SPATIAL DYNAMICS OF THE DIFFUSIVE LOGISTIC EQUATION WITH A SEDENTARY COMPARTMENT

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ABSTRACT. We study an extension of the diffusive logistic equation or Fisher's equation for a situation where one part of the population is sedentary and reproducing, and the other part migrating and subject to mortality. We show that this system is essentially equivalent to a semi-linear wave equation with viscous damping. With respect to persistence in bounded domains with absorbing boundary conditions and with respect to the rate of spread of a locally introduced population, there are two distinct scenarios, depending on the choice of parameters. In the first scenario the population can survive in sufficiently large domains and the linearization at the leading edge of the front yields a unique candidate for the spread rate. In the second scenario the population can survive in arbitrarily small domains and there are two possible candidates for the spread rate. Analysis shows it is the larger candidate which gives the correct spread rate. The phenomenon of spread is also investigated using travelling wave theory. Here the minimal speed of possible travelling front solutions equals the previously calculated spread rate. The results are explained in biological terms.

1 Introduction The diffusive logistic or Verhulst equation or Fisher's equation is a scalar reaction diffusion equation with a simple hump nonlinearity (quadratic nonlinearity in the classical case). This equation describes the immigration of a species into a territory or the

advance of an advantageous gene into a population. The equation provides the classical example for travelling fronts in parabolic equations, [**2, 8, 25**], and it forms the nucleus of more complex multi-species models in ecology, pattern formation and, most notably, epidemiology [**3**]. The equation is also the basis for more elaborate models of the spatial process as in reaction-telegraph equations, Cattaneo systems or reaction transport equations, [**9, 10, 11, 29**], Volterra integral equations and delay equations [**6, 28, 31, 32**].

In recent years several authors have investigated single species reaction diffusion models where only part of the population is migrating and another part is sedentary. Cook [**5**] has studied a Verhulst type population model with a sedentary and a migrating subpopulation. His results appear in [**23**]. His assumption is that there is a joint carrying capacity for both subpopulations and that the offspring of both groups forms one pool which is then distributed to both subpopulations at constant proportions. The resulting equations are

$$v_t = r_v(u+v)(1-(u+v)/K) + Dv_{xx}$$
$$w_t = r_w(u+v)(1-(u+v)/K).$$

In the Verhulst model studied by Lewis and Schmitz [**21**] individuals switch between mobile and stationary states during their lifetime. In their system the migrants have a positive mortality while the sedentary subpopulation reproduces and is subject to a finite carrying capacity. The equations are

$$(1) \qquad \begin{aligned} v_t &= D\Delta v - \mu v - \gamma_2 v + \gamma_1 w \\ w_t &= f(w) - \gamma_1 w + \gamma_2 v \end{aligned}$$

with $f(w) = rw(1 - w/K)$. The authors determined the minimal speed for travelling waves, under the assumption that the emigration rate is less than the intrinsic growth rate for the sedentary class ($\gamma_1 < f'(0)$). This minimal wave speed was obtained from the linearization at the zero equilibrium from the condition that two real eigenvalues coalesce and become complex conjugate. Speeds slower than this minimal speed yield a wave with negative components, thus violating the property that (1) leaves the cone of non-negative functions invariant.

Of course the system (1) could be seen as a highly degenerate two-species model. But it is so close to the scalar case that it should be studied in its own right, even more so, as it shows rather interesting

features which can be best understood by referring to the scalar case and to the underlying biological phenomena.

The biological interpretation suggests the following three scenarios: (i) If the transition rates γ_i are large and the mortality μ is small then the system should behave like the diffusive Verhulst equation with rates suitably adapted. The carrying capacity changes due to the additional compartment of migrating individuals, and the reproduction rate changes because of additional mortality of migrating individuals. (ii) If the transition rates are large and the mortality is also large then the population can be driven to extinction because most individuals start migrating and then die. (iii) For small transition rates there are other types of behavior which require a thorough mathematical investigation.

The paper is organized as follows. In Section 2 we recall properties of reaction-diffusion equations and explain the motivation for studying the present problem. In Section 3 we establish connections to damped wave equations and present the limiting case of large switching rates (diffusion approximation), with some proofs deferred to an Appendix. In Section 4 we study in detail the system without diffusion which, as usual, gives some insight into the uncoupled dynamics and also provides analytical tools. In Section 5 we study the system with diffusion in a bounded domain with zero Dirichlet boundary conditions. For this case we extend the classical stability conditions which can also be phrased as conditions on a domain of minimal size that can sustain the population. We find an interesting situation where arbitrarily small domains can sustain the population. Then, in Section 6, we study the travelling front problem using results on the linear determinacy principle from [**20, 33, 19**], and we investigate in detail the two possible cases together with the appropriate biological interpretation. We close with a discussion of the results.

2 Reaction and diffusion   Consider the classical diffusive logistic equation or Fisher's equation

$$(2) \qquad\qquad u_t = D\Delta u + f(u).$$

The function $u = u(t,x)$ is the density of some population (or the relative proportion of some type within a population). $D > 0$ is the positive diffusion coefficient. Here and throughout the paper we assume a function $f \in C^1(\mathbb{R})$ with $f(0) = f(1) = 0$ and $f(u) > 0$ for $0 < u < 1$. We also assume $f(u) < 0$ for $u \notin [0,1]$, and $f'(0) > 0$, $f'(1) < 0$. This equation has been studied with several boundary conditions. For a bounded domain and zero Neumann (no flux) boundary condition the typical limit

solution is constant in space and time. For a bounded domain with zero Dirichlet condition there is a threshold phenomenon. For large diffusion rates D the individuals move quickly towards the boundary and become absorbed, hence $u = 0$ is a stable stationary solution. For small diffusion rates a stable non-zero solution is established. For the problem on the whole space the typical limit solution is a travelling front, for which the minimal speed depends on the diffusion coefficient and the qualitative features of the source function f. In the standard case where f is a concave function, the minimal speed is given by the formula $c = 2\sqrt{Df'(0)}$, see, e.g., [26].

Now we supply this model system with a compartment of sedentary individuals. Let v denote the migrating part of the population, and let w be the sedentary part, such that $u = v+w$ is the total population density. The diffusion coefficient D has the same meaning as before. The function f describes only the interaction within the sedentary population, i.e., $f = f(w)$ is a function only of the variable w. The rate γ_1 governs the transition from the sedentary to the migrant compartment, whereas γ_2 governs the reverse transition. In order to include the case studied by Lewis and Schmitz [21] we incorporate a death term into the equation for the migrants. Then the system assumes the form (1).

Thus, we think of a population where individuals switch between a sedentary reproduction phase and a migratory phase. For moderate switching rates γ_i an observer will see a sedentary group and a migrating group and, in any given time interval, some migrating individuals which settle down and some sedentary individuals which enter the migrating group. For large switching rates the observer will see essentially one population of indistinguishable individuals and, at any given instant, he will see some sedentary and some moving individuals. Hence the situation where individuals move and interact at the same time is the limiting case. We expect that this case of large switching rates is described by a scalar reaction diffusion equation.

This general concept has been used in [13] to derive epidemic contact distributions from random walk models. Hillen [17] uses the idea to model a migrating population with home ranges: by assuming a space-depending stopping rate he obtains, in the parabolic limit, a taxis term towards preferential habitats or home ranges. Pachepsky et al. [24] study the so-called drift paradox related to populations living in streams in terms of a system (1) with a convection term.

One can imagine the possible effect of the death term $-\mu v$. If the transition rate into the migrant compartment is large and death of migrants occurs frequently, then the whole population can be driven to

extinction.

3 Sedentary states, damped wave equations, and diffusion approximations The system (1) is closely related to nonlinear damped wave equations. In general the connection between certain systems and wave equations can be exploited to gain information on travelling wave solutions, [**7, 11**]. To the system (1) we apply what sometimes is called Kac's trick (cf. [**10**]). This transformation is otherwise used to carry correlated random walk systems or Cattaneo systems into reaction telegraph equations or nonlinear damped wave equations. We differentiate the second equation with respect to time, replace the resulting term v_t from the first equation, then the resulting terms containing v again from the second equation. In this way we end up with an equation containing only the variable w, see the Appendix. With the parameters

$$(3) \qquad \tau = \frac{1}{\gamma_1 + \gamma_2}$$

and

$$(4) \qquad \rho_i = \frac{\gamma_i}{\gamma_1 + \gamma_2}, \quad i = 1, 2,$$

this equation assumes the form

$$(5) \qquad \tau w_{tt} + (1 - \tau(f'(w) - \mu))w_t - \tau D \Delta w_t$$
$$= \rho_1 D \Delta w + (\rho_2 + \tau \mu) f(w) - \rho_1 \mu w - \tau D \Delta f(w).$$

Equation (5) is a damped wave equation of some kind. The first term on the left hand side is the inertia term, the second is a nonlinear damping term, the third a viscous damping term (notice that $-\Delta$ is a positive operator). The first term on the right hand side is the diffusion term with the effective diffusion coefficient $\rho_1 D$ measuring the proportion of time in which diffusion takes place. The second and the third term on the right hand side represent the effective reaction function

$$(6) \qquad f_\tau(w) = (\rho_2 + \tau \mu)\Big(f(w) - \frac{\rho_1 \mu}{\rho_2 + \tau \mu} w\Big)$$

which determines the stationary points. As $\tau \to 0$ it becomes

$$(7) \qquad f_0(w) = \rho_2 f(w) - \rho_1 \mu w.$$

The coefficients ρ_2 and ρ_1 measure the proportions of time the reactions $f(w)$ and $-\mu w$ take actually place. The last term on the right hand side is a nonlinear diffusion term which may strongly effect the character of the problem, as we shall show below.

Now we assume that individuals switch rapidly between the two states v and w, i.e., that the γ_i are large. In the limit of very large rates we expect a single population of individuals which cannot be distinguished as migrating or sedentary. Hence we use the scaling

$$(8) \qquad \gamma_1 \to \gamma_1/\epsilon, \quad \gamma_2 \to \gamma_2/\epsilon$$

and let $\epsilon \to 0$. Notice that this scaling is not equivalent to a simultaneous scaling of space and time. Then also $\tau \to 0$ and we formally arrive at the reaction diffusion equation

$$(9) \qquad w_t = \rho_1 D \Delta w + f_0(w).$$

This diffusion limit equation shows clearly that diffusion and mortality μ act with effective rate ρ_1 and the nonlinearity f acts with effective rate ρ_2. The same idea can be applied to the variable v, see the Appendix.

The special case which is closest to the scalar diffusive logistic equation is that where just a resting state or quiescent state is added, i.e., the case where $\mu = 0$. From equation (9) we observe that the limiting reaction diffusion equation is

$$(10) \qquad w_t = \rho_1 D \Delta w + \rho_2 f(w).$$

The linear case (with $f(w) \equiv 0$, $\mu = 0$), as has been suggested by [4], describes Brownian motion with Poisson stops. In a stochastic interpretation the graphs of the paths are the same as in standard Brownian motion. Following (5) the density is governed by a wave equation with viscous damping

$$(11) \qquad \tau w_{tt} + w_t - \tau D \Delta w_t = \rho_1 D \Delta w$$

with effective diffusion coefficient $\rho_1 D$.

As announced earlier, we discuss the effect of the nonlinear diffusion term $\Delta f(w)$ in equation (5). We linearize at the zero solution and keep only differential operators of order 2 and 3. Hence we find the leading part

$$\tau w_{tt} - \tau D \Delta w_t = D(\rho_1 - \tau r)\Delta w$$

where

$$(12) \qquad\qquad r = f'(0)$$

is the intrinsic growth rate of sedentary individuals. Hence, were it not for the viscosity term Δw_t, the "wave equation" alone would become elliptic rather than hyperbolic for $r > \gamma_1$. It turns out, that the sign of the quantity $r - \gamma_1$ plays an important role in the present problem.

In order to better understand this phenomenon, we compare the system (1) to the Fitzhugh-Nagumo system and to a Fisher equation with a quiescent state. The Fitzhugh-Nagumo system (see [**14, 23**]) describes the interaction of voltage v and membrane activation w in the membrane of a nerve cell (here $q(v) = v(1 - v)(v - \alpha)$, with $0 < \alpha < 1$),

$$(13) \qquad \begin{aligned} v_t &= D\Delta v + q(v) - \delta w \\ w_t &= v - \nu w \end{aligned}$$

which leads to

$$(14) \qquad v_{tt} + (\nu - q'(v))v_t - D\Delta v_t = \nu D\Delta v + \nu q(v) - \delta v.$$

Since $\nu > 0$, the leading part of this equation is always hyperbolic.

3.1 Fisher's equation with a quiescent state We can associate a quiescent state with Fisher's equation,

$$(15) \qquad \begin{aligned} v_t &= D\Delta v + f(v) - \gamma_2 v + \gamma_1 w \\ w_t &= \gamma_2 v - \gamma_1 w. \end{aligned}$$

Individuals in state v move and interact as in the standard Fisher equation while individuals in state w are quiescent. The system (15) could represent a model for a population where individuals migrate and reproduce and are subject to randomly occurring inactive phases. Such behavior is typical for invertebrates living in small ponds in arid climates which dry up and reappear subject to rainfall.

One can eliminate the variable w and derive the damped wave equation

$$(16) \qquad \tau v_{tt} + (1 - \tau f'(v))v_t - \tau D\Delta v_t = \rho_1 D\Delta v + \rho_1 f(v).$$

Studying the three examples (1), (15) and (13) together gives some insight on the transition from formally hyperbolic to formally elliptic in

the case of (1). In the two examples (13) and (15) the second equation describes a negative feedback loop for any biologically meaningful choice of the parameters and this feedback loop leads eventually to the hyperbolicity of the wave equation independent of the viscosity term. On the contrary, the second equation in (1) becomes a positive feedback loop for $r > \gamma_1$ and the wave equation becomes formally elliptic. Hence in the case of the system (1) we have formally a hyperbolic/elliptic transition like in supersonic flow.

4 The system without diffusion   In the absence of diffusion the system (1) reduces to a system of two ordinary differential equations with reproduction in one compartment and mortality in the other,

$$(17) \qquad \begin{aligned} \dot{v} &= -\mu v - \gamma_2 v + \gamma_1 w \\ \dot{w} &= f(w) - \gamma_1 w + \gamma_2 v. \end{aligned}$$

In view of (5) the system is equivalent with the Liénard equation

$$\tau \ddot{w} + (1 - \tau(f'(w) - \mu))\dot{w} = (\rho_2 + \tau\mu)f(w) - \rho_1 \mu w$$

with the limiting case

$$(18) \qquad \dot{w} = f_0(w)$$

for large γ_i, with f_0 defined by (7).

The Jacobian of (17) at any point (v, w) is

$$(19) \qquad J = \begin{pmatrix} -\mu - \gamma_2 & \gamma_1 \\ \gamma_2 & f'(w) - \gamma_1 \end{pmatrix}.$$

Hence (17) is a cooperative system (off-diagonal elements of the Jacobian are positive, see [**30**]). There are no periodic orbits. Every bounded trajectory converges to a stationary point.

With the assumptions on the function f the rectangle

$$Q = \{(v, w) : 0 \leq w \leq 1, \ 0 \leq v \leq \gamma_1/\gamma_2\}$$

is positively invariant with respect to the flow and it attracts all trajectories from $\mathbb{R}_+^2$.

If w is a zero of the function $f_\tau(w)$ as given by (6) and

$$(20) \qquad v = \frac{\gamma_1}{\mu + \gamma_2} w$$

then (v, w) is a stationary point of (17). The determinant and the trace of the Jacobian satisfy

$$(\mu + \gamma_2)\mathrm{tr}\, J = -\det J - (\mu + \gamma_2)^2 - \gamma_1\gamma_2.$$

The trace is negative whenever the determinant is nonnegative. Hence the stability of the stationary point is governed by the determinant alone. Since

$$\det J = -(\mu + \gamma_2)f'_\tau(w),$$

the sign of $f'_\tau(w)$ determines the stability of the stationary point (v, w).

In realistic examples the function f has some monotonicity properties. We assume that the effective growth rate $f(w)/w$ is decreasing,

$$(21) \qquad \frac{d}{dw}\left(\frac{f(w)}{w}\right) < 0 \quad \text{for} \quad w > 0.$$

In other words, we assume that the function f is concave in the sense of Krasnoselskij. This assumption is realistic in biological terms but also a very natural hypothesis for elliptic boundary value problems. The hypothesis is equivalent with the following

$$(22) \qquad f'(w) < f(w)/w \quad \text{for} \quad w > 0.$$

Of course, if f is concave in the standard sense and $f(0) \geq 0$ then it satisfies (21), too. Hence the Verhulst case is always included.

Let (21) be satisfied. Then $1 > w > v > 0$ implies $f(w)/w < f(v)/v = (f(v) - f(0))/(v - 0)$. Hence the function f satisfies also the "subtangential condition"

$$(23) \qquad f(w) \leq f'(0)w \quad \text{for} \quad 0 \leq w \leq 1,$$

which plays a role in the travelling front problem, see Section 6. If $\mu = 0$, i.e., when we consider the system (12), then in all arguments we can replace the assumption (21) by (23).

The point $(0, 0)$ is stationary. If $\mu > 0$ is large then there may be no other stationary points, and $(0, 0)$ is globally attracting. For moderate $\mu > 0$ there may be many stationary points. If (21) is satisfied then there is at most one non-trivial stationary point, and this point exists and is stable whenever $(0, 0)$ is unstable.

The trace and the determinant at the stationary point $(0,0)$ are (recall $r = f'(0)$)

(24) $$\theta = \operatorname{tr} J = r - \mu - \gamma_1 - \gamma_2,$$

(25) $$d = \det J = -\mu r - \gamma_2 r + \mu \gamma_1.$$

Later we shall see that the net production in the sedentary compartment

(26) $$\delta = r - \gamma_1$$

plays an important role. The condition $d < 0$ can also be expressed as

(27) $$r > \frac{\mu \gamma_1}{\mu + \gamma_2}$$

saying that the growth rate in the sedentary compartment exceeds the mortality in the migrant compartment. We rephrase the stability conditions in terms of these quantities.

Lemma 1. *Assume* (21) *holds. If $d < 0$ then the stationary point $(0,0)$ is unstable and there is a unique non-trivial stationary point. If $d \geq 0$ then $(0,0)$ is stable and there is no other stationary point.*

Hence we have two cases depending on the relative sizes of the production rate r, the mortality μ, and the transition rates γ_i.

Case A: $d < 0$ (high production, low mortality). The stationary point $(0,0)$ is unstable. There are non-trivial stationary points. If (21) is satisfied, then the non-trivial stationary point is unique, otherwise there may be generically an uneven number of stationary points.

Case B: $d > 0$ (low production, high mortality). The point $(0,0)$ is stable. If (21) is satisfied, then there are no further stationary points. In a general generic situation, there is an even number of non-trivial stationary points.

Now we consider the case of large switching rates, i.e., the scaling (8) with $\epsilon \to 0$. In the limit the condition (27) for a non-trivial stationary point assumes the form $f_0'(0) = \rho_2 r - \rho_1 \mu > 0$. If there is no non-trivial stationary point then the population dies out. If there is a non-trivial stationary point then the limiting reaction diffusion equation (9) can be seen as a population equation with adapted growth rate and capacity.

These effects can be clearly seen in the Verhulst case $f(u) = ru(1-u)$. Then (18) can be written as (see also (7))

$$(28) \qquad w_t = r_{\text{eff}} w \left(1 - \frac{w}{K_{\text{eff}}}\right)$$

with

$$r_{\text{eff}} = \rho_2 r - \rho_1 \mu, \quad K_{\text{eff}} = \frac{\rho_2 r - \rho_1 \mu}{\rho_2 r}$$

which says that we have another diffusive Verhulst equation with a reduced reproduction factor (because of $\rho_2 < 1$ and the additional mortality μ in the migrating compartment) and reduced capacity, unless $\mu = 0$.

5 Diffusion in a bounded domain The sign of the quantity δ, introduced in (26), plays an important role if one studies the system (1) on a bounded domain Ω. The case of no flux (zero Neumann) conditions can be handled in a straightforward manner. We consider absorption (zero Dirichlet) boundary conditions

$$(29) \qquad v(x) = 0 \quad \text{for} \quad x \in \partial\Omega.$$

We assume that the condition (21) is satisfied. Let $\lambda_1(\Omega)$ be the lowest eigenvalue of $-\Delta$ for the domain Ω with the boundary condition (29). If $d > 0$ then the system without diffusion has only the trivial stationary point $(0,0)$ and also for (1) the solution $(v, w) \equiv (0,0)$ is the only nonnegative stationary solution. Therefore we restrict to Case A, i.e., to $d < 0$.

We linearize the system (1) at the trivial solution. Since the linearization of the right hand side of the system (1) and the Laplacian with zero Dirichlet boundary conditions both generate flows preserving positivity, we can obtain the spectral bound λ for the linearization of the system (1) (29) from the lowest eigenvalue of the (negative) Laplacian, i.e., from the condition

$$(30) \qquad (\lambda + D\lambda_1(\Omega) + \mu + \gamma_2)(\lambda + \gamma_1 - r) - \gamma_1\gamma_2 = 0.$$

This argument works for any standard space, e.g., $L^2(\Omega)$. The equation (30) shows that there are two very different cases.

Proposition 2. *Let the function f have the properties stated in Section 2. Then the stability properties of the zero solution can be described as follows.*

Case 1: $\delta = r - \gamma_1 < 0$. *Then the zero solution is unstable if and only if*

$$(31) \qquad\qquad D\lambda_1(\Omega) < \frac{d}{\delta}$$

where the right hand side is positive. Hence the trivial solution is unstable for sufficiently large domains.

Case 2: $\delta = r - \gamma_1 > 0$. *Then the trivial solution is always unstable. The population can persist in arbitrarily small domains.*

Next we look at the stationary problem

$$(32) \qquad\qquad \begin{aligned} -D\Delta v &= -(\gamma_2 + \mu)v + \gamma_1 w \\ \frac{\gamma_1 w - f(w)}{\gamma_2} &= v \end{aligned}$$

with boundary condition (29). We reduce this problem to a scalar elliptic boundary value problem.

Lemma 3. *Let the function f have the property* (21). *Then the boundary value problem* (32), (29) *for the functions* (v, w) *can be reduced to a boundary value problem for the function v alone,*

$$(33) \qquad\qquad -D\Delta v = g(v)$$

with boundary condition (29). *The function $g : \mathbb{R}_+ \to \mathbb{R}$ has the following properties: $g \in C^1[0, \infty)$, $g(0) \geq 0$, $g(v) < 0$ for large v. The function g is concave in the sense of Krasnoselskij, cf.* (21),

$$(34) \qquad\qquad g'(v) < g(v)/v \quad \text{for} \quad v > 0.$$

There are two cases.

Case 1: $\delta < 0$. *Then $g(0) = 0$, $g'(0) > 0$.*
Case 2: $\delta > 0$. *Then $g(0) > 0$.*

Proof. Define the function $h : \mathbb{R} \to \mathbb{R}$ by $h(w) = (\gamma_1 w - f(w))/\gamma_2$. Then $h(0) = 0$, $h(w) \to +\infty$ for $w \to +\infty$, and $h'(0) = -\delta/\gamma_2$. Furthermore h is "convex in the sense of Krasnoselskij", i.e., $h'(w) > h(w)/w$ for $w > 0$.

Case 1: The function h is strictly monotone for $w > 0$ and defines a bijection of $\mathbb{R}_+$. The inverse function $k : \mathbb{R}_+ \to \mathbb{R}_+$ satisfies $k(0) = 0$, $k'(0) = -\gamma_2/\delta > 0$ and $k'(v) < k(v)/v$ for $v > 0$. Define

(35)
$$g(v) = -(\gamma_2 + \mu)v + \gamma_1 k(v).$$

Then $g'(v) < g(v)/v$ for $v > 0$, $g(0) = 0$, $g'(0) = d/\delta > 0$. In view of $h(1) = \gamma_1/\gamma_2$ we have $g(\gamma_1/\gamma_2) = -\mu\gamma_1/\gamma_2 \le 0$. On the other hand, let v be a non-negative solution of (33), (29). Then define $w = k(v)$, the pair (v, w) is a solution to (32), (29).

Case 2: The function h is negative for small positive v and then becomes positive. There is a unique zero which we denote by $\bar{K}$. From $h(1) = \gamma_1/\gamma_2$ it follows that $\bar{K} < 1$. Then h is strictly increasing for $v \ge \bar{K}$ and $h : [\bar{K}, \infty) \to [0, \infty)$ is a bijection. The inverse function $k : \mathbb{R}_+ \to [\bar{K}, \infty)$ satisfies $k(0) = \bar{K}$ and $k'(v) < k(v)/v$ for $v > 0$. Again, define the function g by (35). Then $g(0) = \gamma_1\bar{K} > 0$, and $g(\gamma_1/\gamma_2) < 0$ as in Case 1. Finally $g'(v) < g(v)/v$ for $v > 0$.

On the other hand, let v be a non-negative solution of (33), (29). Then the pair (v, w) with $w = k(v)$ is a solution to (32), (29). $\square$

Theorem 4. *Let f satisfy the hypothesis (21). Then the boundary value problem (32), (29) has the following properties.*

Case 1: $\delta < 0$. If the domain is sufficiently large, i.e., if condition (31) is satisfied, then there is a non-trivial non-negative solution. This solution is unique.

Case 2: $\delta > 0$. For a given domain of any size there is a unique non-trivial non-negative solution.

Proof. The proof follows from the theory of subsolutions and supersolutions, see, e.g., Theorem 2.1 of [**27**] based earlier work [**1**]. As a supersolution we can take $v(x) \equiv \gamma_1/\gamma_2$. As a subsolution we choose ϵu, where u is the non-negative eigenfunction $-\Delta u = \lambda_1 u$ (see (31)) with $\|u\|_2 = 1$, and $\epsilon > 0$ small. In Case 1 we have $D\Delta(\epsilon u) + g(\epsilon u) = \epsilon(g'(0) - D\lambda_1)u + o(\epsilon u) > 0$ in Ω for small $\epsilon > 0$. In Case 2 we have $D\Delta(\epsilon u) + g(\epsilon u) = g(0) + O(\epsilon u) > 0$ in Ω for $\epsilon > 0$ small.

Uniqueness follows from the argument of [**16**] which covers exactly the present situation (the author does not mention Krasnoselskij monotonicity, but his condition is equivalent to it, with the sign of the condition and that of the Laplacian inverted). $\square$

In the case of the Verhulst nonlinearity $f(w) = rw(1-w)$ we can make things more explicit. Then $h(w) = (\gamma_1 w - rw(1-w))/\gamma_2$ and

$$(36) \qquad k(v) = \frac{1}{2r}\sqrt{(\gamma_1 - r)^2 + 4\gamma_2 rv} - \frac{1}{2r}(\gamma_1 - r),$$

$$(37) \qquad g(v) = \frac{\gamma_1}{2r}\left(\sqrt{(\gamma_1 - r)^2 + 4\gamma_2 rv} - (\gamma_1 - r)\right) - (\gamma_2 + \mu)v.$$

The function $g(v)$ has a unique positive zero (the adjusted carrying capacity for the migrants v)

$$(38) \qquad\qquad K_v = \frac{-\gamma_1 d}{r(\gamma_2 + \mu)^2}$$

which is positive by assumption. One can compute also the carrying capacity for the sedentary population which is

$$(39) \qquad\qquad K_w = \frac{-d}{r(\gamma_2 + \mu)}.$$

One can ask whether any of the inequalities $K_v \le 1$, $K_w \le 1$ or $K_v + K_w \le 1$ hold, in other words, whether the carrying capacity of the total population or its components depends in a simple way on the parameters. In fact a simple relation seems not to exist, except in the case $\mu = 0$ where always $K_v + K_w > 1$.

We interpret Proposition 2 and Theorem 4 in biological terms. Case 1 exhibits a critical domain size and is similar to traditional estimates of patch sizes, whereas Case 2 is unusual as there is no critical domain size. After the calculations have been done, the biological interpretation is obvious. The mortality μ has been restricted by the assumption that $(v, w) = (0, 0)$ is unstable in the system without diffusion. If r is large and γ_1 is small then many individuals are produced in the sedentary compartment and few enter the migrating compartment where they either die or are absorbed at the boundary. Hence in this case the migrating compartment has little influence.

We shall see that the distinction between these two cases is also essential in the travelling front problem.

Now we perform a similar analysis for the system (15). With the hypothesis (21) and the boundary condition (29) we find by direct computation that there is a non-trivial equilibrium if and only if the zero solution is unstable. The zero solution is unstable for any choice of the γ_i. Hence in the case of the system (15) introducing a sedentary compartment does not change the conditions for the population to survive but just changes the total population size at the non-trivial equilibrium.

6 Travelling fronts For the classical reaction diffusion equation (2) where the function f has the properties stated in Section 2 the following is known: There is a minimal speed of travelling fronts $c_0 = c_0(f, D) > 0$. For each $c \geq c_0$ there is a travelling front, i.e., a wave profile, unique up to translation. The profiles are exponentially decaying. Slower fronts have a steeper profile, i.e., decay faster. The front with minimal speed c_0 describes the propagation of initial data with compact support.

The minimal speed can be characterized by variational principles. In general it depends on D and the global shape of the function f. Thus, in general, it is not true that the speed of the front can be obtained from looking at its leading edge; it cannot be determined from a linear analysis.

On the other hand, a linear analysis at the leading edge gives a lower bound $\tilde{c}_0 = \tilde{c}_0(f, D)$ for possible speeds of travelling fronts since for $c < \tilde{c}_0$ all candidates for front profiles are oscillating and hence not uniformly positive. Hence $\tilde{c}_0 = 2\sqrt{Df'(0)} \leq c_0$.

There are certain classes of functions f for which the minimal speed c_0 can be found from a linear analysis, i.e., for which equality $\tilde{c}_0 = c_0$ holds. When this is true it has become customary to say that the equation satisfies the linear conjecture or it is linearly determined. A sufficient, but not necessary, condition is the subtangential inequality $f(u) \leq f'(0)u$ for $0 \leq u \leq 1$, see [26]. There are good reasons to assume that there is no simple necessary and sufficient condition for the linear conjecture to hold [12].

For systems in general, even for those which are close to the scalar case in the sense that the travelling front problem can be reduced to the scalar case (e.g., reaction telegraph equations [12]), there is no analogue of the subtangential condition, although concavity will do. For general systems the problem is wide open except in cases where the nonlinearity has a cooperative structure [19].

The system (1) has the reaction diffusion equation (10) as its limiting case. All results stated above apply to the limiting case. We want to know whether (1) has travelling front solutions and when the linear conjecture holds, away from the limiting case, i.e., for moderate γ_i.

There are several approaches to the travelling front problem. One approach is to transform (1) into travelling wave coordinates and to show the existence of heteroclinic orbits connecting the non-trivial to the trivial stationary state. This approach usually works in scalar problems but becomes extremely cumbersome for systems. But even for systems one can find bounds on the minimal wave speed such as $\tilde{c}_0$ above from

a linear analysis at the leading eadge of the front. We shall use this approach in Subsection 6.3.

Quite another approach, originating from [2], is based on the "spread rate" and uses comparison principles for the time-dependent problem. The spread rate is a number $c^* = c^*(f, D)$ such that, for initial data with compact support, an observer travelling with speed $c > c^*$ will eventually see the trivial state, and an observer travelling with speed $c < c^*$ will see the non-trivial state. Also for the spread rate some information can be gained from linearizing at the leading edge of the front, see [3, 22, 19].

For a large class of scalar equations the travelling wave problem can be carried into an integral equation and then it can be shown that travelling fronts exist and also that the spread rate equals the minimal speed of travelling fronts (again using a subtangential condition), see [32]. Some systems can be carried into a scalar integral equation by solving for one variable in the first equation and replacing it in the second equation. Here we follow a direct approach.

In this section we will give the formula for the spread rate c^* of the system (1) and will show that this spread rate equals the minimal wave speed $\tilde{c}_0$ for the travelling wave problem with condition (21). The equivalence of c^* and $\tilde{c}_0$ is known for the limiting equation (cf. (9)), [2], but has not been previously established for the two-component system (1). Detailed calculations of the minimal wave speed have been made by [21] for $\delta > 0$ (Case 2 above), but have not been previously made for $\delta < 0$ (Case 1 above). Our analysis calculates the spread rate c^* for the two component system using new results from [19], and extends the analysis of [21] to the case $\delta < 0$ (Case 1 above). This allows us to get a complete picture of travelling fronts with mobile and stationary classes. With the subtangential properties required we get $c^* = \tilde{c}_0$ for the nonlinear system (1).

We assume $d < 0$ since otherwise the non-trivial equilibrium $(\bar{v}, \bar{w})$ would not exist.

6.1 Spread rate analysis We follow the approach in [19] and consider a system of reaction diffusion equations

$$(40) \qquad\qquad U_t = \hat{D}\Delta U + F(U)$$

where the nonlinearity F has cooperative structure and $\hat{D}$ is the non-negative diagonal matrix of diffusion rates. Let $F(0) = 0$ and let $F(\bar{U}) = 0$ with $\bar{U} > 0$ componentwise.

We look for a travelling front connecting the non-trivial equilibrium $\bar{U}$ to the trivial equilibrium such that $U = 0$ at the leading edge of the front. Together with (40) we consider the linearization at $U = 0$

$$(41) \qquad \mathbf{u}_t = \hat{D}\mathbf{u}_{xx} + A\mathbf{u}$$

where $A = F'(0)$ is the Jacobian at $U = 0$. There are several quantities related to the minimal speed of travelling fronts. The spread rate for the nonlinear system (40) is a number c^* such that for small $\epsilon > 0$

$$(42) \qquad \lim_{t\to\infty}\Big\{\sup_{|x|\geq(c^*+\epsilon)t}\|U(t,x)\|\Big\} = 0,$$

$$(43) \qquad \lim_{t\to\infty}\Big\{\sup_{|x|\leq(c^*-\epsilon)t}\|U(t,x) - \bar{U}\|\Big\} = 0.$$

There is the spread rate $\bar{c}$ of the linear system (41) defined in a similar manner but with (43) replaced by

$$(44) \qquad \lim_{t\to\infty}\Big\{\sup_{|x|\leq(\bar{c}-\epsilon)t}\|\mathbf{u}(t,x)\|\Big\} > 0.$$

In [19] it was shown that, under certain conditions on $F(U)$, $c^* = \bar{c}$. In turn, $\bar{c}$ can be related to the spectral bound of the matrix $A + \lambda^2\hat{D}$. Intuitively, this spectral bound can be interpreted as a measure of the local growth rate associated with the leading edge of the spreading population which has the shape $\exp\{-\lambda(x - ct)\}$.

Applying the results from [19] requires some further hypotheses about irreducibility of the Jacobian and the absence of other equilibria, see also [20]. These hypotheses are satisfied in our case. In the present context we shall use the following two results.

(i) If the function F satisfies a subtangential condition then c^* and $\bar{c}$ both exist and $c^* = \bar{c}$.

(ii) The spread rate of the linear system is given by

$$(45) \qquad \bar{c} = \inf_{\lambda>0}\sigma_1(\lambda)$$

where $\sigma_1(\lambda)$ is the largest eigenvalue, i.e., the spectral bound, of the matrix

$$(46) \qquad B_\lambda = \frac{A + \lambda^2\hat{D}}{\lambda}.$$

Note that, in view of the assumptions (cooperativeness and instability of the zero solution), the number $\sigma_1(\lambda)$ is positive. It is evident that $\tilde{c}_0 \leq c^*$ and, *if c_0 exists*, also $\tilde{c}_0 \leq c_0$.

6.2 Spread rate analysis for the system (1) In the present case of the system (1) we have, with $U = (v, w)$,

$$(47) \qquad \hat{D} = \begin{pmatrix} D & 0 \\ 0 & 0 \end{pmatrix}, \quad F(U) = \begin{pmatrix} -\mu v - \gamma_2 v + \gamma_1 w \\ f(w) + \gamma_2 v - \gamma_1 w \end{pmatrix},$$

$$(48) \qquad A = \begin{pmatrix} -\mu - \gamma_2 & \gamma_1 \\ \gamma_2 & \delta \end{pmatrix}.$$

It is easy to see that the system satisfies the subtangential condition for the vector function F (see [**19**]) if and only if the scalar function f satisfies a subtangential condition (23).

The characteristic polynomial of the matrix B_λ is, with θ, d, δ from (24)–(26)

$$(49) \qquad p(\sigma, \lambda) = \sigma^2 - \sigma \frac{(\theta + D\lambda^2)}{\lambda} + \frac{d}{\lambda^2} + D\delta = 0.$$

The larger root is $\sigma_1(\lambda)$. We can multiply by λ^2 and look at the polynomial $P(\sigma, \lambda) = \lambda^2 p(\sigma, \lambda)$,

$$(50) \qquad P(\sigma, \lambda) = \lambda^2 \sigma^2 - \lambda \sigma(\theta + D\lambda^2) + d + D\delta\lambda^2$$

as the characteristic polynomial of the two-parameter eigenvalue problem

$$(51) \qquad (A + \lambda^2 \hat{D} - \lambda\sigma I)u = 0.$$

We can expand into powers of λ and get

$$(52) \qquad P(\sigma, \lambda) = e\lambda^3 + a\lambda^2 + b\lambda + d,$$

where the coefficients e, a, and b are given in terms of the original parameters as

$$(53) \qquad e = -D\sigma, \quad a = D\delta + \sigma^2, \quad b = -\sigma\theta$$

and d is given by (25).

Lemma 5. *$\sigma_1(\lambda)$ is positive for all values of λ and achieves its minimum on the interval $0 < \lambda < \infty$ for finite values of λ.*

Case 1: If $\delta = r - \gamma_1 < 0$ then $\sigma_2(\lambda)$ is negative for all λ.
Case 2: If $\delta = r - \gamma_1 > 0$ then $\sigma_2(\lambda)$ is negative for $\lambda^2 < -d/(D\delta)$ and is positive for $\lambda^2 > -d/(D\delta)$. The function $\sigma_2(\lambda)$ achieves a positive maximum for a finite value of λ on the interval $-d/(D\delta) < \lambda < \infty$.

Proof. Since the matrix B_λ is cooperative, the roots of $p(\,\cdot\,, \lambda)$ are real. If $\delta < 0$ then $p(0, \lambda) < 0$ and hence there is one positive root $\sigma_1(\lambda)$ and one negative real root $\sigma_2(\lambda)$ for all values of $\lambda > 0$. Now let $\delta > 0$. The determinant $d/\lambda^2 + D\delta$ increases from large negative values for small λ to $D\delta > 0$ for $\lambda \to \infty$. From the definitions (24)–(26) it follows by direct calculation that $\theta\delta > d$. Then it follows that the inequality $d + D\lambda^2\delta > 0$ implies $\theta + D\lambda^2 > 0$. Hence the polynomial has always one root $\sigma_1 > 0$ and another σ_2 which switches from negative to positive as λ^2 increases through $\lambda^2 = -d/(D\delta)$.

As $\lambda \to 0$, $\sigma_1(\lambda)\lambda \to (\theta + \sqrt{\theta^2 - 4d})/2 > 0$ and thus $\sigma_1(\lambda) \to \infty$. As $\lambda \to \infty$, $\sigma_1(\lambda) \approx D\lambda$ and hence $\sigma_1(\lambda) \to \infty$. As $\lambda \to \infty$, $\sigma_2(\lambda) \approx \delta/\lambda$ and hence $\sigma_2(\lambda) \to 0$. As $\lambda \to 0$, $\sigma_2(\lambda)\lambda \to (\theta - \sqrt{\theta^2 - 4d})/2 < 0$ and thus $\sigma_2(\lambda) \to -\infty$.

The functions $\sigma_1(\lambda)$, $\sigma_2(\lambda)$ are finite for finite values of λ and smooth functions of λ. Thus, $\sigma_1(\lambda)$ has a minimum for a finite value of λ, and, when $\delta > 0$, $\sigma_2(\lambda)$ has a maximum for a finite value of λ greater than $\sqrt{-d/(D\delta)}$. $\qquad\square$

Lemma 6. *If $\bar{\sigma}_i$ is an extremum of $\sigma_i(\lambda)$ assumed at some position $\bar{\lambda}_i > 0$ then $P(\bar{\sigma}_i, \lambda)$ has a double root at $\bar{\lambda}_i$.*

Proof. We have $P(\sigma_i(\lambda), \lambda) = 0$ and hence

$$\frac{\partial P}{\partial \sigma}(\sigma_i(\lambda), \lambda)\frac{d\sigma_i(\lambda)}{d\lambda} + \frac{\partial P}{\partial \lambda}(\sigma_i(\lambda), \lambda) = 0.$$

At an extremum of σ_i, we have $d\sigma_i(\lambda)/d\lambda = 0$ and $P(\sigma_i(\lambda), \lambda) = 0$ and $\frac{\partial P}{\partial \lambda}(\sigma_i(\lambda), \lambda) = 0$. $\qquad\square$

The next lemma shows that the extrema of the functions σ_i are unique. This fact is of interest for characterizing the spread number but also in relating the spread number approach to the travelling wave analysis.

Lemma 7. *The function $\sigma_1(\lambda)$ has a unique minimum*

$$\bar{\sigma}_1 = \min_{\lambda > 0} \sigma_1(\lambda) = \sigma_1(\bar{\lambda}_1) > 0.$$

In Case 1 the function $\sigma_2(\lambda)$ is negative. In Case 2 the function $\sigma_2(\lambda)$ has a unique maximum

$$\bar{\sigma}_2 = \max_{\lambda > 0} \sigma_2(\lambda) = \sigma_2(\bar{\lambda}_2) > 0,$$

and $\sigma_1(\bar{\lambda}_1) > \sigma_2(\bar{\lambda}_2)$.

Proof. By the proof of Lemma 5, the functions $\sigma_1(\lambda)$ and $\sigma_2(\lambda)$ have an odd number of extrema, multiplicities counted. If one of these functions would have three extrema, then for some value of σ, the polynomial $p(\sigma, \lambda)$ would assume that value four times, and the polynomial $P(\sigma, \lambda)$ would have four zeros for that value of σ. Hence $\sigma_1(\lambda)$ has a unique minimum and σ_2 has a unique maximum.

If $\sigma_1(\bar{\lambda}_1) \leq \sigma_2(\bar{\lambda}_2)$ then again the polynomial $P(\sigma, \lambda)$ would vanish four times for some value of σ, multiplicities counted. $\square$

With these Lemmas we have shown the following result.

Theorem 8. *Let the function f have the properties states in Section 2. The spread rate $\bar{c}$ (44) of the linear system (41) can be obtained as the largest value σ such that the polynomial $P(\sigma, \lambda)$ (50) has a real positive double root. If the function f in equation (1) satisfies the subtangential condition (23) then the spread rate c^* of the nonlinear system (42), (43) is given by $c^* = \bar{c}$.*

6.3 Travelling wave analysis We now consider travelling front solutions $v(x + ct)$, $w(x + ct)$ of (1) with speed c. The wave profile (v, w) satisfies the system of ordinary differential equations of order three

$$
\begin{aligned}
c\dot{v} &= D\ddot{v} - \mu v - \gamma_2 v + \gamma_1 w \\
c\dot{w} &= f(w) - \gamma_1 w + \gamma_2 v
\end{aligned}
\tag{54}
$$

and corresponds to a heteroclinic orbit in $\mathbb{R}^3$ connecting the equilibrium (recall that $d < 0$) $(v, w, \dot{v}) = (\bar{v}, \bar{w}, 0)$ to $(0, 0, 0)$.

We linearize about the leading edge of the wave $v = 0, w = 0$ (recall $r = f'(0)$)

$$
\begin{aligned}
c\dot{v} &= D\ddot{v} - \mu v - \gamma_2 v + \gamma_1 w \\
c\dot{w} &= rw - \gamma_1 w + \gamma_2 v.
\end{aligned}
\tag{55}
$$

We look for the eigenvalues of the linearization

$$
\begin{aligned}
c\lambda v &= \lambda^2 D v - \mu v - \gamma_2 v + \gamma_1 w \\
c\lambda w &= rw - \gamma_1 w + \gamma_2 v.
\end{aligned}
\tag{56}
$$

The determinant of this homogeneous system yields the characteristic polynomial which is exactly the same as the polynomial defined in the previous subsection in equation (50):

$$P(c, \lambda) = (D\lambda^2 - \mu - \gamma_2 + c\lambda)(c\lambda + r - \gamma_1) - \gamma_1\gamma_2$$
$$= Dc\lambda^3 + (D\delta + c^2)\lambda^2 + c\theta\lambda + d$$
$$= e\lambda^3 + a\lambda^2 + b\lambda + d$$

with coefficients defined in (53), with σ replaced by c.

The heteroclinic orbit leaves the trivial equilibrium on the unstable manifold defined by the two roots of $P(\lambda, c)$ with positive real part. If these roots are conjugate complex then it spirals in phase space and the v and w components of the orbit become negative. Note that when c is large the pair of roots with positive real part are real and the orbit does not spiral. The minimal allowable wave speed $\tilde{c}_0$ occurs when the pair of positive real roots coalesce and become complex. A necessary condition for this to occur is $P = \partial P/\partial\lambda = 0$. Note that this necessary condition for $\tilde{c}_0$ is the same as the necessary condition for c^* given in the last subsection.

6.4 Evaluating the spread rate and the minimal travelling front speed We now evaluate the double root condition $P = \partial P/\partial\lambda = 0$ which is necessary for c^* and $\tilde{c}_0$. As in [21] we use the resultant of the cubic P, i.e., the resultant of P and $\partial P/\partial\lambda$ which is the homogeneous polynomial of degree 4

$$(57) \qquad R(e, a, b, d) = 18abed - 4a^3d + a^2b^2 - 27e^2d^2 - 4b^3e.$$

The equation $R(e, a, b, d) = 0$ characterizes that manifold in the four-dimensional parameter space for which the cubic P has multiple roots. In the present case we find easily that, given the other parameters, R is a cubic in the variable c^2, i.e., $R(e, a, b, d) \equiv \varphi(c^2)$ with

$$(58) \qquad \begin{aligned} \varphi(c^2) = {} & 18Dc^2(D\delta + c^2)\theta d - 4(D\delta + c^2)^3 d \\ & + c^2(D\delta + c^2)^2\theta^2 - 27D^2c^2d^2 - 4Dc^4\theta^3. \end{aligned}$$

Sorting out terms, we get

$$(59) \qquad \begin{aligned} \varphi(c^2) = {} & c^6(\theta^2 - 4d) - 4D^3\delta^3 d \\ & + c^4 D(18\theta d - 12\delta d + 2\delta\theta^2 - 4\theta^3) \\ & + c^2 D^2(18\delta\theta d - 12\delta^2 d + \delta^2\theta^2 - 27d^2). \end{aligned}$$

As $d < 0$ by assumption, the leading coefficient is positive. Hence the behavior of the problem depends essentially on the sign of δ. Recall the discussion in Section 5.

Lemma 9. *Let $\delta < 0$. Then the function $\varphi(x)$ is convex for $x \geq 0$.*

Proof. If we write $\varphi(x) = a_3 x^3 + a_2 x^2 + a_1 x + a_0$ then $\varphi''(x) = 6a_3 x + 2a_2$. For the coefficient a_2 we find

$$(60) \qquad\qquad a_2 = 2[(9\theta - 6\delta)d + \theta^2(\delta - 2\theta)].$$

We have $d < 0$ and $\theta < \delta < 0$. Hence both terms in (60) are positive. Therefore a_2 is positive as well as a_3.   □

Now we use the information on the functions $\sigma_i(\lambda)$ which we have obtained in Lemmas 5, 6, 7 to show the following theorem.

Theorem 10. *Let the function f satisfy the general hypothesis of Section 2 and and the subtangential condition (23). Let $d < 0$. Then the positive square root of the largest zero of the cubic $\varphi(x)$ is the nonlinear spread rate c^*. The nonlinear spread rate is equal to the bound $\tilde{c}_0$, i.e., $c^* = \tilde{c}_0$.*

Proof. If $\bar{\sigma}$ is an extremal value of either σ_1 or σ_2 then the corresponding value of λ is a double root of $P(\bar{\sigma}, \lambda)$ and hence $\varphi(\bar{\sigma}^2) = 0$, i.e., $\bar{\sigma}^2$ is a positive root of $\varphi(x)$.

Case 1: $\delta = r - \gamma_1 < 0$. Then the constant term of the cubic $\varphi(x)$ is negative, hence $\varphi(0) < 0$ and the cubic has at least one positive root. In view of Lemma 9 this root is unique. Hence there is only one extremum of σ_1 or σ_2. Since we know from Lemma 7 that σ_1 has a unique minimum, which is $\bar{c}$ it follows that $\bar{c}^2$ is the only positive root of $\varphi(x)$. It also follows that the function σ_2, which is negative in this case, has no extrema at all. (It is difficult to show this fact directly). Since in the case of a double eigenvalue the transition from node to focus is generic, solutions for $c < \bar{c}$ are oscillatory. Therefore $c^* = \tilde{c}_0 = \bar{c}$.

Case 2: $\delta = r - \gamma_1 > 0$. Then the constant term in $\varphi(x)$ is positive and hence $\varphi(0) > 0$. There can be two real positive roots (one in the coalescent case) or none at all. In view of Theorem 8 there is a positive root, and hence there are two of them. By Lemma 6 these correspond to the minimum of σ_1 and to the maximum of σ_2. Then Lemma 7 yields that the minimum of σ_1 corresponds to the larger root. The larger root of

$\varphi(x)$ is $\bar{c}^2$. Because f satisfies the subtangential condition, Theorem 8 shows that the nonlinear spread rate is $c^* = \bar{c}$. The proof that the larger of the two roots is also the one that characterizes $\tilde{c}_0$ was given in [**21**], where it was shown that, as c moves through the smaller root, travelling front solutions switch from non-oscillatory negative solutions to oscillatory solutions. □

Hence in the typical situation of a positive net recruitment rate and large γ_i we are in Case 1 and the polynomial φ has exactly one real positive root which is a candidate for both the spread rate and the minimal speed of travelling fronts. This finding completes the discussion in [**21**] where Case 2 has been studied which leads to either two or no real positive roots. In Case 2 the larger positive root of the polynomial φ is the one that characterizes both the spread rate and the minimal speed of travelling fronts. This connection between the spread rate and the minimal speed of travelling fronts, which is well-known for scalar equations [**2**], can also be shown for cooperative systems in general [**18**].

Of course the case $\mu = 0$ is of particular interest. Then $d = -r\gamma_2 < 0$ which says that in absence of migration there is always a non-trivial equilibrium. This finding is obvious in biological terms since there is no mortality in the migrating group. Furthermore $\theta = r - \gamma_1 - \gamma_2$ and $\delta = r - \gamma_1$. Even for $\mu = 0$ both cases 1 and 2 are possible.

6.5 The system with a quiescent stage When individuals reproduce and disperse in a single stage which switches with a quiescent stage, equation (15) pertains. Most results can be carried over to the system (15). The matrix A becomes

$$\begin{pmatrix} r - \gamma_2 & \gamma_1 \\ \gamma_2 & -\gamma_1 \end{pmatrix},$$

hence $\theta = r - \gamma_1 - \gamma_2$, $d = -r\gamma_1 < 0$, and

$$P(\sigma, \lambda) = \lambda^2\sigma^2 - \lambda\sigma(\theta + \lambda^2) + d - D\gamma_1.$$

Hence we always have the situation of Case A ($d < 0$) and of Case 1 ($\sigma_2 < 0$, the cubic $\varphi(x)$ has one or three positive roots).

7 Discussion   We have studied a system of ordinary differential equations (17) with two compartments or subpopulations. In one compartment the population is governed by a law of Verhulst type $\dot{w} = f(w)$

while the other compartment is subject only to mortality $\dot{v} = -\mu v$. The compartments are coupled by linear exchange laws. The population can persist if the zero state is unstable, $d < 0$. In that case there is a unique positive stationary state $(\bar{v}, \bar{w})$. In the diffusion model (1) the subpopulation v diffuses with rate D while the w subpopulation remains sedentary. This system is studied on a bounded domain with zero Dirichlet (absorption) boundary conditions. It turns out that the difference $\delta = r - \gamma_1 = f'(0) - \gamma_1$ determines the fate of the population. If $\delta < 0$ then the population can persist on large domains but not on small domains. If $\delta > 0$ then the system can persist on arbitrarily small domains.

We analyzed the travelling wave problem from two perspectives, that of the spread rate c^* and that of the lower bound $\tilde{c}_0$ for the travelling wave speed, and showed that these were identical. When $\delta < 0$ then the system behaves essentially like the Fisher equation: There is a unique candidate for the speed. When $\delta > 0$ then there are two candidates for the speed, but the larger is the relevant speed.

Explicit calculation of the speed requires finding the largest root of the polynomial $\varphi(c^2)$ in (59). However, simple formulae for the speed can be given for two limiting cases: switching rates very large or very small.

1. For very large switching rates equation (9) applies, and $\tilde{c}_0$ can be calculated from the standard theory for the scalar equation (as outlined in Section 2) to be $c = \tilde{c}_0 = 2\sqrt{\rho_1 D(\rho_2 r - \rho_1 \mu)}$, provided $\rho_2 r > \rho_1 \mu$.

2. For very small and equal switching rates $\gamma_1 = \gamma_2 = \gamma$, and $\mu = 0$, the speed was computed in [21] as $\tilde{c}_0 = \sqrt{rD}$.

In the first of these cases $\delta < 0$. This case is a variant of the classical Fisher formula $c = 2\sqrt{rD}$ where diffusion, reproduction and mortality are weighted by the proportion of time spent in each class. In the second case $\delta > 0$, and the classical formula would not even give a correct lower bound.

Hence, splitting the diffusion and reaction part in Fisher's equation leads to quite unexpected behavior, in particular far from the limiting case of large switching rates, even if there is no mortality in the migrant compartment. This observation may be of importance for modelling actual biological populations since quite often a migrant state can be clearly separated from a sedentary state. Even introducing a quiescent state into a system may change the behavior drastically [15].

Appendix Here we present the steps in the transition from (1) to (5),

$$
\begin{aligned}
w_{tt} &= f'(w)w_t - \gamma_1 w_t + \gamma_2 v_t \\
&= f'(w)w_t - \gamma_1 w_t + \gamma_2[D\Delta v - \mu v - \gamma_2 v + \gamma_1 w] \\
&= f'(w)w_t - \gamma_1 w_t + \gamma_1\gamma_2 w + [D\Delta - \mu - \gamma_2][w_t - f(w) + \gamma_1 w] \\
&= f'(w)w_t - (\gamma_1 + \gamma_2 + \mu)w_t + D\Delta w_t + (\gamma_2 + \mu)f(w) \\
&\quad - D\Delta f(w) - \gamma_1 \mu w + \gamma_1 D\Delta w.
\end{aligned}
$$

Using the parameters (3), (4), one arrives at (5).

The same idea can be applied to the variable v, the resulting equation looks more complicated. From (1) we get

(61)
$$
\begin{aligned}
v_{tt} &= D\Delta v_t - \mu v_t - \gamma_2 v_t + \gamma_1 w_t \\
&= D\Delta v_t - \mu v_t - \gamma_2 v_t + \gamma_1(f(w) - \gamma_1 w + \gamma_2 v) \\
&= D\Delta v_t - (\gamma_1 + \gamma_2 + \mu)v_t + \gamma_1 D\Delta v \\
&\quad + \gamma_1 f\left(\frac{1}{\gamma_1}(v_t - D\Delta v + \mu v + \gamma_2 v)\right) - \gamma_1 \mu v.
\end{aligned}
$$

Hence the new variable

(62)
$$
\tilde{v} = \frac{\gamma_2}{\gamma_1} v
$$

satisfies the damped wave equation
(63)
$$
\tau\tilde{v}_{tt} + (1+\tau\mu)\tilde{v}_t - \tau D\Delta\tilde{v}_t = \rho_1 D\Delta\tilde{v} + \rho_2 f\left(\tilde{v} + \frac{\mu}{\gamma_2}\tilde{v} + \frac{1}{\gamma_2}\tilde{v}_t - \frac{1}{\gamma_2}D\Delta\tilde{v}\right) - \rho_1\mu\tilde{v}
$$

where the Laplacian occurs inside the nonlinearity. In the formal limit (8) of large γ_i we get $\tilde{v}_t = \rho_1 D\Delta\tilde{v} + f_0(\tilde{v})$, i.e., again equation (9). In [**15**] the transition between system diffusion systems and wave equations with viscous damping is studied in general setting.

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