J. Math. Biol. (1992) 30: 457–471

Journal of
Mathematical
Biology

Travelling waves and dominance of ESS's

V. C. L. Hutson and G. T. Vickers

Department of Applied and Computational Mathematics, University of Sheffield, Sheffield S10 2TN, UK

Received December 4, 1990; received in revised form May 6, 1991

Abstract. We consider a simple two strategy game in which each pure strategy is an evolutionarily stable strategy (ESS). Under the usual dynamical equations, the large-time behaviour of the system will depend upon the initial conditions and the pay-off matrix. If spatial effects are included to give a reaction-diffusion system, we prove that travelling wavefronts can occur which in effect replace one ESS by another. The 'strength' or 'dominance' of each ESS which decides the 'winner' in a precisely defined sense is determined by its pay-off and by its diffusion rate. Good strategies have large pay-offs and small diffusion rates.

Key words: Reaction-diffusion – Travelling wave – ESS

1 Introduction

The notion of an evolutionarily stable strategy (ESS) has proved to be very fruitful for the study of contests, especially pair-wise ones, between individuals of a population. The original formulation is to be found in Maynard Smith and Price (1973) and Maynard Smith (1974). The theory develops from a pay-off matrix $A = (a_{ij})$ where a_{ij} is the pay-off (that is increase in fitness) to an individual who plays strategy i against an opponent who plays j. The ESS (if one exists) is then a strategy (usually mixed) which cannot be invaded by any small group of individuals who play a different strategy. The ESS is a static concept. However, the very nature of an ESS implies that there are both temporal and spatial variations.

If $\boldsymbol{p}$ is a probability vector and p_i is the proportion of individuals who play strategy i then Taylor and Jonker (1978) have suggested the time evolution equations

$$dp_i/dt = p_i[(A\boldsymbol{p})_i - \boldsymbol{p}^T A\boldsymbol{p}] \quad (1 \leqslant i \leqslant r), \tag{1.1}$$

where r is the number of strategies. These equations have been widely accepted and the relationship between ESS's and stable equilibrium points of Eqs. (1.1) has been investigated by Zeeman (1980). The inclusion of spatial effects is not so straightforward. There is no difficulty for an ecological model which is formulated in terms of number density, see Hastings (1978), Kishimoto (1982) and

Dunbar (1983). Also if all individuals disperse at the same rate then we are again on a well-worn trial, see Fisher (1937) or Hadeler (1981). But it is quite reasonable to expect that the dispersal rate is affected by, or is indeed part of, the strategy chosen. In this we shall follow Vickers (1989) and adopt the equations

$$\frac{\partial n_i}{\partial t} = n_i\left[\frac{(A\boldsymbol{n})_i}{N} - \frac{\boldsymbol{n}^T A\boldsymbol{n}}{N^2}\right] + D_i \nabla^2 n_i \quad (1 \leqslant i \leqslant r), \tag{1.2}$$

where

$$N = \sum_{i=1}^{r} n_i.$$

In these equations $n_i(\boldsymbol{x}, t)$ is the number density of the i-strategists at position $\boldsymbol{x}$ and time t. Also $N(\boldsymbol{x}, t)$ is the total number density. If the spatial domain is bounded, zero Neumann boundary conditions are imposed. Then the total number of individuals within some finite region can only change by migration across the boundary of the region. So it is being assumed that the carrying capacity for that region has been attained but the strategy-mix may change.

If the matrix A has an interior ESS, that is one in which every strategy is represented, then it is shown in Vickers (1989) that it is stable for all choices of the diffusion coefficients D_i. The situation is more complicated if there is no such ESS, and we consider here the case when there are only two strategies and each pure strategy is an ESS. In the absence of spatial effects each ESS is stable. The inclusion of diffusion creates the possibility of a travelling wave which can replace one ESS by the other. Since any number may be added to any column of A without changing the dynamics, without loss of generality we may take with $\alpha, \beta > 0$,

$$A = \begin{bmatrix} \alpha & 0 \\ 0 & \beta \end{bmatrix},$$

so that each pure strategy is an ESS. With an obvious notation, the system (1.2) then becomes

$$\begin{aligned} \frac{\partial U}{\partial t} &= UV\frac{(\alpha U - \beta V)}{(U+V)^2} + \mu\frac{\partial^2 U}{\partial x^2}, \\ \frac{\partial V}{\partial t} &= -UV\frac{(\alpha U - \beta V)}{(U+V)^2} + \nu\frac{\partial^2 V}{\partial x^2}, \end{aligned} \tag{1.3}$$

where the spatial domain has been taken to be the whole of the x-axis. Our objective is to consider a class of travelling wave (front) solutions of these equations which throws light on the asymptotic (that is large time) behaviour and so on the eventual relative success of the strategies.

To put the investigation into context, consider first the corresponding reaction system, that is (1.3) with $\mu = \nu = 0$ and U, V spatially independent. There are two asymptotically stable equilibria $(1, 0)$ and $(0, 1)$ and one unstable equilibrium $(\beta, \alpha)/(\alpha + \beta)$. If $U < \beta/(\alpha + \beta)$ then the strategy "play option 1 always" will become fixed in the population, but if $U > \beta/(\alpha + \beta)$ then the other ESS will become fixed.

Of course for a given reaction system the asymptotic behaviour depends only on the initial values of the number densities U and V. However, for the system (1.3) matters are not nearly so simple as the initial spatial distributions enter into consideration and the diffusion rates μ, ν play an important role. To investigate this situation we consider the invasion of a region dominated by one strategy by another, and suppose that for $x > 0$ strategy 1 is being played by almost everybody and for $x < 0$ strategy 2 is prevalent. We then look for a travelling wave solution of (1.3), that is a solution of the form

$$U(x, t) = u(x - ct), \qquad V(x, t) = v(x - ct). \tag{1.4}$$

Substitution into (1.3) leads to a pair of nonlinear second-order ordinary differential equations involving an unknown parameter c, and hence to a first-order system of 4 equations in phase space. An equilibrium $(\bar{u}, \bar{v})$ of the reaction system corresponds to an equilibrium $(\bar{u}, 0, \bar{v}, 0)$ in phase space, and we look for two types of heteroclinic connections of such equilibria. The first is a connection of (the equilibrium corresponding to) $(0, 1)$ to $(\beta, \alpha)/(\alpha + \beta)$ which is monotone, that is with $\dot{u} > 0$, $\dot{v} < 0$; this will be called a Fisher wave. The second is a connection of $(1, 0)$ to $(0, 1)$ where one of $\dot{u}$, $\dot{v}$ but not the other may change sign once, and following the standard terminology this is called a bistable wave since the corresponding equilibria of the reaction system are both asymptotically stable.

Our initial aim is to prove the existence of such travelling waves. Of course a great deal is known about travelling wave problems for one species, see Fife (1979) for example. However, two species problems are much more difficult, and it is only relatively recently that there has been much progress with these. In fact the Fisher wave is a saddle-node connection which exists for a range of values of c, and is relatively easy to handle. The bistable wave is a saddle-saddle connection which exists for just one value of c and is a great deal more difficult to tackle. For the bistable case two methods have mainly been used. The first is based on a topological index, see for example Conley and Gardner (1984), Gardner (1984) and Mischaikow and Hutson (1990) where a number of further references are given; this method is potentially extremely powerful but rests on a relatively sophisticated theory. The second method is basically a shooting technique used in conjunction with Wazewski's Theorem, see Dunbar (1984). Our method is related to the second of these but is simpler in conception, and is applicable perhaps because of the simpler sign structure of our solution. The system considered nevertheless presents some possibly unusual difficulties because of the dependence of the critical sets on c, which is reflected in the singular dependence of the travelling wave on the parameters, see Sect. 3 for further comment. In previous examples which have been tackled, where as in the present case the reaction system is neither cooperative nor competitive, it has been found necessary to impose a technical condition, see Gardner (1984), which is probably not intrinsically essential. It has also been found necessary to assume such a condition in the present case, see Theorem 3.2, but we note that the numerical evidence supports the view that a bistable wave exists even when this condition is not satisfied, see Sect. 5 for further details.

Our second main aim is to examine the question of the relative success of the two strategies. As we have seen this is a simple matter for the reaction system. For the reaction-diffusion system, this question has led to the idea of 'dominance' of the equilibria, see Fife (1979), Conley and Gardner (1984) and Hutson (1986). In Fife (1979) dominance is defined for one species by considering circumstances in which a localised population can expand to fill up the whole space. A reasonable alternative definition might be based on the direction of the bistable travelling wave, and for one species these definitions coincide. For the present problem we base the definition of dominance on the direction of the travelling wave, that is on the sign of c; for the model above if $c > 0$ strategy 2 will replace strategy 1 and so will be dominant. There is strong numerical evidence to support the assertion that there is a close relationship between dominance and the growth of a localised strategist in the presence of an established strategist. However, this assertion is probably very difficult to prove. We are able to find an explicit criterion for the sign of c for a bistable wave, and so for the dominance of an ESS.

The plan of the paper is as follows. The terminology and notation are introduced in Sect. 2. In Sect. 3 an outline of the broad picture concerning travelling wave solutions is given, and the main results are stated. Section 4 consists of proofs. Finally, in Sect. 5 we present some numerical results, and comment on the interesting question of the relationship of the sign of c and the diffusion constants, and on their connection with the shape of the travelling wave.

2 Preliminaries

The substitutions (1.4) lead to the following pair of equations for u, v:

$$\mu\ddot{u} + c\dot{u} + f(u, v) = 0, \tag{2.1}$$

$$\nu\ddot{v} + c\dot{v} - f(u, v) = 0, \tag{2.2}$$

where $f(u, v) = uv(\alpha u - \beta v)/(u + v)^2$. Here 'dot' denotes differentiation with respect to the travelling-wave variable $(x - ct)$, and we shall denote this variable by 't' to fit with standard differential equation notation; as this will be used from here on there is little possibility of confusion.

Rewrite (2.1) and (2.2) as a first-order system:

$$\dot{u} = p, \tag{2.3a}$$

$$\mu\dot{p} = -cp - f, \tag{2.3b}$$

$$\dot{v} = q, \tag{2.3c}$$

$$\nu\dot{q} = -cq + f. \tag{2.3d}$$

Adding (2.3b) and (2.3d) and integrating we obtain the equation

$$\mu p + \nu q + c(u + v - \delta) = 0, \tag{2.4}$$

where δ is a constant. Now for any a, b points of the form $(a, 0, 0, 0)$ and $(0, 0, b, 0)$ are equilibria which we seek to connect by a heteroclinic orbit. However, taking limits as $t \to \pm\infty$ in (2.4), we see that necessarily $a = b$ for such a connection if $c \neq 0$. Without loss of generality we may choose $\delta = 1$ (as it is easy to check that rescaling of solutions yields solutions). Our primary aim then is to search for a connection of $(0, 0, 1, 0)$ to $(1, 0, 0, 0)$ in $\mathbb{R}^4$ with $c \neq 0$. Note though that if $c = 0$ orbits must lie in the manifold $\mu u + \nu v = \text{const}$, and if $\mu \neq \nu$ will not be of the above form. This singular behaviour is further commented on in Sect. 3. We remark also that if $\mu = \nu$, from (2.4) the orbit must lie in the manifold $u + v = 1$. The basic equations reduce then to those for the well-known one species case with cubic nonlinearity discussed in detail in Fife (1979).

The next step is to use (2.4) to reduce the dimension of the problem from one in $\mathbb{R}^4$ to one in $\mathbb{R}^3$. Two essentially equivalent systems are obtained, and we shall henceforth use (2.5) as the system governing the problem (and occasionally for technical convenience utilise (2.6));

$$\dot{u} = p, \tag{2.5a}$$

$$\mu\dot{p} = -cp - f, \tag{2.5b}$$

$$\nu\dot{v} = -\mu p - c(u + v - 1), \tag{2.5c}$$

$$\mu\dot{u} = -\nu q - c(u + v - 1), \tag{2.6a}$$

$$\dot{v} = q, \tag{2.6b}$$

$$\nu\dot{q} = -cq + f. \tag{2.6c}$$

The system (2.5) has an additional equilibrium at $(\beta, 0, \alpha)/(\alpha + \beta)$, and we shall also show that there is a connection of $(0, 0, 1)$ to this. Since $(0, 1)$ and $(1, 0)$ are stable equilibria of the reaction system, we shall follow the standard scalar equation terminology in making the following definitions.

Definition. A connection of $A(0, 0, 1)$ to $D(1, 0, 0)$ where one but not both of p, q may change sign once will be called a *bistable wave*. A connection of $A(0, 0, 1)$ to $B(\beta, 0, \alpha)/(\alpha + \beta)$ which is monotone (that is $p > 0$, $q < 0$) will be called a *Fisher wave*.

We shall use the term travelling wave to indicate either the heteroclinic connection in the phase plane or the corresponding solution of the reaction-diffusion system. Strictly these connections should perhaps be referred to as travelling wave fronts as they connect different equilibria, but we follow the standard terminology and drop the 'front'.

The following useful relations are obtained by easy manipulations of the systems (2.5) and (2.6). First, (2.4) may be rewritten in the form

$$(\mu\dot{u} + \nu\dot{v}) = -c(u + v - 1). \tag{2.7}$$

Also

$$\nu(\dot{u} + \dot{v}) = (\nu - \mu)p - c(u + v - 1), \tag{2.8}$$

$$\mu(\dot{u} + \dot{v}) = (\mu - \nu)q - c(u + v - 1). \tag{2.9}$$

On a section of an orbit where v is monotone in u, we can write $v = V(u)$ and $F(u) = f(u, V(u))$. Then

$$\mu\frac{dp}{du} = -c - F/p \tag{2.10}$$

and

$$\frac{\mu}{2}[p^2(u_2) - p^2(u_1)] = -c\int_{u_1}^{u_2} p(s)\,ds - \int_{u_1}^{u_2} F(s)\,ds. \tag{2.11}$$

The first lemma below (whose proof is routine and is omitted) discusses the local behaviour, and the second gives an a priori bound from which existence of orbits follows in the appropriate region of the u–v plane.

Lemma 2.1 *Assume that* $c > 0$. *Then the following hold for* (2.5).
(i) *A has a one-dimensional unstable manifold. The tangent vector at A to this lies in DAE and so is above AD if* $\mu < \nu$ *and below AD if* $\mu > \nu$ *(see Fig.* 1).

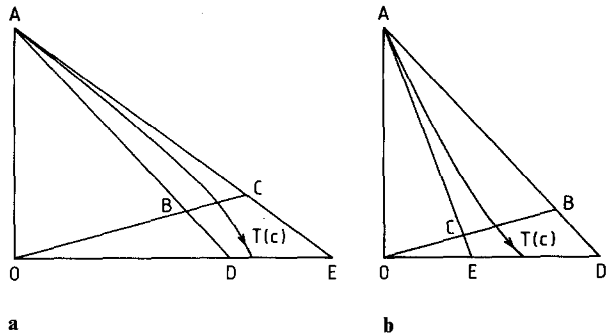

Fig. 1a,b. Projection in $u-v$ plane of phase space, (a) for $\mu < \nu$ and (b) for $\mu > \nu$. The line AE is $\mu u + \nu v = \nu$, AD is $u + v = 1$ and OC is $\alpha u = \beta v$. Also $f < 0$ ($f > 0$) above (below) the line OC respectively

(ii) *B is an asymptotically stable hyperbolic equilibrium. Suppose c_1, c_2 satisfy $0 < c_1 < c_2 < \infty$. Then there is a $\delta > 0$ such that the ball centre B and radius δ lies in the basin of attraction of B for all $c \in [c_1, c_2]$.*

It turns out that D has a two-dimensional stable manifold. The tactics we use are based on shooting along the unstable manifold of A with c as shooting parameter. It is convenient to use $T(c)$ for the projection of this orbit on the $u-v$ plane until its first exit from the region $u \geqslant 0$, $v \geqslant 0$. As the system is autonomous, we shall assume without loss of generality that $T(c)$ cuts a given small ball centre A at $t = 0$.

Lemma 2.2 *Let (u, p, v) denote any point on the orbit corresponding to the unstable manifold of A. Let Δ denote an ε-neighbourhood of the triangle ADE in $\mathbb{R}^2$. Then p is bounded until the first exit of (u, v) from Δ. This ensures existence of $T(c)$.*

Proof. Set

$$m = 2\max\left(1, \frac{\nu}{\mu}\right) \cdot \sup_{(u,v)\in\Delta} |f(u, v)|.$$

We first show that on a section of the orbit starting at A with $p > 0$, $p < 2[c + (c^2 + 2\mu m)^{1/2}]/\mu = p_1$, say. For if not, there is a u_1 with $p(u) < p_1$ for $0 \leqslant u < u_1$ and $p(u_1) = p_1$. Then from (2.11), since $u_1 \leqslant 1 + \varepsilon$ if $\mu \geqslant \nu$ and $u_1 \leqslant \nu/\mu + \varepsilon$ if $\mu < \nu$,

$$\tfrac{1}{2}\mu p_1^2 \leqslant c p_1 + m,$$

whence $p_1 \leqslant [c + (c^2 + 2\mu m)^{1/2}]/\mu < p_1$, a contradiction. Of course p may change sign on the orbit, but an obvious modification of the above argument yields a similar conclusion.

3 Existence of travelling waves

The broad situation exhibits considerable differences from several of the problems for the scalar equation and for higher dimensional problems which have previously been tackled, so we start with some general remarks with the aim of clarification.

Note first that if $c = 0$, the system (2.5) has three *lines* of equilibria OA, OC and OE. Furthermore, $T(0)$ always lies in AE, and will be a heteroclinic connection of A to E if and only if $\beta/\alpha = F(\mu/\nu)$ – see Lemma A1. This will yield a pattern, that is a stationary solution of the reaction-diffusion system (1.3). We might expect this case to form a division between the situations for $\beta/\alpha < F(\mu/\nu)$ and $\beta/\alpha > F(\mu/\nu)$ in that the corresponding travelling waves would proceed in opposite directions. However, this is only true if we interpret the travelling waves as connections of A to D and not of A to E. This singular jump of an A to E connection to an A to D connection is an interesting if complicating mathematical feature of the problem.

One may thus speculate that connections of A to D (since these are both stable equilibria of the reaction systems) will be analogues of the bistable waves for the scalar equation. Suppose then that there is a bistable wave for some $c > 0$ for some fixed value of the parameters. As β/α increases we expect that $T(c)$ for larger c will form a spiral into B, and that for yet larger c, a monotone connection of A to B analogous to a Fisher wave will develop (since the reaction term is of one sign in ABC). All these speculations are strongly supported by numerical evidence, and we would wish to be able to prove the existence of the Fisher and bistable waves. However, as discussed in the introduction, for technical reasons we have had to introduce a certain restriction on the parameters (which is probably not a necessary condition) in order to prove the existence of bistable waves.

The theorems are as follows, the proofs being given in Sect. 4. They are stated for $\beta/\alpha > F(\mu/\nu)$, but this imposes no restriction since the pairs α, μ and β, ν can be interchanged without changing the biological problem.

Theorem 3.1 Set

$$K = \sup_{(u,v) \in \text{int}\, ABC} uv/(u+v)^2,$$

so that $K \leqslant 1/4$, *and assume that* $\beta/\alpha > F(\mu/\nu)$. *Then for* $c > 0$ *with*

$$c^2 > 4K(\beta\mu + \alpha\nu) \max\left(\frac{\mu}{\nu}, \frac{\nu}{\mu}\right),$$

there is a monotone (with $\dot{u} > 0, \dot{v} < 0$*) connection of* A *to* B, *and hence a Fisher wave.*

Theorem 3.2 *Assume that* $\beta/\alpha > F(\mu/\nu)$ *and suppose the following inequality is satisfied*:

$$\frac{\alpha}{\beta} + 2\frac{\mu}{\nu} > 1.$$

Then for some $c > 0$ *there is a connection of* A *to* D *(and hence a bistable wave) such that the following holds. If* $\mu < \nu$, *then* $\dot{v} < 0$, $\dot{u} > 0$ *initially on this, and there is at most one point where* $\dot{u} = 0$; *this lies in* int $BCED$ *and is a strict maximum. If* $\mu \geqslant \nu$, *the connection is monotone with* $\dot{u} > 0, \dot{v} < 0$.

4 Existence proofs

The broad strategy for treating (2.3) is to shoot from A with c as the shooting parameter. The behaviour for small c is approximately known as the system (2.3) may be solved explicitly for $c = 0$ (see Lemma A1); we can thus assert that $T(c)$ cuts DE transversally for small enough c. For large c, we shall show that $T(c)$ never reaches the boundary of ABC; this incidentally establishes the existence of a Fisher wave. In order for $T(c)$ to 'jump' between these two types of behaviour we shall show that a bistable travelling wave must exist for an intermediate value of c. We are going to assume throughout most of this section that $\mu < \nu$; this is the most difficult case to tackle, and at the end of the section we make some remarks on why the case $\mu > \nu$ is easier.

We start the proof by establishing a series of technical lemmas describing the possible qualitative behaviour of orbits. The first concerns the turning points defined as follows.

Definition. A *turning point* (TP) is a point where at least one of $\dot{u}(t_0) = 0$ or $\dot{v}(t_0) = 0$ for some $t_0 \in \mathbb{R}$; if both hold it is counted as 2 TP's. A *strict maximum* (say of u) is a point where $\dot{u}(t_0) = 0$, $\ddot{u}(t_0) < 0$, with a similar definition for a strict minimum. A *strict point of inflexion* is a point where $\dot{u}(t_0) = \ddot{u}(t_0) = 0$ and $\dddot{u}(t_0) \neq 0$.

Lemma 4.1 *Take $c > 0$, $\mu < \nu$ and consider any solution in* cl ADE. *The existence of a* TP *at A, B or D implies that the orbit is the equilibrium of* (2.3) *itself, that is* $(0, 0, 1)$, $(\beta, 0, \alpha)/(\alpha + \beta)$ *or* $(1, 0, 0)$ *respectively. If $\dot{v} = 0$ on DE the solution lies in the vertical plane whose projection is DE. Figure* 2 *shows all the possible turning points (apart from those described above) in* cl ADE, *and all of these are strict.*

Proof. At A, B, D, since $u + v = 1$, from (2.5c) $\dot{v} = 0$ if and only if $p = \dot{u} = 0$. The first statement follows as $f = 0$ at these points. Now suppose $\dot{v} = 0$ on DE. Then the system (2.6) has the solution $u(t)$, $v(t) = q(t) = 0$ where $u(t)$ satisfies $\mu\dot{u} = -c(u - 1)$. The assertion follows by uniqueness.

Consider next the region int ABC where $f < 0$. If $\dot{u} = p = 0$, from (2.5b) $\mu\ddot{u} = -f > 0$, so this is a strict minimum as indicated in Fig. 2. A similar argument applies for $\dot{v}$ and also in int $BCED$.

If $\dot{u} = 0$ on BC, from (2.5c), $\dot{v} < 0$. From (2.5b), $p = 0$ implies $\dot{p} = 0$ and then $\mu\dddot{u} = \mu\ddot{p} = \beta u v \dot{v}/(u + v)^2 < 0$.

A similar calculation holds when $\dot{v} = 0$, and also when $\dot{u} = 0$ on DE. These arguments yield the points of inflexion as marked.

For int AB, from (2.5c), $\dot{u} = 0$ if and only if $\dot{v} = 0$. So a turning point there

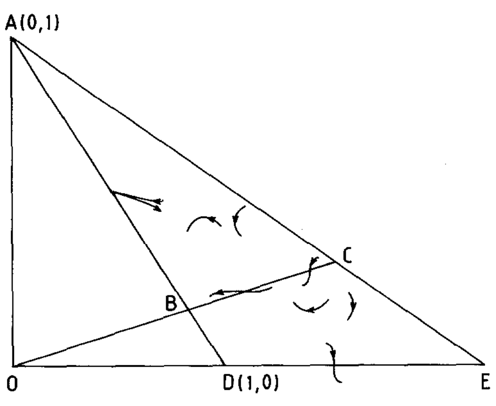

Fig. 2. The case $\mu < \nu$, $c > 0$. Possible turning points are shown – see Lemma 4.1

must be a double turning point. From (2.7) the orbit is tangent to $\mu u + \nu v = \text{const}$. Also from (2.8), $\nu(\ddot{u} + \ddot{v}) = (\nu - \mu)\ddot{u} = -(\nu - \mu)f/\mu > 0$. On BD, the opposite inequality holds, so the orbit does not lie in ADE.

Lemma 4.2 *Take* $c > 0$ *and* $\mu < \nu$. *Then the following hold*:
(i) $T(c)$ *cannot intersect* cl AE.
(ii) *Consider* $T(c)$ *until its first exit from* cl ABC. *Then*
  (a) $p > 0$, $q < 0$
  (b) $T(c) \cap \text{cl}\, AB = \varnothing$.
(iii) *If* $T(c) \cap \text{cl}\, BD \neq \varnothing$, *then* $T(c)$ *intersects* $\{\text{cl}\, BD\} \backslash \{D\}$ *with* $p < 0$, $q > 0$.

Proof (i) An obvious consequence of (2.7).
(ii) (a) If $\dot{u} = 0$ first at t_0, from the allowed behaviour (Fig. 2), $u(t) > u(t_0)$ for $t < t_0$. Hence the orbit cannot have come from A. Similarly for $\dot{v} = 0$. This argument includes B, for if $\dot{u} = 0$ or $\dot{v} = 0$, by the lemma the orbit is an equilibrium.
(b) Suppose the first intersection takes place at t_0. By (2.8), $\nu(\dot{u} + \dot{v})(t_0) = (\nu - \mu)p(t_0) > 0$ by (iia). But at first intersection, the orbit must arrive from the right, that is with $(\dot{u} + \dot{v})(t_0) \leqslant 0$. This is a contradiction.
(iii) Neither $p = 0$ nor $q = 0$ on cl BD by Lemma 4.1. Now on cl BD, from (2.5c), $\nu\dot{v} = -\mu p$ and from (2.8), $\nu(\dot{u} + \dot{v}) = (\nu - \mu)p$. Thus $p < 0$ implies $\dot{v} > 0$ and $p > 0$ implies $(\dot{u} + \dot{v}) > 0$. The last possibility is ruled out as the orbit arrives from the right. Thus $p < 0$ and $q > 0$. Obviously on $T(c)$ this cannot happen at D.

Proof of Theorem 3.1 (Fisher wave). We give this for the case $\mu < \nu$. If $\mu > \nu$, a similar argument is employed, except that the basic equation used is that for u rather than for v.

We shall show that $T(c)$ cannot cut int BC, that is there is no $t_0 \in \mathbb{R}$ such that $(u(t_0), v(t_0)) \in \text{int}\, BC$. The result will then follow. For the orbit must remain in int ABC for all t by Lemma 4.2(i) and (iib), and as it is monotone (by Lemma 4.2(iia)) it must tend to a limit which must be an equilibrium from the standard theory. As this cannot be A it must be B, and the existence of a connection follows.

To prove that $T(c)$ cannot cut int BC we argue by contradiction. Suppose then that $T(c)$ first cuts BC at (u^*, v^*). As $T(c)$ is monotone we may suppose that on $T(c)$, $u = u(v)$ and we may set $H(v) = f(u(v), v)$. Equation (2.2) then becomes

$$\nu\ddot{v} + c\dot{v} - H(v) = 0,$$

and we have $H(v^*) = 0$. The idea in outline is to show by using Lemma A2 that with c as in Theorem 3.1, an orbit in the v–$\dot{v}$ phase plane cannot reach $v = v^*$. To do this we make the changes of variable $w = (v - v^*)/(1 - v^*)$, $t' = t/\sqrt{\nu}$, obtaining the following with w' denoting dw/dt':

$$w'' - \frac{c}{\sqrt{\nu}} w' - \frac{H(v)}{1 - v^*} = 0. \tag{4.1}$$

The substitution changes v^* to 0 and leaves 1 at 1, so we can apply Lemma A2. We thus need an estimate for the following:

$$\sup_{0 < w \leqslant 1} \frac{G(w)}{w} = \sup_{v^* \leqslant v \leqslant 1} -\frac{H(v)}{v - v^*}.$$

Now in ABC, $\mu\dot{u} + v\dot{v} < 0$, whence $\mu(u^* - u) < v(v - v^*)$, and so

$$\frac{\beta v - \alpha u}{v - v^*} \leqslant \beta + \frac{\alpha v}{\mu}.$$

From the expression for f,

$$\sup -\frac{H(v)}{v - v^*} \leqslant \frac{K}{\mu}(\beta\mu + \alpha v).$$

We now set $w' = r$ and rewrite (4.1) in the form given in Lemma A2 with $\varrho = -c/\sqrt{v}$. A short calculation shows that under the assumed condition on c, by Lemma A2, $v(t) < v^*$ for $t \in \mathbb{R}$. This yields the required contradiction and completes the proof of the theorem.

Following the tactics described in the first paragraph of this section, we proceed to establish the existence of a bistable wave. We shall show that this exists for $c = c^+$ with c^+ as in the definition below. Recall in the following that $T(c)$ is the part of an orbit lying in cl AOE and $\beta/\alpha > F(\mu/v)$.

Definition. Let Ω be the set of $c \geqslant 0$ such that $T(c)$ has both the following properties
(i) $T(c)$ intersects $\{\text{cl}\, DE\}\backslash\{D\}$ transversally.
(ii) $T(c)$ has at most one TP.
Put $c^+ = \sup\{c' : c \in \Omega \text{ for } 0 \leqslant c \leqslant c'\}$, and let $\Omega^+ = [0, c^+)$.

We shall use the term 'continuity' several times in the proof to mean continuity of the (one dimensional) unstable manifold $T(c)$ with respect to c on compact t-sets, recalling that from the definition $T(c)$ cuts a small ball with centre A at $t = 0$.

From continuity and Lemma A1, for small enough c, $T(c)$ is close to AE, is monotone, and cuts DE transversally near E. Thus certainly $c^+ > 0$.

Lemma 4.3 *If $c \in \Omega$, then $\dot{v} < 0$ on $T(c)$, $\dot{u} > 0$ on $T(c) \cap$ cl ABC, and precisely one of the following hold on $T(c)$:*
(i) $\dot{u} > 0$
(ii) *u has a strict maximum in* int $BCED$ *and no other* TP
(iii) *u has a strict inflexion with $\dot{u} > 0$ on* int ED *and no other* TP.

Proof. It is clear from Fig. 2 that the first TP must be a maximum in u in int $BCED$ or an inflexion in u on DE. As there is only one TP by the definition of Ω, the possibility that $\dot{v} = 0$ is ruled out.

Lemma 4.4 *Ω is non-empty, bounded above, and open in $\mathbb{R}^+$.*

Proof. Since $\beta/\alpha > F(\mu/v)$ it follows from Lemma A1 that $\Omega \neq \varnothing$. Ω is bounded above by Theorem 3.1. To prove that Ω is open, take some fixed $c_0 \in \Omega$. Continuity yields transversality of intersection on a small enough neighbourhood of c_0. In the following we prove that there is only one TP for c in such a neighbourhood. Suppose the result is false. Then there is a sequence $\{c_n\}$ with $\lim c_n = c_0$ such that $T(c_n)$ has two or more TP's.

We first prove that for large enough n, $T(c_n)$ cannot have a TP in cl ABC. For otherwise there is a subsequence, which we still denote by $\{c_n\}$, such that each $T(c_n)$ has a TP in cl ABC. From continuity in c and compactness, $T(c_0)$ has a TP in cl ABC. This is impossible by Lemma 4.3. We may thus assume without loss of generality that $T(c_n)$ has no TP in cl ABC.

The next step is to prove that $\dot{v} < 0$ on $T(c_n)$. In view of the result of the previous paragraph it is enough to establish this in cl $BCED$. Now by Lemma 4.3, $\dot{v} < 0$ on $T(c_0) \cap \text{cl}\, BCED$. Continuity (of q in c) establishes the claim.

From Fig. 2 the remaining possibility that must be ruled out is that $T(c_n)$ has at least one maximum in u in $BCED$ together with an inflexion on ED. However, from the figure the *combination* of these two is impossible, as u may not have a minimum. We finally conclude that $T(c_n)$ cannot have more than one TP. This yields a contradiction and completes the proof of the lemma.

Lemma 4.5 *If* $\alpha/\beta + 2\mu/\nu > 1$, *no orbit* $T(c)$ *with* $c \in \Omega$ *can touch* BC *at* $t = t_0$ *and then exit from* int $BCED$ *by crossing* int DE.

Proof. We argue by contradiction. Suppose that there is such an orbit, and let it touch int BC at P and cut int DE at R. Then, at P,

$$\alpha u = \beta v, \quad \alpha \dot{u} = \beta \dot{v} \quad \text{and} \quad \mu \dot{u} + \nu \dot{v} + c(u + v - 1) = 0$$

which give

$$\dot{v} = c[\alpha - v(\alpha + \beta)]/(\alpha\nu + \beta\mu). \tag{4.2}$$

In $BCED$, $f > 0$ and so

$$\nu \ddot{v} + c\dot{v} > 0$$

which implies that $\nu\dot{v} + cv$ is increasing. But at R, $\nu\dot{v} + cv < 0$, and so at P

$$\nu\dot{v} + cv < 0. \tag{4.3}$$

The results (4.2) and (4.3) give that at P

$$v > \alpha\nu/(\beta(\nu - \mu)).$$

But at C we see that

$$\alpha u = \beta v \quad \text{and} \quad \mu u + \nu v = \nu,$$

and so

$$v = \alpha\nu/(\alpha\nu + \beta\mu).$$

Clearly v at P has to be less than this and so

$$\frac{\alpha\nu}{\alpha\nu + \beta\mu} > \frac{\alpha\nu}{\beta(\nu - \mu)}$$

or $\alpha/\beta + 2\mu/\nu < 1$, which provides the required contradiction.

The following lemmas give the behaviour of orbits for $c \in \Omega^+$ and for the limiting orbit $T(c^+)$ respectively under the condition of Lemma 4.5.

Proposition 4.6 *Suppose that* $c \in \Omega^+$ *and* $\alpha/\beta + 2\mu/\nu > 1$. *Let* $T(c)$ *have its first exit from* cl ABC *at* t_0. *Then* $\dot{u} > 0$ *for* $t \leqslant t_0$, $\dot{v} < 0$ *for* $t \in \mathbb{R}$, *and* $T(c) \cap$ cl $ABC = \varnothing$ *for* $t > t_0$.

Proof. The first assertions are simply Lemma 4.3. To prove the last assertion, let P_c denote the first intersection of $T(c)$ with BC, and set

$$c_1 = \sup\{c' : T(c) \cap BC = P_c \text{ for } 0 \leqslant c \leqslant c'\}.$$

Note that P_c varies with c, so we are assuming that if $c < c_1$, there is exactly one intersection of $T(c)$ with BC. Now it is given that $c \in \Omega^+$, so $c < c^+$. Thus to prove the result it is enough to show that $c_1 \geqslant c^+$.

Observe first that $T(c_1)$ must intersect BC again, say at $t_1 > t_0$. For if not, by continuity there is an open neighbourhood N of c_1 such that for $c \in N$, $T(c_1)$ does not intersect BC for any $t_1 > t_0$, which contradicts the definition of c_1 as a sup.

We complete the proof by using a contradiction argument. Suppose that $c_1 < c^+$ and consider $T(c_1)$. By Lemma 4.5, since $c_1 \in \Omega^+$, $T(c_1)$ cannot touch BC at t_1. So suppose there is a point $Q \in \operatorname{int} ABC$ on $T(c_1)$. Since $T(c_1)$ is approximated by orbits $T(c)$ with $c < c_1$, these orbits must reenter $\operatorname{int} ABC$. However, by the definition of c_1, orbits $T(c)$ with $c < c_1$ may not intersect BC for $t > t_0$, and so may not reenter $\operatorname{int} ABC$. This contradiction completes the proof.

Lemma 4.7 *If $\alpha/\beta + 2\mu/v > 1$ then $T(c^+)$ does not reenter* int ABC *after its first exit. Also, on $T(c^+)$, $\dot{v} < 0$ and there is one* TP *at most, which can only be a strict maximum in* int $BCED$ *or a strict inflexion on* int DE.

Proof. The first assertion follows from continuity and Proposition 4.6. For $c \in \Omega^+$, $\dot{v} < 0$, again by Proposition 4.6. Thus $\dot{v} \leqslant 0$ on $T(c^+)$ by continuity in c, and so if $\dot{v} = 0$ it must happen at an inflexion, which by Lemma 4.1 must lie on int BC. But this is impossible as then $T(c^+)$ would have to reenter int ABC, which is ruled out above.

Suppose that $\dot{u} = 0$ twice on $T(c^+)$, and let the first two TP's (with respect to increasing t) occur at t_1, t_2 with $t_1 < t_2$. Note that no TP can lie in int ABC (by Proposition 4.6 and continuity in c). By Lemma 4.1 the first TP must be a maximum (for it cannot be a minimum, and if it is an inflexion this must lie on DE, and so the orbit exits from $BCED$ for $t > t_1$, which rules out the existence of a TP at t_2 with $t_2 > t_1$). Consider next the TP at t_2 which obviously cannot be another maximum. Neither can it be a minimum as no TP may lie in int ABC, and a minimum in cl $BCDE$ is not allowed (by Lemma 4.1). If it is an inflexion it cannot lie on BC (from Lemma 4.1 and Fig. 2). Neither can it lie on DE (by Lemma 4.1 as an inflexion on DE cannot follow a maximum). This proves that a second turning point cannot exist.

Proof of Theorem 3.2 Clearly $c^+ \notin \Omega^+$ as Ω^+ is open. Lemma 4.7 rules out the possibility that there are two TP's on $T(c^+)$, so from the definition of Ω^+, $T(c^+)$ cannot intersect $\{\operatorname{cl} ED\}\backslash\{D\}$ transversally, and so not at all as a tangency is ruled out by Lemma 4.1. Neither can $T(c^+)$ intersect cl AB (by Lemma 4.2(iib)) nor cl BD (by Lemma 4.2(iii)) as it has only one TP. Hence $T(c^+)$ must remain in int ADE for all t.

As $T(c^+)$ is eventually monotone, it must tend to an equilibrium, either B or D, as $t \to \infty$. Suppose it is B. Then a sequence of approximating orbits $T(c_n)$ with $c_n \in \Omega^+$ must pass closer and closer to B as $n \to \infty$. But this is ruled out as B is 'uniformly' a hyperbolic sink (see Lemma 2.1(ii)). Thus the orbit tends to D, yielding the required bistable wave.

A final comment on the proof for $\mu > v$ is needed. Note that then the line AC, that is $\mu u + v v = v$, is to the left of AD, and we look at orbits lying in ADE. A repetition of the argument of Lemma 4.1 shows that an orbit $T(c)$ cannot have an inflexion on OD at first exit. Thus using continuity in c, we readily deduce that all orbits $T(c)$ for $c \in \Omega^+$ are monotone. Lemma 4.5 is thus unnecessary, and the proof is as before.

5 Numerical results and discussions

It is a straightforward matter to use a shooting technique (with parameter c) to find numerically a solution of Eq. (2.5) which starts near $(0, 0, 1)$ and approaches $(1, 0, 0)$. Figure 3 illustrates a typical solution. For these parameters $\alpha/\beta + 2\mu/\nu = 7/6$ and so Theorem 3.2 does guarantee the existence of such a solution. Clearly the solution is monotone in v but not u. The reaction-diffusion system (1.3) was solved with the same parameter set to check that the wave is stable and will naturally develop from suitable initial conditions such as those mentioned in the introduction. The agreement between the two approaches was very satisfactory and confirmed that the wave is indeed stable. Other parameter sets were used which had $\alpha/\beta + 2\mu/\nu < 1$. Such experiments support the contention that a stable wave exists in all cases.

For other parameters, the connection may be monotone in both u and v. For example, when $\mu = \nu$ the standard one species case is recovered and it is easy to show that the required solution is

$$u(t) = 1/(1 + \exp(-kt)),$$
$$v(t) = 1/(1 + \exp(kt)),$$

where $k^2 = (\alpha + \beta)/(2\mu)$ and the wave speed is c with

$$c^2 = \mu(\alpha - \beta)^2/(2(\alpha + \beta)).$$

We have seen that in a 2-strategy game with

$$A = \begin{bmatrix} a + \alpha & b \\ a & b + \beta \end{bmatrix}, \qquad \alpha > 0, \beta > 0$$

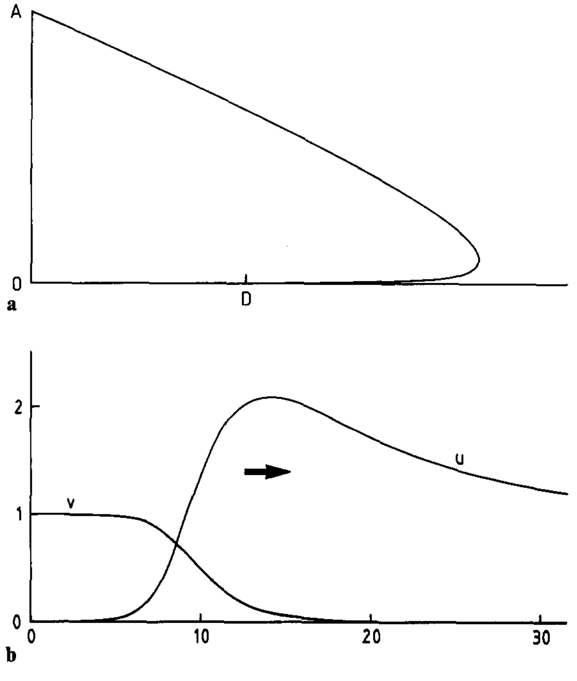

Fig. 3a,b. The travelling wave when $\alpha = 1$, $\beta = 2$, $\mu = 1$, $\nu = 3$. **a** shows the projection of the orbit in the u–v plane, and **b** the functions $u(x - ct)$ and $v(x - ct)$

and diffusion rates μ and ν for the two strategies, the second one can displace the first if

$$\beta/\alpha > F(\mu/\nu),$$

where $F(x)$ is well-approximated by $x^{-0.61}$ for $0.05 < x < 20$. Thus good strategies have large pay-offs and small diffusion rates (suggesting a new interpretation of Sussex University's motto "Be still and know").

In interpreting the result, one must note that the model (1.2) is not appropriate to the spread of a *population*, that is the combination of individual strategists, into unoccupied territory. In this case mobility seems clearly to be an asset at least initially, but it may well be that an inferior strategy does very well at first and only later is replaced by the better one. Our model on the other hand is concerned with a population which has reached its carrying capacity and is being threatened (by invasion or mutation) with a new strategy. Even if a new strategy spreads through the population, there is a rather small, temporary change in population density, so the model will still be valid.

A notable feature of the travelling-wave solutions is that they are not always monotonic. Figure 3 illustrates such a case. The strategy that is being replaced (strategy 1 with density u) initially increases when the new strategy 2 (with density v) enters its territory. At a later time, however, the number of 1-strategists decreases rather sharply and the 2-strategists are left in control. Short-term observations do not always indicate the eventual winner.

Acknowledgement. The first author is grateful to the Leverhulme Trust for a fellowship enabling him to visit the Center for Dynamical Systems and Nonlinear Studies, Georgia Institute of Technology, where the research reported here was partly carried out.

Appendix

We collect together here some technical results. The first notes some consequences of the crucial fact that the system (2.3) may be solved explicitly if $c = 0$. In the following $\bar{u} = \nu/\mu$ is the coordinate of the intersection of the line $\mu u + \nu v = \nu$ with $v = 0$. Also $\lambda = \mu/\nu$.

Lemma A1 *When $c = 0$ the orbit $T(0)$ lies in the plane $\mu u + \nu v = \nu$. Let*

$$I(u) = \int_0^u \frac{uv}{(u+v)^2}(\beta v - \alpha u)\, du,$$

where $v = 1 - \lambda u$. Then $\mu p^2/2 = I(u)$. Also

$$I(\bar{u}) = \alpha G(\lambda)[\beta/\alpha - F(\lambda)],$$

where

$$G(\lambda) = [\lambda(\lambda-1)(\lambda+5) - 2\lambda(2\lambda+1)\log\lambda]/[\lambda(1-\lambda)^4],$$

$$F(\lambda) = \frac{2\lambda(\lambda+2)\log\lambda - (\lambda-1)(5\lambda+1)}{\lambda(\lambda-1)(\lambda+5) - 2\lambda(2\lambda+1)\log\lambda}.$$

For all λ, $G(\lambda) > 0$. Also $F(1) = 1$ and F is strictly decreasing with $F(\lambda) \to \infty$, 0 as $\lambda \to 0$, ∞ respectively. For given α, β, let $\mu_c/\nu_c = \lambda_c(\beta/\alpha)$ be the (obviously unique) solution of $I(\bar{u}) = 0$. Then $I(\bar{u}) > 0$ if either $\beta/\alpha > F(\lambda)$ or equivalently if $\lambda > \lambda_c(\beta/\alpha)$.

If either of these conditions holds, $p > 0$ on $T(0)$ (and so $T(0)$ cuts the plane $v = 0$ transversally).

Proof. the first statement is an obvious consequence of (2.7). It follows that $v = 1 - \lambda u$ on $T(0)$, and (2.10) may be integrated explicitly. The remainder of the proof is merely a (somewhat tedious) algebraic exercise.

The next result is included for convenience of reference; it is a minor amendment of a result due to Fife (1979, p. 109).

Lemma A2 *Assume that $G: [0, 1] \to \mathbb{R}$ is smooth, and suppose that $G(0) = G(1) = 0$ and $G(w) > 0$ $(0 < w < 1)$. Define $G_1 = \sup_{0 < w \leq 1} G(w)/w$, and suppose that $\varrho \leq -2\sqrt{G_1}$. Consider the pair of differential equations*

$$\dot{w} = r$$

$$\dot{r} = -\varrho w - G(w).$$

Let T be an orbit with $\lim_{t \to \infty} (w(t), r(t)) = (1, 0)$ with $w(t) < 1$, $r(t) > 0$ for large t. Then for all t, $r(t) > 0$, $0 < w(t) < 1$, and $\lim_{t \to -\infty} (w(t), r(t)) = (0, 0)$, that is the orbit is a connection of $(0, 0)$ to $(1, 0)$.

References

Conley, C., Gardner, R.: An application of the generalized Morse index to travelling wave solutions of a competitive reaction-diffusion model. Indiana J. Math. **33**, 319–365 (1984)

Dunbar, S.: Travelling wave solutions of diffusive Lotka–Volterra equations: a heteroclinic connection in $\mathbb{R}^4$. Trans. Am. Math. Soc. **286**, 557–594 (1984)

Fife, P.: Mathematical Aspects of Reacting and Diffusing Systems. (Lect. Notes Biomath., vol. 28) Berlin Heidelberg New York: Springer 1979

Fisher, R. A.: The wave of advance of advantageous genes. Ann. Eugen. **7**, 353–369 (1937)

Gardner, R.: Existence of travelling wave solutions of predator-prey systems via the connection index. SIAM J. Appl. Math. **44**, 56–79 (1984)

Hadeler, K. P.: Diffusion in Fisher's population model. Rocky Mt. J. Math. **11**, 39–45 (1981)

Hastings, A.: Global stability in Lotka–Volterra systems with diffusion. J. Math. Biol. **6**, 163–168 (1978)

Hutson, V.: Stability in a reaction diffusion model of mutualism. SIAM J. Math. Anal. **17**, 58–66 (1986)

Kishimoto, K.: The diffusive Lotka–Volterra system with three species can have a stable non-constant equilibrium solution. J. Math. Biol. **16**, 103–112 (1982)

Maynard-Smith, J.: The theory of games and the evolution of animal conflicts. J. Theor. Biol. **47**, 209–221 (1974)

Maynard-Smith, J., Price, G. R.: The logic of animal conflict. Nature (London) **246**, 15–18 (1973)

Mischaikow, K., Hutson, V.: Travelling waves for mutualist species. SIAM J. Math. Anal. (Submitted)

Taylor, P. D., Jonker, L. B.: Evolutionarily stable strategies and game dynamics. Math. Biosci. **40**, 145–156 (1978)

Vickers, G. T.: Spatial patterns and ESS's. J. Theor. Biol. **140**, 129–135 (1989)

Zeeman, E. C.: Population dynamics from game theory. In: Nitecki, A., Robinson, C. (eds.) Global Theory of Dynamical Systems. (Lect. Notes Math., vol. 819, pp. 471–497) Berlin Heidelberg New York: Springer 1980