

SPATIAL SPREAD OF SEXUALLY TRANSMITTED DISEASES WITHIN SUSCEPTIBLE POPULATIONS AT DEMOGRAPHIC STEADY STATE

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ABSTRACT. In this study, we expand on the susceptible-infected-susceptible (SIS) heterosexual mixing setting by including the movement of individuals of both genders in a spatial domain in order to more comprehensively address the transmission dynamics of competing strains of sexually-transmitted pathogens. In prior models, these transmission dynamics have only been studied in the context of nonexplicitly mobile heterosexually active populations at the demographic steady state, or, explicitly in the simplest context of SIS frameworks whose limiting systems are order preserving. We introduce reaction-diffusion equations to study the dynamics of sexually-transmitted diseases (STDs) in spatially mobile heterosexually active populations. To accomplish this, we study a single-strain STD model, and discuss in what forms and at what speed the disease spreads to noninfected regions as it expands its spatial range. The dynamics of two competing distinct strains of the same pathogen on this population are then considered. The focus is on the investigation of the spatial transition dynamics between the two endemic equilibria supported by the non-spatial corresponding model. We establish conditions for the successful invasion of a population living in endemic conditions by introducing a strain with higher fitness. It is shown that there exists a unique spreading speed (where the spreading speed is characterized as the slowest speed of a class of traveling waves connecting two endemic equilibria) at which the infectious population carrying the invading stronger strain spreads into the space where an equilibrium distribution has been established by the population with the weaker strain. Finally, we give sufficient conditions under which an explicit formula for the spreading speed can be found.

1. Introduction. From the time that Sir Ronald Ross [15] identified the similarities (mathematical equivalence) of models for sexually- and vector-transmitted diseases in 1911, efforts to model and understand the transmission dynamics of STDs in heterosexually active populations have been carried out, especially, after the start of the HIV epidemic (see Kasseem et al [8], Kirschner [9], and references

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therein). The first model used for the explicit study of a sexually-transmitted disease, namely gonorrhea, was a simplified two-sex model (Cooke and Yorke [6]). Later, a multi-group (single-sex) model for STD dynamics was formulated and analyzed by Laajmanovich and Yorke [10]. The study of the transmission dynamics and control of STDs has been a direct beneficiary of theoretical work carried out in the context of the transmission dynamics of gonorrhea and the work of Hethcote and Yorke [7] continues to impact current public health policies. These researchers' concept of a core group still drives some control recommendations being implemented today. Hethcote and Yorke's conclusions were derived from the simulations and analysis of a simple system of nonlinear differential equations used to model the transmission dynamics of gonorrhea in a heterosexually-active population with two distinct levels of sexual activity. Their SIS two-sex model, where they introduced the concept of *core group*, provides the historical foundation of this paper. Extensions have been carried out, for example in, Brauer et al. [1], Castillo-Chavez et al. [4, 2, 3] and references therein. The recent work on heterosexually-transmitted HIV found in Kasseem et al. [8] focuses on the role of the core group and mobile (transient) populations on its dynamics. The work in Kirschner [9] focuses on mobility in risk space in the context of sexually-transmitted HIV in heterosexually-active populations. Nevertheless, limited research has been carried out on the study of the transmission dynamics of STDs in heterosexual mobile populations. The work in this manuscript, we hope, suggests additional worthwhile expansions.

Most of the research on heterosexually-transmitted STDs has been driven by an interest on their impact on human populations. In contrast, the work here is *motivated* by the study of the dynamics of STDs in populations, such as mammal populations, where spatially dependent interactions may be critical. The complications associated with the study of STD dynamics in, for example, populations of mammals in the wild, is rather complex. A *realistic* model would include the possibility of high fluctuation densities (that is, it would not be based on an assumption of populations at a demographic steady state), mating preferences and possibly, specific social structure (hierarchies). Hence, this paper is just an *initial attempt* to start a discussion on the study of the dynamics of STDs in populations of mammals in the wild. The modeling approach and results in this manuscript provide a starting point used to identify potential dynamics (two strain results). We also hope that the framework used here can be used to build realistic model extensions in the future [1].

Following the vision already communicated in Ross [15] that recognizes that vector- and sexually-transmitted diseases have intersecting mathematical formulations, we proceed to use his modeling philosophy to formulate models for the study of the spatial dynamics of vector-transmitted diseases. Clearly, there are critical differences between STDs and VTDs (Vector Transmitted Diseases). For example, VTDs involve coexisting highly distinct time scales, and vectors do not recover from infection. Specifically, implementing the framework and methods of analysis introduced here, we plan to extend our study of dengue dynamics in Peru (see [5].)

The spatial spread of a disease can be seen as a process in which infectious individuals move while multiplying their numbers. Models in which mobility is formulated as a random diffusion process take the form of reaction-diffusion equations, which have proven successful in modeling the spatial spread of diseases such as the Black Death, red fox, and rabies in human populations (see, for example,

Murray [14], and Shigesada and Kawasaki [16]). Here we incorporate the standard reaction-diffusion formulation to study the spatial spread of STDs. First, a reaction-diffusion model that accounts for the impact of local individuals' mobility on single-strain STD dynamics is introduced. The focus of the analysis is primarily that of capturing the forms and speed of disease propagation to non-infected regions as the pathogen expands its spatial range. It is shown that the spread of the STD is determined by the speed of propagation computed from the model's linearization about the leading edge of the epidemic invasion wave. It is shown that the speed of propagation can be characterized as the smallest speed of traveling wave solutions. We follow up this analysis by introducing a model that puts two distinct strains of the same pathogen in competition and focus on the study of spatial transition dynamics between the endemic equilibria supported by the corresponding non-spatial version of our model. Particularly, we study the spatial invasion of an established infected population by a stronger strain. It is shown that there exists a unique spreading speed at which the infectious population with the stronger strain spreads and at which the infectious population with the weaker strain retreats in space. We prove that the spreading speed can be characterized as the slowest speed of a class of traveling waves connecting two endemic equilibria. It is shown that under certain conditions, an explicit formula for the spreading speed can be found. The mathematical analysis presented in this paper relies on theory about spreading speed and traveling waves for cooperative systems developed by Weinberger, Lewis, and Li [12, 17, 18].

This paper is organized as follows: Section 2 introduces the single-strain STD model and examines the dynamics of spatial spread in this context; in Section 3, we discuss the two-strain STD model and study the spreading speed and traveling waves in the presence of interference pathogen competition; in Section 4, we provide some concluding remarks and discuss possibilities for expansions and applications.

2. Spread of a single-strain STD model. We let $S^k(x, t)$, $k = m, f$ and $I^k(x, t)$, $k = m, f$ represent the local densities of susceptible and infected males and females, respectively, as we proceed to introduce and study the simplest spatially-explicit SIS STD model. The spatial dynamics are modeled in this simple setting, just through the addition of diffusion terms. Hence, d^k ($k = m, f$) are used to denote the diffusion coefficients of males and females, respectively. The model includes some simple demographics; that is, sexually-mature individuals are regularly recruited. In fact, Λ^k ($k = m, f$) denote the recruitment rates of males and females, while μ^k ($k = m, f$) are natural death rates for males and females, respectively. In other words, males and females exit the reproductive (sexually-active) life-stage at the rates μ^k ($k = m, f$). In addition, γ^k are the per-capita rates of recovery for males and females; β^k denote transmission rates of infection; and r^k , ($k = m, f$), as functions of T^m and T^f , give the average rates of partner acquisition per male and per female (respectively). These last rates satisfy the constraint $r^m(T^m, T^f)T^m = r^f(T^m, T^f)T^f$; that is, the total average contact rate of females equals the total average contact rate of males. These assumptions and definitions lead us to the following model:

$$\begin{aligned}
\frac{\partial S^m}{\partial t} &= d^m \frac{\partial^2 S^m}{\partial x^2} + \Lambda^m - B^m - \mu^m S^m + \gamma^m I^m \\
\frac{\partial I^m}{\partial t} &= d^m \frac{\partial^2 I^m}{\partial x^2} + B^m - (\mu^m + \gamma^m) I^m \\
\frac{\partial S^f}{\partial t} &= d^f \frac{\partial^2 S^f}{\partial x^2} + \Lambda^f - B^f - \mu^f S^f + \gamma^f I^f \\
\frac{\partial I^f}{\partial t} &= d^f \frac{\partial^2 I^f}{\partial x^2} + B^f - (\mu^f + \gamma^f) I^f
\end{aligned} \tag{1}$$

where

$$\begin{aligned}
B^m &= r^m(T^m, T^f) \beta^f S^m I^f / T^f, B^f = r^f(T^m, T^f) \beta^m S^f I^m / T^m, T^m = S^m + I^m, T^f \\
&= S^f + I^f.
\end{aligned}$$

By adding the first two equations and the last two equations in (1) respectively, one obtains

$$\frac{\partial T^m}{\partial t} = d^m \frac{\partial^2 T^m}{\partial x^2} + \Lambda^m - \mu^m T^m \tag{2}$$

and

$$\frac{\partial T^f}{\partial t} = d^f \frac{\partial^2 T^f}{\partial x^2} + \Lambda^f - \mu^f T^f. \tag{3}$$

The linear reaction-diffusion equations (2) and (3) describe the distributions of males and females as functions of the space variable x and time variable t , respectively. It may be worth noticing that relaxing our assumptions immediately leads to potential novel and challenging systems of coupled nonlinear partial differential equations. For example, one could assume that Λ^k ($k = m, f$) are functions of the local (or global) densities of males and females. If this were the case, then the system (3 and 2) would become not only quite challenging but also the kind of extension that may be relevant for the study of the transmission dynamics of STDs in mammal populations in the wild.

Here, it is assumed that the initial distributions of males and females $T^m(x, 0)$ and $T^f(x, 0)$ are bounded continuous functions. Solving (2) with the initial value function $T^m(x, 0)$, and (3) with the initial value function $T^f(x, 0)$, one finds that $T^m(x, t)$ and $T^f(x, t)$ satisfy

$$|\Lambda^m / \mu^m - T^m(x, t)| \leq \|T^m(x, 0)\| e^{-\mu^m t}$$

and

$$|\Lambda^f / \mu^f - T^f(x, t)| \leq \|T^f(x, 0)\| e^{-\mu^f t}$$

where $\|\cdot\|$ denote the supremum norm. This shows that $T^m(x, t)$ and $T^f(x, t)$ approach equilibrium values uniformly and exponentially. We have the following limiting system

$$\begin{aligned}
\frac{\partial I^m}{\partial t} &= d^m \frac{\partial^2 I^m}{\partial x^2} - \sigma^m I^m + a^m (p^m - I^m) I^f \\
\frac{\partial I^f}{\partial t} &= d^f \frac{\partial^2 I^f}{\partial x^2} - \sigma^f I^f + a^f (p^f - I^f) I^m
\end{aligned} \tag{4}$$

where $a^m = \frac{\mu^f c^m \beta^f}{\Lambda^f}$, $a^f = \frac{\mu^m c^f \beta^m}{\Lambda^m}$, and $c^k = r^k (\lambda^m / \mu^m, \Lambda^f / \mu^f)$, $\sigma^k = \mu^k + \gamma^k$, $p^k = \frac{\Lambda^k}{\mu^k}$, $k = m, f$.

System (4) is cooperative in the biologically realistic range $0 \leq I^m \leq p^m, 0 \leq I^f \leq p^f$. The reproductive number of system (4) is

$$R = \frac{a^m p^m a^f p^f}{\sigma^m \sigma^f},$$

which represents a threshold value. If $R < 1$, system (4) has a unique stable constant equilibrium $E^0 = (0, 0)$. If $R > 1$, E_0 is unstable and there is a globally asymptotically stable constant positive equilibrium $E^* = (I_*^m, I_*^f)$ where

$$I_*^m = \frac{\sigma^m \sigma^f (R - 1)}{a^f (p^f a^m + \sigma^m)}, \quad I_*^f = \frac{\sigma^m \sigma^f (R - 1)}{a^m (p^m a^f + \sigma^f)}.$$

In what follows we assume that $R > 1$. Since there are only two equilibria E_0 and E^* , the results from [12, 17, 18] show that system (4) has a unique spreading speed at which the disease spreads to non-infected regions as it expands its spatial range. To find a formula for the spreading speed of (4), we use the following linearization of (4) about E_0

$$\begin{aligned} \frac{\partial I^m}{\partial t} &= d^m \frac{\partial^2 I^m}{\partial x^2} - \sigma^m I^m + a^m p^m I^f \\ \frac{\partial I^f}{\partial t} &= d^f \frac{\partial^2 I^f}{\partial x^2} - \sigma^f I^f + a^f p^f I^m. \end{aligned} \tag{5}$$

System (4) is always bounded above by its linearization system (5). Theorem 4.2 in [17] shows that system (4) is linear-determinant; that is, the spreading speed of (4) is that of a truncation of (5). The conditions of this theorem involve a matrix C_μ , defined to be the coefficient matrix for the vector of linear combinations of α_1 and α_2 obtained by substituting $I^m = \alpha_1 e^{-\mu x}$, $I^f = \alpha_2 e^{-\mu x}$ into the right-hand side of (5) and setting $x = 0$:

$$C_\mu = \begin{pmatrix} d^m \mu^2 - \sigma^m & a^m p^m \\ a^f p^f & d^f \mu^2 - \sigma^f \end{pmatrix}.$$

This is an irreducible matrix for $\mu \geq 0$ with the principle eigenvalue given by

$$\lambda(\mu) = \frac{1}{2} \{ (d^m + d^f) \mu^2 - (\sigma^m + \sigma^f) + \sqrt{[(d^m - d^f) \mu^2 - \sigma^m + \sigma^f]^2 + 4 a^m a^f p^m p^f} \}. \tag{6}$$

It follows from Theorem 4.2 in [17] that the spreading speed of (4) is given by

$$c^* = \inf_{\mu > 0} \lambda(\mu) / \mu. \tag{7}$$

Since

$$2\lambda(0) = -(\sigma^m + \sigma^f) + \sqrt{(\sigma^m - \sigma^f)^2 + 4 a^m a^f p^m p^f} = \sqrt{(\sigma^m + \sigma^f)^2 + 4 \sigma^m \sigma^f (R - 1)}$$

$-(\sigma^m + \sigma^f) > 0$, $\lim_{\mu \rightarrow 0^+} \lambda(\mu) / \mu = +\infty$. On the other hand, it is also obvious that $\lim_{\mu \rightarrow +\infty} \lambda(\mu) / \mu = +\infty$. Therefore the infimum in (7) is attained at a finite number and c^* is a positive number.

In general, it is difficult to find an explicit formula for c^* in terms of model parameters. However, one can easily find that

$$\text{if } d^m = d^f = d, \quad c^* = \lambda(\bar{\mu}) / \bar{\mu} = \sqrt{2d[\sqrt{(\sigma^m + \sigma^f)^2 + 4 \sigma^m \sigma^f (R - 1)} - (\sigma^m + \sigma^f)]}, \tag{8}$$

with

$$\bar{\mu} = \sqrt{[\sqrt{(\sigma^m + \sigma^f)^2 + 4\sigma^m\sigma^f(R-1)} - (\sigma^m + \sigma^f)]/(2d)}.$$

Thus, we have obtained the following proposition that is a paraphrase of Theorems 4.1 and 4.4 of [17].

Proposition 1. *The spreading speed of the limit system (4) is c^* given by (7) in the following sense: If $0 \leq I^m(x, 0) < I_*^m$, $0 < I^f(x, 0) < I_*^f$, $I^m(x, 0)$ and $I^f(x, 0)$ are zero outside a bounded set, and $I^f(x, 0) \not\equiv 0$ and $I^m(x, 0) \not\equiv 0$, then for every positive number ϵ*

$$\lim_{t \rightarrow \infty} \sup_{|x| \geq (c^* + \epsilon)t} \{(I^m(x, t))^2 + (I^f(x, t))^2\} = 0,$$

and

$$\lim_{t \rightarrow \infty} \sup_{|x| \leq (c^* - \epsilon)t} \{(I_*^m - I^m(x, t))^2 + (I_*^f - I^f(x, t))^2\} = 0.$$

Since the limit system (4) has only two equilibria, Theorem 3 in [12] shows that c^* can be characterized as the slowest speed of a class of traveling wave solutions connecting E_0 to E^* , as described by the following proposition.

Proposition 2. *For $c \geq c^*$, the limiting system (4) has a nonincreasing traveling wave solution $(I^m(x - ct), I^f(x - ct))$ with $(I^m(-\infty), I^f(-\infty)) = (I_*^m, I_*^f)$ and $(I^m(+\infty), I^f(+\infty)) = (0, 0)$. A traveling wave solution $(I^m(x - ct), I^f(x - ct))$ with $(I^m(-\infty), I^f(-\infty)) = (I_*^m, I_*^f)$ and $(I^m(+\infty), I^f(+\infty)) = (0, 0)$ does not exist if $c < c^*$.*

Remark 1. The traveling wave solution described in Proposition 2 propagates to the right with a speed $c \geq c^*$. Similarly one can establish a traveling wave that propagates to the left. In fact, for $c \leq -c^*$, the limiting system (4) has a nondecreasing traveling wave solution $(I^m(x - ct), I^f(x - ct))$ with $(I^m(-\infty), I^f(-\infty)) = (0, 0)$ and $(I^m(+\infty), I^f(+\infty)) = (I_*^m, I_*^f)$, and such a traveling wave solution does not exist if $c > -c^*$.

If the males and females have initial equilibrium distributions

$$T^m(x, 0) \equiv \lambda^m/\mu^m, T^f(x, 0) \equiv \lambda^f/\mu^f, \quad (9)$$

then equations (2) and (3) show that $T^m(x, t) \equiv \lambda^m/\mu^m$ and $T^f(x, t) \equiv \lambda^f/\mu^f$ for all x and $t \geq 0$. In this case in the full system (1), $I^m(x, t)$ and $I^f(x, t)$ satisfy (4), and $S^m = \lambda^m/\mu^m - I^m(x, t)$ and $S^f = \lambda^f/\mu^f - I^f(x, t)$ satisfy the S^m and S^f equations in (1), respectively. Therefore if (9) holds, c^* is the spreading speed for the full system (1). On the other hand, clearly, if $(I^m(x - ct), I^f(x - ct))$ is a traveling wave solution of (4) then $(\lambda^m/\mu^m - I^m(x - ct), I^m(x - ct), \lambda^f/\mu^f - I^f(x - ct), I^f(x - ct))$ is a traveling wave solution of (1). We therefore have the following theorem based on Proposition 1 and Proposition 2.

Theorem 2.1. *Assume $R > 1$.*

(i) *The spreading speed of system (1) is c^* given by (7) in the following sense: If $0 \leq I^m(x, 0) < I_*^m$, $0 < I^f(x, 0) < I_*^f$, $I^m(x, 0)$ and $I^f(x, 0)$ are zero outside a bounded set, $I^f(x, 0) \not\equiv 0$ and $I^m(x, 0) \not\equiv 0$, and $S^m(x, 0) = \lambda^m/\mu^m - I^m(x, 0)$ and $S^f(x, 0) = \lambda^f/\mu^f - I^f(x, 0)$, then for every positive number ϵ*

$$\lim_{t \rightarrow \infty} \sup_{|x| \geq (c^* + \epsilon)t} \{(\lambda^m/\mu^m - S^m(x, t))^2 + (I^m(x, t))^2 + (\lambda^f/\mu^f - S^f(x, t))^2 + (I^f(x, t))^2\} = 0,$$

$)^2\} = 0$,
 and
 $\lim_{t \rightarrow \infty} \sup_{|x| \leq (c^* - \epsilon)t} \{(\Lambda^m/\mu^m - I_*^m - S^m(x, t))^2 + (I_*^m - I^m(x, t))^2 + (\Lambda^f/\mu^f - I_*^f - S^f(x, t))^2 + (I_*^f - I^f(x, t))^2\} = 0$.
 (ii) For $c \geq c^*$, the system (1) has a monotone traveling wave solution $(S^m(x - ct), I^m(x - ct), S^f(x - ct), I^f(x - ct))$ with $(S^m(+\infty), I^m(+\infty), S^f(+\infty), I^f(+\infty)) = (\Lambda^m/\mu^m, 0, \Lambda^f/\mu^f, 0)$ and $(S^m(-\infty), I^m(-\infty), S^f(-\infty), I^f(-\infty)) = (\Lambda^m/\mu^m - I_*^m, I_*^m, \Lambda^f/\mu^f - I_*^f, I_*^f)$. A traveling wave solution with $(\Lambda^m/\mu^m, 0, \Lambda^f/\mu^f, 0)$ at $+\infty$ and $(\Lambda^m/\mu^m - I_*^m, I_*^m, \Lambda^f/\mu^f - I_*^f, I_*^f)$ at $-\infty$, and speed c does not exist in (1) if $c < c^*$.

We provide a graphical description of Theorem 2.1 in Figure 1.

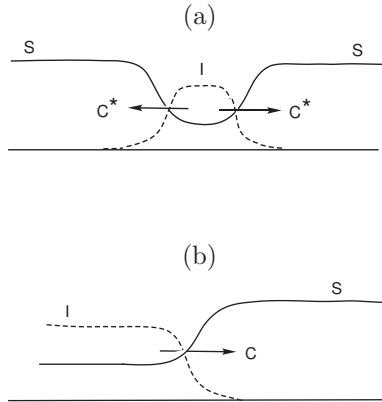


FIGURE 1. Spread of a single strain of a sexually-transmitted pathogen in case of $R > 1$. (a) Spread of infectious individuals in a region pre-occupied by susceptible individuals with an equilibrium distribution. The infectious individuals succeed in invasion and establish a wave that proceeds at a speed c^* . At the rear of the wave both susceptible individuals and infectious individuals coexist. (b) Traveling wave propagation of susceptible individuals and infectious individuals. At the front of the traveling wave there are very small numbers of infectious individuals, and a large number of susceptible individuals. At the rear of the traveling wave both susceptible individuals and infectious individuals coexist. The traveling wave solution has speed c with $c \geq c^*$.

3. Spread of a two-strain STD model. In this section, we study the following model that puts two distinct strains of the same pathogen in competition:

$$\begin{aligned}\frac{\partial S^m}{\partial t} &= d^m \frac{\partial^2 S^m}{\partial x^2} + \Lambda^m - B^m - \mu^m S^m + \gamma_1^m I_1^m + \gamma_2^m I_2^m \\ \frac{\partial I_i^m}{\partial t} &= d^m \frac{\partial^2 I_i^m}{\partial x^2} + B_i^m - (\mu^m + \gamma_i^m) I_i^m, \quad i = 1, 2 \\ \frac{\partial S^f}{\partial t} &= d^f \frac{\partial^2 S^f}{\partial x^2} + \Lambda^f - B^f - \mu^f S^f + \gamma_1^f I_1^f + \gamma_2^f I_2^f \\ \frac{\partial I_i^f}{\partial t} &= d^f \frac{\partial^2 I_i^f}{\partial x^2} + B_i^f - (\mu^f + \gamma_i^f) I_i^f, \quad i = 1, 2\end{aligned}\tag{10}$$

where for $k = m, f$, $B^k = B_1^k + B_2^k$ with $B_i^m = r^m(T^m, T^f)S^m\beta_i^m\frac{I_i^f}{T^f}$, $B_i^f = r^f(T^m, T^f)S^f\beta_i^m\frac{I_i^m}{T^m}$, and $T^k = S^k + I_1^k + I_2^k$. Here variables and parameters without subscripts are the same as those in (1); variables and parameters labeled with subscript i correspond to those without subscripts in (1) and are associated with strain i .

The distributions of males and females $T^m(x, t)$ and $T^f(x, t)$ still satisfy (2) and (3). As in the previous section, we assume that the initial distributions $T^m(x, 0)$ and $T^f(x, 0)$ are continuous and bounded. $T^k(x, t)$ converges exponentially and uniformly to Λ^k/μ^k for $k = m, f$. We have the following limiting system with four equations

$$\begin{aligned}\frac{\partial I_i^m}{\partial t} &= d^m \frac{\partial^2 I_i^m}{\partial x^2} - \sigma_i^m I_i^m + a_i^m(p^m - I_1^m - I_2^m)I_i^f, \quad i = 1, 2, \\ \frac{\partial I_i^f}{\partial t} &= d^f \frac{\partial^2 I_i^f}{\partial x^2} - \sigma_i^f I_i^f + a_i^f(p^f - I_1^f - I_2^f)I_i^m, \quad i = 1, 2,\end{aligned}\tag{11}$$

where $a_i^m = \frac{\mu^f c^m \beta_i^f}{\Lambda^f}$, $a_i^f = \frac{\mu^m c^f \beta_i^m}{\Lambda^m}$, and $c^k = r^k(\lambda^m/\mu^m, \Lambda^f/\mu^f)$, $\sigma_i^k = \mu^k + \gamma_i^k$, $p^k = \frac{\Lambda^k}{\mu^k}$, $k = m, f$.

The reproductive number for strain i is

$$R_i = \frac{a_i^m a_i^f p^m p^f}{\sigma_i^m \sigma_i^f}, \quad i = 1, 2.$$

We shall assume that $R_i > 1$ for $i = 1, 2$, so that each strain can persist in the absence of its competitor. There are three equilibria in the limiting system (11): $E_0 = (0, 0, 0, 0)$, $E_1^* = (I_{1*}^m, I_{1*}^f, 0, 0)$, and $E_2^* = (0, 0, I_{2*}^m, I_{2*}^f)$ where

$$I_{i*}^m = \frac{\sigma_i^m \sigma_i^f (R_i - 1)}{a_i^f (p^f a_i^m + \sigma_i^m)}, \quad I_{i*}^f = \frac{\sigma_i^m \sigma_i^f (R_i - 1)}{a_i^m (p^m a_i^f + \sigma_i^f)}, \quad i = 1, 2.$$

System (11) is a monotone system. The monotone dynamical system theory can be used to determine the global stability of the ODE system corresponding to (11). It is shown in Castillo-Chavez et al. [3] that if $R_i > R_j > 1$ then E_j^* is unstable and E_i^* is the global attractor in the corresponding ODE system. This indicates that the system exhibits **Competitive Exclusion**, that is, the strain with the stronger competitive ability survives and the strain with weaker competitive ability dies out.

For convenience, we shall assume

$$R_1 > R_2 > 1$$

so that strain 1 is a stronger competitor. We assume that the strain 2 has established an equilibrium distribution before the invasion of strain 1. We investigate in what forms and at what speeds strain 1 invades and strain 2 retreats in space.

We use the change of variables $I_1^m := I_1^m, I_1^f := I_1^f$, and $L_2^m := I_{2*}^m - I_2^m, L_2^f := I_{2*}^f - I_2^f$ to convert the model (11) into the system

$$\begin{aligned} \frac{\partial I_1^m}{\partial t} &= d^m \frac{\partial^2 I_1^m}{\partial x^2} - \sigma_1^m I_1^m + a_1^m (p^m - I_{2*}^m - I_1^m + L_2^m) I_1^f \\ \frac{\partial I_1^f}{\partial t} &= d^f \frac{\partial^2 I_1^f}{\partial x^2} - \sigma_1^f I_1^f + a_1^f (p^f - I_{2*}^f - I_1^f + L_2^f) I_1^m \\ \frac{\partial L_2^m}{\partial t} &= d^m \frac{\partial^2 L_2^m}{\partial x^2} - \sigma_2^m L_2^m + a_2^m [I_{2*}^f (I_1^m - L_2^m) + L_2^f (p^m - I_{2*}^m - I_1^m + L_2^m)] \\ \frac{\partial L_2^f}{\partial t} &= d^f \frac{\partial^2 L_2^f}{\partial x^2} - \sigma_2^f L_2^f + a_2^f [I_{2*}^m (I_1^f - L_2^f) + L_2^m (p^f - I_{2*}^f - I_1^f + L_2^f)]. \end{aligned} \tag{12}$$

System (12) has three equilibria: the origin $\mathbf{0} = (0, 0, 0, 0)$, the positive equilibrium $\beta = (I_{1*}^m, I_{1*}^f, I_{2*}^m, I_{2*}^f)$, and the equilibrium $\nu = (0, 0, I_{2*}^m, I_{2*}^f)$ that lies on the boundary of the rectangular box region with vertices $\mathbf{0}$ and β . It is a cooperative system in the rectangular box region $G = \{(I_1^m, I_1^f, L_2^m, L_2^f) : 0 \leq I_1^m \leq I_{1*}^m, 0 \leq I_1^f \leq I_{1*}^f, 0 \leq L_2^m \leq I_{2*}^m, 0 \leq L_2^f \leq I_{2*}^f\}$. We study the spatial transition from the origin $\mathbf{0}$ to the positive equilibrium β in set G . Let $\mathbf{f}(I_1^m, I_1^f, L_2^m, L_2^f)$ denote the vector representing the reaction terms on the right hand side of (12). We define the matrix

$$C_\mu = \mu^2 \text{diag}[d^m, d^m, d^f, d^f] + \mathbf{f}'(\mathbf{0}) = \begin{bmatrix} C_{\mu 11} & 0 \\ C_{\mu 21} & C_{\mu 22} \end{bmatrix}$$

where

$$\begin{aligned} C_{\mu 11} &= \begin{bmatrix} d^m \mu^2 - \sigma_1^m & a_1^m (p^m - I_{2*}^m) \\ a_1^f (p^f - I_{2*}^f) & d^f \mu^2 - \sigma_1^f \end{bmatrix}, \\ C_{\mu 21} &= \begin{bmatrix} a_2^m I_{2*}^f & 0 \\ 0 & a_2^f I_{2*}^m \end{bmatrix}, \end{aligned}$$

and

$$C_{\mu 22} = \begin{bmatrix} d^m \mu^2 - (\sigma_2^m + a_2^m I_{2*}^f) & a_2^m (p^m - I_{2*}^m) \\ a_2^f (p^f - I_{2*}^f) & d^m \mu^2 - (\sigma_2^f + a_2^f I_{2*}^m) \end{bmatrix}.$$

C_μ is a matrix associated with the linearization of (12) about $\mathbf{0}$. Here C_μ is in Frobenius form. Let $\lambda_1(\mu)$ and $\lambda_2(\mu)$ denote the principle eigenvalues of $C_{\mu 11}$ and $C_{\mu 22}$, respectively. Then

$$\begin{aligned} \lambda_1(\mu) &= \frac{1}{2} \{ (d^m + d^f) \mu^2 - (\sigma_1^m + \sigma_1^f) \\ &\quad + \sqrt{[(d^m - d^f) \mu^2 - \sigma_1^m + \sigma_1^f]^2 + 4a_1^m a_1^f (p^m - I_{2*}^m)(p^f - I_{2*}^f)} \} \end{aligned}$$

and

$$\begin{aligned} \lambda_2(\mu) &= \frac{1}{2} \{ (d^m + d^f) \mu^2 - (\sigma_2^m + \sigma_2^f + a_2^m I_{2*}^f + a_2^f I_{2*}^m) \\ &\quad + \sqrt{[(d^m - d^f) \mu^2 - (\sigma_2^m + a_2^m I_{2*}^f) + \sigma_2^f + a_2^f I_{2*}^m]^2 + 4a_2^m a_2^f (p^m - I_{2*}^m)(p^f - I_{2*}^f)} \}. \end{aligned}$$

One can verify that $R_1 > R_2$ shows that $4a_1^m a_1^f (p^m - I_{2*}^m)(p^f - I_{2*}^f) > 4\sigma_1^m \sigma_1^f$, which implies $\lambda_1(0) > 0$. One can also find that $R_1 > 1$ and $R_2 > 1$ imply that $4a_2^m a_2^f (p^m - I_{2*}^m)(p^f - I_{2*}^f) < 4(\sigma_2^m + a_2^m I_{2*}^f)(\sigma_2^f + a_2^f I_{2*}^m)$ so that $\lambda_2(0) < 0$. Note that $C_{\mu 21}$ has positive diagonal entries. We therefore have that Hypotheses 4.1 in [17] are valid, and the theory developed in [17] can be applied to (12).

System (11) has an additional equilibrium ν besides $\mathbf{0}$ and β . It is shown in [12, 17] that for a cooperative system that has an equilibrium other than the origin and the positive equilibrium, components of the system may spread at different speeds. The following proposition shows that this is not the case for (12), and all the components in (12) spread at the same speed.

Proposition 3. *System (12) has a single spreading speed c^* in the following sense: If $0 \leq I_1^m(x, 0) < I_{1*}^m$, $0 < I_1^f(x, 0) < I_{1*}^f$, $0 \leq L_2^m(x, 0) < I_{2*}^m$, $0 \leq L_2^f(x, 0) < I_{2*}^f$, $I_1^m(x, 0)$, $I_1^f(x, 0)$, $L_2^m(x, 0)$, $L_2^f(x, 0)$ are zero outside a bounded set, and $I^f(x, 0) \neq 0$ and $I^m(x, 0) \neq 0$, $L_2^m(x, 0) \neq 0$ and $L_2^f(x, 0) \neq 0$, then for every positive number ϵ*

$$\lim_{t \rightarrow \infty} \left[\sup_{|x| \geq (c^* + \epsilon)t} \{(I_1^m(x, t))^2 + (I_1^f(x, t))^2 + (L_2^m(x, t))^2 + (L_2^f(x, t))^2\} \right] = 0,$$

and

$$\lim_{t \rightarrow \infty} \left[\sup_{|x| \leq (c^* - \epsilon)t} \{(I_{1*}^m - I_1^m(x, t))^2 + (I_{1*}^f - I_1^f(x, t))^2 + (I_{2*}^m - L_2^m(x, t))^2 + (I_{2*}^f - L_2^f(x, t))^2\} \right] = 0.$$

The proof of this proposition will be given in the Appendix.

The results in the previous section show that

$$\bar{c} = \inf_{\mu > 0} \lambda_1(\mu) / \mu > 0 \quad (13)$$

represents the spreading speed of I_1^m and I_1^f in the absence of L_2^m and L_2^f . Since system (11) is cooperative, we have the following result.

Proposition 4.

$$c^* \geq \bar{c}. \quad (14)$$

The following proposition shows that c^* can be characterized as the slowest speed of a class of traveling wave solutions connecting $\mathbf{0}$ with β .

Proposition 5. *For $c \geq c^*$, the system (12) has a nonincreasing traveling wave solution $(I_1^m(x-ct), I_1^f(x-ct), L_2^m(x-ct), L_2^f(x-ct))$ with $(I_1^m(+\infty), I_1^f(+\infty), L_2^m(+\infty), L_2^f(+\infty)) = \mathbf{0}$ and $(I_1^m(-\infty), I_1^f(-\infty), L_2^m(-\infty), L_2^f(-\infty)) = \beta$. A traveling wave solution with $\mathbf{0}$ at $+\infty$, β at $-\infty$ and speed c does not exist in (12) if $c < c^*$.*

The proof of this proposition will be presented in the Appendix.

If

$$T^m(x, 0) \equiv \Lambda^m / \mu^m, \quad T^f(x, 0) \equiv \Lambda^f / \mu^f \quad (15)$$

for all x , then $T^m(x, t) \equiv \Lambda^m / \mu^m$, $T^f(x, t) \equiv \Lambda^f / \mu^f$ for all x and $t > 0$. In this case, $(S^m(x, t), I_1^m(x, t), I_1^f(x, t), S^f(x, t), I_2^m(x, t), I_2^f(x, t)) = (\Lambda^m / \mu^m - I_1^m(x, t) - (I_{2*}^m - L_2^m(x, t)), I_1^m(x, t), I_1^f(x, t), \Lambda^f / \mu^f - I_1^f(x, t) - (I_{2*}^f - L_2^f(x, t)), I_{2*}^m - L_2^m(x, t), I_{2*}^f - L_2^f(x, t))$ is a solution of (10) if $(I_1^m(x, t), I_1^f(x, t), L_2^m(x, t), L_2^f(x, t))$ is a solution of (12).

We have the following theorem about the spreading speed and traveling waves in (10) based on Proposition 3 and Proposition 5.

Theorem 3.1. *Assume that $R_1 > R_2 > 1$.*

(i) *System (10) has a single spreading speed c^* in the following sense: If $0 \leq I_1^m(x, 0) < I_{1*}^m$, $0 \leq I_1^f(x, 0) < I_{1*}^f$, $0 < I_2^m(x, 0) \leq I_{2*}^m$, $0 < I_2^f(x, 0) \leq I_{2*}^f$, both $I_1^m(x, 0)$ and $I_1^f(x, 0)$ are zero, and $I_2^m(x, 0)$ is I_{2*}^m and $I_2^f(x, 0)$ is I_{2*}^f outside a*

bounded set, and $I_1^m(x, 0) \not\equiv 0$ and $I_1^f(x, 0) \not\equiv 0$, $I_2^m(x, 0) \not\equiv I_{2*}^m$ and $I_2^f(x, 0) \not\equiv I_{2*}^f$, and $S^m(x, 0) = \Lambda^m/\mu^m - I_1^m(x, 0) - I_2^m(x, 0)$ and $S^f(x, 0) = \Lambda^f/\mu^f - I_1^f(x, 0) - I_2^f(x, 0)$, then for every positive number ϵ

$$\lim_{t \rightarrow \infty} [\sup_{|x| \geq (c^* + \epsilon)t} \{(S^m - \Lambda^m/\mu^m - I_{2*}^m)^2 + (I_1^m(x, t))^2 + (I_1^f(x, t))^2 + (S^f - \Lambda^f/\mu^f - I_{2*}^f)^2 +$$

$$(I_{2*}^m - I_2^m(x, t))^2 + (I_{2*}^f - I_2^f(x, t))^2\}] = 0,$$

and

$$\lim_{t \rightarrow \infty} [\sup_{|x| \leq (c^* - \epsilon)t} \{(S^m - \Lambda^m/\mu^m - I_{1*}^m)^2 + (I_{1*}^m - I_1^m(x, t))^2 + (S^f - \Lambda^f/\mu^f - I_{1*}^f)^2 + (I_{1*}^f - I_1^f(x, t))^2 + (I_2^m(x, t))^2 + (I_2^f(x, t))^2\}] = 0.$$

(ii) For $c \geq c^*$, the system (10) has a monotone traveling wave solution $(S^m(x - ct), I_1^m(x - ct), I_1^f(x - ct), S^f(x - ct), I_2^m(x - ct), I_2^f(x - ct))$ with $(S^m(+\infty), I_1^m(+\infty), I_1^f(+\infty), S^f(+\infty), I_2^m(+\infty), I_2^f(+\infty)) = (\Lambda^m/\mu^m - I_{2*}^m, 0, 0, \Lambda^f/\mu^f - I_{2*}^f, I_{2*}^m, I_{2*}^f)$ and $(S^m(-\infty), I_1^m(-\infty), I_1^f(-\infty), S^f(-\infty), I_2^m(-\infty), I_2^f(-\infty)) = (\Lambda^m/\mu^m - I_{1*}^m, I_{1*}^m, I_{1*}^f, \Lambda^f/\mu^f - I_{1*}^f, 0, 0)$. A traveling wave solution with $(\Lambda^m/\mu^m - I_{2*}^m, 0, 0, \Lambda^f/\mu^f - I_{2*}^f, I_{2*}^m, I_{2*}^f)$ at $+\infty$, $(\Lambda^m/\mu^m - I_{1*}^m, I_{1*}^m, I_{1*}^f, \Lambda^f/\mu^f - I_{1*}^f, 0, 0)$ at $-\infty$ and speed c does not exist in (10) if $c < c^*$.

This theorem describes the spread of infectious individuals with strain 1 and the retreat of infectious individuals with strain 2 in space. We depict the results of this theorem in Figure 2.

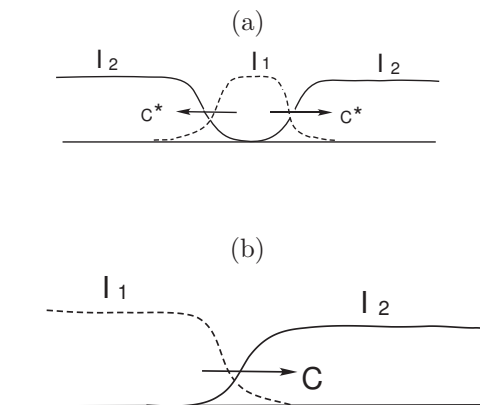


FIGURE 2. Spread of strain 1 and retreat of strain 2 in space in case of $R_1 > R_2$. (a) Spread of infectious males and females with strain 1 in a region initially occupied by infectious males or females with strain 2. The infectious individuals with strain 1 establish a wave that proceeds by completely displacing infectious individuals with strain 2. The wave propagates at a speed c^* . (b) Traveling wave propagation of infectious individuals with strain 1 and strain 2. At the front of the traveling wave there are very small number of infectious individuals with strain 1, and a large number of infectious individuals with strain 2. At the rear of the traveling wave infectious individuals with strain 1 occupy the region and infectious individuals with strain 2 retreat from the region. The traveling wave solution has a speed c with $c \geq c^*$.

According to [17, 18], \bar{c} given in (13) represents the spreading speed of a truncation of the linear system obtained by linearizing (12) at E_0 . Proposition 4 shows that \bar{c} is a lower bound for the spreading speed c^* . We show that under certain conditions $c^* = \bar{c}$. Let $\xi = (\bar{I}_1^m(\mu), \bar{I}_1^f(\bar{\mu}), \bar{I}_2^m(\mu), \bar{I}_2^f(\mu))$ be an eigenvector of C_μ corresponding to $\lambda_1(\mu)$. If $\lambda_1(\mu) > \lambda_2(\mu)$ then every component of ξ is positive.

We have the following result that gives a formula for the spreading speed c^* .

Theorem 3.2. *Assume that $R_1 > R_2 > 1$ and $\lambda_1(\bar{\mu}) > \lambda_2(\bar{\mu})$ where $\bar{\mu}$ denotes the value at which $\inf_{\mu>0} \lambda_1(\mu)/\mu$ is attained. If*

$$\bar{I}_1^m(\bar{\mu}) < \bar{L}_2^m(\bar{\mu}), \bar{I}_1^f(\bar{\mu}) < \bar{L}_2^f(\bar{\mu}), \quad (16)$$

then $c^* = \bar{c}$.

The proof of this theorem will be given in the Appendix.

4. Discussion. In this paper, we use reaction-diffusion equations to model the spatial transmission dynamics of STDs in heterosexually active populations. This work has been motivated by our effort to analyze a model that may become the initial stepping stone in the development of a theoretical mathematical framework for the study of the transmission dynamics and control of STDs in heterosexual-active populations in spatial domains. Since, studying the dynamics of STDs in the context of mobile populations in the wild requires the incorporation of complex demographics and mating systems, the emphasis here is on the mathematics in a rather simplified biological context. We analyze a model for STD dynamics in a crude setting which already offers considerable mathematical challenges. First, we analyze a one-strain SIS STD model that describes the spread of infectious males and females. We show that when the reproductive number is greater than 1, infectious males and females spread at the same spreading speed, and that the spreading speed can be characterized as the slowest speed of a class of traveling waves. We proceed to examine a two-strain SIS STD model with emphasis on the study of the ability of the stronger strain to invade a domain where the weaker strain has established an equilibrium spatial distribution. It is shown that there is a unique spreading speed at which the stronger strain spreads and the weaker strain retreats, and that the spreading speed can be characterized as the slowest speed of a class of traveling waves connecting two endemic equilibria.

In studying the spatial spread of a disease, it is crucial to find the spreading speed of the disease. To determine the spreading speed of an STD, we use the concept of linear determinacy, which states that the spreading speed of a nonlinear model equals that of a truncate of a linear system obtained by linearizing the nonlinear model about the leading edge of the wave front. We found that linear determinacy always holds for the one-strain STD model, and that it holds for the two-strain model provided that condition (16), is satisfied. In general, if a nonlinear system is always dominated by its linearization at the leading edge of invasion, then the a nonlinear system is linear-determinate; otherwise linear determinacy may not be true (see Lewis, Li and Weinberger [11]). When (16) is not satisfied, the problem of determining the spreading speed for the two-strain model remains unsolved.

The results of this paper are an *initial attempt* to study the dynamics of sexually-transmitted pathogens in heterosexual mammal populations. We have ignored, among other things, the role of differential mortality in our models. However, we hope that the models and their analysis will mark the beginning of a series of studies that examine the impact of disease on mammal mating systems. One could modify

model (1) and model (10) by allowing the recruitment rates Λ^k ($k = m, f$) to depend on the size of the infective populations as well as on total population sizes as a way of incorporating differential mortality. The mathematical analysis for the resulting models is considerably more complicated and so, we leave it for future work.

The framework provided in this paper can also be used to study the spatial dynamics of Vector Transmitted Disease models in the form

$$\begin{aligned}
 \frac{\partial S^h}{\partial t} &= d^h \frac{\partial^2 S^h}{\partial x^2} + \Lambda^h - \beta^h S^h I^v / T^v - \mu^h S^h + \gamma^h I^h \\
 \frac{\partial I^h}{\partial t} &= d^h \frac{\partial^2 I^h}{\partial x^2} + \beta^h S^h I^v / T^v - (\mu^h + \gamma^h) I^h \\
 \frac{\partial S^v}{\partial t} &= d^v \frac{\partial^2 S^v}{\partial x^2} + \Lambda^v - \beta^v S^v I^h / T^h - \mu^v S^v \\
 \frac{\partial I^v}{\partial t} &= d^v \frac{\partial^2 I^v}{\partial x^2} + \beta^v S^v I^h / T^h - \mu^v I^v
 \end{aligned}
 \tag{17}$$

where for $k = h, v$, S^k and I^k are for susceptible and infected humans and vectors, respectively; and other variables and parameters are analogs of those in (1). In model (17), it is assumed that vectors do not recover from infection. It can be shown that the limiting system of (17) is cooperative and linear-determinant. The spreading speeds and traveling waves can be determined using the methods in this paper. This model provides a platform to pursue a study of dengue dynamics ([5]).

We have only considered the spread of STD diseases in one-dimensional space. One can use the results in [12, 13, 17, 18] to determine the spreading speeds and traveling waves in higher-dimensional habitats by looking at one direction at a time.

5. Appendix. 1. Proof of Proposition 3.

We use Lemma 4.2 in [17] to prove this proposition. We need to find a matrix $E^{(\nu)}$ that satisfies the following conditions:

- (i) $E^{(\nu)} \geq P_1 \mathbf{f}'(\nu) + (I - P_1) \mathbf{f}'(\mathbf{0})$ componentwise;
- (ii) $P_1 E^{(\nu)} = P_1 \mathbf{f}'(\nu)$; and
- (iii) The maximum spreading speed of a truncate of the linear system associated with $E^{(\nu)}$ is determined by the upper left corner 2 by 2 submatrix.

In (i) and (ii), P_1 is the projection operator in the sense that $P_1[\mathbf{v}]$ has the same first two components as \mathbf{v} and last two components zero, and I is the identity operator. Standard linearization shows that

$$\mathbf{f}'(\mathbf{0}) = \begin{bmatrix} -\sigma_1^m & a_1^m(p^m - I_{*2}^m) & 0 & 0 \\ a_1^f(p^f - I_{2*}^f) & -\sigma_1^f & 0 & 0 \\ a_2^m I_{2*}^m & 0 & -\sigma_2^m - a_2^m I_{2*}^m & a_2^m(p^m - I_{2*}^m) \\ 0 & a_2^f I_{2*}^f & a_2^f(p^f - I_{2*}^f) & -\sigma_2^f - a_2^f I_{2*}^m \end{bmatrix}$$

and

$$\mathbf{f}'(\nu) = \begin{bmatrix} -\sigma_1^m & a_1^m p^m & 0 & 0 \\ a_1^f p^f & -\sigma_1^f & 0 & 0 \\ 0 & 0 & -\sigma_2^m & a_2^m p^m \\ 0 & 0 & a_2^f p^f & -\sigma_2^f \end{bmatrix}.$$

We choose

$$E^{(\nu)} = \begin{bmatrix} -\sigma_1^m & a_1^m p^m & 0 & 0 \\ a_1^f p^f & -\sigma_1^f & 0 & 0 \\ \sigma_2^m I_{2*}^f & 0 & -\sigma_2^m - a_2^m I_{2*}^f & a_2^m (p^m - I_{2*}^m) \\ 0 & a_2^f I_{2*}^f & a_2^f (p^f - I_{2*}^f) & -\sigma_2^f - a_2^f I_{2*}^m \end{bmatrix}.$$

It is easy to see that conditions (i) and (ii) are satisfied. In $E^{(\nu)}$ the principle eigenvalue of the upper left 2 by 2 matrix is positive and the principle eigenvalue of the lower right 2 by 2 matrix is negative. By Theorem 4.1 in [18], the maximum spreading speed of a truncate of the linear system associated with $E^{(\nu)}$ is the spreading speed of the subsystem associated with the upper left 2 by 2 matrix of $E^{(\nu)}$. The Proposition then follows from Lemma 4.2 in [17].

2. Proof of Proposition 5.

Since system (12) has a single speed c^* , Theorem 4.1 in [12] shows that for $c \geq c^*$, (12) has a nonincreasing traveling wave solution $(I_1^m(x - ct), I_1^f(x - ct), L_2^m(x - ct), L_2^f(x - ct))$ with $(I_1^m(+\infty), I_1^f(+\infty), L_2^m(+\infty), L_2^f(+\infty)) = \mathbf{0} = (0, 0, 0, 0)$ and $(I_1^m(-\infty), I_1^f(-\infty), L_2^m(-\infty), L_2^f(-\infty))$ an equilibrium other than $\mathbf{0}$, and that there is no traveling wave solution with $\mathbf{0}$ at $+\infty$, an equilibrium other than $\mathbf{0}$ at $-\infty$, and a speed less than c^* . We need show $(I_1^m(-\infty), I_1^f(-\infty), L_2^m(-\infty), L_2^f(-\infty)) = \beta$. For the sake of contradiction, we assume $(I_1^m(-\infty), I_1^f(-\infty), L_2^m(-\infty), L_2^f(-\infty)) = \nu = (0, 0, I_{2*}^m, I_{2*}^f)$. It follows that $I_1^m(x - ct) \equiv 0$ and $I_1^f(x - ct) \equiv 0$ for all x and $t \geq 0$ and consequently $(L_2^m(x - ct), L_2^f(x - ct))$ is a nonincreasing traveling wave solution of the system

$$\begin{aligned} \frac{\partial L_2^m}{\partial t} &= d^m \frac{\partial^2 L_2^m}{\partial x^2} - \sigma_2^m L_2^m + a_2^m [-I_{2*}^f L_2^m + L_2^f (p^m - I_{2*}^m + L_2^m)] \\ \frac{\partial L_2^f}{\partial t} &= d^f \frac{\partial^2 L_2^f}{\partial x^2} - \sigma_2^f L_2^f + a_2^f [-I_{2*}^m L_2^f + L_2^m (p^f - I_{2*}^f + L_2^f)] \end{aligned} \tag{18}$$

with $(L_2^m(-\infty), L_2^f(-\infty)) = (I_{*2}^m, I_{*2}^f)$ and $(L_2^m(+\infty), L_2^f(+\infty)) = (0, 0)$. We therefore have that $(I_2^m(x - ct), I_2^f(x - ct)) = (I_{2*}^m - L_2^m(x - ct), I_{2*}^f - L_2^f(x - ct))$ is a nondecreasing traveling wave solution of

$$\begin{aligned} \frac{\partial I_2^m}{\partial t} &= d^m \frac{\partial^2 I_2^m}{\partial x^2} - \sigma_2^m I_2^m + a_2^m (p_2^m - I_2^m) I_2^f \\ \frac{\partial I_2^f}{\partial t} &= d^f \frac{\partial^2 I_2^f}{\partial x^2} - \sigma_2^f I_2^f + a_2^f (p_2^f - I_2^f) I_2^m \end{aligned} \tag{19}$$

with $(I_2^m(-\infty), I_2^f(-\infty)) = (0, 0)$ and $(I_2^m(+\infty), I_2^f(+\infty)) = (I_{2*}^m, I_{2*}^f)$. System (19) has the same form as (4). According to Remark 1, $c < 0$. This contradicts that $c \geq c^* > 0$. The proof is complete.

3. Proof of Theorem 3.2.

We use Theorem 4.2 in [17] to prove this Theorem. We only need to verify the condition $\mathbf{f}(\rho \boldsymbol{\xi}(\bar{\mu})) \leq \rho \mathbf{f}'(\mathbf{0}) \boldsymbol{\xi}(\bar{\mu})$ for all positive ρ . One can easily find that this condition is equivalent to $\bar{I}_1^m(\bar{\mu}) < \bar{L}_2^m(\bar{\mu})$ and $\bar{I}_1^f(\bar{\mu}) < \bar{L}_2^f(\bar{\mu})$. The proof is complete.

This manuscript is our contribution to honor of our dear friend and teacher Thomas G Hallam.

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