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ORIGINAL ARTICLE

Traveling Waves and Spread Rates for a West Nile Virus Model

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Abstract A reaction–diffusion model for the spatial spread of West Nile virus is developed and analysed. Infection dynamics are based on a modified version of a model for cross infection between birds and mosquitoes (Wonham et al., 2004, An epidemiological model for West-Nile virus: Invasion analysis and control application. Proc. R. Soc. Lond. B 271), and diffusion terms describe movement of birds and mosquitoes. Working with a simplified version of the model, the cooperative nature of cross-infection dynamics is utilized to prove the existence of traveling waves and to calculate the spatial spread rate of infection. Comparison theorem results are used to show that the spread rate of the simplified model may provide an upper bound for the spread rate of a more realistic and complex version of the model.

Keywords West Nile virus model · Traveling waves · Spread rate · Comparison theorems

1. Introduction

West Nile (WN) virus is an infectious disease spreading through interacting bird and mosquito populations. Although WN virus is endemic in Africa, the Middle East and western Asia, the first recorded North American epidemic was detected in New York state as recently as 1999. In the subsequent 5 years the epidemic has

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spread spatially across to most of the west coast of North America. It is likely that the spread of WN virus comes from the interplay of disease dynamics and bird and mosquito movement.

Here we mathematically investigate the spread of WN virus by spatially extending the non-spatial dynamical model of Wonham et al. (2004) to include diffusive movement of birds and mosquitoes. Diffusive movement provides the simplest possible movement model for birds and mosquitoes. It is likely that both bird and mosquito movements actually involve a mixture of local interactions, long-distance dispersal and, in the case of birds, migratory flights. Despite these complicating factors, diffusion models for birds have proved useful in the analysis of related problems, such as avian range expansion (Okubo, 1998). Our approach is to focus on the implications of diffusive motion coupled to a dynamical model for WN virus.

1.1. Wonham et al. Model

In Wonham et al. (2004), a non-spatial susceptible-infectious-removed (SIR) model for the emerging West Nile virus in North America is formulated and discussed. The model, which is for one season, includes cross-infection between female mosquitoes (vectors) and birds (reservoirs) that is modeled by mass action incidence normalized by the total population of birds. This arises since female mosquitoes only take a fixed number of blood meals per unit time, and follows a similar term used to model malaria. The female mosquito classes are larval, susceptible, exposed and infectious (infective) adult with the numbers in each class denoted by L_V, S_V, E_V and I_V, respectively, and with total population $N_V = L_V + S_V + E_V + I_V$. Bird classes are susceptible, infectious, removed and dead with the numbers in each class denoted by S_R, I_R, R_R, X_R, respectively, and with total live population $N_R = S_R + I_R + R_R$. Here we generalize the model of Wonham et al. (2004) by assuming that removed birds may return to the susceptible class (i.e., WN virus confers temporary immunity on birds). As in Wonham et al. (2004), human and other dead-end hosts (for example, horses) are ignored.

The time rate of change for mosquitoes (V) and birds (R) is modeled by the following ODE dynamical system.

$$\begin{aligned}
\frac{\mathrm{d}L_V}{\mathrm{d}t} &= b_V(S_V + E_V + I_V) - m_V L_V - d_L L_V \\
\frac{\mathrm{d}S_V}{\mathrm{d}t} &= -\alpha_V \beta_R \frac{I_R}{N_R} S_V + m_V L_V - d_V S_V \\
\frac{\mathrm{d}E_V}{\mathrm{d}t} &= \alpha_V \beta_R \frac{I_R}{N_R} S_V - (\kappa_V + d_V) E_V \\
\frac{\mathrm{d}I_V}{\mathrm{d}t} &= \kappa_V E_V - d_V I_V \qquad (1) \\
\frac{\mathrm{d}S_R}{\mathrm{d}t} &= -\alpha_R \beta_R \frac{S_R}{N_R} I_V + \eta_R R_R \\
\frac{\mathrm{d}I_R}{\mathrm{d}t} &= \alpha_R \beta_R \frac{S_R}{N_R} I_V - (\delta_R + \gamma_R) I_R
\end{aligned}$$

$$\frac{\mathrm{d}R_R}{\mathrm{d}t} = \gamma_R I_R - \eta_R R_R$$
$$\frac{\mathrm{d}X_R}{\mathrm{d}t} = \delta_R I_R$$

The parameters in the above system are defined as follows.

- b_V: mosquito birth rate;
- d_L, d_V: larval, adult mosquito death rate;
- δ_R: bird death rate, caused by virus;
- α_V, α_R: WN transmission probability per bite to mosquitoes, birds;
- β_R: biting rate of mosquitoes on birds;
- m_V: mosquito maturation rate;
- κ_V: virus incubation rate in mosquitoes;
- γ_R: bird recovery rate from WN;
- η_R: bird loss of immunity rate (0 in Wonham et al. (2004)).

With non-negative initial conditions, variables in (1) remain non-negative. The parameter constraint $b_V = d_V(m_V + d_L)/m_V$ is assumed so as to guarantee the existence of a disease-free equilibrium (see assumption (B1) in Section 2).

1.2. Spread rate and traveling waves

Here we consider spatial extensions of the equations (1). The general form for the model will be

$$\mathbf{u}_t = \mathcal{D}\mathbf{u}_{xx} + \mathbf{f}(\mathbf{u}), \tag{2}$$

where $\mathbf{u}$ denotes the numbers in classes of mosquitoes and birds, $\mathbf{f}(\mathbf{u})$ describes the infection dynamics, and $\mathcal{D}$ is a non-negative diagonal diffusion matrix. The dynamics are assumed to have a disease-free (i.e., all infected components equal to zero) equilibrium $\mathbf{u_0}$ satisfying $\mathbf{f}(\mathbf{u_0}) = \mathbf{0}$, and a disease-endemic equilibrium $\mathbf{u}^* > 0$ satisfying $\mathbf{f}(\mathbf{u}^*) = \mathbf{0}$. Note that $\mathbf{u}^* \neq \mathbf{u_0}$. We also consider a simplified version of problem (2) in which $\mathbf{u} = (I_V, I_R)^T$ represents the numbers in the infectious classes of mosquitoes and birds. A trivial (disease-free) equilibrium for the simplified model is $\mathbf{0}$ since $\mathbf{f}(\mathbf{0}) = \mathbf{0}$. Details on the simplification of system (1) to the two-component model are given in Sections 2 and 3.

Our focus is on spatial spread of the infection. Two alternative approaches for investigating spatial spread of the infection are through analysing *traveling wave solutions* and calculating *spread rates*. We now give some relevant definitions, which we use in Sections 4–6.

One approach for analyzing the spread of infection involves traveling waves. Here equation (2) is rewritten in terms of a coordinate frame moving with speed c to the right, thus $\mathbf{u}(x, t) = \mathbf{U}(z)$, with $z = x - ct$, and $\dot{\mathbf{U}}$ denotes the derivative with respect to z. Equation (2) becomes

$$c\dot{\mathbf{U}} + \mathcal{D}\ddot{\mathbf{U}} + \mathbf{f}(\mathbf{U}) = \mathbf{0}. \tag{3}$$

Boundary conditions that join up the disease-free and disease-endemic equilibria are assumed, namely

$$\lim_{z\to-\infty} \mathbf{U}(z) = \mathbf{u}^*, \qquad \lim_{z\to\infty} \mathbf{U}(z) = \mathbf{u_0}. \tag{4}$$

An alternative approach is by calculating spread rates: the next two definitions come from Weinberger et al. (2002); see also Hadeler and Lewis (2002).

Definition 1.1. The spread rate for the non-linear system (2) with initial conditions not equal to $\mathbf{u_0}$ on a compact set, is a number c_G^* such that for $\mathbf{u_0} \neq \mathbf{u}^*$ and small $\epsilon > 0$

$$\lim_{t\to\infty}\left\{\sup_{|x|\geq(c_G^*+\epsilon)t} \|\mathbf{u}(x,t)-\mathbf{u_0}\|\right\} = 0, \qquad \lim_{t\to\infty}\left\{\sup_{|x|\leq(c_G^*-\epsilon)t} \|\mathbf{u}(x,t)-\mathbf{u}^*\|\right\} = 0.$$

For the simplified two-component model with $\mathbf{u_0} = \mathbf{0}$, it is useful to also define the spread rate for the corresponding linear system.

Definition 1.2. The spread rate $\bar{c}$ for the simplified linear system corresponding to (2)

$$\mathbf{u}_t = \mathcal{D}\mathbf{u}_{xx} + \mathcal{A}\mathbf{u},$$

where $\mathbf{f(0)} = \mathbf{0}$ and $\mathcal{A} = \mathbf{Df(0)}$ is the Jacobian matrix, is defined as a number satisfying

$$\lim_{t\to\infty}\left\{\sup_{|x|\geq(\bar{c}+\epsilon)t} \|\mathbf{u}(x,t)\|\right\} = 0, \qquad \lim_{t\to\infty}\left\{\sup_{|x|\leq(\bar{c}-\epsilon)t} \|\mathbf{u}(x,t)\|\right\} > 0.$$

When the spread rates for the non-linear and linear systems are identical, then the spread rate for the non-linear system is said to be *linearly determinate*. Certain classes of models with cooperative dynamics have linearly determinate spread rates, but this is not the case for all non-linear systems. Linear determinacy for discrete time recursion systems is discussed by Lui (1989a,b).

Here we use the methods of Li et al. (2005) to show existence of a class of traveling wave solutions for the simplified system and use the methods of Weinberger et al. (2002) to relate the speed c to the spread rates for the non-linear and linear systems.

2. Spatially-independent model

We start by proposing modifications of equations (1) that allow us to simplify the ODE system and so analyze the dynamics.

2.1. *ODE model simplification*

We begin analysis by simplifying system (1) and reducing the number of variables. To do this we make assumptions about the model structure ((A1)–(A6)) and others about the model parameters ((B1)–(B2)), which we now list together with the sequential simplifications.

(A1) *There is no bird death due to WN virus:* $\delta_R = 0$.

Since we include all WN virus susceptible birds, this approximation is reasonable, as only a small number of species (for example, corvid species such as crows) have a high WN virus related death rate. Many other species such as Rock Dove (pigeons) carry WN virus with low mortality rates Komar et al. (2003). Then from (1) it follows that

$$\frac{\mathrm{d}N_R}{\mathrm{d}t} = 0$$

so $N_R(t) = N_R$ is a constant for all $t \geq 0$.

(A2) *Removed birds become immediately susceptible*: $\eta_R \to \infty$.

This assumes that there is no temporary immunity arising from WN virus. While simplifying our model, the assumption of immediate return to the susceptible class tends to overestimate the rate of disease progression. This statement is justified in Section 6, in which this assumption is relaxed and comparison theorems are applied.

The equation for $R_R(t)$ can be solved in terms of $I_R(t)$. Assuming that $R_R(0) = 0$, the result is

$$R_R(t) = \mathrm{e}^{-\eta_R t} \int_0^t \gamma_R I_R(\tau) \mathrm{e}^{\eta_R \tau} d\tau \leq \frac{\gamma_R}{\eta_R} N_R \tag{5}$$

Thus, $R_R(t) \to 0$ as $\eta_R \to \infty$. Therefore, $N_R = S_R(t) + I_R(t)$, and we need consider only the equation for infectious birds, which takes the form

$$\frac{dI_R}{dt} = \alpha_R \beta_R \frac{N_R - I_R}{N_R} I_V - \gamma_R I_R \tag{6}$$

(A3) *Exposed mosquitoes are immediately infective*: $\kappa_V \to \infty$.

Biological data indicate that the exposed (but not yet infective) class can last approximately 9 days in mosquitoes. The assumption of immediate infectivity, as for (A2) above, tends to overestimate the rate of disease progression. This statement is also justified in Section 6, in which this assumption is relaxed and comparison theorems are applied.

Using integration as above, $E_V(t) \leq \dfrac{\alpha_V \beta_R}{\kappa_V + d_V} N_V$ implying that $E_V(t) = 0$ in the limit as $\kappa_V \to \infty$. The equations for mosquitoes become

$$\frac{\mathrm{d}L_V}{\mathrm{d}t} = b_V(S_V + I_V) - m_V L_V - d_L L_V$$

$$\frac{\mathrm{d}S_V}{\mathrm{d}t} = -\alpha_V \beta_R \frac{I_R}{N_R} S_V + m_V L_V - d_V S_V \tag{7}$$
$$\frac{\mathrm{d}I_V}{\mathrm{d}t} = \alpha_V \beta_R \frac{I_R}{N_R} S_V - d_V I_V$$

(B1) *Non-trivial disease-free equilibria exist*: $b_V = \dfrac{d_V(m_V + d_L)}{m_V}$.

For the existence of a disease-free equilibrium it is assumed that vector birth and death rates balance in the absence of disease. This is expressed by the above parameter constraint (identical to the one made in Wonham et al. (2004)), and ensures that, in the absence of disease, the larval and adult mosquito populations remain constant at values determined by their initial values. Denoting the population of adult mosquitoes in (7) by A_V, i.e., $A_V = S_V + I_V$, we now study the two-dimensional linear system for A_V and L_V:

$$\frac{\mathrm{d}A_V}{\mathrm{d}t} = -d_V A_V + m_V L_V$$
$$\frac{\mathrm{d}L_V}{\mathrm{d}t} = b_V A_V - (m_V + d_L) L_V \tag{8}$$

We can analyze the phase plane portrait in L_V, A_V variables. By assumption (B1), system (8) has infinitely many degenerate stationary points satisfying $L_V = \dfrac{d_V}{m_V} A_V$. Trajectories are straight lines of the form

$$A_V(t) = -\frac{m_V}{m_V + d_L} L_V(t) + A_V(0) + \frac{m_V}{m_V + d_L} L_V(0)$$

and solutions tend to stationary points (Fig. 1). Using the trajectories in (8), the equation for A_V can be written as

$$\frac{\mathrm{d}^2 A_V}{\mathrm{d}t^2} + (m_V + d_V + d_L)\frac{\mathrm{d}A_V}{\mathrm{d}t} = 0$$

which has solution

$$A_V(t) = A_V(0) - B(1 - \mathrm{e}^{-(m_V + d_V + d_L)t})$$
$$\text{with} \quad B = \frac{d_V A_V(0) - m_V L_V(0)}{m_V + d_V + d_L} \tag{9}$$

from the first equation in (8). Then

$$L_V(t) = L_V(0) + \frac{m_V + d_L}{m_V} B(1 - \mathrm{e}^{-(m_V + d_V + d_L)t})$$

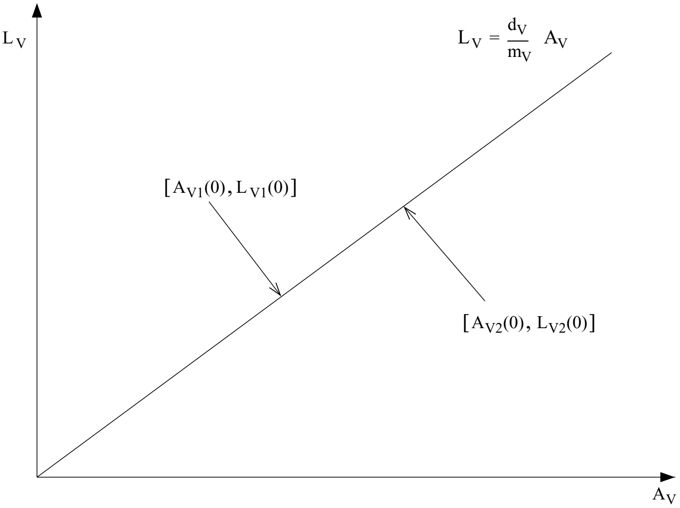

Fig. 1 Stationary solutions and trajectories for L_V, A_V system.

In particular,

$$\min(A_V(0), A_V(0) - B) < A_V(t) < \max(A_V(0), A_V(0) - B), \tag{10}$$

and similar estimates hold for $L_V(t)$. Using the above in (7), the equations for mosquitoes can be reduced to one non-autonomous equation:

$$\frac{\mathrm{d}I_V}{\mathrm{d}t} = \alpha_V \beta_R \frac{I_R}{N_R} \left(A_V(0) - B(1 - \mathrm{e}^{-(m_V + d_V + d_L)t}) - I_V \right) - d_V I_V$$

Note, that as $t \to \infty$, $A_V(t) \to A_V = A_V(0) - B$, a constant, motivating our next assumption.

(A4) *$A_V(t)$ and $L_V(t)$ are constant and equal to stationary solutions of the system* (8).

Under this assumption

$$\frac{\mathrm{d}I_V}{\mathrm{d}t} = \alpha_V \beta_R \frac{I_R}{N_R} (A_V - I_V) - d_V I_V \tag{11}$$

From (11) together with the infectious bird equation (6), we obtain the simplified system

$$\begin{aligned} \frac{\mathrm{d}I_V}{\mathrm{d}t} &= \alpha_V \beta_R \frac{I_R}{N_R} (A_V - I_V) - d_V I_V \\ \frac{\mathrm{d}I_R}{\mathrm{d}t} &= \alpha_R \beta_R \frac{N_R - I_R}{N_R} I_V - \gamma_R I_R \end{aligned} \tag{12}$$

where N_R, A_V are constants denoting the total population of birds and adult mosquitoes, respectively.

2.2. *Analysis in I_V, I_R phase plane*

The system (12) can be written in the form

$$\begin{bmatrix} I_V \\ I_R \end{bmatrix}_t = \mathbf{f}\left(\begin{bmatrix} I_V \\ I_R \end{bmatrix}\right) \tag{13}$$

with $\mathbf{f} = (f_1, f_2)^T$ given as

$$f_1(I_V, I_R) = \alpha_V \beta_R \frac{I_R}{N_R}(A_V - I_V) - d_V I_V$$

$$f_2(I_V, I_R) = \alpha_R \beta_R \frac{N_R - I_R}{N_R} I_V - \gamma_R I_R$$

The Jacobian matrix at the trivial stationary solution $(I_V, I_R) = (0, 0)$ is given by

$$\mathcal{J} = \mathbf{Df}(\mathbf{0}) = \begin{bmatrix} -d_V & \alpha_V \beta_R \frac{A_V}{N_R} \\ \alpha_R \beta_R & -\gamma_R \end{bmatrix} \tag{14}$$

Denoting the eigenvalues of $\mathcal{J}$ by λ_1 and λ_2, it follows that

$$\lambda_1 + \lambda_2 = \mathrm{tr}\mathcal{J} = -(d_V + \gamma_R) < 0$$

$$\lambda_1 \lambda_2 = \det \mathcal{J} = d_V \gamma_R - \alpha_V \alpha_R \beta_R^2 \frac{A_V}{N_R} = d_V \gamma_R (1 - \mathcal{R}_0^2)$$

where $\mathcal{R}_0 = \sqrt{\frac{\alpha_V \alpha_R \beta_R^2 A_V}{d_V \gamma_R N_R}}$ is the *basic reproduction number* for the WN virus model (13) (see van den Driessche and Watmough (2002) for a definition and detailed calculations needed for $\mathcal{R}_0$). Thus the stability of the zero solution is determined by the sign of $\det \mathcal{J}$, it is linearly stable (a node) for $\det \mathcal{J} > 0$, i.e., $\mathcal{R}_0 < 1$, and unstable (a saddle point) for $\det \mathcal{J} < 0$, i.e., $\mathcal{R}_0 > 1$. In the latter case, there exists a positive eigenvalue with positive components of the corresponding eigenvector. This motivates our second assumption on the parameters.

(B2) $d_V \gamma_R < \alpha_V \alpha_R \beta_R^2 \frac{A_V}{N_R}$ *giving* $\det \mathcal{J} < 0$ *and* $\mathcal{R}_0 > 1$.

We also consider the positive stationary solution (I_V^*, I_R^*) given by the system $\mathbf{f}\left[(I_V^*, I_R^*)^T\right] = 0$. From the first and second equations of this system, respectively:

$$I_R^* = \frac{d_V}{\alpha_V \beta_R} \frac{I_V^* N_R}{A_V - I_V^*}, \qquad I_V^* = \frac{\gamma_R}{\alpha_R \beta_R} \frac{I_R^* N_R}{N_R - I_R^*}$$

Solving for non-trivial values gives

$$I_V^* = \frac{\alpha_V \alpha_R \beta_R^2 A_V - d_V \gamma_R N_R}{\alpha_R \beta_R (d_V + \alpha_V \beta_R)}, \quad I_R^* = \frac{\alpha_V \alpha_R \beta_R^2 A_V - d_V \gamma_R N_R}{\alpha_V \beta_R (\gamma_R + \alpha_R \beta_R \frac{A_V}{N_R})} \tag{15}$$

For a biologically reasonable (i.e., positive) solution, the constraint

$$\alpha_V \alpha_R \beta_R^2 A_V - d_V \gamma_R N_R > 0 \Leftrightarrow \det \mathcal{J} < 0 \Leftrightarrow R_0 > 1$$

is needed. Thus the assumption (B2) is necessary for the existence of a non-trivial stationary solution. Notice that the disease-free stationary point $(0, 0)$ and the disease-endemic stationary point (I_V^*, I_R^*) are the only stationary solutions of system (13).

We now study linear stability of the positive solution given by (15). For $\mathcal{R}_0 > 1$, the Jacobian

$$\mathcal{J}^* = \mathbf{Df}\left[(I_V^*, I_R^*)^T\right] = \begin{bmatrix} -d_V - \dfrac{\alpha_V \beta_R}{N_R} I_R^* & \dfrac{\alpha_V \beta_R}{N_R}(A_V - I_V^*) \\ \dfrac{\alpha_R \beta_R}{N_R}(N_R - I_R^*) & -\gamma_R - \dfrac{\alpha_R \beta_R}{N_R} I_V^* \end{bmatrix}$$

Consequently, on using (15)

$$\begin{aligned} \det(\mathcal{J}^*) &= d_V \gamma_R - \alpha_V \alpha_R \beta_R^2 \frac{A_V}{N_R} + \alpha_R \beta_R \frac{I_V^*}{N_R}(d_V + \alpha_V \beta_R) \\ &\quad + \alpha_V \beta_R \frac{I_R^*}{N_R}\left(\gamma_R + \alpha_R \beta_R \frac{A_V}{N_R}\right) \\ &= \det \mathcal{J} - 2 \det \mathcal{J} = -\det \mathcal{J} > 0 \end{aligned}$$

$$\operatorname{tr}(\mathcal{J}^*) = -d_V - \gamma_R + \det \mathcal{J}\left[\frac{1}{d_V + \alpha_V \beta_R} + \frac{1}{\gamma_R + \alpha_R \beta_R \frac{A_V}{N_R}}\right] < 0$$

showing that the positive stationary solution of (13) is a stable node.

Proposition 2.1 Global stability of the endemic equilibrium. *If* $\mathcal{R}_0 > 1$ *and* $I_V(0) + I_R(0) > 0$, *then the endemic equilibrium* (I_V^*, I_R^*) *of (12) is globally asymptotically stable in the positive quadrant.*

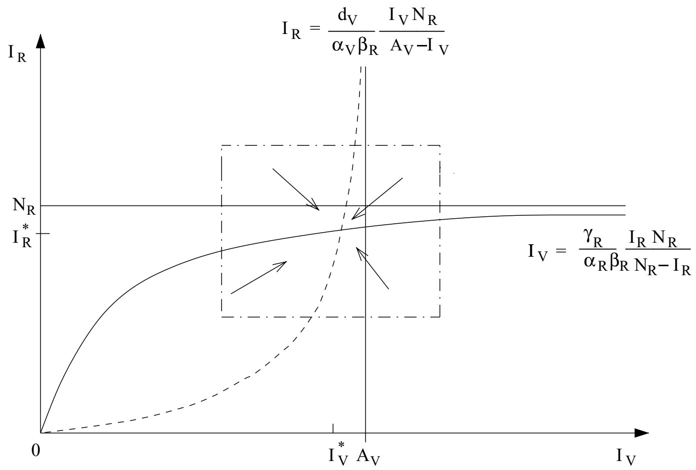

Fig. 2 Phase portrait for I_V, I_R.

Proof. From (13)

$$\nabla \cdot \mathbf{f} = \frac{\partial f_1}{\partial I_V} + \frac{\partial f_2}{\partial I_R} = -d_V - \gamma_R - \alpha_V\beta_R\frac{I_R}{N_R} - \alpha_R\beta_R\frac{I_V}{N_R} < 0$$

Thus, periodic solutions are excluded by Bendixson's Criterion. Application of the Poincaré–Bendixson theorem completes the proof that the endemic equilibrium is globally asymptotically stable.

The method of contracting rectangles (Smoller, 1983), can also be used to show that the endemic equilibrium is globally stable, as illustrated in Fig. 2.

3. Spatially-dependent model

To include the possible impact of spatial movement of reservoirs (birds) and, on a much smaller scale, vectors (mosquitoes), diffusion terms are included, giving the following spatially-dependent model in which the variables are function of space x, with $-\infty < x < \infty$, and time t, and non-negative initial values are assumed.

$$\begin{aligned}
\frac{\partial L_V}{\partial t} &= b_V(S_V + E_V + I_V) - m_V L_V - d_L L_V \\
\frac{\partial S_V}{\partial t} &= -\alpha_V\beta_R\frac{I_R}{N_R}S_V + m_V L_V - d_V S_V + \varepsilon\frac{\partial^2 S_V}{\partial x^2} \\
\frac{\partial E_V}{\partial t} &= \alpha_V\beta_R\frac{I_R}{N_R}S_V - (\kappa_V + d_V)E_V + \varepsilon\frac{\partial^2 E_V}{\partial x^2} \\
\frac{\partial I_V}{\partial t} &= \kappa_V E_V - d_V I_V + \varepsilon\frac{\partial^2 I_V}{\partial x^2}
\end{aligned} \qquad (16)$$

$$\frac{\partial S_R}{\partial t} = -\alpha_R\beta_R\frac{S_R}{N_R}I_V + \eta_R R_R + D\frac{\partial^2 S_R}{\partial x^2}$$
$$\frac{\partial I_R}{\partial t} = \alpha_R\beta_R\frac{S_R}{N_R}I_V - (\delta_R + \gamma_R)I_R + D\frac{\partial^2 I_R}{\partial x^2}$$
$$\frac{\partial R_R}{\partial t} = \gamma_R I_R - \eta_R R_R + D\frac{\partial^2 R_R}{\partial x^2}$$
$$\frac{\partial X_R}{\partial t} = \delta_R I_R$$

Here the diffusion coefficient for birds is $D > 0$ and the diffusion coefficient for mosquitoes is $\varepsilon > 0$ with $\epsilon \ll D$, since they do not move as quickly as birds. (In Section 5, the limiting case $\epsilon = 0$ is studied.) It is assumed that birds (mosquitoes) in each class have the same diffusion coefficient, except that larval mosquitoes do not diffuse.

3.1. Model simplification

We put some assumptions on initial conditions for this system. The conditions below, together with the structural assumptions (A1)–(A4), lead to the simplified spatially-dependent model.

(A5) *$N_R(x, t)$ is initially constant in space.*
This assumption is $N_R(x, 0) = N_R$, a constant. By (A1),

$$\frac{\partial N_R}{\partial t} = D\frac{\partial^2 N_R}{\partial x^2}$$

Then $N_R(x, t) = N_R$ for all $t \geq 0$.

As with our analysis of the ODE system (1), assumption (A2) can be used to show that R_R approaches zero in the limit $\eta_R \to \infty$. This is facilitated by Fourier transforming (in space) the recovered birds equation and proceeding as for (5). Thus, we can replace the bird equations in the system (16) with the single equation for infectious birds

$$\frac{\partial I_R}{\partial t} = \alpha_R\beta_R\frac{N_R - I_R}{N_R}I_V - \gamma_R I_R + D\frac{\partial^2 I_R}{\partial x^2} \tag{17}$$

Consider $N_V(x, t) = L_V(x, t) + S_V(x, t) + E_V(x, t) + I_V(x, t)$, then

$$\frac{\partial N_V}{\partial t} = (b_V - d_V)(S_V + E_V + I_V) - d_L L_V + \varepsilon\frac{\partial^2}{\partial x^2}(S_V + E_V + I_V)$$

Thus, it is hard to predict the total number of mosquitoes at a given time. Nevertheless, we can set $A_V(x, t) = S_V(x, t) + E_V(x, t) + I_V(x, t)$ and study the system of two equations for A_V and L_V:

$$\begin{aligned}\frac{\partial A_V}{\partial t} &= -d_V A_V + m_V L_V + \varepsilon \frac{\partial^2 A_V}{\partial x^2}\\ \frac{\partial L_V}{\partial t} &= b_V A_V - (m_V + d_L) L_V \end{aligned} \tag{18}$$

(A6) *The adult and larval mosquito densities* $A_V(x,t)$, $L_V(x,t)$ *are initially constant in space.*
With this assumption, the system (18) implies that $A_V(x,t)$ and $L_V(x,t)$ remain constant in space for all time. This can be seen rigorously by analysing the Fourier-transformed version of (18), by solving the initial value problem for each wave number and by showing that non-zero wave numbers cannot grow. Similarly, we use (A3) and, arguing as in the spatially-independent case, assuming (A4) and (B1), the mosquito equations in (16) simplify to

$$\frac{\partial I_V}{\partial t} = \alpha_V \beta_R \frac{I_R}{N_R}(A_V - I_V) - d_V I_V + \varepsilon \frac{\partial^2 I_V}{\partial x^2} \tag{19}$$

The simplified spatial model now reads

$$\begin{aligned}\frac{\partial I_V}{\partial t} &= \alpha_V \beta_R \frac{I_R}{N_R}(A_V - I_V) - d_V I_V + \varepsilon \frac{\partial^2 I_V}{\partial x^2}\\ \frac{\partial I_R}{\partial t} &= \alpha_R \beta_R \frac{N_R - I_R}{N_R} I_V - \gamma_R I_R + D \frac{\partial^2 I_R}{\partial x^2}\end{aligned} \tag{20}$$

where A_V, N_R are constant and $I_V(x,0) + I_R(x,0) > 0$.

With the assumption (B2) there is a positive stationary solution of (20), namely (I_V^*, I_R^*) given by (15). From Fig. 2, it can be seen that there exits a family of contracting rectangles in the positive (I_V, I_R) quadrant, containing (I_V^*, I_R^*) (see Fig. 2). Denote such a rectangle by G. By using Theorem 14.19 in Smoller (1983) taking $w = (I_V, I_R)$, a norm $|w|_G = \inf\{a \geq 0 : w \in aG\}$ and the Lyapunov functional

$$L_G(w) = \sup\{|w(x)|_G : x \in R\},$$

it follows that (I_V^*, I_R^*) is a global attractor in the positive quadrant for the spatially-dependent system (20).

The system (20) can be written as

$$\begin{bmatrix} I_V \\ I_R \end{bmatrix}_t = \mathcal{D} \begin{bmatrix} I_V \\ I_R \end{bmatrix}_{xx} + \mathbf{f}\left(\begin{bmatrix} I_V \\ I_R \end{bmatrix}\right) \tag{21}$$

with $\mathbf{f} = (f_1, f_2)^T$ given as before in Section 2.2 and

$$\mathcal{D} = \begin{bmatrix} \varepsilon & 0 \\ 0 & D \end{bmatrix}$$

System (12) is the spatially-independent version of the simplified system (20) and the results of the phase plane analysis in Section 2.2 hold.

4. Traveling wave solutions

We start by defining traveling waves for the system (20).

Definition 4.1. A traveling wave solution with speed c for (20) is a solution that has the form $(I_V(x-ct), I_R(x-ct))$ and connects the disease-free and disease-endemic stationary points of the system so that

$$\lim_{(x-ct)\to-\infty} (I_V, I_R) = (I_V^*, I_R^*) \quad \text{and} \quad \lim_{(x-ct)\to\infty} (I_V, I_R) = (0, 0).$$

The traveling front solution with speed c satisfies the ODE system

$$-c\dot{I}_V = \varepsilon \ddot{I}_V + \alpha_V \beta_R \frac{I_R}{N_R}(A_V - I_V) - d_V I_V$$
$$-c\dot{I}_R = D\ddot{I}_R + \alpha_R \beta_R \frac{N_R - I_R}{N_R} I_V - \gamma_R I_R$$

with boundary conditions at ±∞ determined by stationary solutions of the system as above.

We use the theorem on existence of traveling waves proved in Li et al. (2005). To this end, we examine and list the properties of the non-linear system (20), as written in (21), that are necessary to apply the result.

1. **f** has two stationary solutions: the zero solution $(0, 0)$ and the positive solution (I_V^*, I_R^*).
2. **f** is cooperative, i.e., f_1, f_2 are non-decreasing in off-diagonal components.
3. **f** does not depend explicitly on either x or t.
4. **f** is continuous, has uniformly bounded continuous first partial derivatives for $0 \le (I_V, I_R) \le (I_V^*, I_R^*)$ and is differentiable at zero. The Jacobian matrix $\mathcal{J} = \mathbf{Df(0)}$, given by (14) has non-negative off-diagonal entries and has a positive eigenvalue whose eigenvector has positive components.
5. Matrix $\mathcal{D}$ is diagonal with constant strictly positive diagonal entries.

With the properties (1)–(5) we can use the result of Li et al. (2005) Theorem 4.2 (see also Volpert et al., 1994, Theorem 4.2) to claim the following traveling wave result.

Theorem 4.1. *There exists a minimal speed of traveling fronts c_0 such that for every $c \ge c_0$ the non-linear system (20) has a non-increasing traveling wave solution*

$(I_V(x-ct), I_R(x-ct))$ with speed c so that

$$\lim_{(x-ct)\to-\infty}(I_V, I_R) = (I_V^*, I_R^*) \quad \text{and} \quad \lim_{(x-ct)\to\infty}(I_V, I_R) = (0,0).$$

If $c < c_0$, there is no traveling wave of this form.

The alternative approach to spatial disease spread involves calculation of the spread rate of system (20), as given by Definition (1). With assumptions (1)–(5), results in Li et al. (2005) can be used to describe the spread rate in terms of the traveling wave minimal speed.

Theorem 4.2. *The minimal wave speed c_0 for the non-linear system (20) is equal to c^*, the spread rate for this system.*

5. Spread-rate analysis

We now consider how to calculate the spread rate c^* for the non-linear system (20); see Definition 1.1. Cases in which the spread rate is linearly determinate are outlined in Section 4 of Weinberger et al. (2002). To apply these results, Hypotheses 4.1 of Weinberger et al. (2002) must be satisfied. The properties (1)–(4) above are equivalent to the Hypotheses 4.1.i–4.1.iv of Weinberger et al. (2002), and the Jacobian $\mathcal{J}$, given by (14), is irreducible and so satisfies Hypothesis 4.1.v of Weinberger et al. (2002).

Theorem 4.2 of Weinberger et al. (2002) states that under the above hypotheses if a *subtangential condition*

$$\mathbf{f}\left(\rho\begin{bmatrix} I_V \\ I_R \end{bmatrix}\right) \le \rho\mathbf{Df}(\mathbf{0})\begin{bmatrix} I_V \\ I_R \end{bmatrix} = \rho\mathcal{J}\begin{bmatrix} I_V \\ I_R \end{bmatrix} \tag{22}$$

for all positive ρ is satisfied, then the spread rate for the non-linear system c^* is linearly determinate. In other words $c^* = \bar{c}$ where $\bar{c}$ is the spread rate for the linearisation of (20), namely

$$\begin{bmatrix} I_V \\ I_R \end{bmatrix}_t = \mathcal{D}\begin{bmatrix} I_V \\ I_R \end{bmatrix}_{xx} + \mathcal{J}\begin{bmatrix} I_V \\ I_R \end{bmatrix} \tag{23}$$

(see Definition 1.2.) The subtangential condition is satisfied naturally by function $\mathbf{f}$ in (13). Moreover, using Lemma 4.1 in Weinberger et al. (2002) gives a formula for $\bar{c}$.

Theorem 5.1.

(i) The spread rate c^* of the non-linear system (20) and the spread rate $\bar{c}$ of the linearized system (23) both exist and $c^* = \bar{c}$.
(ii) The spread rate $\bar{c}$ of (23) is given by

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

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

$$\mathcal{B}_\lambda = \frac{\mathcal{J} + \lambda^2 \mathcal{D}}{\lambda}$$

Note that Theorem 5.1 does not rely upon the positivity of the diagonal elements of $\mathcal{D}$ (i.e. property (5) above) and hence remains true in the limiting case $\varepsilon = 0$.

By the above theorem, the single speed can be found from the linear analysis, which is more convenient than using the definition of spread rate for the non-linear system. From the formula in Theorem 5.1, for system (23)

$$\mathcal{B}_\lambda = \begin{bmatrix} -\dfrac{d_V}{\lambda} + \varepsilon\lambda & \dfrac{\alpha_V \beta_R}{\lambda}\dfrac{A_V}{N_R} \\ \dfrac{\alpha_R \beta_R}{\lambda} & -\dfrac{\gamma_R}{\lambda} + D\lambda \end{bmatrix}.$$

Denoting

$$\operatorname{tr}\mathcal{J} = -(d_V + \gamma_R) \equiv \theta < 0$$

$$\det \mathcal{J} = d_V \gamma_R - \alpha_V \alpha_R \beta_R^2 \frac{A_V}{N_R} \equiv j < 0$$

the characteristic polynomial of $\mathcal{B}_\lambda$ is

$$p(\sigma; \lambda, \varepsilon) = \sigma^2 - \sigma \tfrac{\theta + (D+\varepsilon)\lambda^2}{\lambda} + \tfrac{j}{\lambda^2} - D d_V - \varepsilon \gamma_R + \varepsilon D \lambda^2 = 0 \qquad (24)$$

Thus, the following statement holds.

Lemma 5.1. *For any finite λ, the roots $\sigma_i(\lambda, \varepsilon)$, $i = 1, 2$ of the characteristic polynomial $p(\sigma; \lambda, \varepsilon)$ of the matrix $\mathcal{B}_\lambda$ depend continuously on ε at zero, i.e.,*

$$\lim_{\varepsilon \to 0} \sigma_i(\lambda, \varepsilon) = \sigma_i(\lambda, 0)$$

In the general case $\varepsilon > 0$, it is difficult to obtain a result for the minimal spread rate by examining roots of $p(\sigma; \lambda, \varepsilon)$ as the larger root $\sigma_1(\lambda, \varepsilon)$ can have more than one extremum. Consequently we study the limiting case $\varepsilon = 0$ for which a more precise characterization is possible.

For $\varepsilon = 0$, we can apply the results of Hadeler and Lewis (2002), Section 6 (Lemmas 5, 6, 7 and Theorem 8), since the polynomial $p(\sigma; \lambda, 0)$ has the structure required there. This leads to the following result for $\bar{c}$.

Theorem 5.2. *Let* $\det \mathcal{J} \equiv j < 0$ *and* $\varepsilon = 0$. *Consider*

$$P(\sigma; \lambda) = \lambda^2 p(\sigma; \lambda, 0) = -D\sigma\lambda^3 + (\sigma^2 - D d_V)\lambda^2 - \theta\sigma\lambda + j$$

The spread rate $\bar{c}$ *of the linear system (23) can be obtained as the largest value* σ *such that the polynomial* $P(\sigma;\lambda)$ *has a real-positive double root.*

To study the double root condition $P(c;\lambda) = \partial P/\partial\lambda = 0$ necessary for $\bar{c}$, we can use the resultant of the polynomial P and its derivative, which is cubic in c^2. This resultant is

$$\begin{aligned} Q(c^2) = c^6(c^4 D(-4\theta^3 + 12 d_V j - 2 d_V \theta^2 + 18\theta j) \\ + c^2 D^2(-18\theta d_V j - 12 d_V^2 j + d_V^2 \theta^2 - 27 j^2) + 4 D^3 d_V^3 j \end{aligned} \tag{25}$$

With $x = c^2$, from Hadeler and Lewis (2002) Lemma 9, it follows that the polynomial $Q(x)$ is convex (concave up) for $x > 0$.

Thus the cubic $Q(x)$ has one positive root.

Using Theorems 4.1, 4.2, 5.1 and 5.2 and Lemma 5.1, we can infer the following result.

Theorem 5.3. *Assume that the conditions* $\det \mathcal{J} < 0$ *and* $\varepsilon > 0$ *hold. Then the spread rate* c^* *of the non-linear system (20) is the lower bound* c_0 *for the speed of a class of traveling waves solutions* ($c^* = c_0$)*, and the spread rate is linearly determinate,* ($c^* = \bar{c}$)*. As* $\varepsilon \to 0$*, the spread rate for the non-linear system approaches the positive square root of the largest zero of the cubic* $Q(x)$*.*

6. Comparison results

We now consider the system (16) assuming only (A1), (A5), (A6) and (B1), which we recall now for convenience of the reader.

(A1) $\delta_R = 0$
(A5) $N_R(x, 0) = \widetilde{N}_R$, constant
(A6) $A_V(x, 0)$ and $L_V(x, 0)$ are constant
(B1) $b_V = \dfrac{d_V(m_V + d_L)}{m_V}$

We prove the following result by using the comparison theorem for parabolic systems that can be found, for example, in Lu and Sleeman (1993).

Theorem 6.1. *Assume that (A1), (A5), (A6) and (B1) hold. Let*

$$\max\left(A_V(x,0),\, A_V(x,0) - \frac{d_V A_V(x,0) - m_V L_V(x,0)}{m_V + d_V + d_L}\right) \le \widetilde{A}_V$$

where $A_V = \widetilde{A}_V$ *and* $N_R = \widetilde{N}_R$ *in the simplified system (20), and*

$$(E_V(0) + I_V(0),\, I_R(0)) \le (\bar{I}_V(0),\, \bar{I}_R(0))$$

where $(\bar{I}_V, \bar{I}_R)$ *are the solutions of (20). Then the solution components* (I_V, I_R) *for the system (16) are bounded above by the solution* $(\bar{I}_V, \bar{I}_R)$ *of the simplified system (20).*

Proof. The essential assumption of the comparison result that we want to apply is a uniform parabolicity of operators in all equations. We note that some operators in (16) do not have this property so we need to modify the system.

The simplified system (20) reads, in variables $(\bar{I}_V, \bar{I}_R)$:

$$\begin{aligned}\frac{\partial \bar{I}_V}{\partial t} - \varepsilon\frac{\partial^2 \bar{I}_V}{\partial x^2} &= \alpha_V\beta_R\frac{\bar{I}_R}{\widetilde{N}_R}\left(\widetilde{A}_V - \bar{I}_V\right) - d_V\bar{I}_V\\ \frac{\partial \bar{I}_R}{\partial t} - D\frac{\partial^2 \bar{I}_R}{\partial x^2} &= \alpha_R\beta_R\frac{\widetilde{N}_R - \bar{I}_R}{\widetilde{N}_R}\bar{I}_V - \gamma_R\bar{I}_R\end{aligned} \tag{26}$$

where $\widetilde{N}_R$, $\widetilde{A}_V$ are constant.

From the system (16),

$$\begin{aligned}&\frac{\partial(E_V + I_V)}{\partial t} - \varepsilon\frac{\partial^2(E_V + I_V)}{\partial x^2} \\ &\qquad = \alpha_V\beta_R\frac{I_R}{N_R}(A_V - (E_V + I_V)) - d_V(E_V + I_V).\end{aligned} \tag{27}$$

By assumption $A_V(x, t)$ is initially constant in space, thus it remains constant for all times (that can be seen from the analysis of the system in (A_V, L_V), as observed in Section 3). Consequently, by (10)

$$\begin{aligned}A_V(x, t) = A_V(t) &\le \max\left(A_V(x, 0), A_V(x, 0) - \frac{d_V A_V(x, 0) - m_V L_V(x, 0)}{m_V + d_V + d_L}\right)\\ &\le \widetilde{A}_V\end{aligned}$$

Next, since $N_R(x, t) = S_R(x, t) + I_R(x, t) + R_R(x, t)$ is initially constant, equal to $\widetilde{N}_R$, and satisfies the heat equation, as $\delta_R = 0$, then $N_R(x, t) = \widetilde{N}_R$. Thus, from (16) the equation for I_R can be written as

$$\begin{aligned}\frac{\partial I_R}{\partial t} - D\frac{\partial^2 I_R}{\partial x^2} &= -\gamma_R I_R + \alpha_R\beta_R\frac{\widetilde{N}_R - I_R - R_R}{\widetilde{N}_R}I_V\\ &\le -\gamma_R I_R + \alpha_R\beta_R\frac{\widetilde{N}_R - I_R - R_R}{\widetilde{N}_R}(E_V + I_V)\end{aligned} \tag{28}$$

Variables $(E_V + I_V, I_R)$ satisfy the system (27)–(28) for which the right hand side functions are bounded above by the right-hand side functions of the system (26), since

$$A_V(x, t) \le \widetilde{A}_V$$

and, since $R_R(x, t) \ge 0$,

$$\frac{\widetilde{N}_R - I_R - R_R}{\widetilde{N}_R} \le \frac{\widetilde{N}_R - I_R}{\widetilde{N}_R}.$$

Then, using the comparison result for parabolic systems, as stated, for example, in Lu and Sleeman (1993), Theorem 2.9, it follows that $(\bar{I}_V, \bar{I}_R)$ are supersolutions to $(E_V + I_V, I_R)$ and thus to (I_V, I_R) if this relation holds initially.

Our final result bounds the spread rate of the original system by the corresponding values for the simplified system. For this, the following extension of (B2) is needed for existence of the disease-endemic equilibrium for the system (16) with finite κ_V.

(B2′) $d_V \gamma_R \left(1 + \frac{d_V}{\kappa_V}\right) < \alpha_V \alpha_R \beta_R^2 \frac{\widetilde{A}_V}{\widetilde{N}_R}$

The system (16) has, in infected variables $(E_V + I_V, I_R)$, the disease-free equilibrium $(0, 0)$ and the disease-endemic equilibrium

$$\mathbf{u}^* = \left(\frac{\alpha_V \alpha_R \beta_R^2 \widetilde{A}_V - \left(d_V + \frac{d_V^2}{\kappa_V}\right) \gamma_R \widetilde{N}_R}{\alpha_R \beta_R \left[d_V \left(1 + \frac{\gamma_R}{\eta_R}\right) + \alpha_V \beta_R \right]}, \frac{\alpha_V \alpha_R \beta_R^2 \widetilde{A}_V - \left(d_V + \frac{d_V^2}{\kappa_V}\right) \gamma_R \widetilde{N}_R}{\alpha_V \beta_R \left[\gamma_R \left(1 + \frac{d_V}{\kappa_V}\right) + \alpha_R \beta_R \frac{\widetilde{A}_V}{\widetilde{N}_R} \left(1 + \frac{\gamma_R}{\eta_R}\right) \right]} \right) \tag{29}$$

which is positive by (B2′). Note that the condition (B2′) is an extension of (B2) for finite κ_V. It is also equivalent to

$$\sqrt{\frac{\alpha_V \alpha_R \beta_R^2 \widetilde{A}_V \kappa_V}{d_V \gamma_R \widetilde{N}_R (\kappa_V + d_V)}} > 1$$

where the left-hand side is the basic reproduction number for the ODE WN virus model with the exposed class E_V included. This reduces to $\mathcal{R}_0 > 1$ when $\kappa_V \to \infty$, as in Section 2.2.

Theorem 6.2. *Let the assumptions of Theorem 6.1 and (B2′) be satisfied. If the spread rate for the system (16) exists and is equal to c_G^* then $c_G^* \leq c^*$, where c^* is the spread rate for the simplified system (20).*

Proof. From the above considerations, the infected classes for the system (16) satisfy the system (27)–(28). Therefore, using Definition 1.1 for the spread rate of (16)

$$\lim_{t\to\infty} \left\{ \sup_{|x| \geq (c_G^* + \epsilon)t} \|\mathbf{u}(t, x)\| \right\} = 0, \qquad \lim_{t\to\infty} \left\{ \sup_{|x| \leq (c_G^* - \epsilon)t} \|\mathbf{u}(t, x) - \mathbf{u}^*\| \right\} = 0,$$

with $\mathbf{u} = (E_V + I_V, I_R)$, $\mathbf{u_0} = \mathbf{0}$ and the disease-endemic equilibrium $\mathbf{u}^*$ as in (29). Similarly, for the spread rate of (20)

$$\lim_{t\to\infty} \left\{ \sup_{|x| \geq (c^* + \epsilon)t} \|\bar{\mathbf{u}}(t, x)\| \right\} = 0, \qquad \lim_{t\to\infty} \left\{ \sup_{|x| \leq (c^* - \epsilon)t} \|\bar{\mathbf{u}}(t, x) - \bar{\mathbf{u}}^*\| \right\} = 0,$$

where $\bar{\mathbf{u}} = (\bar{I}_V, \bar{I}_R)$ and $\bar{\mathbf{u}}^*$ is given by (15). Assume that $c^* < c_G^*$, then taking $\epsilon = \frac{c_G^* - c^*}{2} > 0$ and using the above with $c_G^* - \epsilon = c^* + \epsilon = \frac{c_G^* + c^*}{2} = c$ gives

$$\lim_{t\to\infty}\left\{\sup_{|x|\le ct} \|\mathbf{u}(t,x) - \mathbf{u}^*\|\right\} = 0 \quad \text{and} \quad \lim_{t\to\infty}\left\{\sup_{|x|\ge ct} \|\bar{\mathbf{u}}(t,x)\|\right\} = 0.$$

Thus

$$\lim_{t\to\infty}\left\{\sup_{|x|=ct} ||\mathbf{u}(t,x) - \mathbf{u}^*||\right\} \le \lim_{t\to\infty}\left\{\sup_{|x|\le ct} ||\mathbf{u}(t,x) - \mathbf{u}^*||\right\} = 0,$$

$$\lim_{t\to\infty}\left\{\sup_{|x|=ct} ||\bar{\mathbf{u}}(t,x)||\right\} \le \lim_{t\to\infty}\left\{\sup_{|x|\ge ct} ||\bar{\mathbf{u}}(t,x)||\right\} = 0.$$

Since by the comparison result (Theorem 6.1) it follows that

$$\mathbf{u}(x,t) = \begin{bmatrix} E_V + I_V \\ I_R \end{bmatrix}(x,t) \le \begin{bmatrix} \bar{I}_V \\ \bar{I}_R \end{bmatrix}(x,t) = \bar{\mathbf{u}}(x,t)$$

we conclude the following

$$\lim_{t\to\infty}\left\{\sup_{|x|=ct} ||\mathbf{u}(t,x) - \mathbf{u}^*||\right\} = 0,$$

$$\lim_{t\to\infty}\left\{\sup_{|x|=ct} ||\mathbf{u}(t,x)||\right\} \le \lim_{t\to\infty}\left\{\sup_{|x|=ct} ||\bar{\mathbf{u}}(t,x)||\right\} = 0.$$

This implies $\mathbf{u}^* = \mathbf{0}$, which contradicts the assumption $\mathbf{u}^* \ne \mathbf{0}$ in Definition 1.1. Therefore, $c_G^* \le c^*$.

Combining the above results with those of Theorem 5.3 for system (20), gives $c_G^* \le c^* = \bar{c} = c_0$, if the spread rate c_G^* for the system (16) exists.

7. Discussion

Figure 3 shows a plot of the numerical estimate for the spread rate $\bar{c} = c^*$ km/day of the simplified system (20) with $\varepsilon = 0$, calculated as the positive square root of the largest zero of the cubic Q, given by (25), versus the bird diffusion coefficient D. We consider the range of D between 0 and 14 km^2/day, as estimated in Okubo (1998). For illustrative purposes, we set the ratio $A_V/N_R = 20$, $\beta_R = 0.3$ and $\gamma_R = 0.01$/day. For other parameters, we use mean values as estimated in Wonham et al. (2004), namely, $d_V = 0.029$, $\alpha_V = 0.16$, $\alpha_R = 0.88$/day.

As noted in the Introduction section, West Nile virus has spread across North America in about 5 years, thus the observed spread rate is about 1000 km/year, i.e., 2.74 km/day. From Fig. 3, to achieve this observed value for c^*, a diffusion

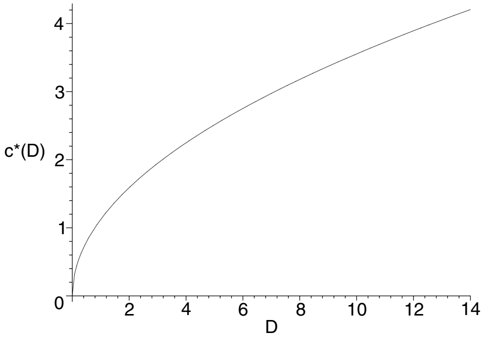

Fig. 3 Spread rate c^* $([\frac{\text{km}}{\text{day}}])$ as the function of bird diffusion $D([\frac{\text{km}^2}{\text{day}}])$.

coefficient of about 5.94 is needed in our model. The spread rate c^* is an increasing function of D and also increases slowly with the ratio A_V/N_R.

The reaction-diffusion system (16) that we have discussed is a first approximation for the spatial spread of West Nile virus. To incorporate more biology, a model should contain more realistic bird and mosquito movements. For a model with seasonality, these include bird migration and regular changes in the number of mosquitoes. Different species of birds with different characteristics need to be included, especially if control strategies are incorporated in the model. In addition, spatial models other than those using reaction-diffusion equations remain to be explored.

We have analyzed a simplified version of system (16), namely system (20), and proved that the spread rate, which is linearly determinate, is equal to the minimal wave speed for this non-linear system. By comparison results, it then follows that this spread rate is an upper bound for the spread rate of the original system (16), provided that the spread rate for (16) exists. Conditions for this existence remain to be determined.

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