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## SPREADING SPEEDS FOR A PARTIALLY COOPERATIVE 2-SPECIES REACTION-DIFFUSION MODEL.

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ABSTRACT. It is shown that a trick introduced by H. R.Thieme [6] to study a one-species integral equation model with a nonmonotone operator can be used to show that some multispecies reaction-diffusion systems which are cooperative for small population densities but not for large ones have a spreading speed. The ideas are explained by considering a model for the interaction between ungulates and grassland.

**1. Introduction.** Horst Thieme showed in [6] that one could define a spreading speed for a single-species integral equation or integral recursion model in which the fecundity ceases to be a nondecreasing function of the population density at large densities. Such a phenomenon, which is sometimes called overcompensation, was used in [1] to model the growth dynamics of an ungulate population. A plausible explanation for this phenomenon may be that while a small population density of ungulates helps the grassland on which they live by aerating and fertilizing it, a large population density of ungulates hardens the soil and kills the grass, which harms the ungulates. Since this explanation really represents an interaction between the

grass and the ungulates, it is natural to study it by means of a 2-species model. In this work we shall examine the two-species reaction-diffusion model

$$\begin{aligned} u_t &= a_1 u_{xx} + u[-\alpha - \beta u + \gamma v] \\ v_t &= a_2 v_{xx} + rv[1 - v + f(u)], \end{aligned} \tag{1.1}$$

where  $a_1$ ,  $\alpha$ ,  $\beta$ ,  $\gamma$ ,  $a_2$ , and  $r$  are positive parameters, and  $f(u)$  is a prescribed function of  $u$ . This system models the interaction between ungulates with linear density  $u(x, t)$  and grass with linear density  $v(x, t)$ .

The function  $f(u)$  models the increase in the specific growth rate of the grass due to the presence of ungulates. It describes the net benefit of the beneficial and the harmful effects. When the density  $u$  is small the net effect is increasingly beneficial, but as the density increases above a certain value, the benefits decrease with increasing  $u$ , and eventually, the benefit becomes negative. For example, McNaughton ([4], [5]) observed that the above-ground grassland productivity showed a one-humped shape as a function of grazing intensity of wildebeest. We take the unit of grass density so that the density at which this negative effect sets in is  $u = 1$ . The interesting fact about the system (1.1) is that it is not cooperative, because the function  $f(u)$  is not nondecreasing. While this function increases for all sufficiently small  $u$ , it must then decrease in order to return to the value 0 at  $u = 1$ . That is, a small increase in  $u$  is beneficial to the grass when  $u$  is small, but harmful when  $u$  is large. The purpose of this work is to provide conditions on the parameters and the function  $f$  under which one can make a meaningful definition of the asymptotic speed at which a population of ungulates which invades a bounded set of an infinite grassland at equilibrium density spreads out to occupy more and more of the grassland.

The first equation of (1.1) shows that  $u$  approaches 0 when  $v < \alpha/\gamma$ . That is, the ungulates cannot survive without a sufficient supply of grass. On the other hand, when  $u \equiv 0$ ,  $v$  satisfies a Fisher equation, with a stable equilibrium at 1 and an unstable equilibrium at 0. The latter fact shows that the extinction equilibrium (0,0) is unstable for the system (1.1). When  $\gamma > \alpha$ , the second factor in the nonlinear term of the first equation is positive at (0,1). Therefore, the monoculture equilibrium (0,1) is invadable, so that it is also unstable.

The coexistence equilibria of the system (1.1) are found by equating the second factor of the nonlinear term of each equation to zero. By eliminating  $v$ , we find that the  $u$ -component  $u^*$  of such an equilibrium is a solution of the equation

$$\gamma - \alpha - \beta u + \gamma f(u) = 0. \tag{1.2}$$

We shall assume that  $\gamma > \alpha$  and the function  $f(u)/u$  is decreasing. Then there is a single root  $u^* = u^*(\beta)$ , and it decreases from 1 to 0 as  $\beta$  increases from  $\gamma - \alpha$  to infinity. Once  $u^*$  is known, the  $v$ -component  $v^*$  of the coexistence equilibrium is given by the formula

$$v^* = 1 + f(u^*).$$

In particular, we see that  $v^*$  is greater than the value 1 in the monoculture equilibrium, so that the grass benefits from the presence of the ungulates, if and only if  $u^* < 1$ . This is equivalent to the inequality  $\beta > \gamma - \alpha$ . Our method will, in fact, require a stronger inequality.

Section 2 is devoted to making hypotheses about the system (1.1), and to stating a theorem which shows that this system has an asymptotic spreading speed. An example and numerical simulations to illustrate these results are presented in Section 3. The proofs of Theorem 1 and Proposition 2.1 are presented in Section 4.

**2. Hypotheses and the main result.** In this work we shall prove that, in spite of the fact that the system (1.1) is not cooperative when  $u$  is too large, one can define a speed  $c^*$  for the the spread of ungulates which invade a habitat consisting of the grassland in the stable equilibrium state  $(0,1)$ . In order to keep the results as simple as possible, we shall use the following definition.

**Definition 2.1.** *The function  $f(u)$  is said to be **unimodal** on the interval  $[0, 1]$  if there is a number  $u_m$  with  $0 < u_m < 1$  such that  $f$  is increasing on the interval  $[0, u_m]$  and decreasing on  $[u_m, 1]$ .*

We shall make the following assumptions about the function  $f$ .

**Hypotheses 2.1.** *The function  $f$  is continuous, and has the following properties.*

- : i.  $f(0) = f(1) = 0$ .
- : ii.  $f(u)/u$  is bounded above and decreasing for  $0 \leq u \leq 1$ , and negative for  $u > 1$ .
- : iii.  $f(u)$  is unimodal on the interval  $[0, 1]$  with its maximum attained at  $u_m$ .

We define two functions of  $\beta$ .

$$\begin{aligned} u^{*(+)} &:= \begin{cases} [\gamma - \alpha + \gamma f(u_m)]/\beta & \text{when } \beta \leq [\gamma - \alpha + \gamma f(u_m)]/u_m \\ u^* & \text{when } \beta \geq [\gamma - \alpha + \gamma f(u_m)]/u_m \end{cases} \\ v^{*(+)} &:= \begin{cases} 1 + f(u_m) & \text{when } \beta \leq [\gamma - \alpha + \gamma f(u_m)]/u_m \\ v^* & \text{when } \beta \geq [\gamma - \alpha + \gamma f(u_m)]/u_m \end{cases} \end{aligned} \quad (2.1)$$

It is easily checked that  $u^{*(+)} \geq u^*$  and  $v^{*(+)} \geq v^*$ , with strict inequalities when  $\beta < [\gamma - \alpha + \gamma f(u_m)]/u_m$  and equalities when  $\beta \geq [\gamma - \alpha + \gamma f(u_m)]/u_m$ .

In order to obtain a spreading result for solutions of the system (1.1), we shall assume that

$$\beta > \gamma - \alpha + \gamma f(u_m), \quad (2.2)$$

so that  $u^{*(+)} < 1$ , and define another pair of functions of  $\beta$ .

$$\begin{aligned} u^{*(-)} &:= \min\{u^*, [\gamma - \alpha + \gamma f(u^{*(+)})]/\beta\} \\ v^{*(-)} &:= \min\{v^*, 1 + f(u^{*(+)})\}. \end{aligned} \quad (2.3)$$

Our main result is the following theorem, which is the natural extension to the two-species system (1.1) of the single-species result of Thieme [6]. It states that if the parameters satisfy three inequalities and the function  $f$  and the parameters satisfy an inequality, then an invasion by ungulates of a grassland in which  $v$  has the value 1 outside a bounded set spreads at the asymptotic speed

$$c^* := 2\sqrt{(\gamma - \alpha)a_1}. \quad (2.4)$$

**Theorem 1.** *Suppose that the Hypotheses 2.1 are satisfied. Also suppose that the inequalities*

$$\gamma > \alpha$$

and

$$\frac{a_2}{a_1} < 2 + \frac{r}{\gamma - \alpha}, \quad (2.5)$$

are valid, and that, in addition to (2.2),  $\beta$  satisfies the inequality

$$\beta \geq \frac{\gamma f'(0)}{1 + \frac{\gamma - \alpha}{r} \left[ 2 - \frac{a_2}{a_1} \right]}. \quad (2.6)$$

Also assume that the inequality

$$- \left\{ 1 + \frac{\gamma - \alpha}{r} \left[ 2 - \frac{a_2}{a_1} \right] \right\}^2 \left[ 1 - \frac{f(u)}{f'(0)u} \right] + \left\{ 1 + \frac{\gamma - \alpha}{r} \left[ 2 - \frac{a_2}{a_1} \right] \right\} f(u) - f'(0)u \leq 0 \text{ when } 0 < u \leq u_m \quad (2.7)$$

holds. Then the solutions  $(u(x, t), v(x, t))$  of the system (1.1) have the following properties.

- : i. If the functions  $u(x, 0)$  and  $v(x, 0) - 1$  are bounded and vanish outside a bounded interval, then

$$\lim_{t \rightarrow \infty} \left\{ \sup_{|x| \geq ct} [u(x, t) + |v(x, t) - 1|] \right\} = 0 \text{ for any } c > c^*. \quad (2.8)$$

- : ii. If, in addition,  $u(x, 0) \not\equiv 0$ , then

$$\liminf_{t \rightarrow \infty} \left\{ \min_{|x| \leq ct} u(x, t) \right\} \geq u^{*(-)} \text{ and } \liminf_{t \rightarrow \infty} \left\{ \min_{|x| \leq ct} v(x, t) \right\} \geq v^{*(-)} \quad (2.9)$$

for any  $c < c^*$ .

**Remarks.** 1. This Theorem states that any level set  $u(x, t) = \rho$  with  $\rho < u^{*(-)}$ , and any level set  $v = 1 + \sigma$  with  $0 < \sigma < v^{*(-)} - 1$  must spread at a speed which is no lower than  $c^*$ , while no level set can spread at a speed greater than  $c^*$ . In general, it does not say that level sets with higher levels cannot move more slowly, or that the solution converges behind the front.

2. When  $\beta \geq [\gamma - \alpha + \gamma f(u_m)]/u_m$ , we have  $u^{*(+)} = u^{*(-)} = u^*$  and  $v^{*(+)} = v^{*(-)} = v^*$ , and the Theorem gives the usual convergence result for a cooperative system. Theorem 1 gives new results when the inequalities

$$\frac{r\gamma f'(0)}{(\gamma - \alpha)[2 + \{r/(\gamma - \alpha)\} - (a_2/a_1)]} \leq \beta < [\gamma - \alpha + \gamma f(u_m)]/u_m$$

are satisfied.

3. The quadratic formula shows that the inequality (2.7) is equivalent to the statement that at least one of the inequalities

i.  $f(u)^2 + 4f(u) - 4f'(0)u \leq 0$ , or

ii.  $1 + \{(\gamma - \alpha)/r\}\{2 - (a_2/a_1)\} \geq \frac{f(u) + \sqrt{f(u)^2 + 4f(u) - 4f'(0)u}}{2[1 - \{f(u)/(f'(0)u)\}]}$ , or (2.10)

iii.  $1 + \{(\gamma - \alpha)/r\}\{2 - (a_2/a_1)\} \leq \frac{2f'(0)u}{f(u) + \sqrt{f(u)^2 + 4f(u) - 4f'(0)u}}$ .

must be satisfied for every  $u$  in the interval  $0 < u \leq u_m$ . Continuity shows that if the inequality (i) is violated in an interval, then one of the inequalities (ii) or (iii) must hold throughout this interval.

4. The right-hand side of the inequality (ii) in (2.10) can be replaced by any upper bound for it on the set where (i) is violated. If  $f$  has the additional property  $f''(0) < 0$ , then L'Hôpital's rule shows that there is such an upper bound. Similarly, the right-hand side of (iii) may be replaced by a lower bound for it. It can be shown that 1 is such a lower bound, so that the inequality  $a_2 \geq 2a_1$  implies (2.7). If  $f''(0) < 0$ , there is a lower bound which is greater than 1, so that a slightly weaker inequality suffices.

In view of Hypothesis 2.1.i, it is natural to write  $f$  in the form  $f(u) = u(1 - u)\psi(u)$ . The following proposition gives a large family of  $\psi$  for which  $f$  satisfies Hypotheses 2.1.

**Proposition 2.1.** *Let  $\psi(u)$  be a twice continuously differentiable function with the properties*

- : i.  $\psi(u) > 0$  and  $\psi'(u) \leq 0$  for  $u \geq 0$ ; and
- : ii.  $\psi''(u) \leq 0$  for  $0 \leq u \leq 1/2$ .

*Then the function  $f(u) = u(1 - u)\psi(u)$  satisfies the Hypotheses 2.1 with  $u_m \leq 1/2$ , with  $u_m = 1/2$  if and only if  $\psi$  is constant for  $0 \leq u \leq 1/2$ .*

*Moreover, any of the three inequalities*

- i.  $\psi(0) \leq 4$  or
- ii.  $a_2/a_1 \leq 2 - r[\psi(0) - 2 + \sqrt{(\psi(0) - 2)^2 - 4}]/[2(\gamma - \alpha)]$  or
- iii.  $a_2/a_1 \geq 2 - r[\psi(0) - 2 - \sqrt{(\psi(0) - 2)^2 - 4}]/[2(\gamma - \alpha)]$

*implies that the inequality (2.7) is satisfied by this function  $f$ .*

**3. An example and its simulation.** We observe that if  $a$ ,  $b$ , and  $\rho$  are any constants such that

$$0 < a < b \text{ and } \rho > 0,$$

then the function

$$\psi(u) = a + (b - a)/[e^{\rho(2u-1)} + 1] \quad (3.1)$$

decreases from  $b$  to  $a$  as  $u$  goes from  $-\infty$  to  $\infty$ . Differentiation shows that  $\psi' < 0$  for all  $u$ , and that  $\psi''(u) \leq 0$  when  $u \leq 1/2$ . Hence this  $\psi$  satisfies the conditions of Proposition 2.1. Since  $\psi'(1/2) < 0$ , the Proposition shows that when  $f(u) = u(1 - u)\psi(u)$ , then  $u_m < 1/2$ . If, in addition,  $b \leq 4$ , the inequality (2.7) is automatically satisfied. We present below the results of the numerical simulation of the system

$$\begin{aligned} u_t &= 0.5u_{xx} + u(-1.9 - \beta u + 4.75v) \\ v_t &= 0.01v_{xx} + 3.405v(1 - v + u(1 - u)[0.3 + 2.7/[e^{100(2u-1)} + 1]]) \end{aligned} \quad (3.2)$$

with the initial values

$$u(x, 0) = \begin{cases} 0.5 & \text{for } |x| \leq 5 \\ 0 & \text{for } |x| > 5 \end{cases}, \quad v(x, 0) = 1.$$

This system is of the form (1.1) with  $f = u(1-u)\psi(u)$ , and  $\psi$  has the form (3.1) with  $\rho = 100$ ,  $a = 0.3$ , and  $b = 3$ . Since  $b \leq 4$ , the inequality (2.7) is automatically satisfied. It is easily seen that the inequality (2.5) is also satisfied. Simple calculations show that  $u_m = 0.467$ , so that the condition (2.6) becomes  $\beta \geq \max\{6.393, 5.363\} = 6.393$ . The value of  $\beta$  at which  $u^{*(+)} = u^{*(-)} = u^* = u_m$  is  $[\gamma - \alpha + \gamma f(u_m)]/u_m = 13.679$ .

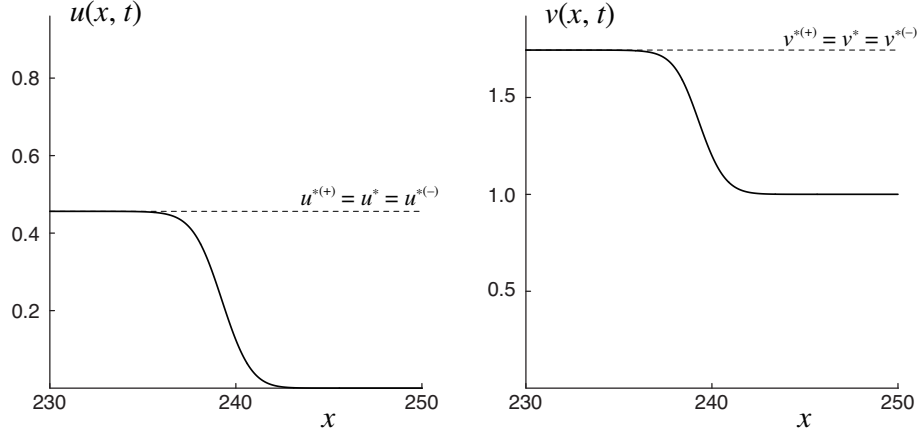


Figure 1

Figure 1 shows the graph of the solution  $(u(x, t), v(x, t))$  at the large value  $t = 100$  when  $\beta = 14 > 13.679$ . Because  $f$  is increasing all the way up to  $u^{*(+)}$ , the solution looks like that of a monotone system.

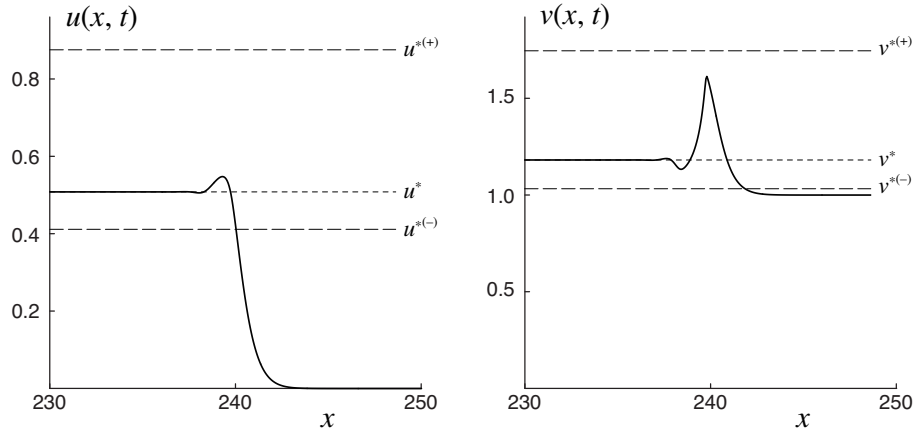


Figure 2

Figure 2 shows the graph of the solution  $(u(x, t), v(x, t))$  at the large value  $t = 100$  when  $\beta = 7.3 < 13.679$ . Since  $u^{*(+)} > u_m$ , the solution cannot be expected to behave like that of a monotone system. In fact, Theorem 1 permits oscillations in  $u$  and  $v$  bounded above by  $u^{*(+)}$  and  $v^{*(+)}$  and below by  $u^{*(-)}$  and  $v^{*(-)}$ , respectively, behind the front, followed by convergence to the equilibrium values  $u^*$  and  $v^*$ . Such oscillations are visible on the graphs in Figure 2.

**4. Proofs. Proof of Theorem 1.** Our principal tool is the following well-known consequence of the maximum principle.

**Lemma 4.1. Comparison Principle.** *Suppose that the vector-valued functions  $\mathbf{u}^{(1)}(x, t)$  and  $\mathbf{u}^{(2)}$  satisfy the inequality*

$$\mathbf{u}_t^{(1)} - D\mathbf{u}_{xx}^{(1)} - \mathbf{f}(\mathbf{u}^{(1)}) \leq \mathbf{u}_t^{(2)} - D\mathbf{u}_{xx}^{(2)} - \mathbf{f}(\mathbf{u}^{(2)})$$

where  $D$  is a positive definite diagonal matrix. Also suppose that the underlying system is **cooperative** in the sense that for each  $i$  the  $i$ th component of  $\mathbf{f}(\mathbf{u})$  is nondecreasing in all but the  $i$ th component of  $\mathbf{u}$ . If at some time  $t_0$  the components of  $\mathbf{u}^{(1)}$  are bounded above by those of  $\mathbf{u}^{(2)}$  for all  $x$ , then this same property is true for all  $t \geq t_0$ .

In order to apply this result, we shall use a pair of related cooperative systems. Horst Thieme [6] showed that for a single-species integral recursion model with overcompensation, one obtains a spreading speed by bounding the growth function above and below by monotone functions with the same derivative at zero. We shall show that the same idea works for the system (1.1), even though the function  $f$  is far from being a growth function. We define the upper function

$$\begin{aligned} f^{(+)}(u) &:= \max_{0 \leq w \leq u} f(w) \\ &= \begin{cases} f(u) & \text{when } 0 \leq u \leq u_m \\ f(u_m) & \text{when } u \geq u_m. \end{cases} \end{aligned} \quad (4.1)$$

This function is nondecreasing and satisfies the inequality  $f^{(+)}(u) \geq f(u)$ . Consequently, the system

$$\begin{aligned} u_t^{(+)} &= a_1 u_{xx}^{(+)} + u^{(+)}[-\alpha - \beta u^{(+)} + \gamma v^{(+)}] \\ v_t^{(+)} &= a_2 v_{xx}^{(+)} + r v^{(+)}[1 - v^{(+)} + f^{(+)}(u^{(+)})] \end{aligned} \quad (4.2)$$

is cooperative. Because a solution of the system (1.1) satisfies the system (4.2) with the  $=$  sign in the second equation replaced by  $\leq$ , the Comparison Principle shows that the components of a solution  $(u^{(+)}, v^{(+)})$  of (4.2) are upper bounds for the corresponding components of the solution  $(u, v)$  of the system (1.1) with the same initial values.

Roughly speaking, we are interested in the invasion by ungulates on a bounded interval of the monoculture state  $(0, 1)$ . We shall apply the methods of [7] with the change of variable  $v = 1 + w$  to the cooperative systems (4.2). We see from the formula (4.1) that the function  $f^{(+)}(u)$  is equal to  $f(u)$  for  $u \leq u_m$ . Hence, this system has the linearization

$$\begin{aligned} U_t &= a_1 U_{xx} + (\gamma - \alpha)U \\ W_t &= a_2 W_{xx} + r(f'(0)U - W) \end{aligned} \quad (4.3)$$

at the monoculture equilibrium  $u = 0$ ,  $1 + w = 1$ . If we look for a solution of this system of the form  $(U, W) = e^{-\mu(x-ct)}(\zeta_1, \zeta_2)$  where  $\mu$ ,  $\zeta_1$ , and  $\zeta_2$  are positive constants, we find the system

$$\begin{pmatrix} a_1 \mu^2 - c\mu + \gamma - \alpha & 0 \\ r f'(0) & a_2 \mu^2 - c\mu - r \end{pmatrix} \begin{pmatrix} \zeta_1 \\ \zeta_2 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}. \quad (4.4)$$

R. Lui [3] has shown that for problems where the matrix is irreducible (that is, off-diagonal elements are not zero), this equation leads to a formula for the spreading speed of the linearized system. The present problem, in which one of the off-diagonal elements is zero, was considered in [7] and [2], and we sketch a part of the proof of Theorem 4.2 of [7]. We note that the system (4.4) has a solution with both  $\zeta_1$  and  $\zeta_2$  positive if and only if its upper diagonal element is zero and its lower diagonal element is negative. These conditions lead to the upper bounds

$$c = a_1\mu + (\gamma - \alpha)/\mu, \quad (4.5)$$

for the spreading speed of the linearized system (4.3) for all  $\mu$  such that the constraint

$$(a_2 - a_1)\mu^2 - (r + \gamma - \alpha) < 0 \quad (4.6)$$

is satisfied. If  $a_2 \leq a_1$ , the constraint is automatically satisfied, and one obtains Lui's formula by minimizing the right-hand side of (4.5):

$$c^* := 2\sqrt{(\gamma - \alpha)a_1} \quad (4.7)$$

(This is, of course, the spreading speed of the Fisher equation obtained by setting  $v \equiv 1$  in the first equation.) If  $a_2 > a_1$ , the same formula is still valid, provided the minimizer  $\mu = \tilde{\mu} := \sqrt{(\gamma - \alpha)/a_1}$  of the right-hand side of (4.5) satisfies the constraint (4.6). That is, it is sufficient to assume that

$$\frac{a_2}{a_1} < 2 + r/(\gamma - \alpha), \quad (4.8)$$

which is the inequality (2.5) in the Theorem.

It is shown in [7] that under this condition, (4.7) gives a lower bound for the spreading speeds of both components of (4.2). In order to show that the components both have the spreading speed  $c^*$ , it is sufficient to show that the formula (4.7) also gives an upper bound for the spreading speed of (4.2). For this purpose, it is enough to show that if we set  $(U, W) = e^{-\mu(x-ct)}(\zeta_1, \zeta_2)$  where  $(\zeta_1, \zeta_2)$  is a solution of (4.4) with  $\mu = \sqrt{(\gamma - \alpha)/a_1}$  and  $c = 2\sqrt{(\gamma - \alpha)a_1}$ , then  $(U, 1 + W)$  is a supersolution of the equation (4.2). That is, the left-hand sides of this system with  $(u^{(+)}, v^{(+)}) = (U, 1 + W)$  are bounded below by the right-hand sides. Since  $(U, W)$  satisfies the linearized system (4.3), these inequalities are equivalent to the inequalities

$$\begin{aligned} U(-\beta U + \gamma W) &\leq 0 \\ r[(1 + W)(-W + f^{(+)}(U)) - (-W + f'(0)U)] &\leq 0, \end{aligned} \quad (4.9)$$

which are obtained by subtracting the linearizations from the nonlinear functions on the right-hand sides. (See Theorem 4.1 of [7].)

We recall that the linearized system (4.3) with  $\mu = \sqrt{(\gamma - \alpha)/a_1}$  has the solution  $(U, W) = e^{-\mu(x-c^*t)}(\zeta_1, \zeta_2)$ , where  $(\zeta_1, \zeta_2)$  is a solution of the system (4.4). Any such solution is a multiple of  $(\zeta_1, \zeta_2) = (1 + (\gamma - \alpha)[2 - (a_2/a_1)]/r, f'(0))$ . This shows that

$$\frac{W}{U} = \frac{f'(0)}{1 + (\gamma - \alpha)[2 - (a_2/a_1)]/r} \quad (4.10)$$

for all positive  $U$  and  $W$ . This immediately shows that the first inequality in (4.9) is satisfied if and only if

$$\beta \geq \frac{\gamma f'(0)}{1 + (\gamma - \alpha)[2 - (a_2/a_1)]/r},$$



which is the assumption (2.6).

We eliminate  $W$  from the second inequality of (4.9) by using (4.10) and multiply the resulting inequality by  $\{1 + (\gamma - \alpha)[1 - (a_2/a_1)]/r\}^2/[f'(0)U]$  to obtain the equivalent inequality

$$-\left\{1 + \frac{\gamma - \alpha}{r} \left[2 - \frac{a_2}{a_1}\right]\right\}^2 \left[1 - \frac{f^{(+)}(U)}{f'(0)U}\right] + \left\{1 + \frac{\gamma - \alpha}{r} \left[2 - \frac{a_2}{a_1}\right]\right\} f^{(+)}(U) - f'(0)U \leq 0. \quad (4.11)$$

When  $0 < U \leq u_m$ , we have  $f^{(+)}(U) = f(U)$ , and this inequality follows from the assumption (2.7). When  $U \geq u_m$ ,  $f^{(+)}(U)$  is the positive constant  $f(u_m)$ , so that the left-hand side of (4.11) is decreasing in  $U$ . Therefore, the fact that the inequality is satisfied at  $U = u_m$  implies that it is also valid for  $U > u_m$ .

We have shown that when the assumptions of Theorem 1 are satisfied, then the function  $(e^{-\sqrt{\gamma-\alpha/a_1}(x-c^*t)}\zeta_1, 1 + e^{-\sqrt{\gamma-\alpha/a_1}(x-c^*t)}\zeta_2)$  is a supersolution of the cooperative system (4.2). The same is still true if we translate the function by replacing  $x$  by  $x + a$  for any constant  $a$ . If the initial functions  $u(x, 0)$  and  $v(x, 0)$  are bounded and vanish to the right of some value of  $x$ , we can find an  $a$  so that  $u(x, 0) \leq e^{-\sqrt{\gamma-\alpha/a_1}(x+a)}\zeta_1$  and  $v(x, 0) \leq 1 + e^{-\sqrt{\gamma-\alpha/a_1}(x+a)}\zeta_2$ . The Comparison Principle (Lemma 4.1) then shows that  $u(x, t) \leq u^{(+)}(x, t) \leq e^{-\sqrt{\gamma-\alpha/a_1}(x+a-c^*t)}\zeta_1$ . Thus,  $\sup_{x \geq ct} u(x, t) \leq e^{-\sqrt{\gamma-\alpha/a_1}(a+[c-c^*]t)}\zeta_1$ , and this bound goes to 0 if  $c > c^*$ . We have shown that

$$\lim_{t \rightarrow \infty} [\sup_{x \geq ct} u(x, t)] = 0 \text{ when } c > c^*. \quad (4.12)$$

Similarly, we show that

$$\limsup_{t \rightarrow \infty} [\sup_{x \geq ct} \{v(x, t) - 1\}] \leq 0 \text{ when } c > c^*. \quad (4.13)$$

To finish the proof of Statement i, we need to show that the minimum of  $v$  does not remain below 1. By the Comparison Principle, the components  $(u, v)$  of a solution of (1.1) are bounded above by the solution of the system (4.2) with the initial values  $u^{(+)}(x, 0) = \sup_x u(x, 0)$ ,  $v^{(+)}(x, 0) = \sup_x v(x, 0)$ . It is easily seen that  $u^{(+)}$  and  $v^{(+)}$  are independent of  $x$ , and the resulting system of ordinary differential equations shows that  $u^{(+)}$  approaches  $u^{*(+)}$  and  $v^{(+)}$  approaches  $v^{*(+)}$  as  $t$  goes to infinity. Because  $\beta > \gamma - \alpha + \gamma f^{(+)}(u_m)$ ,  $u^{*(+)} < 1$ . Thus we have proved that

$$\begin{aligned} \limsup_{t \rightarrow \infty} [\sup_x u(x, t)] &\leq u^{*(+)}, \text{ and} \\ \limsup_{t \rightarrow \infty} [\sup_x v(x, t)] &\leq v^{*(+)}. \end{aligned} \quad (4.14)$$

Because of the inequality  $\beta > \gamma - \alpha + \gamma f(u_m)$ ,  $u^{*(+)} < 1$ . Therefore, there is a time  $t_0$  such that  $u(x, t) \leq 1$  for all  $x$  when  $t \geq t_0$ . Then  $f(u) \geq 0$ , and therefore  $v$  satisfies the inequality

$$v_t \geq v_{xx} + rv(1 - v) \text{ for } t \geq t_0.$$

Since  $v(x, t_0) > 0$  by the strong maximum principle, and  $v(\pm\infty, t) = 1$  because this is true at  $t = 0$ , we see that  $v(x, t_0)$  is uniformly positive. The application of the

Comparison Principle to the single differential inequality then shows that

$$\liminf_{t \rightarrow \infty} \sup_x [1 - v(x, t)] \leq 0.$$

We combine this with (4.13) to see that

$$\lim_{t \rightarrow \infty} [\sup_{|x| \geq ct} |v(x, t) - 1|] = 0 \text{ when } c > c^*. \quad (4.15)$$

Finally, we observe that if  $(u(x, t), v(x, t))$  is a solution of (1.1), the same is true of  $(u(-x, t), v(-x, t))$ . Applying (4.12) and (4.15) to both of these solutions gives (2.8), which is Statement i of Theorem 1.

In order to prove Statement ii of Theorem 1, we need to bound solutions of (1.1) from below. For this purpose, we recall that the hypothesis  $\beta > \gamma - \alpha + \gamma f(u_m)$  of Theorem 1 implies that  $u^{*(+)} < 1$ . We choose an arbitrary number  $\hat{u}$  such that

$$\begin{aligned} u^{*(+)} < \hat{u} < 1 \text{ when } \gamma - \alpha + \gamma f(u_m) < \beta \leq [\gamma - \alpha + \gamma f(u_m)]/u_m \\ \hat{u} = u_m > u^* = u^{*(+)} \text{ when } \beta > [\gamma - \alpha + \gamma f(u_m)]/u_m. \end{aligned} \quad (4.16)$$

We imitate a trick from [6] by defining the lower function

$$\begin{aligned} \hat{f}^{(-)}(u) &:= \min_{u \leq w \leq \hat{u}} f(w) \\ &= \min\{f(u), f(\hat{u})\}. \end{aligned} \quad (4.17)$$

This function is only defined on the interval  $0 \leq u \leq \hat{u}$ . It is nondecreasing in  $u$  on this interval. Thus, the system

$$\begin{aligned} u_t^{(-)} &= a_1 u_{xx}^{(-)} + u^{(-)}[-\alpha - \beta u^{(-)} + \gamma v^{(-)}] \\ v_t^{(-)} &= a_2 v_{xx}^{(-)} + r v^{(-)}[1 - v^{(-)} + \hat{f}^{(-)}(u^{(-)})] \end{aligned} \quad (4.18)$$

is cooperative, provided  $0 \leq u^{(-)} \leq \hat{u}$ .

Because  $\hat{u} > u^{*(+)}$  in all cases, (4.14) shows that for any solution  $(u, v)$  of (1.1) there is a  $t_1 \geq 0$  such that  $u(x, t) \leq \hat{u}$  for  $t \geq t_1$ . We see from (4.17) that  $\hat{f}^{(-)}(u) \leq f(u)$  when  $u \leq \hat{u}$ . Therefore,  $(u, v)$  is a supersolution of the system (4.18) for  $t \geq t_1$ . Then if  $(u^{(-)}, v^{(-)})$  is the solution of the system (4.18), with  $u^{(-)}(x, t_1) = u(x, t_1)$ ,  $v^{(-)}(x, t_1) = v(x, t_1)$ , it follows that  $u^{(-)} \leq u$  and  $v^{(-)} \leq v$  for  $t \geq t_1$ .

We now define the time-one map  $Q^{(-)}$  of the system (4.18) by saying that if  $(u^{(-)}(x, t), v^{(-)}(x, t))$  is the solution of the system (4.18) with the initial values  $u^{(-)}(x, 0) = p(x)$  and  $v^{(-)}(x, 0) = q(x)$ , then

$$Q^{(-)}[(p, q)] := (u^{(-)}(x, 1), v^{(-)}(x, 1)).$$

It is easily checked that if  $\beta > \gamma - \alpha + \gamma f(u_m)$ , the operator  $Q^{(-)}$  satisfies the conditions of Theorem 3.2 of [3] with the monoculture equilibrium  $(0, 1)$  as Lui's  $\tau$ , and the coexistence equilibrium  $(\hat{u}^{*(-)}, \hat{v}^{*(-)})$  as Lui's  $\beta$ . This coexistence equilibrium is easily found to be

$$\begin{aligned} \hat{u}^{*(-)} &= \min\{u^*, [\gamma - \alpha + \gamma f(\hat{u})]/\beta\} \\ \hat{v}^{*(-)} &= \min\{v^*, 1 + f(\hat{u})\} \end{aligned} \quad (4.19)$$

Lui's Theorem 3.2 states that for every positive  $\sigma$  there is a positive number  $r_\sigma$  with the property that if at some time

$$u^{(-)} \geq \sigma \text{ and } v^{(-)} \geq 1 + \sigma \text{ on an interval of length } 2r_\sigma \quad (4.20)$$

then for any  $0 \leq c < \hat{c}^{*(-)}$ ,

$$\begin{aligned} \liminf_{t \rightarrow \infty} [\min_{|x| \leq ct} u^{(-)}(x, t)] &\geq \hat{u}^{*(-)} \text{ and} \\ \liminf_{t \rightarrow \infty} [\min_{|x| \leq ct} v^{(-)}(x, t)] &\geq \hat{v}^{*(-)}. \end{aligned} \quad (4.21)$$

Because  $\hat{f}^{(-)} \leq f^{(+)}$ , the above-proved Statement i of the Theorem shows that  $c^{*(-)} \leq c^{*(+)} = 2\sqrt{(\gamma - \alpha)a_1}$ . Because  $\hat{f}^{(-)}(u) = f^{(+)}(u)$  for all sufficiently small  $u$ , the system (4.18) has the same linearization as (4.2) about the equilibrium (0,1). As before, one cannot apply Lui's lower bound for  $c^{*(-)}$ , but the results of [7] and the inequality (2.5) show that  $c^{*(-)} \geq c^*$ . We conclude that  $c^{*(-)} = c^* = 2\sqrt{(\gamma - \alpha)a_1}$ .

It remains to show that the condition (4.20) is automatically satisfied at some time. The derivation of (4.15) applied to the function  $v^{(-)}$  shows that for any positive  $\epsilon$  there is a number  $t_\epsilon$  such that  $v^{(-)}(x, t) \geq 1 - \epsilon$  when  $t \geq t_\epsilon$ . The first equation of (4.18) now implies that

$$u_t^{(-)} \geq a_1 u_{xx}^{(-)} + u^{(-)}(\gamma - \alpha - \gamma\epsilon - \beta u^{(-)})$$

for  $t \geq t_\epsilon$ . We take  $\epsilon < (\gamma - \alpha)/\gamma$  and choose positive constants  $\rho$  and  $\eta$  so small that

$$-a_1 \rho^2 + \gamma - \alpha - \gamma\epsilon - \beta\eta > 0. \quad (4.22)$$

We also require that

$$\eta \leq u(x, t_\epsilon) \text{ for } |x| \leq \pi/(2\rho),$$

which can be done by decreasing the size of  $\eta$  if necessary. If  $(\tilde{u}^{(-)}, \tilde{v}^{(-)})$  is the solution of (4.18) with the initial values

$$\begin{aligned} \tilde{u}^{(-)}(x, t_\epsilon) &= \begin{cases} \eta \cos \rho x & \text{for } |x| \leq \pi/(2\rho) \\ 0 & \text{for } |x| \geq \pi/(2\rho) \end{cases} \\ \tilde{v}^{(-)}(x, t_\epsilon) &\equiv 1 - \epsilon, \end{aligned}$$

the Comparison Principle shows that the components of  $(\tilde{u}^{(-)}, \tilde{v}^{(-)})$  are lower bounds for  $u^{(-)}$  and  $v^{(-)}$  when  $t \geq t_\epsilon$ . The inequality (4.22) shows that both  $\tilde{u}_t^{(-)}$  and  $\tilde{v}_t^{(-)}$  are nonnegative at  $t = t_\epsilon$ , and the Comparison Principle then implies that  $\tilde{u}^{(-)}$  and  $\tilde{v}^{(-)}$  are nondecreasing in  $t$ . It follows that  $\tilde{u}^{(-)}$  increases to a smooth function  $\phi(x) \leq \hat{u}^{*(-)}$  and  $\tilde{v}^{(-)}$  increases to a smooth function  $\psi(x) \leq \hat{v}^{*(-)}$ , uniformly on every bounded interval, and that  $(\phi, \psi)$  is a stationary solution of (4.18). Because the right-hand side of the  $u$  equation is bounded below by  $\tilde{u}^{(-)}[-\alpha - \beta\tilde{u}^{(-)} + \gamma(1 - \epsilon)]$ , comparison with the Fisher equation shows that  $\phi \geq [\gamma - \alpha - \gamma\epsilon]\beta > 0$ . It then follows from comparing the solution,  $(\phi, \psi)$  with the solution of (4.18) with the constant initial values  $(\gamma - \alpha - \gamma\epsilon, 1 - \epsilon)$  shows that, in fact,  $\phi \equiv \hat{u}^{*(-)}$  and  $\psi \equiv \hat{v}^{*(-)}$ . Thus, we see that  $\hat{u}^{*(-)} - \tilde{u}^{(-)}(x, t)$  and  $\hat{v}^{*(-)} - \tilde{v}^{(-)}(x, t)$  approach 0 as  $t \rightarrow \infty$ , uniformly in  $x$  on every bounded  $x$ -interval. Because  $u^{(-)} \geq \tilde{u}^{(-)}$  and  $v^{(-)} \geq \tilde{v}^{(-)}$ , it follows that if we choose any positive  $\sigma$  with  $\sigma < \min\{\hat{u}^{*(-)}, \hat{v}^{*(-)} - 1\}$  then for all sufficiently large  $t$ , the condition (4.20) is automatically satisfied on the fixed interval  $|x| \leq 2r_\sigma$ . We thus obtain the statement (4.21) without an extra condition.

We recall that when  $\beta > [\gamma - \alpha + \gamma f(u_m)]/u_m$ , we have  $\hat{u} = u_m$ , so that  $\hat{f}^{(-)} = f$ , and hence  $\hat{u}^{*(-)} = u^* = \hat{u}^{*(+)}$  and  $\hat{v}^{*(-)} = v^* = \hat{v}^{*(+)}$ . This immediately gives Statement ii of Theorem 1 for this case. When  $\gamma - \alpha + \gamma f(u_m) < \beta \leq [\gamma -$

$\alpha + \gamma f(u_m)]/u_m$ , (4.19) shows that  $\hat{u}^{*(-)}$  and  $\hat{v}^{*(-)}$  are decreasing functions of  $\hat{u}$ . Therefore, we can improve the statements (4.21) by decreasing  $\hat{u}$  to its lower bound  $u^{*(+)}$ . The limit of  $(\hat{u}^{*(-)}, \hat{v}^{*(-)})$  as  $\hat{u}$  approaches  $u^{*(+)}$  is easily seen to be the point  $(u^{*(-)}, v^{*(-)})$  given by the formulas (2.3). Thus, the limiting process applied to (4.21) yields (2.9), which is Statement ii. This finishes the proof of Theorem 1.

**Proof of Proposition 2.1.** We shall first show that the function

$$f(u) = u(1-u)\psi(u)$$

satisfies the Hypotheses 2.1. Part i, the fact that  $f(0) = f(1) = 0$  is obviously satisfied. Since  $f(u)/u = (1-u)\psi(u)$  we see that  $[f(u)/u]' = -\psi(u) + (1-u)\psi'(u)$ , which is negative for  $0 \leq u \leq 1$ . Therefore Part ii is satisfied. In order to show that  $f$  is unimodal, we observe that  $f'(u) = (1-2u)\psi(u) + u(1-u)\psi'(u)$ , which is negative for  $1/2 < u < 1$ . That is,  $f$  is strictly decreasing on this interval, so that its maximum must occur at a point  $u_m \leq 1/2$ . We now observe that

$$f''(u) = u(1-u)\psi''(u) + 2(1-2u)\psi'(u) - 2\psi(u).$$

Because  $\psi > 0$ ,  $\psi' \leq 0$ , and  $\psi'' \leq 0$  for  $0 \leq u \leq 1/2$ , we conclude that  $f'' < 0$  for  $0 \leq u \leq 1/2$ . Therefore,  $f'$  has exactly one maximum at a point  $u_m \leq 1/2$  and no other extrema in  $(0,1)$ . Thus  $f$  is unimodal, which shows that  $f$  satisfies all the Hypotheses 2.1. We observe that  $f'(1/2) = (1/4)\psi'(1/2)$ , so that  $u_m = 1/2$  if and only if  $\psi'(1/2) = 0$ . Since  $\psi' \leq 0$  and  $\psi'' \leq 0$ , this implies that  $\psi$  is constant for  $0 \leq u \leq 1/2$ .

In connection with Remark 4 after Theorem 1, we observe that  $f''(0) = -2\psi(0) + 2\psi'(0) < 0$ .

Finally, we observe that because  $\psi(u)$  is nonincreasing, the quantity  $-1 + f(u)/[f'(0)u] = [-\psi(0) + (1-u)\psi(u)]/\psi(0)$  in the first term of (2.7) is bounded above by  $-u$ , and the quantity  $f(u) = u(1-u)\psi(u)$  is bounded above by  $\psi(0)u$ . Therefore, the inequality

$$-\left\{1 + \frac{\gamma - \alpha}{r} \left[2 - \frac{a_2}{a_1}\right]\right\}^2 u + \left\{1 + \frac{\gamma - \alpha}{r} \left[2 - \frac{a_2}{a_1}\right]\right\} \psi(0)u - \psi(0)u \leq 0$$

implies (2.7). The quadratic formula shows that this inequality is satisfied for  $u \geq 0$  when one of the three inequalities (2.11) is satisfied. Thus, all parts of Proposition 2.1 have been established.

**5. Discussion.** We have shown some multispecies reaction-diffusion systems which are cooperative at low population densities but not at higher densities have a spreading speed. The proof uses an idea of Thieme [6] for obtaining spreading speeds for some integral recursions with overcompensation.

We remark that the assumption that  $f$  is unimodal was only used to obtain simple formulas for the functions  $f^{(+)}$  and  $\hat{f}^{(-)}$  and for the coexistence equilibria  $(u^{*(+)}, v^{*(+)})$  and  $(\hat{u}^{*(-)}, \hat{v}^{*(-)})$ . If  $f^\pm$  are defined by the first lines of (4.1) and (4.17), respectively and  $(u^{*(\pm)}, v^{*(\pm)})$  are their positive equilibria, the two statements of Theorem 1 are still valid when unimodality is replaced by the much weaker assumption that  $f(u)$  is positive in the interval  $(0, 1)$ , and increasing on some open interval with the left end-point 0.

While we have only considered one space dimension, the spreading results in [3], [7], and [2] show how to obtain spreading results in higher-dimensional habitats by looking at one direction at a time.

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