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SOME VECTOR BORNE DISEASES WITH STRUCTURED HOST POPULATIONS: EXTINCTION AND SPATIAL SPREAD*

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Abstract. We derive from a structured population model a system of delay differential equations describing the interaction of five subpopulations, namely susceptible and infected adult and juvenile reservoirs and infected adult vectors, for a vector borne disease with particular reference to West Nile virus, and we also incorporate spatial movements by considering the analogue reaction-diffusion systems with nonlocal delayed terms. Specific conditions for the disease eradication and sharp conditions for the local stability of the disease-free equilibrium are obtained using comparison techniques coupled with the spectral theory of monotone linear semiflows. A formal calculation of the minimal wave speed for the traveling waves is given and compared with field observation data.

Key words. stage-structure, epidemic, delay, traveling front, vector borne disease

AMS subject classifications. 34K20, 34K60, 35K57, 92D25

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1. Introduction.

Vector borne diseases are infectious diseases that are carried by insects from one host to another. Examples include malaria, West Nile virus, yellow fever, dengue fever, lyme disease, and plague. In many of these diseases it is the mosquito that carries the virus, but ticks and fleas can also be responsible. The diseases can be spread to humans, birds, and other animals.

Much has been done in terms of modeling and analysis of the transmission dynamics and spatial spread of vector borne diseases; see Anderson and May [1], Murray [20], Brauer and Castillo-Chavez [4], Edelstein-Keshet [6], Hethcote [10], Kot [13], Jones and Sleeman [12], Wonham and coworkers [26, 27], etc. However, one important biological aspect of the hosts—the stage structure—seems to have received little attention, although structured population models have been intensively studied (see Diekmann and Heesterbeek [5]) in the context of population dynamics and spatial ecology, and the interaction of stage-structure with spatial dispersal has been receiving considerable attention in association with the theoretical development of the so-called reaction-diffusion equations with nonlocal delayed feedback (see the papers by Gourley, So, and Wu [7] and Gourley and Wu [8] and the references therein).

The developmental stages of hosts have a profound impact on the transmission dynamics of vector borne diseases. In the case of West Nile virus the transmission cycle involves both mosquitoes and birds, the crow species being particularly important. *Nestling* crows are crows that have hatched but are helpless and stay in the nest, receiving more-or-less continuous care from the mother for up to two weeks and less

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continuous care thereafter. *Fledgling* crows are old enough to have left the nest (they leave it after about five weeks), but they cannot fly very well. After three or four months these fledglings will be old enough to obtain all of their food by themselves. As these facts demonstrate, the maturation stages of adult birds, fledglings, and nestlings are all very different from a biological and an epidemiological perspective, and a realistic model needs to take these different stages into account. For example, in comparison with grown birds, the nestlings and fledglings have much higher disease-induced death rate, much poorer ability to avoid being bitten by mosquitoes, and much less spatial mobility [18, 2, 22]. In this paper we shall, in fact, assume that there is only one preadult stage for the host population, which in the West Nile virus context could be thought of as the fledgling stage of crows.

The aim of this paper is to formulate a model for the evolution of some vector borne diseases whose transmission dynamics and patterns are similar to those of West Nile virus. Other recent mathematical models for this disease include the works of Bowman et al. [3], Lewis, Renclawowicz, and van den Driessche [16], and Wonham et al. [26, 27], some of which use a different incidence function normalized by bird density. We start with the classical McKendrick von-Foerster equations for an age-structured reservoir population divided into two epidemiological compartments of susceptible and infected (and infectious), coupled with a scalar delay differential equation for the adult vector population under the assumption that the total vector population is maintained at a constant level. We then use the standard technique of integration along characteristics to reduce the model to a system of five coupled delay differential equations for the susceptible and infected juvenile and adult reservoir populations and the adult infected vector. If spatial diffusion is allowed, a similar derivation leads to a reaction-diffusion system with nonlocal and highly nonlinear delayed interactions. The model derivation is carried out in detail in sections 2 (for ODE models) and 3 (for PDE models), together with some detailed biological and epidemiological explanations of all terms involved.

We consider the qualitative behaviors of the reduced ordinary delay differential system in subsections 2.1–2.4. We establish the positiveness and boundedness of the reduced system, and we emphasize the need to restrict the initial data to the subset which is biologically and epidemiologically realistic. We then establish a concrete criterion, expressed in terms of the model parameters, for disease eradication. This is achieved using some comparison techniques and differential inequalities. We also obtain a necessary and sufficient condition for the disease-free equilibrium to be locally asymptotically stable—this is done using an application of the spectral properties of a linear delay differential system due to Smith [23]. The sharpness of the disease eradication condition is then tested using the available data and parameters for West Nile virus, and our simulations show that sustained oscillation can occur, should this disease eradication condition be violated.

In section 3, consider the issue of spatial spread of the disease in a one-dimensional setting. We provide a detailed formal calculation of the so-called minimal wave speed that is expected to coincide with the propagation speed of the disease, and we compare the predicted wave speed with data in the literature relating to the observed speed of spread of West Nile virus across North America. Finally, in section 4, we discuss our findings together with some of the corresponding results for a modified model with a different incidence function.

2. Model derivation. We shall think of the disease as mosquito borne, since mosquitoes are responsible for transmitting many of the vector borne diseases that

currently constitute significant public health issues in various parts of the world.

We will also refer to the reservoir as the host, and assume that the host population is age-structured. We start with a simple division of the host population into susceptible hosts $s(t,a)$ and infected hosts $i(t,a)$ at time t and age a. These host populations are assumed to evolve according to the McKendrick von-Foerster equations for an age-structured population:

$$\frac{\partial s}{\partial t} + \frac{\partial s}{\partial a} = -d_s(a)s(t,a) - \beta(a)s(t,a)m_i(t) \tag{2.1}$$

and

$$\frac{\partial i}{\partial t} + \frac{\partial i}{\partial a} = -d_i(a)i(t,a) + \beta(a)s(t,a)m_i(t), \tag{2.2}$$

where $m_i(t)$ is the number of infected adult mosquitoes satisfying another equation below, and $\beta(a)$ is the age-dependent transmission coefficient, and it is assumed that conversion of hosts from susceptible to infected occurs through interaction of susceptible hosts with infected mosquitoes, and at this stage we assume that the rate of conversion is given by mass action. We shall discuss the limitations of the model involving mass action and shall indicate how our work can be extended to include a more standard incidence term that includes dividing by the density of the host population. The functions $d_s(a)$ and $d_i(a)$ are the age-dependent death rates of susceptible and infected hosts.

We shall further split the host population into juveniles and adults, defined respectively as those of age less than some number τ and those of age greater than τ. We will work with the following choices for the death rates and the transmission coefficient $\beta(a)$:

$$d_s(a) = \begin{cases} d_{sj}, & a < \tau, \\ d_{sa}, & a > \tau, \end{cases} \qquad d_i(a) = \begin{cases} d_{ij}, & a < \tau, \\ d_{ia}, & a > \tau, \end{cases} \tag{2.3}$$

and

$$\beta(a) = \begin{cases} \beta_j, & a < \tau, \\ \beta_a, & a > \tau. \end{cases} \tag{2.4}$$

The subscripts in these quantities refer to disease and juvenile/adult status; thus, for example, the per capita death rates for susceptible juveniles and infected adults would be d_{sj} and d_{ia}, respectively. The above choices enable us to formulate a closed system of delay differential equations involving only the total numbers of hosts classified as adult susceptibles, adult infected, juvenile susceptibles, and juvenile infected. These total numbers are given respectively, using self-explanatory notations, by

$$\begin{aligned} A_s(t) &= \int_\tau^\infty s(t,a)\,da, \qquad A_i(t) = \int_\tau^\infty i(t,a)\,da, \qquad J_s(t) = \int_0^\tau s(t,a)\,da, \\ &\qquad\qquad J_i(t) = \int_0^\tau i(t,a)\,da. \end{aligned} \tag{2.5}$$

We assume no vertical transmission in the system (both from host and vector). On the further assumption that the birth rate is a function of the total number of susceptible adult hosts, we have the following expressions for the birth rates $s(t,0)$ and $i(t,0)$:

$$s(t,0) = b(A_s(t)), \qquad i(t,0) = 0, \tag{2.6}$$

where $b(\cdot)$ is the birth rate function for hosts (we shall later introduce $B(\cdot)$ as the birth rate function for mosquitoes). Equations (2.1) and (2.2) are solved subject to (2.6).

Let us now find a differential equation for $A_s(t)$. Differentiating the expression for $A_s(t)$ in (2.5), making use of (2.1), (2.3), and (2.4), and assuming (reasonably) that $s(t,\infty)=0$, we quickly find that

$$\frac{dA_s}{dt} = s(t,\tau) - d_{sa}A_s(t) - \beta_a m_i(t)A_s(t). \tag{2.7}$$

Next we need to find $s(t,\tau)$. This will be achieved by solving (2.1) for $0<a<\tau$. Set

$$s_\xi(a) = s(\xi+a,a).$$

Then

$$\begin{aligned}\frac{ds_\xi}{da} &= \left[\frac{\partial s}{\partial t} + \frac{\partial s}{\partial a}\right]_{t=\xi+a}\\ &= -s_\xi(a)[d_s(a) + \beta(a)m_i(\xi+a)],\end{aligned}$$

so that

$$\begin{aligned}s(\xi+a,a) = s_\xi(a) &= s_\xi(0)\exp\left(-\int_0^a (d_s(\eta)+\beta(\eta)m_i(\xi+\eta))\,d\eta\right)\\ &= b(A_s(\xi))\exp\left(-\int_0^a (d_s(\eta)+\beta(\eta)m_i(\xi+\eta))\,d\eta\right).\end{aligned} \tag{2.8}$$

Setting $a=\tau$ and $\xi = t-\tau$ and using (2.3), (2.4) gives

$$s(t,\tau) = b(A_s(t-\tau))\exp\left(-\int_0^\tau (d_{sj}+\beta_j m_i(t-\tau+\eta))\,d\eta\right).$$

Substituting this into (2.7) gives, after a change of variables in the integral,

$$\frac{dA_s}{dt} = b(A_s(t-\tau))\exp\left(-\int_{t-\tau}^t (d_{sj}+\beta_j m_i(u))\,du\right) - d_{sa}A_s(t) - \beta_a m_i(t)A_s(t). \tag{2.9}$$

In much the same way, we obtain the following equation for $J_s(t)$:

$$\begin{aligned}\frac{dJ_s}{dt} &= b(A_s(t)) - b(A_s(t-\tau))\exp\left(-\int_{t-\tau}^t (d_{sj}+\beta_j m_i(u))\,du\right)\\ &\quad - d_{sj}J_s(t) - \beta_j m_i(t)J_s(t).\end{aligned} \tag{2.10}$$

The differential equation for $A_i(t)$ turns out to be more complicated. Differentiating the expression for $A_i(t)$ in (2.5), assuming $i(t,\infty)=0$, and using (2.3) and (2.4) gives

$$\frac{dA_i(t)}{dt} = i(t,\tau) - d_{ia}A_i(t) + \beta_a m_i(t)A_s(t), \tag{2.11}$$

and we need to find $i(t,\tau)$, by solving (2.2) for $0<a<\tau$. Setting $i_\xi(a) = i(\xi+a,a)$ and differentiating with respect to a, we find from (2.2) that

$$\frac{di_\xi(a)}{da} + d_{ij}i_\xi(a) = \beta_j m_i(\xi+a)s(\xi+a,a).$$

Integrating this from 0 to a and recalling that $i_\xi(0) = i(\xi, 0) = 0$ by (2.6), we find that

$$i(\xi + a, a) = i_\xi(a) = \beta_j \int_0^a e^{-d_{ij}(a-\eta)} m_i(\xi + \eta) s(\xi + \eta, \eta)\, d\eta.$$

Therefore,

$$\begin{aligned} i(t, \tau) &= \beta_j \int_0^\tau e^{-d_{ij}(\tau-\eta)} m_i(t - \tau + \eta) s(t - \tau + \eta, \eta)\, d\eta \\ &= \beta_j \int_{t-\tau}^t e^{-d_{ij}(t-\xi)} m_i(\xi) s(\xi, \xi + \tau - t)\, d\xi. \end{aligned} \tag{2.12}$$

In this integral the second argument of $s(\xi, \xi + \tau - t)$ goes from 0 to τ, and therefore an expression for $s(\xi, \xi + \tau - t)$ can be obtained from the earlier analysis. From (2.8),

$$s(\xi, \xi + \tau - t) = b(A_s(t - \tau)) \exp\left(- \int_{t-\tau}^\xi [d_{sj} + \beta_j m_i(v)]\, dv \right).$$

Insertion of this expression into (2.12) yields an expression for $i(t, \tau)$ that involves only the state variables in (2.5) and $m_i(t)$, and insertion of this expression for $i(t, \tau)$ into (2.11) finally gives the differential equation for $A_i(t)$ to be

$$\begin{aligned} \frac{dA_i(t)}{dt} &= -d_{ia} A_i(t) + \beta_a m_i(t) A_s(t) \\ &\quad + \beta_j b(A_s(t - \tau)) \int_{t-\tau}^t m_i(\xi) e^{-d_{ij}(t-\xi)} \exp\left(- \int_{t-\tau}^\xi (d_{sj} + \beta_j m_i(v))\, dv \right) d\xi. \end{aligned} \tag{2.13}$$

Similarly, the differential equation for $J_i(t)$ can be shown to be

$$\begin{aligned} \frac{dJ_i(t)}{dt} &= -d_{ij} J_i(t) + \beta_j m_i(t) J_s(t) \\ &\quad - \beta_j b(A_s(t - \tau)) \int_{t-\tau}^t m_i(\xi) e^{-d_{ij}(t-\xi)} \exp\left(- \int_{t-\tau}^\xi (d_{sj} + \beta_j m_i(v))\, dv \right) d\xi. \end{aligned} \tag{2.14}$$

To close the system we still need a differential equation for the variable $m_i(t)$, but first we would like to discuss the ecological interpretation of the complicated integral term appearing in (2.13) and (2.14). The first two terms in the right-hand side of (2.13) are easy to interpret. They are, respectively, the death rate of infected adults and conversion of susceptible adults to infected adults via contact with infected mosquitoes. The last term in (2.13) tells us the rate at which infected immatures become infected adults having contracted the disease in childhood. This term is the rate at which infected individuals pass through age τ. Now, an individual that is of age τ at time t will have been born at time $t - \tau$. Recall, however, that all individuals are born as susceptibles. This is why the birth rate $b(A_s(t-\tau))$ is involved. The individuals we are presently discussing have each acquired the infection at some stage during childhood, so assume that a particular individual acquires it at a time $\xi \in (t - \tau, t)$. This particular individual remained susceptible from its birth at time $t - \tau$ until time ξ, and the probability of this happening is

$$\exp\left(- \int_{t-\tau}^\xi (d_{sj} + \beta_j m_i(v))\, dv \right).$$

The probability that the individual will survive from becoming infected at time ξ until becoming an adult at time t is

$$e^{-d_{ij}(t-\xi)}.$$

These two exponentials both feature in the last term in (2.13). The product $\beta_j m_i(\xi)$ is the per capita conversion rate of susceptible juveniles to infected juveniles at time ξ, and ξ running from $t-\tau$ to t totals up the contributions from all possible times at which infected individuals passing into adulthood might have acquired the infection.

Finally, we need differential equations for the mosquitoes. Let $m_T(t)$ be the total number of (adult) mosquitoes, divided into infected mosquitoes $m_i(t)$ and susceptible mosquitoes $m_T(t) - m_i(t)$. Death and reproductive activity for mosquitoes are assumed not to depend on whether they are carrying the disease or not, and so the total number of adult mosquitoes is assumed to obey

$$\frac{dm_T(t)}{dt} = e^{-d_l\sigma}B(m_T(t-\sigma)) - d_m m_T(t), \tag{2.15}$$

where d_l and d_m denote the death rates of larval and adult mosquitoes, respectively, and σ is the length of the larval phase from egg to adult. The function $B(\cdot)$ is the birth rate function for mosquitoes. It is possible but unnecessary to write down a differential equation for larval mosquitoes. Infected adult mosquitoes $m_i(t)$ are assumed to obey

$$\frac{dm_i(t)}{dt} = -d_m m_i(t) + \beta_m(m_T(t) - m_i(t))(J_i(t) + \alpha A_i(t)). \tag{2.16}$$

Thus, the rate at which mosquitoes become infected is given by mass action as the product of susceptible mosquitoes $m_T(t) - m_i(t)$ and infected birds which may be either juvenile or adult. The presence of the factor α is to account for the possibility that juvenile and adult birds might not be equally vulnerable to being bitten. Again, we defer the discussion of a more standard incidence term to the final section.

Certain assumptions will be made concerning the birth function $B(\cdot)$ for the mosquitoes. These assumptions, which are ecologically reasonable, are geared towards ensuring that the total number $m_T(t)$ of mosquitoes stabilizes and does not tend to zero (otherwise the disease is automatically eradicated and the model is not interesting). These assumptions are

$$\left.\begin{array}{l} B(0) = 0,\ B(\cdot) \text{ is strictly monotonically increasing, there exists } m_T^* > 0 \\ \text{such that } e^{-d_l\sigma}B(m) > d_m m \text{ when } m < m_T^* \text{ and } e^{-d_l\sigma}B(m) < d_m m \text{ when} \\ m > m_T^*. \end{array}\right\} \tag{2.17}$$

The quantity $m_T^* > 0$ in (2.17) is an equilibrium of (2.15), and $m_T(t) \to m_T^*$ as $t \to \infty$, provided $m_T(\theta) \geq 0$ and $m_T(\theta) \not\equiv 0$ on $\theta \in [-\sigma, 0]$ (see Kuang [14]). Accordingly, (2.16) is asymptotically autonomous, and we may replace $m_T(t)$ by m_T^* in (2.16), thereby lowering the order of the system to be studied, which we now note consists of (2.9), (2.10), (2.13), and (2.14) together with

$$\frac{dm_i(t)}{dt} = -d_m m_i(t) + \beta_m(m_T^* - m_i(t))(J_i(t) + \alpha A_i(t)), \tag{2.18}$$

which is the asymptotically autonomous limiting form of (2.16). Note that this system does not explicitly involve the delay σ, but this delay is still involved via the quantity m_T^*.

2.1. Positivity of solutions. We will prove that the system consisting of (2.9), (2.10), (2.13), (2.14), and (2.18) has a positivity preserving property. It is easy to appreciate that this system cannot have a positivity preserving property for completely arbitrary nonnegative initial data (a glance at the terms in the right-hand side of (2.14) makes this clear). However, positivity preservation does hold when some components of the initial data satisfy certain relations. These relations are easily seen to be the only ones that make sense ecologically and therefore are easily admitted. We therefore now append to the above-mentioned system the following initial data:

$$
\begin{aligned}
&A_s(\theta) = A_s^0(\theta) \geq 0, \qquad \theta \in [-\tau, 0],\\
&m_i(\theta) = m_i^0(\theta) \in [0, m_T^*], \qquad \theta \in [-\tau, 0],\\
&A_i(0) = A_i^0(0) \geq 0,\\
&J_s(0) = \int_{-\tau}^{0} b(A_s^0(\xi)) \exp\left(- \int_{\xi}^{0} [d_{sj} + \beta_j m_i^0(u)]\, du \right) d\xi,\\
&J_i(0) = \int_{-\tau}^{0} b(A_s^0(\xi)) \left\{ \int_{\xi}^{0} \beta_j m_i^0(\eta) e^{d_{ij}\eta} e^{-\int_{\xi}^{\eta} [d_{sj} + \beta_j m_i^0(v)]\, dv} d\eta \right\} d\xi,
\end{aligned}
\tag{2.19}
$$

where $A_s^0(\theta)$ and $m_i^0(\theta)$ are prescribed continuous functions of the variable $\theta \in [-\tau, 0]$, and $A_i^0(0)$ is also a given value. Note that $J_s(0)$ and $J_i(0)$ have to be calculated from the initial data for A_s and m_i. This is ecologically reasonable; after all, $J_s(0)$ is the number of juvenile susceptibles at time $t = 0$. The integral on the right in the expression for $J_s(0)$ is simply accounting for all these juvenile susceptibles at $t = 0$. Each one was born at some time $\xi \in [-\tau, 0]$—hence the presence of the birth rate $b(A_s^0(\xi))$—and each has to have survived and remained susceptible until time 0, hence the exponential term which represents the probability of this actually happening. The interpretation of the expression for $J_i(0)$ is similar but more complicated. Of the infected juveniles $J_i(0)$ at time 0, each one was born at some time $\xi \in [-\tau, 0]$ as a susceptible, and each of these newborns at time ξ then became infected at some subsequent time $\eta \in [\xi, 0]$.

We will now prove the following positivity preservation result.

PROPOSITION 2.1. *Let* (2.17) *hold. Then each component of the solution of the system consisting of* (2.9), (2.10), (2.13), (2.14), *and* (2.18) *for* $t > 0$, *subject to the initial conditions* (2.19), *remains nonnegative for all* $t > 0$. *Also,* $m_i(t) \leq m_T^*$ *for all* $t > 0$. *If, furthermore, the function* b *is bounded, then each component of the above solution is also bounded for all* $t > 0$.

Proof. First we will show that $m_i(t) \leq m_T^*$ for all $t > 0$. Suppose the contrary; then there must exist a time t_1 such that $m_i(t_1) = m_T^*$ and $dm_i(t_1)/dt \geq 0$. Evaluating (2.18) at time t_1 immediately gives a contradiction.

Next we prove nonnegativity of $A_s(t)$, for $t \in (0, \tau]$ in the first instance. On this interval,

$$
\frac{dA_s(t)}{dt} \geq -d_{sa} A_s(t) - \beta_a m_i(t) A_s(t).
$$

By comparison, $A_s(t)$ is bounded below by the solution of the corresponding differential equation obtained by replacing $\geq$ by $=$, and this differential equation contains a factor of $A_s(t)$ in its right-hand side. Since $A_s(0) \geq 0$, it follows that $A_s(t) \geq 0$ for all $t \in (0, \tau]$. This argument can be continued using the method of steps, and we conclude that $A_s(t) \geq 0$ for all $t > 0$.

Nonnegativity of $J_s(t)$ will be shown next. This can be seen by noting that the solution of (2.10), subject to the initial value for $J_s(0)$ given in (2.19), is

$$J_s(t) = \int_{t-\tau}^{t} b(A_s(\xi)) \exp\left(-\int_{\xi}^{t} [d_{sj} + \beta_j m_i(u)]\, du\right) d\xi, \tag{2.20}$$

which is nonnegative because A_s is nonnegative.

We still have to prove the nonnegativity of $A_i(t)$, $J_i(t)$, and $m_i(t)$. It will be helpful to note that the solution of (2.14), subject to the initial value for $J_i(0)$ given in (2.19), is

$$J_i(t) = \int_{t-\tau}^{t} b(A_s(\xi)) \left\{ \int_{\xi}^{t} \beta_j m_i(\eta) e^{-d_{ij}(t-\eta)} e^{-\int_{\xi}^{\eta} [d_{sj} + \beta_j m_i(v)]\, dv} d\eta \right\} d\xi, \tag{2.21}$$

which is nonnegative if $m_i(t)$ is nonnegative. Therefore, it suffices to prove nonnegativity of $A_i(t)$ and $m_i(t)$. These two functions can be viewed as the solution $(A_i(t), m_i(t))$ of the system of differential equations consisting of (2.13) and

$$\begin{aligned} \frac{dm_i(t)}{dt} &= -d_m m_i(t) + \beta_m (m_T^* - m_i(t)) \\ &\times \left(\int_{t-\tau}^{t} b(A_s(\xi)) \left\{ \int_{\xi}^{t} \beta_j m_i(\eta) e^{-d_{ij}(t-\eta)} e^{-\int_{\xi}^{\eta} [d_{sj} + \beta_j m_i(v)]\, dv} d\eta \right\} d\xi + \alpha A_i(t) \right) \end{aligned} \tag{2.22}$$

for $t > 0$, with initial data taken from (2.19), but with $A_s(t)$ thought of simply as some prescribed nonnegative function. Recalling that $m_i(t) \le m_T^*$, we now note that, even though this system does not satisfy a quasi monotonicity condition, Theorem 2.1 of Smith [23, p. 81] is applicable and gives us the nonnegativity of $A_i(t)$ and $m_i(t)$ immediately. The proof of the nonnegativity of each component of the solution is then complete.

The boundedness of $A_s(t)$ is simple since, by (2.9),

$$\frac{d}{dt} A_s(t) \le b_{\sup} - d_{sa} A_s(t) - \beta_a m_i(t) A_s(t),$$

where $b_{\sup} = \sup_{A \ge 0} b(A) < \infty$. The boundedness of $A_i(t)$ follows from (2.13) and the boundedness of $m_i(t)$. The boundedness of $J_s(t)$ and $J_i(t)$ follows from (2.20) and (2.21) directly. This completes the proof.

2.2. Global convergence to disease-free state. In this section we shall prove a theorem giving sufficient conditions for the system to evolve to the disease-free state (i.e., conditions that ensure A_i, J_i, and m_i go to zero as $t \to \infty$). Since the differential equations (2.10) and (2.14) can be solved to give (2.20) and (2.21), respectively, it is sufficient to study the system consisting of (2.9), (2.13), and (2.22), with initial data taken from (2.19). These equations form a closed system for $A_s(t)$, $A_i(t)$, and $m_i(t)$. Our aim will be to establish, using these three equations, a differential inequality for the variable $m_i(t)$ only, and to use this to find conditions which ensure that $m_i(t) \to 0$ as $t \to \infty$. Note that if $m_i(t) \to 0$, then from (2.21) it follows immediately that $J_i(t) \to 0$ and, furthermore, (2.13) then becomes an asymptotically autonomous ODE, from which it is easily seen that $A_i(t)$ tends to zero.

We will make certain assumptions concerning the birth rate function $b(\cdot)$ for hosts. These assumptions are

$$\left.\begin{array}{l} b(0)=0,\ b(A)>0 \text{ when } A>0,\ b_{\sup}:=\sup_{A\geq 0} b(A)<\infty, \text{ there exists} \\ A_s^*>0 \text{ such that } e^{-d_{sj}\tau}b(A)>d_{sa}A \text{ when } A<A_s^* \text{ and } e^{-d_{sj}\tau}b(A)< \\ d_{sa}A \text{ when } A>A_s^*. \end{array}\right\} \tag{2.23}$$

These assumptions are not the same as those for the birth rate function $B(\cdot)$ for mosquitoes (assumptions (2.17)); note in particular that we do not require $b(\cdot)$ to be monotone.

The reader will realize that the quantity A_s^* in (2.23) is, in fact, a nonzero equilibrium value for $A_s(t)$ in the case when the disease is absent. Assumptions (2.23) are geared towards ensuring that the population $A_s(t)$ of adult susceptible hosts does not go to zero even without the disease; otherwise the model is not interesting. This is important because if $e^{-d_{sj}\tau}b(A)<d_{sa}A$ for all $A>0$ (which means that, in the absence of the disease, adult recruitment of susceptible hosts is insufficient to offset natural death of adult susceptible hosts), then it is natural to expect that $A_s(t)\to 0$ even without the disease, and this can be mathematically shown to be the case, using (2.9).

We will prove the following theorem. Assumption (2.17) is needed to ensure the existence of m_T^*. We shall need the functions a_1 and a_0 defined by

$$\begin{aligned} a_1(\epsilon) &= d_m d_{ia}+d_m d_{ij}+d_{ia}d_{ij} \\ &\quad -\frac{\beta_m m_T^* b_{\sup}\beta_j}{d_{sj}}-\beta_m m_T^*\alpha\beta_a\left(\frac{b_{\sup}e^{-d_{sj}\tau}}{d_{sa}}+\epsilon\right) \\ &\quad -e^{-d_{sj}\tau}\left(\frac{1-e^{-\tau(d_{ij}-d_m-d_{sj})}}{d_{ij}-d_m-d_{sj}}\right)\beta_m m_T^*\alpha\beta_j b_{\sup} \end{aligned} \tag{2.24}$$

and

$$\begin{aligned} a_0(\epsilon) &= d_m d_{ia}d_{ij}-\frac{d_{ia}\beta_m m_T^* b_{\sup}\beta_j}{d_{sj}}-d_{ij}\beta_m m_T^*\alpha\beta_a\left(\frac{b_{\sup}e^{-d_{sj}\tau}}{d_{sa}}+\epsilon\right) \\ &\quad -d_{ij}e^{-d_{sj}\tau}\left(\frac{1-e^{-\tau(d_{ij}-d_m-d_{sj})}}{d_{ij}-d_m-d_{sj}}\right)\beta_m m_T^*\alpha\beta_j b_{\sup}. \end{aligned} \tag{2.25}$$

THEOREM 2.2. *Let* (2.17) *and* (2.23) *hold, and let* $A_s(t)$, $A_i(t)$, *and* $m_i(t)$ *satisfy* (2.9), (2.13), *and* (2.22), *with initial data taken from* (2.19). *Assume further that*

$$a_1(0)>0, \quad a_0(0)>0, \quad \textit{and} \quad (d_m+d_{ia}+d_{ij})a_1(0)>a_0(0), \tag{2.26}$$

where the functions a_1, a_0 *are defined by* (2.24) *and* (2.25). *Then* $(A_i(t),m_i(t))\to(0,0)$ *as* $t\to\infty$.

Remark. It is not hard to check that (2.26) can be satisfied for some parameter values. It is satisfied, for example, when the contact rates β_a, β_j, and β_m are sufficiently small, or when the mosquito capacity m_T^* is sufficiently small. These are situations in which we intuitively expect the theorem to hold. As such, an obvious control measure for achieving disease eradication is to reduce the mosquito capacity. Reducing β_m is an alternative approach.

Proof of Theorem 2.2. For the reasons explained above, we may concentrate on showing that $m_i(t)\to 0$ as $t\to\infty$. From positivity of solutions, we find from (2.9)

that

$$\begin{aligned}\frac{dA_s}{dt} &\le b(A_s(t-\tau))e^{-d_{sj}\tau} - d_{sa}A_s(t)\\ &\le b_{\sup}e^{-d_{sj}\tau} - d_{sa}A_s(t).\end{aligned}$$

Hence

$$\limsup_{t\to\infty} A_s(t) \le \frac{b_{\sup}e^{-d_{sj}\tau}}{d_{sa}}.$$

By hypothesis (2.26) and by a continuity argument we may choose $\epsilon > 0$ sufficiently small that

$$a_1(\epsilon) > 0, \quad a_0(\epsilon) > 0, \quad \text{and} \quad (d_m + d_{ia} + d_{ij})a_1(\epsilon) > a_0(\epsilon). \tag{2.27}$$

There exists $T_1 > 0$ such that, for $t \ge T_1$,

$$A_s(t) \le \frac{b_{\sup}e^{-d_{sj}\tau}}{d_{sa}} + \epsilon.$$

Using this estimate in (2.13), we find that, for $t \ge T_1$,

$$\begin{aligned}\frac{dA_i(t)}{dt} &\le -d_{ia}A_i(t) + \beta_a m_i(t)\left(\frac{b_{\sup}e^{-d_{sj}\tau}}{d_{sa}} + \epsilon\right)\\ &+ \beta_j b_{\sup}\int_{t-\tau}^{t} m_i(\xi)e^{-d_{ij}(t-\xi)}\exp\left(-\int_{t-\tau}^{\xi}(d_{sj} + \beta_j m_i(v))\,dv\right)d\xi.\end{aligned} \tag{2.28}$$

Solving this differential inequality and ignoring a transient term involving $A_i(0)$, we find that

$$\begin{aligned}A_i(t) &\le \beta_a\left(\frac{b_{\sup}e^{-d_{sj}\tau}}{d_{sa}} + \epsilon\right)\int_0^t e^{-d_{ia}(t-\psi)}m_i(\psi)\,d\psi\\ &+ \beta_j b_{\sup}\int_0^t e^{-d_{ia}(t-\psi)}\int_{\psi-\tau}^{\psi} m_i(\xi)e^{-d_{ij}(\psi-\xi)}\exp\left(-\int_{\psi-\tau}^{\xi}(d_{sj} + \beta_j m_i(v))\,dv\right)d\xi\,d\psi.\end{aligned} \tag{2.29}$$

We shall use this estimate for $A_i(t)$ to obtain a differential inequality for $m_i(t)$ as follows. From (2.22), and using positivity of $m_i(t)$ and the bound on $b(\cdot)$,

$$\begin{aligned}\frac{dm_i(t)}{dt} &\le -d_m m_i(t) + \beta_m m_T^*\\ &\times\left(b_{\sup}\int_{t-\tau}^{t}\int_{\xi}^{t}\beta_j m_i(\eta)e^{-d_{ij}(t-\eta)}e^{-\int_{\xi}^{\eta}[d_{sj}+\beta_j m_i(v)]\,dv}d\eta\,d\xi + \alpha A_i(t)\right),\end{aligned}$$

so that, from (2.29),

$$\begin{aligned}
\frac{dm_i(t)}{dt} &\le -d_m m_i(t) \\
&+ \beta_m m_T^* b_{\sup} \int_{t-\tau}^{t} \int_{\xi}^{t} \beta_j m_i(\eta) e^{-d_{ij}(t-\eta)} e^{-\int_{\xi}^{\eta} [d_{sj}+\beta_j m_i(v)]\, dv} d\eta\, d\xi \\
&+ \beta_m m_T^* \alpha \beta_a \left(\frac{b_{\sup} e^{-d_{sj}\tau}}{d_{sa}} + \epsilon \right) \int_0^t e^{-d_{ia}(t-\psi)} m_i(\psi)\, d\psi \\
&+ \beta_m m_T^* \alpha \beta_j b_{\sup} \int_0^t e^{-d_{ia}(t-\psi)} \int_{\psi-\tau}^{\psi} m_i(\xi) e^{-d_{ij}(\psi-\xi)} \\
&\qquad \times \exp\left(- \int_{\psi-\tau}^{\xi} (d_{sj} + \beta_j m_i(v))\, dv \right) d\xi\, d\psi.
\end{aligned}$$

From this it is easy to see, using the positivity of $m_i(t)$, that $m_i(t)$ also obeys the following simpler linear differential inequality:

$$\begin{aligned}
\frac{dm_i(t)}{dt} &\le -d_m m_i(t) \\
&+ \beta_m m_T^* b_{\sup} \int_{t-\tau}^{t} \int_{\xi}^{t} \beta_j m_i(\eta) e^{-d_{ij}(t-\eta)} e^{-d_{sj}(\eta-\xi)} d\eta\, d\xi \\
&+ \beta_m m_T^* \alpha \beta_a \left(\frac{b_{\sup} e^{-d_{sj}\tau}}{d_{sa}} + \epsilon \right) \int_0^t e^{-d_{ia}(t-\psi)} m_i(\psi)\, d\psi \\
&+ \beta_m m_T^* \alpha \beta_j b_{\sup} \int_0^t e^{-d_{ia}(t-\psi)} \int_{\psi-\tau}^{\psi} m_i(\xi) e^{-d_{ij}(\psi-\xi)} e^{-d_{sj}(\xi-\psi+\tau)} d\xi\, d\psi.
\end{aligned} \tag{2.30}$$

To make progress we need to estimate some of these integrals. If we change the order of integration in the first double integral of (2.30), we reach the following estimate:

$$\begin{aligned}
&\int_{t-\tau}^{t} \int_{\xi}^{t} \beta_j m_i(\eta) e^{-d_{ij}(t-\eta)} e^{-d_{sj}(\eta-\xi)} d\eta\, d\xi \\
&= \int_{t-\tau}^{t} \int_{t-\tau}^{\eta} \beta_j m_i(\eta) e^{-d_{ij}(t-\eta)} e^{-d_{sj}(\eta-\xi)} d\xi\, d\eta \\
&\le \frac{\beta_j}{d_{sj}} \int_{t-\tau}^{t} m_i(\eta) e^{-d_{ij}(t-\eta)} d\eta \\
&\le \frac{\beta_j}{d_{sj}} \int_{0}^{t} m_i(\eta) e^{-d_{ij}(t-\eta)} d\eta,
\end{aligned} \tag{2.31}$$

assuming $t > \tau$.

From (2.18) and Proposition 2.1 we have

$$\frac{dm_i(t)}{dt} \ge -d_m m_i(t).$$

Integrating from ξ to ψ gives

$$m_i(\xi) \le m_i(\psi) e^{d_m(\psi-\xi)}, \qquad \xi \le \psi.$$

Using this and (2.31), we obtain

$$\begin{aligned}\frac{dm_i(t)}{dt} &\le -d_m m_i(t) + \frac{\beta_m m_T^* b_{\sup}\beta_j}{d_{sj}} \int_0^t m_i(\eta) e^{-d_{ij}(t-\eta)}\, d\eta \\ &+ \beta_m m_T^* \alpha\beta_a \left(\frac{b_{\sup} e^{-d_{sj}\tau}}{d_{sa}} + \epsilon\right) \int_0^t e^{-d_{ia}(t-\psi)} m_i(\psi)\, d\psi \\ &+ \beta_m m_T^* \alpha\beta_j b_{\sup} e^{-d_{sj}\tau} \left(\frac{1 - e^{-\tau(d_{ij}-d_m-d_{sj})}}{d_{ij}-d_m-d_{sj}}\right) \int_0^t e^{-d_{ia}(t-\psi)} m_i(\psi)\, d\psi.\end{aligned} \tag{2.32}$$

By the theory of monotone systems [23], $m_i(t) \le M_i(t)$, where $M_i(t)$ is the solution of the differential equation obtained from (2.32) by replacing $\le$ by $=$, subject to the same initial data as that for m_i. Applying to this differential equation the Laplace transform, letting p be the transform variable and $\bar{M}_i(p)$ denote the Laplace transform of $M_i(t)$, we find after some algebra that

$$\bar{M}_i(p)\,\Lambda(p) = m_i(0)(p + d_{ia})(p + d_{ij}), \tag{2.33}$$

where

$$\Lambda(p) = p^3 + (d_m + d_{ia} + d_{ij})p^2 + a_1(\epsilon)p + a_0(\epsilon) \tag{2.34}$$

with $a_1(\epsilon)$ and $a_0(\epsilon)$ given by (2.24) and (2.25). Recall that the small number $\epsilon > 0$ has been chosen such that (2.27) holds. This fact, together with the Routh Hurwitz criteria, implies that all the roots of the cubic equation $\Lambda(p) = 0$ satisfy $\operatorname{Re} p < 0$, and so the same is true of all singularities of $\bar{M}_i(p)$. By the inversion formula for Laplace transforms, $M_i(t) \to 0$ as $t \to \infty$. Since $0 \le m_i(t) \le M_i(t)$, $m_i(t) \to 0$ as $t \to \infty$. By (2.13), $A_i(t) \to 0$ as $t \to \infty$. The proof of Theorem 2.2 is complete.

2.3. Local stability of disease-free equilibrium. If (2.23) holds, then the model (2.9), (2.10), (2.13), (2.14), and (2.18) has a disease-free equilibrium (DFE), obtained by substituting $J_i = 0$, $A_i = 0$, and $m_i = 0$ into the right-hand sides of those equations and setting them to zero, given by

$$E_0 = (A_s^*, J_s^*, 0, 0, 0), \tag{2.35}$$

where $A_s^* > 0$ and $J_s^* > 0$ are given by

$$\begin{cases} b(A_s^*)e^{-d_{sj}\tau} - d_{sa}A_s^* = 0, \\ J_s^* = \dfrac{b(A_s^*)}{d_{sj}}(1 - e^{-d_{sj}\tau}). \end{cases} \tag{2.36}$$

The previous section of this paper presented sufficient conditions for disease eradication (Theorem 2.2). In this section we investigate the linear stability of the DFE E_0 to gain further insight, and we shall present a condition (namely, condition (2.38) below) which is both necessary and sufficient for E_0 to be linearly stable. Though we do not establish disease eradication *globally* under this particular condition, it is clearly the weakest possible condition for disease eradication.

We first require the following simple preliminary result, which provides a condition for the linear stability of the DFE E_0 to perturbations in which the disease remains absent.

LEMMA 2.3. *Let* (2.23) *hold. Then* (A_s^*, J_s^*)*, given by* (2.36)*, is a locally asymptotically stable equilibrium of the subsystem*

$$\begin{cases} \dfrac{d\bar{J}_s(t)}{dt} = b(\bar{A}_s(t)) - b(\bar{A}_s(t-\tau))e^{-d_{sj}\tau} - d_{sj}\bar{J}_s(t), \\ \dfrac{d\bar{A}_s(t)}{dt} = b(\bar{A}_s(t-\tau))e^{-d_{sj}\tau} - d_{sa}\bar{A}_s(t) \end{cases} \tag{2.37}$$

if $d_{sa} > |b'(A_s^*)|e^{-d_{sj}\tau}$.

Proof. Obviously, (A_s^*, J_s^*) is an equilibrium of system (2.37). The linearization of (2.37) at this equilibrium has solutions of the form $\exp(\lambda t)$ whenever λ satisfies

$$\begin{vmatrix} -\lambda - d_{sj} & b'(A_s^*)(1 - e^{-(\lambda+d_{sj})\tau}) \\ 0 & -\lambda - d_{sa} + b'(A_s^*)e^{-(\lambda+d_{sj})\tau} \end{vmatrix} = 0.$$

Therefore, (A_s^*, J_s^*) is a locally stable solution of (2.37) if and only if all the roots λ of $-\lambda - d_{sa} + b'(A_s^*)e^{-(\lambda+d_{sj})\tau} = 0$ have negative real part. It is straightforward to show that this is the case if $d_{sa} > |b'(A_s^*)|e^{-d_{sj}\tau}$. The proof is complete.

Our main result of this section is the following theorem, which gives a necessary and sufficient condition for the linear stability of the disease-free state.

THEOREM 2.4. *Let* (2.17) *and the hypotheses of Lemma* 2.3 *hold, and assume additionally that*

$$\begin{aligned} d_m > \beta_m m_T^* \Bigg\{ & \frac{b(A_s^*)\beta_j}{d_{ij} - d_{sj}} \left[\frac{1 - e^{-d_{sj}\tau}}{d_{sj}} - \frac{(1 - e^{-d_{ij}\tau})}{d_{ij}} \right] \\ & + \frac{\alpha}{d_{ia}} \left[\beta_a A_s^* + \beta_j b(A_s^*) e^{-d_{sj}\tau} \frac{(1 - e^{-(d_{ij}-d_{sj})\tau})}{d_{ij} - d_{sj}} \right] \Bigg\}. \end{aligned} \tag{2.38}$$

Then the disease-free equilibrium E_0 *given by* (2.35) *is linearly asymptotically stable as a solution of the full model* (2.9), (2.10), (2.13), (2.14), (2.18).

Remark. The hypotheses of Theorem 2.4 are the weakest possible hypotheses that can guarantee the stated result. Recall from earlier remarks that if (2.17) or (2.23) is violated, then the mosquito or host population is doomed, irrespective of the disease. If the two sides of (2.38) are equal, then zero is an eigenvalue of the characteristic equation of the linearization about E_0 ((2.40) below), signaling the bifurcation of an endemic equilibrium. As will be shown numerically at the end of this section, a Hopf bifurcation of periodic solutions may further bifurcate from this endemic equilibrium. It remains a challenging problem to determine whether the hypotheses of Theorem 2.4 are sufficient to guarantee the global stability of E_0.

Proof. We aim for a linear equation in m_i only. Making use of the expression (2.21) for $J_i(t)$, solving for $A_i(t)$ the differential equation (2.13) on the interval $(-\infty, t)$, and then linearizing about $m_i = 0$, we obtain

$$\begin{aligned} \frac{dm_i(t)}{dt} &= -d_m m_i(t) \\ &+ \beta_m m_T^* b(A_s^*) \int_{t-\tau}^{t} \int_{\xi}^{t} \beta_j m_i(\eta) e^{-d_{ij}(t-\eta)} e^{-d_{sj}(\eta-\xi)} d\eta \, d\xi \\ &+ \beta_m m_T^* \alpha \beta_a A_s^* \int_{-\infty}^{t} e^{-d_{ia}(t-\psi)} m_i(\psi) \, d\psi \\ &+ \beta_m m_T^* \alpha \beta_j b(A_s^*) \int_{-\infty}^{t} e^{-d_{ia}(t-\psi)} \int_{\psi-\tau}^{\psi} m_i(\xi) e^{-d_{ij}(\psi-\xi)} e^{-d_{sj}(\xi-\psi+\tau)} d\xi \, d\psi. \end{aligned} \tag{2.39}$$

Solutions of the form $m_i(t) = e^{\lambda t}$ exist whenever λ satisfies

$$\lambda + d_m = \beta_m m_T^* \left\{ \frac{b(A_s^*)\beta_j}{\lambda + d_{ij} - d_{sj}} \left[\frac{1 - e^{-d_{sj}\tau}}{d_{sj}} - \frac{(1 - e^{-(\lambda + d_{ij})\tau})}{\lambda + d_{ij}} \right] + \frac{\alpha}{\lambda + d_{ia}} \left[\beta_a A_s^* + \beta_j b(A_s^*) e^{-d_{sj}\tau} \frac{(1 - e^{-(\lambda + d_{ij} - d_{sj})\tau})}{\lambda + d_{ij} - d_{sj}} \right] \right\}. \tag{2.40}$$

The structure of the linear equation (2.39) is such that the linear stability of its zero solution can be determined by considering only the real roots of the characteristic equation (2.40). This follows from Theorem 5.1 of Smith [23, p. 92] and Theorem 3.2 of Wu [28]. Our aim is therefore to show that, under condition (2.38), equation (2.40) does not have any nonnegative real roots. From simple graphical arguments, we see that it is sufficient to show that the right-hand side of (2.40) is monotonically decreasing as a function of $\lambda \in \mathbf{R}$ for $\lambda \geq 0$.

Let $F(\lambda)$ denote the right-hand side of (2.40), excluding the $\beta_m m_T^*$ factor. It is sufficient to show that $F'(\lambda) < 0$ for all $\lambda \geq 0$. Now

$$\begin{aligned} F(\lambda) &= \frac{\tau b(A_s^*)\beta_j}{\lambda + d_{ij} - d_{sj}} \left[f(d_{sj}\tau) - f((\lambda + d_{ij})\tau) \right] \\ &\quad + \frac{\alpha}{\lambda + d_{ia}} \left[\beta_a A_s^* + \tau \beta_j b(A_s^*) e^{-d_{sj}\tau} f((\lambda + d_{ij} - d_{sj})\tau) \right] \\ &=: F_1(\lambda) + \alpha F_2(\lambda), \end{aligned} \tag{2.41}$$

in which the function f is defined by

$$f(x) = \frac{1 - e^{-x}}{x}.$$

It is reasonably straightforward to see that f satisfies

$$f(x) > 0, \qquad f'(x) < 0, \qquad f''(x) > 0 \qquad \text{for all } x \in \mathbf{R}. \tag{2.42}$$

Indeed, (2.42) follows from the following inequalities:

$$(x + 1)e^{-x} \leq 1, \qquad x \in \mathbf{R},$$

and

$$\begin{aligned} e^{-x}(x^2 + 2x + 2) &< 2, \qquad x > 0, \\ e^{-x}(x^2 + 2x + 2) &> 2, \qquad x < 0. \end{aligned}$$

It is sufficient to show that $F_1'(\lambda) < 0$ and $F_2'(\lambda) < 0$ for all $\lambda \geq 0$, with the $F_i(\lambda)$ defined by (2.41). It is very easily seen, using (2.42), that $F_2'(\lambda) < 0$ for all $\lambda \geq 0$ (in fact for all $\lambda > -d_{ia}$). To show that $F_1'(\lambda) < 0$, introduce $\xi = \lambda + d_{ij} - d_{sj}$ and the function $g(\xi)$ defined by

$$g(\xi) = \frac{1}{\xi}(f(d_{sj}\tau) - f((\xi + d_{sj})\tau));$$

then it is more than sufficient to show that $g'(\xi) < 0$ for all $\xi \in \mathbf{R}$. However,

$$\begin{aligned} g'(\xi) &= \frac{1}{\xi^2}[f((\xi + d_{sj})\tau) - f(d_{sj}\tau)] - \frac{\tau}{\xi} f'((\xi + d_{sj})\tau) \\ &= \frac{\tau}{\xi} \left[f'((\theta\xi + d_{sj})\tau) - f'((\xi + d_{sj})\tau) \right] \\ &= (\theta - 1)\tau^2 f''(c) \end{aligned}$$

for some numbers $\theta \in (0,1)$ and $c \in \mathbf{R}$ which arise from applications of the mean value theorem. Since $f''(c) > 0$ by (2.42) it follows that $g'(\xi) < 0$, as desired. Thus, (2.40) does not have any nonnegative real roots.

With $m_i(t) \to 0$ it follows from (2.21) and (2.13) that $J_i(t) \to 0$ and $A_i(t) \to 0$. Then the hypotheses of Lemma 2.3, which are embodied within those of Theorem 2.4, imply that $A_s(t) \to A_s^*$ and $J_s(t) \to J_s^*$ in the linearized equations. The proof of Theorem 2.4 is complete.

2.4. Numerical simulations. Let us introduce the new variable W_1 defined by

$$W_1(t) = \int_{t-\tau}^{t} m_i(\xi) e^{-d_{ij}(t-\xi)} \exp\left(- \int_{t-\tau}^{\xi} (d_{sj} + \beta_j m_i(v))\, dv \right) d\xi,$$

so that we can rewrite the model (2.9), (2.10), (2.13), (2.14), and (2.18) in the form

(2.43)

$$\begin{aligned}
\frac{dJ_s(t)}{dt} &= b(A_s(t)) - b(A_s(t-\tau)) e^{-d_{sj}\tau} e^{-\int_{t-\tau}^{t} \beta_j m_i(v) dv} - d_{sj} J_s(t) - \beta_j m_i(t) J_s(t), \\
\frac{dA_s(t)}{dt} &= b(A_s(t-\tau)) e^{-d_{sj}\tau} e^{-\int_{t-\tau}^{t} \beta_j m_i(v) dv} - d_{sa} A_s(t) - \beta_a m_i(t) A_s(t), \\
\frac{dJ_i(t)}{dt} &= -d_{ij} J_i(t) + \beta_j m_i(t) J_s(t) - \beta_j b(A_s(t-\tau)) W_1(t), \\
\frac{dA_i(t)}{dt} &= -d_{ia} A_i(t) + \beta_a m_i(t) A_s(t) + \beta_j b(A_s(t-\tau)) W_1(t), \\
\frac{dm_i(t)}{dt} &= -d_m m_i(t) + (m_T(t) - m_i(t)) \beta_m (J_i(t) + \alpha A_i(t)), \\
\frac{dW_1(t)}{dt} &= W_1(t)(d_{sj} - d_{ij} + \beta_j m_i(t-\tau)) + m_i(t) e^{-d_{sj}\tau} e^{-\int_{t-\tau}^{t} \beta_j m_i(v) dv} \\
&\qquad - e^{-d_{ij}\tau} m_i(t-\tau).
\end{aligned}$$

The DFE of model (2.43) is the equilibrium in which

$$(J_s, A_s, J_i, A_i, m_i, W_1) \equiv (J_s^*, A_s^*, 0, 0, 0, 0).$$

In the simulations reported below, we take the birth function of mosquitoes and that of birds as

$$B(m_T) = b_m m_T e^{-a_m m_T}, \qquad b(A_s) = b_b A_s e^{-a_b A_s}, \tag{2.44}$$

respectively. These forms for the birth function have been used, for example, in the well-studied Nicholson blowflies equation [9].

Various parameter values are given in Table 1, taken from [18, 19, 3, 26] with reference to West Nile virus. We took the initial conditions to be

$$A_s(t) = 500, \qquad M_I(t) = 0$$

for $t \in [-\tau, 0]$ and $A_i(0) = 2$. This, together with the matching condition (2.19), gives $J_s(0) = 16700$ and $J_i(0) = 0$.

In Figure 1 the condition (2.38) is satisfied, and the infected populations go to zero. However, as we increase the contact rates, the condition (2.38) fails, and the disease sustains in the bird and mosquito population, as shown in Figure 2. If we continue to increase the contact rates, we eventually find oscillatory behaviors, as shown in Figure 3, suggesting the possibility of a Hopf bifurcation to periodic solutions.

TABLE 1
Meaning of parameters.

Parameter	Meaning of the parameter	Value
b_b	Maximum per capita daily bird production rate	0.5
$1/a_b$	Size of bird population at which the number of newborn birds is maximized	1000
b_m	Maximum per capita daily mosquito egg production rate	5
$1/a_m$	Size of mosquito population at which egg laying is maximized	10000
d_{sj}	Mortality rate of uninfected juveniles (per day)	0.005
d_{ij}	Mortality rate of infected juveniles (per day)	0.05
d_{sa}	Mortality rate of uninfected adults (per day)	0.0025
d_{ia}	Mortality rate of infected adults (per day)	0.015
d_m	Mortality rate of mosquito (per day)	0.05
β_j	Contact rate between uninfected juvenile and infected mosquito	Variable
β_a	Contact rate between uninfected adult and infected mosquito	Variable
β_m	Contact rate between uninfected mosquito and infected juvenile	Variable
$\alpha\beta_m$	Contact rate between uninfected mosquito and infected juvenile	Variable
τ	Duration of more vulnerable period of bird (day)	160
σ	Maturation time of mosquito (day)	10
d_l	Mortality rate of larva mosquito (per day)	0.1

3. Spatial speed of spread. In this section we will derive a reaction-diffusion analogue of the system we have studied thus far, and we will use this system to formally estimate the speed at which the disease epidemic would spread through space. For simplicity, diffusion will be modeled using Fick's law. Equations (2.1) and (2.2) become

$$\frac{\partial s}{\partial t} + \frac{\partial s}{\partial a} = D_s(a)\frac{\partial^2 s}{\partial x^2} - d_s(a)s(t,a,x) - \beta(a)s(t,a,x)m_i(t,x) \tag{3.1}$$

and

$$\frac{\partial i}{\partial t} + \frac{\partial i}{\partial a} = D_i(a)\frac{\partial^2 i}{\partial x^2} - d_i(a)i(t,a,x) + \beta(a)s(t,a,x)m_i(t,x) \tag{3.2}$$

on a one-dimensional spatial domain $x \in (-\infty, \infty)$, where $m_i(t,x)$ is the number of infected adult mosquitoes at (t,x) satisfying a reaction-diffusion equation mentioned later. We shall assume that the age-dependent diffusivities $D_s(a)$, $D_i(a)$ have the special form

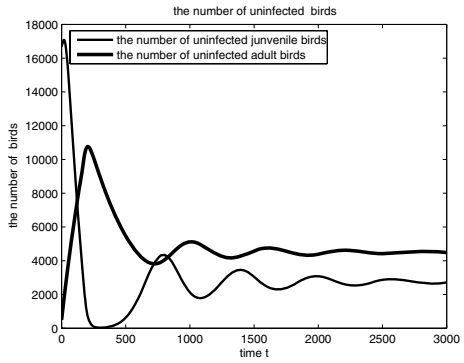
$$D_s(a) = \begin{cases} D_{sj}, & a < \tau, \\ D_{sa}, & a > \tau, \end{cases} \qquad D_i(a) = \begin{cases} D_{ij}, & a < \tau, \\ D_{ia}, & a > \tau. \end{cases} \tag{3.3}$$

With this choice for the diffusivities, our concern for the moment is with deriving a system of four reaction-diffusion equations for the quantities

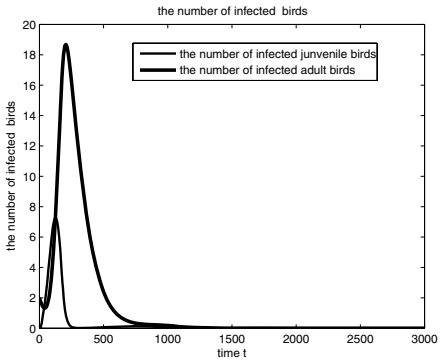
$$\begin{aligned} A_s(t,x) &= \int_\tau^\infty s(t,a,x)\,da, \qquad A_i(t,x) = \int_\tau^\infty i(t,a,x)\,da, \\ J_s(t,x) &= \int_0^\tau s(t,a,x)\,da, \qquad J_i(t,x) = \int_0^\tau i(t,a,x)\,da, \end{aligned} \tag{3.4}$$

which are analogous to the total numbers in (2.5). Differentiating the expression for $A_s(t,x)$ and using (3.1) and (3.3) gives

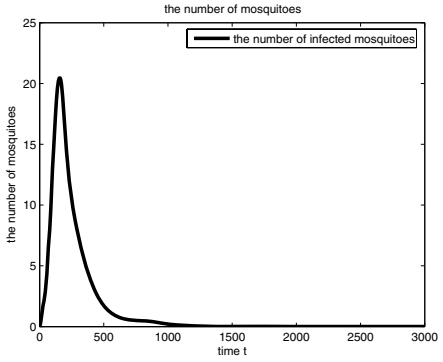
$$\frac{\partial A_s}{\partial t} = s(t,\tau,x) + D_{sa}\frac{\partial^2 A_s}{\partial x^2} - d_{sa}A_s - \beta_a m_i(t,x)A_s,$$



(a) Uninfected birds



(b) Infected birds



(c) Infected mosquitoes

FIG. 1. *Parameter values are* $\beta_j = 3.5 \times 10^{-6}$, $\beta_a = 1.5 \times 10^{-6}$, $\beta_m = 3.25 \times 10^{-6}$, $\alpha\beta_m = 7.5 \times 10^{-7}$, *and other parameters have the values shown in Table* 1. *In this case* d_m *is larger than the right-hand side of* (2.38), *which equals* 0.0343. *The DFE is stable.*

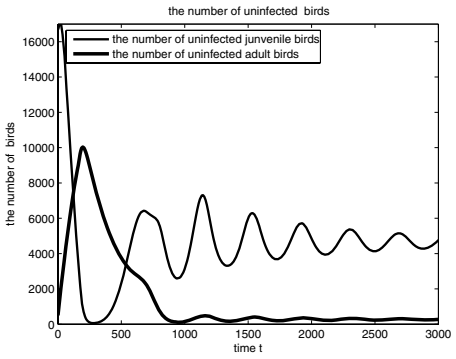
and we need to find $s(t, \tau, x)$. Set

$$s_\xi(a, x) = s(\xi + a, a, x).$$

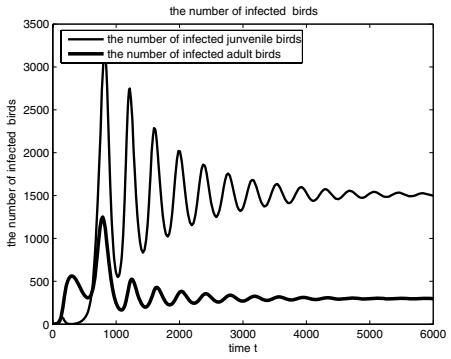
Differentiating with respect to a and using (3.1) gives

$$\frac{\partial s_\xi}{\partial a} = D_s(a)\frac{\partial^2 s_\xi}{\partial x^2} - d_s(a)s_\xi(a, x) - \beta(a)s_\xi(a, x)m_i(\xi + a, x). \tag{3.5}$$

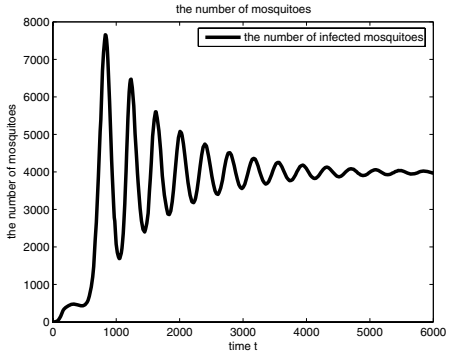
We would like to solve (3.5) exactly for $s_\xi(a, x)$, but this is impossible because the equation is nonautonomous. (The variable m_i satisfies a separate nonlinear partial differential equation, which appears below.) Our aim, however, will be to study the spatial spread of the disease by looking for traveling wave solutions which move leftwards through the spatial domain $x \in (-\infty, \infty)$, and which constitute a connection between the disease-free state and an endemic state. The PDEs we derive for the



(a) Uninfected birds



(b) Infected birds



(c) Infected mosquitoes

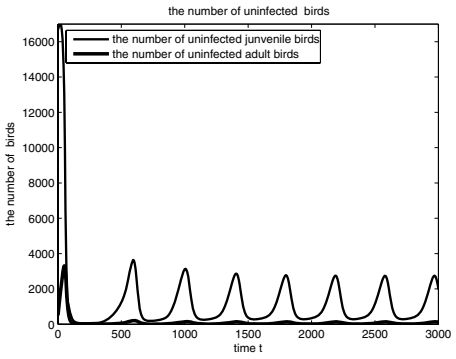
FIG. 2. *Parameter values are* $\beta_j = 4.0883 \times 10^{-6}$, $\beta_a = 2.3705 \times 10^{-6}$, $\beta_m = 3.7962 \times 10^{-6}$, $\alpha\beta_m = 1.1853 \times 10^{-6}$, *and other parameters have the values shown in Table* 1. *In this case* d_m *is less than the right-hand side of* (2.38), *which equals* 0.0613. *The DFE is unstable, and the solution evolves to an endemic equilibrium.*

variables (3.4), and for $m_i(t,x)$, will be studied only in the region far ahead of the advancing epidemic, i.e., as $x \to -\infty$, because we shall be assuming that the linearized equations in this region determine the speed of the epidemic wave. In the disease-free region $x \approx -\infty$, the variables $A_i(t,x)$, $J_i(t,x)$, and $m_i(t,x)$ are all close to zero. Thus, we solve (3.5) in the case when m_i is zero to find that in this case the solution subject to the first condition appearing below,

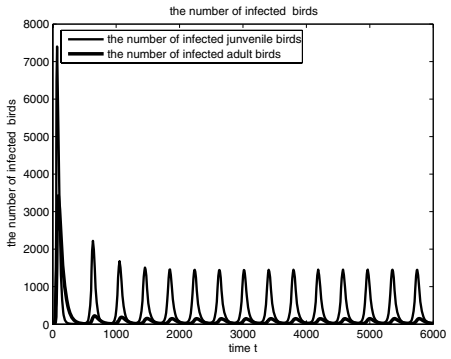
$$s(t,0,x) = b(A_s(t,x)), \qquad i(t,0,x) = 0 \tag{3.6}$$

(the analogue of (2.6)) is, for $a \le \tau$ and $\xi \ge 0$,

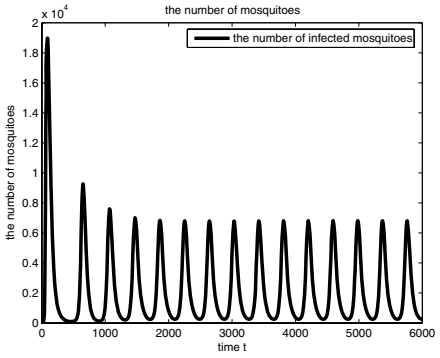
$$s_\xi(a,x) = s(\xi + a, a, x) = \int_{-\infty}^{\infty} \Gamma(D_{sj}a, x-y) b(A_s(\xi,y)) e^{-d_{sj}\tau}\, dy, \tag{3.7}$$



(a) Uninfected birds



(b) Infected birds



(c) Infected mosquitoes

FIG. 3. *Parameter values are* $\beta_j = 9.4030 \times 10^{-6}$, $\beta_a = 2.2388 \times 10^{-6}$, $\beta_m = 8.7313 \times 10^{-6}$, $\alpha\beta_m = 4.0299 \times 10^{-6}$, *and other parameters have the values shown in Table* 1. *In this case* d_m *is less than the right-hand side of* (2.38), *which equals* 0.2475. *The DFE is unstable, and the solution is oscillating.*

where

$$\Gamma(t,x) = \frac{1}{\sqrt{4\pi t}} e^{-x^2/4t}. \tag{3.8}$$

From (3.7) we find an expression for $s(t,\tau,x)$, and we deduce that for $t \geq \tau$ the PDE for $A_s(t,x)$ is

$$\begin{aligned} \frac{\partial A_s}{\partial t} &= \int_{-\infty}^{\infty} \Gamma(D_{sj}\tau, x-y) b(A_s(t-\tau,y)) e^{-d_{sj}\tau}\, dy \\ &\quad + D_{sa}\frac{\partial^2 A_s}{\partial x^2} - d_{sa}A_s(t,x) - \beta_a m_i(t,x) A_s(t,x), \end{aligned} \tag{3.9}$$

valid in the far left of the spatial domain $x \in (-\infty, \infty)$. Similarly, we obtain the following approximate equation for $J_s(t,x)$, also valid only in the far field $x \to -\infty$:

$$\begin{aligned}\frac{\partial J_s}{\partial t} &= b(A_s(t,x)) - \int_{-\infty}^{\infty} \Gamma(D_{sj}\tau, x-y) b(A_s(t-\tau,y)) e^{-d_{sj}\tau}\, dy \\ &\quad + D_{sj}\frac{\partial^2 J_s}{\partial x^2} - d_{sj} J_s(t,x) - \beta_j m_i(t,x) J_s(t,x).\end{aligned} \tag{3.10}$$

Next we shall derive the PDE for $A_i(t,x)$. Differentiating the expression for A_i in (3.4) and using (3.2) and (3.3) gives

$$\frac{\partial A_i}{\partial t} = i(t,\tau,x) + D_{ia}\frac{\partial^2 A_i}{\partial x^2} - d_{ia}A_i + \beta_a m_i(t,x) A_s,$$

and we need to find $i(t,\tau,x)$. Set

$$i_\xi(a,x) = i(\xi + a, a, x).$$

Since the calculation of $i(t,\tau,x)$ involves immature ages $a \in [0,\tau]$ only, from (3.2) we obtain

$$\frac{\partial i_\xi}{\partial a} = D_{ij}\frac{\partial^2 i_\xi}{\partial x^2} - d_{ij} i_\xi(a,x) + \beta_j m_i(\xi + a, x) s(\xi + a, a, x).$$

The solution of this equation satisfying the second condition in (3.6) is

$$i_\xi(a,x) = \beta_j \int_0^a e^{-d_{ij}(a-\zeta)} \int_{-\infty}^{\infty} \Gamma(D_{ij}(a-\zeta), x-y) m_i(\xi+\zeta, y) s(\xi+\zeta, \zeta, y)\, dy\, d\zeta,$$

where Γ is again given by (3.8). For $s(\xi+\zeta,\zeta,y)$ we use expression (3.7). Then, setting $a = \tau$ and $\xi = t - \tau$ in the above expression gives us $i(t,\tau,x)$, and thus we conclude that the evolution PDE for the variable $A_i(t,x)$ representing the number of adult infected hosts is, for $t \geq \tau$,

$$\begin{aligned}\frac{\partial A_i}{\partial t} &= D_{ia}\frac{\partial^2 A_i}{\partial x^2} - d_{ia}A_i(t,x) + \beta_a m_i(t,x) A_s(t,x) \\ &\quad + \beta_j \int_0^\tau e^{-d_{ij}(\tau-\zeta)} \int_{-\infty}^{\infty} \Gamma(D_{ij}(\tau-\zeta), x-y) m_i(t-\tau+\zeta, y) \\ &\quad \times \int_{-\infty}^{\infty} \Gamma(D_{sj}\zeta, y-\eta) b(A_s(t-\tau,\eta)) e^{-d_{sj}\zeta}\, d\eta\, dy\, d\zeta.\end{aligned} \tag{3.11}$$

This is again valid only in the far field $x \to -\infty$, since we have used expression (3.7). The last term in the right-hand side of (3.11) is the rate at which infected immatures become infected adults and has a similar interpretation to a term in the right-hand side of (2.13). This time the term involves additional integrals because of diffusion, but the reader may notice that in certain other respects the term in (3.11) is a little simpler than we might expect based on comparison with (2.13); this is due to the approximations we have made to derive (3.11) because of the restriction to the $x \approx -\infty$ zone. The interpretation of the term we are discussing is as follows. Each individual that reaches adulthood at point x at time t as an infected individual was born as a susceptible at time $t - \tau$ at some other point η. For an amount of time ζ that individual drifted around as a susceptible individual with diffusivity D_{sj} until

reaching a point y, where it became infected at time $t-\tau+\zeta$. For an amount of time $\tau-\zeta$, constituting the remainder of its childhood, it drifted around as an infected individual with diffusivity D_{ij} to reach point x at time t, where it becomes an adult. The two exponential factors represent the probability of surviving the susceptible and infected portions of childhood.

The PDE for $J_i(t,x)$ is derived similarly and turns out to be

$$\begin{aligned}\frac{\partial J_i}{\partial t} &= D_{ij}\frac{\partial^2 J_i}{\partial x^2} - d_{ij}J_i(t,x) + \beta_j m_i(t,x)J_s(t,x)\\ &\quad - \beta_j \int_0^\tau e^{-d_{ij}(\tau-\zeta)} \int_{-\infty}^{\infty} \Gamma(D_{ij}(\tau-\zeta), x-y) m_i(t-\tau+\zeta, y)\\ &\quad \times \int_{-\infty}^{\infty} \Gamma(D_{sj}\zeta, y-\eta) b(A_s(t-\tau,\eta)) e^{-d_{sj}\zeta}\, d\eta\, dy\, d\zeta.\end{aligned} \tag{3.12}$$

Finally we need a reaction-diffusion equation for the infected adult mosquitoes $m_i(t,x)$. We shall take

$$\frac{\partial m_i}{\partial t} = D_m\frac{\partial^2 m_i}{\partial x^2} - d_m m_i(t,x) + \beta_m(m_T^* - m_i(t,x))(J_i(t,x)+\alpha A_i(t,x)). \tag{3.13}$$

The system of PDEs to be solved thus consists of (3.9), (3.10), (3.11), (3.12), and (3.13). As explained previously, we shall look for solutions which constitute a leftward moving traveling wave-front and which invade what was formerly a disease-free zone; in other words, as $x \to -\infty$ we shall assume that the variables tend to the disease-free values in which A_i, J_i, and m_i are zero while $A_s^* > 0$ and $J_s^* > 0$ are given by (2.36), assuming that (2.23) holds. (If (2.23) does not hold, then the host population is eradicated even in the absence of the disease.)

We shall, in fact, look for a wave-front that constitutes a transition from the disease-free state to an endemic steady state, and so we need to be assured of the existence of an endemic state. The endemic state cannot be found explicitly, but fortunately we know the condition for its existence. This condition is the opposite of (2.38). Therefore, we assume in this section that

$$\begin{aligned}d_m < \beta_m m_T^* \Bigg\{ &\frac{b(A_s^*)\beta_j}{d_{ij}-d_{sj}}\left[\frac{1-e^{-d_{sj}\tau}}{d_{sj}} - \frac{(1-e^{-d_{ij}\tau})}{d_{ij}}\right]\\ &+ \frac{\alpha}{d_{ia}}\left[\beta_a A_s^* + \beta_j b(A_s^*)e^{-d_{sj}\tau}\frac{(1-e^{-(d_{ij}-d_{sj})\tau})}{d_{ij}-d_{sj}}\right]\Bigg\}.\end{aligned} \tag{3.14}$$

We linearize the equations for A_i, J_i, and m_i ((3.11), (3.12), and (3.13)) in the region $x \to -\infty$, where $A_s \to A_s^*$, $J_s \to J_s^*$, and the other variables approach zero. The linearized equations are then converted to traveling wave form by looking for solutions that are functions only of the variable $z = x + ct$ with $c \geq 0$. Then we look for nontrivial solutions of the linearized traveling wave equations of the form $(A_i, J_i, m_i) = (q_1, q_2, q_3)\exp(\lambda z)$. After a fair amount of algebra we find that the characteristic equation determining λ is

$$G_1(\lambda; c) = G_2(\lambda; c)G_3(\lambda; c), \tag{3.15}$$

where

$$\begin{aligned}G_1(\lambda;c) &= (D_{ia}\lambda^2 - d_{ia} - c\lambda)(D_{ij}\lambda^2 - d_{ij} - c\lambda)(D_m\lambda^2 - d_m - c\lambda)\\ &\quad - \beta_m m_T^*[\beta_j J_s^*(D_{ia}\lambda^2 - d_{ia} - c\lambda) + \alpha\beta_a A_s^*(D_{ij}\lambda^2 - d_{ij} - c\lambda)],\end{aligned} \tag{3.16}$$

$$G_2(\lambda;c) = \alpha(D_{ij}\lambda^2 - d_{ij} - c\lambda) - (D_{ia}\lambda^2 - d_{ia} - c\lambda), \tag{3.17}$$

and

$$G_3(\lambda;c) = \beta_m m_T^* \left(\frac{\beta_j b(A_s^*)(e^{-d_{sj}\tau} - e^{-d_{ij}\tau - \lambda c\tau + \lambda^2 D_{ij}\tau})}{d_{ij} - d_{sj} + \lambda c - \lambda^2 D_{ij}} \right). \tag{3.18}$$

Recall that A_s^* and J_s^* are given by (2.36) and that m_T^* is given by (2.17).

An epidemiologically feasible wave-front is one in which all the variables remain nonnegative as $x \to -\infty$ (as $z \to -\infty$ in the traveling wave variable formulation). The decay of A_i, J_i, and m_i to zero as $z \to -\infty$ must not be oscillatory. It is therefore necessary that there should exist at least one strictly positive real root λ of the characteristic equation (3.15) with the property that the corresponding eigenvector (q_1, q_2, q_3) points into the positive octant in $\mathbf{R}^3$. This actually happens only for c above some minimum value $c_{\min} > 0$. Define

$$c_{\min} = \inf\{c : \quad \exists \lambda \in (0, \tfrac{1}{2D_{ia}}(c + \sqrt{c^2 + 4d_{ia}D_{ia}})] \text{ satisfying (3.15)}\}. \tag{3.19}$$

The reason why the search for positive real roots λ of (3.15) is confined to the finite interval in (3.19) is that the eigenvector (q_1, q_2, q_3) corresponding to an eigenvalue λ exceeding $\frac{1}{2D_{ia}}(c + \sqrt{c^2 + 4d_{ia}D_{ia}})$ has q_1 and q_3 of opposite sign (implying that one of A_i or m_i is negative) so that such an eigenvalue corresponds to an infeasible solution. Note that the interval of λ in (3.19) is c dependent.

A calculation shows that, because of (3.14),

$$G_1(0;c) - G_2(0;c)G_3(0;c) > 0.$$

If for a fixed c one plots the graph of $G_1(\lambda;c) - G_2(\lambda;c)G_3(\lambda;c)$ against λ on the feasible domain $\lambda \in [0, \frac{1}{2D_{ia}}(c + \sqrt{c^2 + 4d_{ia}D_{ia}})]$, one finds that for a very small value of c the graph is always above the horizontal axis. The effect of increasing c is that a minimum begins to form within the feasible domain, and this minimum moves down and touches the horizontal axis at a critical c, the value $c_{\min}$ defined in (3.19) above. Figure 4 shows the critical situation for a particular set of parameter values shown in the caption, and for the two birth functions $b(\cdot)$ and $B(\cdot)$ chosen as in section 2.4. The value $c_{\min}$ can be found by numerically solving the simultaneous equations

$$G_1(\lambda;c) - G_2(\lambda;c)G_3(\lambda;c) = 0,$$
$$\frac{d}{d\lambda}[G_1(\lambda;c) - G_2(\lambda;c)G_3(\lambda;c)] = 0,$$

for c and λ with $c > 0$ and $\lambda \in (0, \frac{1}{2D_{ia}}(c + \sqrt{c^2 + 4d_{ia}D_{ia}})]$.

4. Discussion. The minimum speed of spread computed in the previous section according to the predictions of the linearized analysis was about 2.62 km/day, i.e., about 956 km/year. This is certainly roughly consistent with the speed at which West Nile virus has spread across the USA. The disease first emerged in New York in 1999 and had reached the West coast five years later. We should point out, however, that there is some uncertainty regarding the choice of parameter values, especially the diffusivities. We have availed ourselves of what data there is concerning the diffusivity of adult crows, but our choice of a value for the fledgling crows, which do not fly so well and may well spend some time on the ground (where they are, of course, vulnerable to predators such as cats) is purely our estimate. While the speed of spread does show a dependence on the diffusivities, we noted a lack of sensitivity to the values of

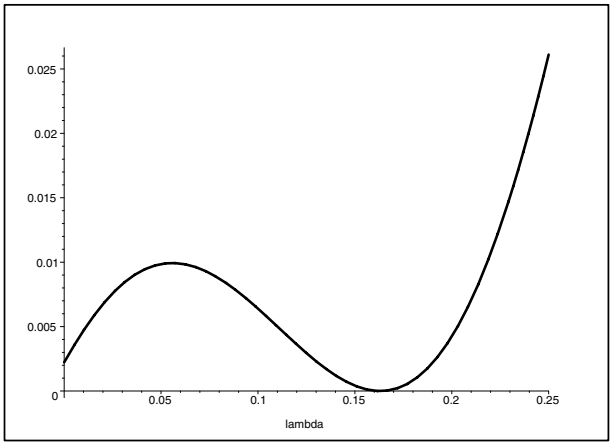


FIG. 4. *Parameter values are* $\beta_j = 3.15 \times 10^{-5}$, $\beta_a = 1.5 \times 10^{-5}$, $\beta_m = 2.925 \times 10^{-5}$, $\alpha\beta_m = 0.75 \times 10^{-5}$, $D_{ia} = 13$ km^2/day [16, 21] *(the diffusion rate of infected adult),* $D_{ij} = 6$ km^2/day *(the diffusion rate of infected juvenile),* $D_m = 0.1$ km^2/day *(the diffusion rate of mosquito), and other parameters have the values shown in Table* 1. *For these values, the minimum speed* $c_{\min}$*, computed as described in the text, equals* 2.623164094 *km/day.*

some of them (e.g., the diffusivity of mosquitoes) and a sensitivity to the values of other parameters, particularly the contact rates.

Ideally it would be desirable to have some information on whether the minimum speed $c_{\min}$ computed as described in section 3 is really the speed that solutions would evolve to, from ecologically realistic initial data such as a localized introduction of infectives. One must remember that in deriving the reaction-diffusion model, we were restricted to the vicinity of the DFE because the model derivation requires an explicit solution to a certain linear parabolic PDE that is nonautonomous except near that equilibrium. The inability to formulate a model that is valid everywhere in the spatial domain has made it impossible to numerically simulate the spatially extended model (such a simulation might have confirmed that the spread rate is indeed the minimal wave speed $c_{\min}$). The mathematical theory of the speed of spread in reaction-diffusion equations with functional terms is still far from complete, especially for coupled systems such as those in this paper. Relating the spread rate of the disease to the traveling wave with the minimal wave speed relies on the so-called linear conjecture (see [25, 15]). The fact that the minimal speed coincides with the spread rate has been theoretically verified only for dynamical systems enjoying certain order-preserving properties (see the two recent articles [24, 17]), and counterexamples when these properties do not hold have been reported [11]. Establishing this fact for our system (3.9)–(3.13) is even more difficult due to the interaction of time delay and spatial diffusion, in addition to the nonlocality of the nonlinear terms. Therefore, it has to be emphasized that our calculation of $c_{\min}$ is nothing more than a formal calculation of the minimum ecologically feasible speed according to the linearized equations ahead of the front.

Throughout this paper simple mass action terms have been used. In some virus infections, possibly including mosquito borne disease, one might argue for the inclusion of a term which represents the fact that a female mosquito takes a fixed number of blood meals per unit time (Anderson and May [1]). Such a modification involves dividing by bird density and has recently been utilized by Lewis, Renclawowicz, and

van den Driessche [16] and by Bowman et al. [3] in some simpler models for West Nile virus. In the present paper such a modification can be implemented only in the model without diffusion, which we have studied in section 2, and unfortunately not for the reaction-diffusion model of section 3, which becomes intractable. The type of modification we are discussing involves replacing (2.1) by

$$\frac{\partial s}{\partial t} + \frac{\partial s}{\partial a} = -d_s(a)s(t,a) - \frac{\beta(a)s(t,a)m_i(t)}{N(t)}, \tag{4.1}$$

with another similar modification to (2.2). The variable $N(t)$ stands for the total bird population,

$$N(t) = A_s(t) + A_i(t) + J_s(t) + J_i(t),$$

in which the variables are defined by (2.5). Equation (2.18) would be replaced by

$$\frac{dm_i(t)}{dt} = -d_m m_i(t) + \frac{\beta_m(m_T^* - m_i(t))}{N(t)}(J_i(t) + \alpha A_i(t)). \tag{4.2}$$

For this modified model it is possible to develop a parallel theory including equations for the total number variables analogous to (2.9), (2.10), (2.13), (2.14) and to prove theorems concerning positivity, boundedness, and global convergence. We shall confine ourselves in this paragraph only to a discussion of the linear stability of the DFE in the modified model involving division by bird density. The DFE itself is still given precisely by (2.35). Lemma 2.3, which concerns stability to perturbations in which the disease remains absent, still holds. For the modified model a necessary and sufficient condition for the DFE to be linearly asymptotically stable to arbitrary small perturbations is

$$\begin{aligned} d_m > \frac{\beta_m m_T^*}{N^*}\Bigg\{ & \frac{b(A_s^*)\beta_j}{N^*(d_{ij}-d_{sj})}\left[\frac{1-e^{-d_{sj}\tau}}{d_{sj}} - \frac{(1-e^{-d_{ij}\tau})}{d_{ij}}\right] \\ & + \frac{\alpha}{d_{ia}N^*}\left[\beta_a A_s^* + \beta_j b(A_s^*)e^{-d_{sj}\tau}\frac{(1-e^{-(d_{ij}-d_{sj})\tau})}{d_{ij}-d_{sj}}\right]\Bigg\}, \end{aligned} \tag{4.3}$$

which is similar to condition (2.38). Here, $N^* = A_s^* + J_s^*$, where A_s^* and J_s^* are given by (2.36).

There are a number of ways in which one could interpret conditions (2.38) and (4.3) for the simple mass action model and the modified model, respectively. First let us note that as far as the stability of the DFE is concerned the two models are similar: to get from one to the other we simply divide the contact rates by the total bird population at the equilibrium. Not surprisingly, in reality in the control of West Nile virus a great deal of emphasis goes into mosquito control. This may mean larval control, i.e., reducing the number of places mosquito larvae may inhabit such as old tires, blocked gutters, bird baths, flower pots, swimming pool covers, etc. Adult mosquito control using adulticides, which are sprayed into the air from a sprayer truck as very tiny droplets, is also practiced, especially when larval control measures are clearly inadequate or disease is imminent. The per capita mortality rate for adult mosquitoes manifests itself in our model as the parameter d_m. The per capita mortality rate for mosquito larvae is d_l, which does not feature directly in (2.38) or (4.3) but features indirectly through the quantity m_T^*. (In fact, m_T^* depends on both d_l and d_m.) If the birth function $B(\cdot)$ for mosquitoes is chosen as

in (2.44), then $m_T^* = \frac{1}{a_m}\ln(b_m/d_m) - d_l\sigma/a_m$, and so the right-hand side of (2.38) or (4.3) decreases linearly with d_l so that sufficiently effective larval control eradicates the disease. On the other hand, as d_m increases, the left-hand side increases linearly while the right-hand side decreases, suggesting that in percentage terms an increase in d_m might be more effective than an increase in larval mortality d_l. However, adult mosquito control is more expensive and more difficult to organize.

There are a number of other factors we have not considered in this paper at all. It seems that in reality seasonal effects probably play an important role and should be modeled. It is really only in the breeding season that crows, once paired, seek to establish individual territories to raise their broods. In the nonbreeding season crow activities tend to be centered around large communal roosts to which they return in the evenings after searching for food during the day (some roost locations may have been gathering points for crows for many decades). Crows also have a strong flocking instinct, something which Fickian diffusion does not model at all. Northern birds tend to fly south during the winter. All these considerations indicate possible areas for further investigation.

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