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SPATIAL SPREAD OF RABIES REVISITED: INFLUENCE OF AGE-DEPENDENT DIFFUSION ON NONLINEAR DYNAMICS*

CHUNHUA OU† AND JIANHONG WU‡

Abstract. We consider the spatio-temporal patterns of disease spread involving structured populations. We start with a general model framework in population biology and spatial ecology where the individual's spatial movement behaviors depend on its maturation status, and we show how delayed reaction diffusion equations with nonlocal interactions arise naturally. We then consider the impact of this delayed nonlocal interaction on the disease spread by revisiting the spatial spread of rabies in continental Europe during the period between 1945 and 1985. We show how the distinction of territorial patterns between juvenile and adult foxes, the main carriers of the rabies under consideration, yields a class of partial differential equations involving delayed and nonlocal terms that are implicitly defined by a hyperbolic-parabolic equation, and we show how incorporating this distinction into the model leads to a formula describing the relation of the minimal wave speed and the maturation time of foxes. We show how the homotopy argument developed by Chow, Lin, and Mallet-Paret can be applied to obtain the existence of a heteroclinic orbit between a disease-free equilibrium and an endemic state for the spatially averaged system of delay differential equations, and we illustrate how the technique developed by Faria, Huang, and Wu can be used to establish the existence of a family of traveling wavefronts in the neighborhood of the heteroclinic orbit for the corresponding spatial model.

Key words. time delay, nonlocal, reaction, reaction diffusion, traveling waves, fronts, stability, structured model, disease modeling, minimal wave speed

AMS subject classifications. 34C25, 34K15, 34K18, 35K55

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1. Introduction.

Spatial movement and reaction time lag are certainly two intrinsic features in biological systems; their interaction seems to be one of the many factors for possible complicated spatio-temporal patterns in a single species population without an external time-dependent forcing term. Modeling this interaction is nevertheless a highly nontrivial task, and recent progress indicates diffusive (partial or lattice) systems with nonlocal and delayed reaction nonlinearities arise very naturally. Such systems were investigated in the earlier work of Yamada [34], Pozio [24, 25], Redlinger [26, 27], and the modeling and analysis effort in the ground-breaking work by Britton [3], Gourley and Britton [9], Smith and Thieme [28] marked the beginning of the systematic study of a new class of nonlinear dynamical systems directly motivated by consideration of biological realities [10, 11].

This new class of nonlinear dynamical systems can be derived from the classical structured population model involving maturation-dependent spatial diffusion rates and nonlinear birth and natural maturation processes. More specifically, if we use $u(t,x)$ to denote the total number of matured individuals in a single species population

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†Department of Mathematics and Statistics, Memorial University of Newfoundland, St. John's, Newfoundland, A1C 5S7, Canada (ou@math.mun.ca).

‡Laboratory for Industrial and Applied Mathematics, Department of Mathematics and Statistics, York University, Toronto, Ontario, M3J 1P3, Canada (wujh@mathstat.yorku.ca).

and if we assume the maturation time is a fixed constant τ, then we have

$$\frac{\partial}{\partial t}u(t,x) = D\frac{\partial^2}{\partial x^2}u(t,x) - du(t,x) + j(t,\tau,x), \tag{1.1}$$

where D and d are the diffusion and death rates of the adult population (that are assumed to be age-independent), and $j(t,\tau,x)$ is the maturation rate that is given by the rate where an individual was born exactly time $t-\tau$ ago in all possible spatial locations but moved to the current position x upon maturation. This maturation rate is thus regulated by the birth process and the dynamics of the individual during the maturation phase. In the work of So, Wu, and Zou [29], this is derived from the structured population model

$$\Big(\frac{\partial}{\partial t} + \frac{\partial}{\partial a}\Big)j(t,a,x) = D_I\frac{\partial^2}{\partial x^2}j(t,a,x) - d_I j(t,a,x) \tag{1.2}$$

for the density $j(t,a,x)$ of the immature individual with $a \in (0,\tau]$ as the variable for age, subject to some (spatial) boundary conditions (if the space is bounded) and the following (age) boundary condition:

$$j(t,0,x) = b(u(t,x)), \tag{1.3}$$

where b is the birth rate function that is assumed to be dependent on the matured population, and D_I and d_I are the diffusion and death rates of the immature individual (these rates are allowed to depend on the age a in [29]). The maturation rate $j(t,\tau,x)$ can be obtained by solving the linear hyperbolic-parabolic equation (1.2) subject to the boundary condition (1.3). In the case of unbounded one-dimensional space, we have

$$j(t,\tau,x) = e^{-d_I\tau}\int_R b(u(t-\tau,y))f(x-y)dy. \tag{1.4}$$

In other words, the maturation rate at time t and spatial location x is the sum of the birth rate at time $t-\tau$ at the spatial location y, times the probability $f(x-y)$ of the individual moved from y to the current position x, and then times the survival rate $e^{-d_I\tau}$ during the entire maturation phase. Incorporating (1.4) into (1.1), we then obtain a closed system of reaction diffusion equations with nonlocal delayed nonlinearity as follows:

$$\frac{\partial}{\partial t}u(t,x) = D\frac{\partial^2}{\partial x^2}u(t,x) - du(t,x) + e^{-d_I\tau}\int_R b(u(t-\tau,y))f(x-y)dy, \tag{1.5}$$

where

$$f(x) = \frac{1}{\sqrt{4\pi D_I\tau}}e^{\frac{-x^2}{4D_I\tau}}.$$

For the existence of positive solutions to (1.5) with various initial and boundary conditions, we refer to [19, 33]. Recently, there has been some rapid development towards a qualitative theory for the asymptotic behaviors of solutions to the above equation with various types of assumptions on the birth functions. Notably, in comparison with the ordinary reaction diffusion analogue, we will have more prototypes than the so-called monostable and bistable cases. See [11].

The analytic form above for f was derived in [29]. It is possible to obtain such an analytic form here since the dynamical process during the maturation phase is governed by a linear hyperbolic-parabolic equation with time-independent constant coefficients. Such a possibility disappears in an ecological system consisting of multiple species with age- or stage-dependent diffusion rates when these species interact during their maturation phases. This is also the case for the spread of a disease even if its main carrier involves only a single species, since the model describing the infection process must involve the transfers of individuals from one compartment to another, and some of these transfers such as the force of infection from the susceptible compartment to the infective compartment are nonlinear.

We will illustrate the above difficulty and usefulness of modeling the spread of diseases involving stage-dependent spatial diffusion by considering the spatial spread of rabies in continental Europe during the period 1945–1985. Our focus is on the front of the epizootic wave of rabies, starting on the edge of the German/Polish border and moved westward at an average speed of about 30–60 km a year. This traveling wavefront has been investigated quite successfully (see [15, 22]), where the minimal wave speed was calculated from basic epidemiological and ecological parameters, and compared well with field observation data. It was also noted that juvenile foxes leave their home territory in the autumn traveling distances that typically may be 10 times a territory size in search of a new territory. If a fox happened to have contracted rabies around the time of such long-distance movement, it could certainly increase the spreading of the disease into uninfected areas. This observation has not been considered in the existing models. It turns out that incorporating the differential spatial movement behaviors of adult and juvenile foxes into a deterministic model yields a much more complicated system of reaction diffusion equations with delayed nonlinear nonlocal interactions.

More precisely, the celebrated work [15, 22] used a system of a reaction diffusion equation for the infective, coupled with an ODE for the susceptible foxes—the main carrier of the disease—under the assumption that the infective compartment consists of both rabid foxes and those in the incubation stage, and that susceptible foxes are territorial and thus their spatial movement can be ignored. It was already pointed out, in both papers mentioned above and their later extensions and further detailed studies, that the spatial movement behaviors of susceptible juvenile foxes are different since they prefer to leave their home territories in search of new territories of their own. How to describe this stage-dependent diffusion pattern of susceptible foxes and how stage-dependent diffusion affects the spatial spread of rabies are the main focus of the current paper.

It turns out, as will be shown in section 2, that such a stage-dependent diffusion of susceptible foxes and the random movement of rabid foxes due to the loss of the sense of direction and territorial behaviors yield a coupled system of reaction diffusion equations with nonlocal delayed nonlinearity for the juvenile susceptible foxes $M(t,x)$ and total rabies foxes $J(t,x)$. Unlike system (1.5) for a single species population with simple dynamics during the maturation phase, the coupled system for (M,J) involves the density of the juvenile foxes $S(t,a,y)$ for all $y \in R$ and the maturation rate $S(t,\tau,x)$ (again, τ is assumed to be a constant maturation time of the foxes) and the force of infection that is proportional to the product of $J(t,x)\int_0^\tau S(t,a,x)da$. This density of the juvenile foxes cannot be solved explicitly in terms of $M(s,\cdot)$ with $s \leq t$ although it is given implicitly by solving a hyperbolic-parabolic equation with a nonlinear term.

Some of the key issues related to the spatial spread can nevertheless be addressed, despite the aforementioned difficulty in obtaining an explicit analytic formula of $S(t,a,x)$ in terms of the historical values of M at all spatial locations. As shall be shown in section 3, the linear stability of two spatially homogeneous equilibria can be fully investigated and the minimal wave speed can be calculated. One of the results we obtain from this calculation is that the minimal wave speed is a function of the average maturation time. More precisely, knowing the carrying capacities for the adult and juvenile foxes, the minimal wave speed is a decreasing function of the maturation period. This results coincide in principle with the speculation in [15, 22], and give a more precise qualitative description of the influence of maturation time on the propagation of the disease in space.

Establishing the existence of traveling waves turns out to be a very difficult task due to the loss of monotonicity of the nonlocal delayed nonlinearity. In section 4, we utilize a general result of Faria, Huang, and Wu [8] that claims the existence of traveling waves in the neighborhood of a heteroclinic orbit between the two equilibria of a corresponding ordinary delay differential system obtained from the delayed reaction diffusion system for (J, M) through a spatial average, and we obtain the existence of this heteroclinic orbit by an approach based on a combination of perturbation analysis [23], the Fredholm theory, and some fixed point theorems [5, 13]. This will be developed in detail in section 4, along with some numerical simulations to show how the maturation time affects the calculation of the minimal wave speed, and how the diffusion of the juvenile foxes impacts the amplitudes and frequencies of the oscillatory long tails of the traveling wavefronts.

2. Derivation of the model.

Here we use a deterministic approach to describe the spatial spread of rabies. Following [15, 22], we divide the fox population into two groups: the infective and the susceptible. The former consists of both rabid foxes and those in the incubation stage. The basic facts and assumptions of our model are as follows:

- (H1) The rabies virus is contained in the saliva of the rabid fox and is normally transmitted by bite. Therefore, contact between a rabid and a susceptible fox is necessary for the transmission of the disease.
- (H2) Rabies is invariably fatal in foxes.
- (H3) Adult susceptible foxes are territorial and seem to divide the countryside into nonoverlapping home ranges which are marked out by scent. They do occasionally travel considerable distances but always return to their home territory. However, for young susceptible juvenile foxes, their behaviors are different, because they prefer to leave their home territories in search of new territories of their own.
- (H4) The rabies virus enters the central nervous system and induces behavioral changes of foxes. If the spinal cord is involved, it often takes the form of paralysis. However, if the virus enters the limbic system, the foxes become aggressive, lose their sense of direction and territorial behavior, and wander about in a more or less random way.

Modeling the distinction of diffusion patterns of young and adult susceptible foxes, already observed in [15, 22], is the main focus of this paper. Because of this distinction, we shall incorporate age structure into our model and consider the fox population with two age classes: the immature and the mature. Let $I(t, a, x)$ and $S(t, a, x)$ denote the population density at time t, age $a \geq 0$, and spatial location $x \in R = (-\infty, \infty)$ for the infective and the susceptible foxes, respectively, and let τ be the maturation time which is assumed to be a constant. Then the integral

$$J(t, x) = \int_0^\infty I(t, a, x) da \tag{2.1}$$

is the total population of the infective foxes and

$$M(t,x)=\int_{\tau}^{\infty}S(t,a,x)da \tag{2.2}$$

is the total population of the adult susceptible foxes. Using Fick's diffusive law and the mass active incidence, we have

$$\left(\frac{\partial}{\partial t}+\frac{\partial}{\partial a}\right)I(t,a,x)=D_I\frac{\partial^2}{\partial x^2}I(t,a,x)+\beta S(t,a,x)J(t,x)-d_I I(t,a,x), \tag{2.3}$$

where D_I is the diffusive coefficient, d_I is the death rate for the infective foxes, and β is the transmission rate. Using $I(t,\infty,x)=0$ and $I(t,0,x)=0$, we obtain from (2.1) and (2.3) that

$$\begin{aligned}\frac{\partial J(t,x)}{\partial t}&=\int_0^{\infty}\frac{\partial I(t,a,x)}{\partial t}da\\&=D_I\frac{\partial^2 J(t,x)}{\partial x^2}+\beta M(t,x)J(t,x)-d_I J(t,x)\\&\quad+\beta J(t,x)\int_0^{\tau}S(t,a,x)da.\end{aligned} \tag{2.4}$$

For $S(t,a,x)$ with $a\geq\tau$, we have the structured population model (see [20] or [32])

$$\left(\frac{\partial}{\partial t}+\frac{\partial}{\partial a}\right)S(t,a,x)=-\beta S(t,a,x)J-d_S S(t,a,x), \tag{2.5}$$

where the constant d_S is the death rate for the susceptible foxes. Using $S(t,\infty,x)=0$, we get from (2.2) and (2.5) that

$$\frac{\partial M(t,x)}{\partial t}=-\beta M(t,x)J(t,x)-d_S M(t,x)+S(t,\tau,x). \tag{2.6}$$

To obtain a closed system for (J,M), we need to formulate $S(t,a,x)$ with $0\leq a\leq\tau$ in terms of (J,M). This is achieved by using the following structured hyperbolic-parabolic equation with the initial condition given by the birth process:

$$\begin{cases}\left(\frac{\partial}{\partial t}+\frac{\partial}{\partial a}\right)S(t,a,x)=D_Y\frac{\partial^2}{\partial x^2}S(t,a,x)-\beta S(t,a,x)J(t,x)-d_Y S(t,a,x),\\ S(t,0,x)=b(M(t,x)),\end{cases} \tag{2.7}$$

where D_Y is the diffusive coefficient for the immature susceptible foxes and $b(\cdot)$ is the birth function of the susceptible foxes.

Combining (2.4) and (2.6) together gives

$$\begin{cases}\frac{\partial J(t,x)}{\partial t}=D_I\frac{\partial^2 J(t,x)}{\partial x^2}+\beta M(t,x)J(t,x)-d_I J(t,x)+\beta J(t,x)\int_0^{\tau}S(t,a,x)da,\\ \frac{\partial M(t,x)}{\partial t}=-\beta M(t,x)J(t,x)-d_S M(t,x)+S(t,\tau,x),\end{cases} \tag{2.8}$$

where $S(t,a,x)$, $0\leq a\leq\tau$, is determined by solving the hyperbolic-parabolic system (2.7).

Remark 2.1. *$S(t,a,x)$ in (2.7) depends on t, a, $M(t,y)$, and $J(s,y)$ for all $0 \le s \le t$ and $y \in R$, but an explicit formula for $S(t,a,x)$ cannot be found. We shall write $F(t,a,x) = F(a,M,J)(t,a,x)$ to indicate this functional relation. It is easy to show that*

$$F(a,M,J_1)(t,a,x) \ge F(a,M,J_2)(t,a,x) \quad \text{if } 0 \le J_1(s,y) \le J_2(s,y) \tag{2.9}$$

for $0 \le s \le t$ and $y \in R$, and for $t \ge a$,

$$F(a,M,J_1)(t,a,x) = b(M(t-a,x))e^{-\int_{t-a}^{t}(d_Y+\beta J(u,x))du} \quad \text{when } D_Y = 0. \tag{2.10}$$

Remark 2.2. *When $\tau = 0$, system (2.8) reduces to*

$$\begin{cases} \frac{\partial J(t,x)}{\partial t} = D_I \frac{\partial^2 J(t,x)}{\partial x^2} + \beta J(t,x)S(t,x) - d_I J(t,x), \\ \frac{\partial M(t,x)}{\partial t} = -\beta J(t,x)M(t,x) - d_S M(t,x) + b(M(t,x)). \end{cases} \tag{2.11}$$

This model was studied in [7] and [15] by assuming that the birth function obeys the well-known logistic growth, that is, the (gross) birth function $b(M) := d_S M + b_0 M(1 - M/S_0)$, where S_0 is the carrying capacity of the susceptible fox population and b_0 is the net birth rate for the susceptible foxes when the population density is close to zero. After rescaling by

$$u(t,x) = J(t,x)/S_0,\ v(t,x) = M(t,x)/S_0,\ x^* = (\beta S_0/D_I)^{1/2}x,\ t^* = \beta S_0 t,\ r = \frac{d_I}{\beta S_0}$$

and dropping the asterisk, we can transform (2.11) into

$$\begin{cases} \frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + u(v - r), \\ \frac{\partial v}{\partial t} = -uv + kv(1 - v), \end{cases} \tag{2.12}$$

where $k = b_0/\beta S_0$. In [7], it was proved that if $r = \frac{d_I}{\beta S_0} < 1$, then the infective and the susceptible foxes coexist, and there exists a family of traveling wavefronts $(J = S_0 u(x+ct), M = S_0 v(x+ct))$ for (2.11) which connect $(0, S_0)$ to $(kS_0(1-r), S_0 r)$ with the wave speed c satisfying

$$c \ge c_{\min} = 2\sqrt{\beta S_0 D_I}\sqrt{1 - \frac{d_I}{\beta S_0}} = 2\sqrt{D_I(\beta S_0 - d_I)}.$$

In addition, it was shown that there is a constant $k^* > 0$ so that (a) *if $k = b_0/\beta S_0 > k^*$, then the wavefront (u,v) approaches $(k(1-r)S_0, rS_0)$ monotonically;* (b) *if $k = b_0/\beta S_0 \le k^*$, then the wavefront (u,v) approaches $(k(1-r)S_0, rS_0)$ with oscillatory damping.*

In [14] and [15], instead of the logistic growth, a static population of the susceptible is assumed in the sense that deaths are equally balanced by births. This yields the simple model

$$\begin{cases} \frac{\partial J}{\partial t} = D_I \frac{\partial^2 J}{\partial x^2} + \beta JM - d_I J, \\ \frac{\partial M}{\partial t} = -\beta JM, \end{cases} \tag{2.13}$$

where M and J are the total numbers of susceptible and infective foxes, respectively. It was shown that with initial (maximum) susceptible population S_0, if $r = \frac{d_I}{\beta S_0} > 1$

(that is, the mortality rate of the infective foxes is greater than the rate of recruitment of new infective), the infection dies out quickly. If $r = \frac{d_I}{\beta S_0} < 1$*, there is a family of traveling wavefronts to the system* (2.13) *with the minimal speed*

$$c_{\min} = 2[D_I(\beta S_0 - d_I)]^{1/2}.$$

See [1, 6] for related work.

REMARK 2.3. *When* $D_Y = 0$*, system* (2.7)–(2.8) *reduces to the following model:*

$$\begin{cases} \frac{dJ}{dt} = D_I \frac{\partial^2 J}{\partial x^2} + \beta MJ - d_I J + \beta J \int_0^\tau b(M(t-a)) e^{\int_0^a -(d_Y + \beta J(t-s))ds} da, \\ \frac{dM}{dt} = -\beta MJ - d_S M + b(M(t-\tau)) e^{\int_{t-\tau}^t -(d_Y + \beta J(s))ds}. \end{cases} \tag{2.14}$$

This is a delayed reaction diffusion system with distributed delay but without spatial averaging. We will numerically compare the behavior of solutions to (2.14) *with that of* (2.7)–(2.8) *in section* 4.3.

In the remaining part of this paper, we consider the dynamics of (2.7)–(2.8) using the birth function

$$b(M) = b_0 M e^{-\bar{a} M},$$

where $\bar{a} > 0$ is a positive parameter, and $b_0 = b'(0)$ is the birth rate when the population size is small. This birth function exhibits the logistic growth nature of the fox population in the absence of the disease. Such a function has been used in the well-studied Nicholson blowfly model [12] and is common in models of fish. The specific form of such a function is not so important for the method developed below, though the specific form facilitates and simplifies our qualitative analysis since, as will be shown, constant equilibria can be explicitly described.

3. Structure of equilibria. In this section, we describe the structure of equilibria of biological interest. At an equilibrium, (J, M) takes on a constant value, namely,

$$J \equiv J_0, \quad M \equiv M_0,$$

for constants J_0 and M_0. Then from (2.7) we have

$$\begin{cases} (\frac{\partial}{\partial t} + \frac{\partial}{\partial a})S = D_Y \frac{\partial^2}{\partial x^2} S - d_Y S - \beta S J_0, \\ S(t, 0, x) = b(M_0). \end{cases} \tag{3.1}$$

To solve (3.1), we define $V^s(t, x) = S(t, t-s, x)$ and obtain, for $t \geq s$, that

$$\begin{aligned} \frac{\partial}{\partial t} V^s(t, x) &= \frac{\partial S}{\partial t}(t, a, x)|_{a=t-s} + \frac{\partial S(t, a, x)}{\partial a}|_{a=t-s} \\ &= D_Y \frac{\partial^2}{\partial x^2} V^s(t, x) - d_Y V^s(t, x) - \beta J_0 V^s(t, x). \end{aligned} \tag{3.2}$$

Note that (3.2) is a linear reaction diffusion equation with constant coefficients. The associated initial condition is

$$V^s(s, x) = b(M_0), \quad x \in R. \tag{3.3}$$

To ensure uniqueness of solutions, we also impose biologically realistic boundary conditions as follows:

$$|V^s(t, \pm\infty)| < \infty. \tag{3.4}$$

The solution of (3.2)–(3.4) is given by

$$V^s(t, x) = b(M_0)e^{-(d_Y+\beta J_0)(t-s)}. \tag{3.5}$$

That is,

$$S(t, t-s, x) = b(M_0)e^{-(d_Y+\beta J_0)(t-s)} \tag{3.6}$$

and

$$S(t, a, x) =: F(a, M_0, J_0) =: b(M_0)e^{-(d_Y+\beta J_0)a},\ 0 \le a \le \tau,$$

from which, with (2.8), it follows that equilibrium (M_0, J_0) is given by the following algebraic equations:

$$\begin{cases} \beta M_0 J_0 - d_I J_0 + \beta J_0 \frac{b(M_0)}{(d_Y+\beta J_0)}(1 - e^{-(d_Y+\beta J_0)\tau}) = 0, \\ -\beta M_0 J_0 - d_S M_0 + b(M_0)e^{-(d_Y+\beta J_0)\tau} = 0. \end{cases} \tag{3.7}$$

We now solve (3.7) for equilibria.

When $J_0 = 0$, the second equation in (3.7) gives

$$-d_S M_0 + b(M_0)e^{-d_Y\tau} = 0. \tag{3.8}$$

Thus M_0 can take on two different values: $M_0 = 0$ or $M_0 = M^{\tau}_{\max} = \frac{1}{\bar{a}}\ln(b_0/d_S e^{d_Y\tau}))$. Biological consideration requires that

$$\frac{b_0}{d_S e^{d_Y\tau}} > 1$$

or, equivalently,

$$\tau < \tau_{\max} = \frac{1}{d_Y}\ln\frac{b_0}{d_S}, \tag{3.9}$$

so that $M^{\tau}_{\max} > 0$.

When $J_0 \neq 0$, obviously from the second equation of (3.7) we can simplify the relation between J_0 and M_0 to yield

$$M_0 = \frac{1}{\bar{a}}\left(\ln\frac{b_0}{\beta J_0 + d_S} - (d_Y + \beta J_0)\tau\right).$$

Viewing M_0 as a function of J_0, that is, $M_0 = h_0(J_0)$ with h_0 being given by

$$h_0(J_0) = \frac{1}{\bar{a}}\left(\ln\frac{b_0}{\beta J_0 + d_S} - (d_Y + \beta J_0)\tau\right), \tag{3.10}$$

we find that $h_0(J_0)$ is decreasing for $J_0 \ge 0$ with

$$h_0(0) = M^{\tau}_{\max} > 0 \quad \text{and} \quad h_0(+\infty) < 0.$$

From the first equation of (3.7) we have

$$\frac{\beta b(M_0)}{d_I - \beta M_0} = \frac{d_Y + \beta J_0}{1 - e^{-(d_Y + \beta J_0)\tau}}. \tag{3.11}$$

The monotonic increasing property of the function on the right-hand side of (3.11) is obvious for $J_0 \in [0, \infty)$. We now check the monotonicity of the function on the left-hand side. Using the definition of $b(\cdot)$ and defining $f(x) := \beta b(x)/(d_I - \beta x)$, we have

$$\begin{aligned} f'(x) &= \beta \frac{b'(x)(d_I - \beta x) + \beta b(x)}{(d_I - \beta x)^2} \\ &= \beta \frac{b_0 e^{-\bar{a}x}(\bar{a}\beta x^2 - \bar{a} d_I x + d_I)}{(d_I - \beta x)^2}. \end{aligned}$$

It is easy to know that the function $f(x) = \beta b(x)/(d_I - \beta x)$ is increasing with respect to x provided that

$$\bar{a} d_I < 4\beta.$$

Therefore, under the above condition, a careful examination of the left-hand side of (3.11) shows that (3.11) gives a unique function $M_0 = h_1(J_0)$ ($M_0 < d_I/\beta$, $J_0 \geq 0$) which is increasing for $J_0 \in (0, \infty)$ and satisfies

$$h_1(\infty) = \frac{d_I}{\beta}.$$

It is easy to see that the intersection point of the two curves $M_0 = h_0(J_0)$ and $\mathrm{M}_0 = h_1(J_0)$ corresponds to the third equilibrium (J_*^τ, M_*^τ) of our system. As to the existence and positivity of this particular point, we have the following.

THEOREM 3.1. *Assume $\tau < \tau_{\max}$ and $ad_I < 4\beta$. Then system (2.7)–(2.8) has a unique positive equilibrium (J_*^τ, M_*^τ) if and only if*

$$C_0(\tau) := \frac{d_I}{\beta M_{\max}^\tau} - \frac{b(M_{\max}^\tau)(1 - e^{-d_Y \tau})}{M_{\max}^\tau d_Y} < 1, \tag{3.12}$$

where

$$M_{\max}^\tau = \frac{1}{\bar{a}} \ln \frac{b_0}{d_S e^{d_Y \tau}}.$$

Proof. The condition $\tau < \tau_{\max}$ implies that $M_{\max}^\tau$ is positive and the condition $ad_I < 4\beta$ guarantees that h_1 is increasing. Note that $h_0(0) = M_{\max}^\tau$. By the monotonicity properties of functions h_0 and h_1 and the fact that $h_0(\infty) < 0$ and $h_1(\infty) = \frac{\beta}{d_I} > 0$, it follows that the functions h_0 and h_1 have a positive intersection point if and only if $h_1(0) < h_0(0) = M_{\max}^\tau$. Now we show that $h_1(0) < h_0(0) = M_{\max}^\tau$ if and only if $C_0(\tau) < 1$. We consider two cases:

(i) $M_{\max}^\tau \geq \beta/d_I$;
(ii) $M_{\max}^\tau < \beta/d_I$.

In the first case, the proof is obvious and will be omitted here. For the second case, the inequality $C_0(\tau) < 1$ is actually equivalent to

$$\frac{d_I}{\beta M_{\max}^\tau} - \frac{b(M_{\max}^\tau)(1 - e^{-d_Y \tau})}{M_{\max}^\tau d_Y} < 1,$$

or to

$$\frac{d_Y}{(1-e^{-d_Y\tau})} < \frac{\beta b(M^\tau_{\max})}{d_I - \beta M^\tau_{\max}}. \tag{3.13}$$

From (3.11) we note that $h_1(0)$ $(< \frac{d_I}{\beta})$ is determined by

$$\frac{\beta b(h_1(0))}{d_I - \beta h_1(0)} = \frac{d_Y}{1-e^{-d_Y\tau}}. \tag{3.14}$$

This means by (3.13) that $C_0(\tau) < 1$ is equivalent to

$$\frac{\beta b(h_1(0))}{d_I - \beta h_1(0)} = \frac{d_Y}{1-e^{-d_Y\tau}} < \frac{\beta b(M^\tau_{\max})}{d_I - \beta M^\tau_{\max}}. \tag{3.15}$$

Since the function $f(y) = \beta b(y)/(d_I - \beta y)$ is strictly increasing for $y \in (-\infty, d_I/\beta)$, from (3.15) we have the desired result that $h_1(0) < M^\tau_{\max} \Longleftrightarrow C_0(\tau) < 1$, and the proof is complete.

Remark 3.2. *Inequality* (3.12) *can be rewritten as*

$$\frac{d_I}{\beta} < M^\tau_{\max} + b(M^\tau_{\max})\frac{(1-e^{-d_Y\tau})}{d_Y}. \tag{3.16}$$

The right side of (3.16) *is the sum of the population of the mature and the immature foxes when they reach equilibria in the disease-free case. This sum is the carrying capacity of the environment. The left-hand side d_I/β is the critical minimum threshold fox density; see* [14]. *Theorem* 3.1 *means that when the carrying capacity of the environment is greater than the critical threshold-value d_I/β, the rabid foxes and the susceptible foxes can coexist and a positive equilibrium exists.*

4. Traveling wave solutions.

In this section, we consider the behavior of solutions to system (2.7)–(2.8) in unbounded domain $(-\infty, \infty)$ under the conditions in Theorems 3.1. In section 4.1, we use the standard stability analysis to investigate possible patterns of traveling waves. An explicit formula for the minimal wave speed is given and this wave solution is confirmed by numerical simulations in section 4.3. In section 4.2, we prove that traveling wavefronts with large wave speeds indeed exist by using perturbation analysis developed in [8].

4.1. Local analysis of the traveling wavefronts.

Standard stability analysis is employed here to discuss the existence of traveling wavefronts. As usual, we linearize the wave equation of (2.7)–(2.8) near their equilibria and find the associated eigenvalues and eigenvectors. Sketching this information in the system's phase plane yields a useful suggestion about a possible heteroclinic connection between these equilibria. We show the details as follows.

First of all, we linearize (2.7)–(2.8) around its equilibrium (J_0, M_0). Recall that when $J \equiv J_0$, $M \equiv M_0$, we have $S(t, t-s, x) = F(t-s, M_0, J_0)$. Assume that

$$J = J_0 + \Delta J, \quad M = M_0 + \Delta M, \quad S(t, t-s, x) = F(t-s, M_0, J_0) + \Delta S.$$

We first obtain the following linearized system for ΔS:

$$\begin{cases} \frac{\partial \Delta S}{\partial t} = D_Y \frac{\partial^2}{\partial x^2}\Delta S - d_Y \Delta S - \beta J_0 \Delta S - \beta F(t-s, M_0, J_0)\Delta J, \\ \Delta S|_{t=s} = b'(M_0)\Delta M. \end{cases} \tag{4.1}$$

We then use Fourier transforms to solve this equation. Let

$$\Delta\tilde{S} = \int_{-\infty}^{\infty} \Delta S\, e^{i\omega y} dy,$$

and let f be the Fourier transform of the term $-\beta F(t-s, M_0, J_0)\Delta J$, that is,

$$f = -\beta F(t-s, M_0, J_0) \int_{-\infty}^{\infty} \Delta J\, e^{i\omega y} dy.$$

Then, after taking Fourier transforms to both sides of (4.1), we arrive at a new linear equation for $\Delta\tilde{S}$ that can be solved easily to yield

$$\begin{aligned}
\Delta\tilde{S} &= e^{-(D_Y\omega^2+d_Y+\beta J_0)(t-s)} \int_{-\infty}^{\infty} b'(M_0)\Delta M(s,y) e^{i\omega y} dy \\
&\quad + \int_s^t f\, e^{-\int_{u-s}^{t-s}(D_Y\omega^2+d_Y+\beta J_0)dv} du \\
&= e^{-(D_Y\omega^2+d_Y+\beta J_0)(t-s)} \int_{-\infty}^{\infty} b'(M_0)\Delta M(s,y) e^{i\omega y} dy \\
&\quad - \beta \int_s^t F(u-s, M_0, J_0) \int_{-\infty}^{\infty} \Delta J(u,y)\, e^{i\omega y} dy\, e^{-(D_Y\omega^2+d_Y+\beta J_0)(t-u)} du.
\end{aligned}$$

We now take inverse Fourier transforms to obtain

$$\begin{aligned}
\Delta S(t,s,x) &= \frac{1}{2\pi} \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} b'(M_0)\Delta M(s,y) e^{i\omega y} dy\, e^{-(D_Y\omega^2+d_Y+\beta J_0)(t-s)} e^{-i\omega x} d\omega \\
&\quad - \frac{\beta}{2\pi} \int_{-\infty}^{\infty} \int_s^t F(u-s, M_0, J_0) \\
&\quad \times \int_{-\infty}^{\infty} \Delta J(u,y)\, e^{-(D_Y\omega^2+d_Y+\beta J_0)(t-u)+i\omega(y-x)} dy\, du d\omega \\
&= \frac{b'(M_0)}{\sqrt{4\pi D_Y(t-s)}} e^{-(d_Y+\beta J_0)(t-s)} \int_{-\infty}^{\infty} \Delta M(s,y) e^{-(x-y)^2/(4D_Y(t-s))} dy \\
&\quad - \frac{\beta}{2\pi} \int_{-\infty}^{\infty} dy \int_s^t F(u-s, M_0, J_0)\Delta J(u,y) e^{-(d_Y+\beta J_0)(t-u)} \\
&\quad \times \int_{-\infty}^{\infty} e^{-\omega^2 D_Y(t-u)+i\omega(y-x)} du d\omega \\
&= \frac{b'(M_0)}{\sqrt{4\pi D_Y(t-s)}} e^{-(d_Y+\beta J_0)(t-s)} \int_{-\infty}^{\infty} \Delta M(t-a,y) e^{-(x-y)^2/(4D_Y(t-s))} dy \\
&\quad - \beta \int_{-\infty}^{\infty} dy \int_0^{t-s} F(t-v-s, M_0, J_0)\Delta J(t-v,y) \\
&\quad \times e^{-(d_Y+\beta J_0)v} \frac{e^{-(x-y)^2/(4D_Y v)}}{\sqrt{4\pi D_Y v}} dv
\end{aligned}$$

and

$$\begin{aligned}\Delta S(t,a,x) = {} & \frac{b'(M_0)}{\sqrt{4\pi D_Y a}} e^{-(d_Y+\beta J_0)a} \int_{-\infty}^{\infty} \Delta M(t-a,y) e^{-(x-y)^2/(4D_Y a)} dy \\ & - \beta \int_{-\infty}^{\infty} dy \int_0^a F(a-v, M_0, J_0) \Delta J(t-v,y) \\ & \times e^{-(d_Y+\beta J_0)v} \frac{e^{-(x-y)^2/(4D_Y v)}}{\sqrt{4\pi D_Y v}} dv.\end{aligned}$$

Thus we obtain from (2.4) and (2.6) the following linearized system:

$$(4.2) \quad \begin{cases} \frac{\partial \Delta J}{\partial t} = D_I \frac{\partial^2 \Delta J}{\partial x^2} + \beta M_0 \Delta J + \beta J_0 \Delta M - d_I \Delta J + \beta \Delta J \int_0^\tau F(a, M_0, J_0) da \\ \qquad + \beta J_0 \int_0^\tau \Delta S(t,a,x) da, \\ \frac{\partial \Delta M}{\partial t} = -\beta M_0 \Delta J - \beta J_0 \Delta M - d_S \Delta M + \Delta S(t,\tau,x). \end{cases}$$

Near the equilibrium $(J, M) = (0, M^\tau_{\max})$, it gives

$$(4.3) \quad \begin{cases} \frac{\partial \Delta J}{\partial t} = D_I \frac{\partial^2 \Delta J}{\partial x^2} + \beta M^\tau_{\max} \Delta J - d_I \Delta J + \beta b(M^\tau_{\max}) \frac{1-e^{d_Y \tau}}{d_Y} \Delta J, \\ \frac{\partial \Delta M}{\partial t} = -\beta M^\tau_{\max} \Delta J - d_S \Delta M + \Delta S(t,\tau,x), \end{cases}$$

where

$$\begin{aligned}\Delta S(t,\tau,x) = {} & \frac{b'(M^\tau_{\max})}{\sqrt{4\pi D_Y \tau}} e^{-d_Y \tau} \int_{-\infty}^{\infty} \Delta M(t-\tau,y) e^{-(x-y)^2/(4D_Y \tau)} dy \\ & - \beta \int_{-\infty}^{\infty} dy \int_0^\tau F(\tau-v, M_0, J_0) \Delta J(t-v,y) e^{-d_Y v} \frac{e^{-(x-y)^2/(4D_Y v)}}{\sqrt{4\pi D_Y v}} dv.\end{aligned}$$

Looking for a traveling wavefront $\Delta J = f_1(x+ct)$, $\Delta M = g(x+ct)$, we have from (4.3) that

$$(4.4) \quad \begin{cases} c f_1' = D_I f_1'' + f_1(\beta M^\tau_{\max} - d_I + \frac{\beta b(M^\tau_{\max})}{d_Y}(1-e^{-d_Y \tau})), \\ c g' = -\beta M^\tau_{\max} f_1 - d_S g + \frac{b'(M^\tau_{\max})}{\sqrt{4\pi D_Y \tau}} e^{-d_Y \tau} \int_{-\infty}^{\infty} g(y-c\tau) e^{-(\xi-y)^2/(4D_Y \tau)} dy \\ \qquad - \beta \int_{-\infty}^{\infty} dy \int_0^\tau F(\tau-v, M_0, J_0) f_1(y-cv) e^{-d_Y v} \sqrt{\frac{1}{4\pi D_Y v}} e^{-(\xi-y)^2/(4D_Y v)} dv. \end{cases}$$

This is a linear system of functional differential equations with mixed arguments. The corresponding eigenvalues are determined by either

$$(4.5) \quad \lambda^2 - \frac{c}{D_I}\lambda + \frac{k_1}{D_I} = 0$$

or

$$-d_S + e^{-d_Y \tau} b'(M^\tau_{\max}) e^{\alpha \lambda^2 - \lambda c \tau} = c\ \lambda,$$

where

$$k_1 = \beta M^\tau_{\max} - d_I + \frac{\beta b(M^\tau_{\max})}{d_Y}(1 - e^{-\tau d_Y}).$$

Solving (4.5) yields

$$\lambda_{1,2} = \frac{c \pm \sqrt{c^2 - 4k_1 D_I}}{2D_I}.$$

The corresponding eigenvectors to the following system, which is equivalent to (4.4) by letting $f_2 = f_1'$,

$$\begin{cases} f_1' = f_2, \\ D_I f_2' = cf_2 - f_1(\beta M^\tau_{\max} - d_I + \frac{\beta b(M^\tau_{\max})}{d_y}(1 - e^{-d_y \tau})), \\ cg' = -\beta M^\tau_{\max} f_1 - d_S g + \frac{b'(M^\tau_{\max})}{\sqrt{4\pi D_Y \tau}} e^{-d_Y \tau} \int_{-\infty}^{\infty} g(y - c\tau) e^{-(\xi - y)^2/(4D_Y \tau)} dy \\ \qquad - \beta \int_{-\infty}^{\infty} dy \int_0^\tau S_0(\tau - v) f_1(y - cv) e^{-d_Y v} \sqrt{\frac{1}{4\pi D_Y v}} e^{-(\xi - y)^2/(4D_Y v)} dv \end{cases}$$

are

$$\vec{v}_1 = \begin{pmatrix} 1 \\ \lambda_1 \\ 0 \end{pmatrix}, \ \vec{v}_2 = \begin{pmatrix} 1 \\ \lambda_2 \\ 0 \end{pmatrix}.$$

When

$$0 < c < 2\sqrt{k_1 D_I},$$

the eigenvalues $\lambda_{1,2}$ are complex and the eigensolutions are oscillatory and can be negative. This is not biologically meaningful. Therefore, a natural condition for the existence of traveling wavefronts starting from $(0, M^\tau_{\max})$ is

$$\begin{aligned} c \geq c_{\min}(\tau) &:= 2\sqrt{\beta M^\tau_{\max} D_I} \sqrt{1 - \frac{d_I}{\beta M^\tau_{\max}} + \frac{b(M^\tau_{\max})}{M^\tau_{\max} d_Y}(1 - e^{-d_Y \tau})} \\ &= 2\sqrt{\beta M^\tau_{\max} D_I} \sqrt{1 - C_0(\tau)}. \end{aligned} \tag{4.6}$$

We should mention that the minimal speed can also be expressed as

$$c_{\min}(\tau) = 2\sqrt{\beta D_I} \sqrt{M^\tau_{\max} + b(M^\tau_{\max}) \frac{1 - e^{-d_Y \tau}}{d_Y} - \frac{d_I}{\beta}},$$

from which we find the speed $c_{\min}$ depends not only on the diffusive coefficient D_I and the transmission rate β, but also on the difference between the carrying capacity $M^\tau_{\max} + b(M^\tau_{\max}) \frac{1 - e^{-d_Y \tau}}{d_Y}$ and the critical threshold value d_I/β.

We now argue that it is impossible for a positive trajectory to go from $(0, M^\tau_{\max})$ to $(0, 0)$. To see this, linearizing around $(0, 0)$, we obtain

$$\begin{cases} \frac{\partial \Delta J}{\partial t} = D_I \frac{\partial^2 \Delta J}{\partial x^2} - d_I \Delta J, \\ \frac{\partial \Delta M}{\partial t} = -d_S \Delta M + \frac{b'(0)}{\sqrt{4\pi D_Y \tau}} e^{-d_Y \tau} \int_{-\infty}^{\infty} \Delta M(t - \tau, y) e^{-(x - y)^2/(4D_Y \tau)} dy. \end{cases}$$

This gives, by substituting $\Delta J = f_1(x + ct)$, $\Delta M = g(x + ct)$, the following:

$$\begin{cases} cf_1' = D_I f_1'' - d_I f_1, \\ cg' = -d_S g + \frac{b'(0)}{\sqrt{4\pi D_Y \tau}} e^{-d_Y \tau} \int_{-\infty}^{\infty} g(y - c\tau) e^{-(\xi - y)^2/(4D_Y \tau)} dy. \end{cases} \tag{4.7}$$

Thus at $(0, 0)$, the eigenvalues satisfy

$$\left[\lambda \left(\lambda - \frac{c}{D_I}\right) - \frac{d_I}{D_I}\right] \left[\frac{1}{c} \left(-d_S + e^{-d_Y \tau} b'(0) e^{\alpha \lambda^2 - \lambda c \tau}\right) - \lambda\right] = 0. \tag{4.8}$$

The second factor corresponds to the second equation of (4.7) that is in fact decoupled from the first equation of (4.7).

By (3.9) it is easy to see that every eigenvalue to equation

$$\frac{1}{c}\left(-d_S + e^{-d_Y\tau}b'(0)e^{\alpha\lambda^2-\lambda c\tau}\right) - \lambda = 0$$

cannot be negative and real, and hence there is no positive solution g such that $\lim_{t\to\infty} g(t) = 0$. This means that there's no positive orbit of (2.7)–(2.8) starting from $(0, M^\tau_{\max})$ and approaching $(0, 0)$.

So the solution starting from $(0, M^\tau_{\max})$ could arrive at (J^τ_*, M^τ_*) under the condition (4.6). The asymptotic behavior of traveling wavefronts approaching (J^τ_*, M^τ_*) depends on eigenvalues of system (4.2) near the equilibrium (J^τ_*, M^τ_*). If all the eigenvalues with negative real parts are complex, then the traveling wave will tend to (J^τ_*, M^τ_*) with oscillatory damping. Otherwise it will approach (J^τ_*, M^τ_*) monotonically. We will see numerical evidence for oscillatory damping of wave patterns in later sections.

4.2. A rigorous proof of traveling wavefronts with large wave speeds.

In this section, the existence of traveling wavefronts is rigorously established for system (2.7)–(2.8). To present our result, we first show the existence of a heteroclinic connection for a nondiffusive delayed system and then show that this is perturbed to a traveling wavefront with large wave speed for (2.7)–(2.8).

4.2.1. Heteroclinic connection for a nondiffusion delay system.

We now study the heteroclinic connection of the delayed system

$$\begin{cases} \frac{dJ}{dt} = \beta MJ - d_I J + \beta J \int_0^\tau b(M(t-a))e^{\int_0^a -(d_Y+\beta J(t-s))ds}da, \\ \frac{dM}{dt} = -\beta MJ - d_S M + b(M(t-\tau))e^{\int_{t-\tau}^t -(d_Y+\beta J(s))ds}, \end{cases} \tag{4.9}$$

which is a reduced version of (2.7)–(2.8) when $D_I = D_Y = 0$. It is easy to see that (4.9) has three equilibria: $E_1 := (0, 0)$, $E_2 := (0, M^\tau_{\max})$, and $E_3 := (J^\tau_*, M^\tau_*)$.

For initial continuous data $(J, M) = (j_0(s), m_0(s)) \geq 0$ for $s \in [-\tau, 0]$ with $(j_0(0), m_0(0)) > 0$, we claim that

$$(J(t), M(t)) > 0$$

for all $t > 0$. Indeed, dividing the first equation in (4.9) by J and integrating it from 0 to t, we have

$$J(t) = J(0)\exp\left(\beta M - d_I + \beta\int_0^\tau b(M(t-a)e^{\int_0^a -(d_Y+\beta J(t-s))ds}\right) > 0.$$

We then use the variation-of-constants formula in consecutive interval $[0, \tau], [\tau, 2\tau], \ldots$ to obtain

$$M(t) > 0$$

for $t \geq 0$.

When $\tau = 0$, the above system reduces to the ODE system

$$\begin{cases} \frac{dJ}{dt} = \beta MJ - d_I J, \\ \frac{dM}{dt} = -\beta MJ - d_S M + b(M). \end{cases} \tag{4.10}$$

Obviously, the three equilibria reduces to $E_1 = (0, 0)$, $E_2 = (0, M^0_{\max})$, and $E_3 = (J^0_*, M^0_*) = (\frac{1}{\beta}(-d_S + b_0 e^{-\bar{a}d_I/\beta}), \frac{d_I}{\beta})$, and we have $J^0_* > 0$ if and only if $C_0(0) = \frac{d_I}{\beta M^0_{\max}} < 1$.

THEOREM 4.1. *When* $\tau = 0$ *and* $C_0(0) = \frac{d_I}{\beta M^0_{\max}} < 1$*, system* (4.9) *has a heteroclinic orbit* $(J_0(t), M_0(t))$ *connecting* E_2 *and* E_3*.*

Proof. First, we prove that the third equilibrium E_3 is a global attractor in the sense that it attracts every positive solution of (4.9) when $\tau = 0$. To see this, define a Lyapunov function as

$$V = \left[M - M^0_* - M^0_* \log \frac{M}{M^0_*}\right] + \left[J - J^0_* - J^0_* \log \frac{J}{J^0_*}\right].$$

Differentiating the function V along the solution (4.10) yields

$$\frac{dV}{dt} = b_0(e^{-\bar{a}M} - e^{-\bar{a}d_I/\beta})\left(M - \frac{d_I}{\beta}\right) < 0$$

provided that $M \neq d_I/\beta$. This means that the equilibrium E_3 is a global attractor by LaSalle's well-known invariance principle. Linearizing (4.10) around E_2 gives

$$\begin{pmatrix} \beta M^0_{\max}(1 - C_0(0)) - \lambda & 0 \\ -\beta M^0_{\max} & -d_S + b'(M^0_{\max}) - \lambda \end{pmatrix}$$

and the following characteristic equation:

$$(\beta M^0_{\max} - d_I - \lambda)(-d_S + b'(M^0_{\max}) - \lambda) = 0. \tag{4.11}$$

For $\lambda_1 = \beta M^0_{\max}(1 - C_0(0)) > 0$, we find an eigenvector $\vec{v}_1$ which points into the first quadrant of the $J - M$ plane. Therefore, the solution starting from the local unstable manifold of E_2 along the $\vec{v}_1$ direction will permanently stay in the first quadrant and tends to $(J^0_*, M^0_*)^T$ as $t \to \infty$ due to the global attractivity of E_3. This completes the proof.

When $\tau \neq 0$, deriving the global stability of the equilibrium E_3 is nontrivial. Even for the local stability, providing an explicit criterion is not easy. To demonstrate this, we linearize (4.9) around E_3 to obtain

$$\begin{aligned} \frac{dJ}{dt} = {} & \left(\beta M^\tau_* - d_I + \beta b(M^\tau_*)\frac{1 - e^{-(d_Y + \beta J^\tau_*)\tau}}{(d_Y + \beta J^\tau_*)}\right) J \\ & - \beta^2 J^\tau_* b(M^\tau_*) \int_0^\tau e^{-(d_Y + \beta J^\tau_*)a} \int_0^a J(t-s)\,ds\,da + \beta J^\tau_* M \\ & + \beta J^\tau_* b'(M^\tau_*) \int_0^\tau M(t-a) e^{-(d_Y + \beta J^\tau_*)a}\,da \end{aligned} \tag{4.12}$$

and

$$\begin{aligned} \frac{dM}{dt} = {} & -\beta M^\tau_* J - \beta b(M^\tau_*) e^{-(d_Y + \beta J^\tau_*)\tau} \int_0^\tau J(t-s)\,ds \\ & + \beta J^\tau_* M - d_S M + b'(M^\tau_*) e^{-(d_Y + \beta J^\tau_*)\tau} M(t - \tau). \end{aligned} \tag{4.13}$$

In order to understand the linear system (4.12) and (4.13), we first consider the special case when $\tau = 0$. In this case the characteristic equation is given by

$$\lambda^2 + (\beta J^0_* + d_S - b'(M^0_*))\lambda + \beta^2 M^0_* J^0_* = 0.$$

Since (4.10) yields $\beta J_*^0 + d_S = b(M_*^0)/M_*^0$, the above equation becomes

$$\lambda^2 + \bar{a}b_0 e^{-\bar{a}M_*^0}\lambda + \beta^2 M_*^0 J_*^0 = 0.$$

Hence, the eigenvalues are given by

$$\lambda_{1,2} = \frac{-\bar{a}b_0 e^{-\bar{a}M_*^0} \pm \sqrt{(\bar{a}b_0)^2 e^{-2\bar{a}M_*^0} - 4\beta^2 M_*^0 J_*^0}}{2}, \tag{4.14}$$

the real parts of which are negative as long as $J_*^0 > 0$ (or, equivalently, $C_0(0) < 1$). Because λ depends continuously on the parameter τ, we conclude that there exists a number $\tau_1 > 0$ so that when $\tau < \tau_1$, all the eigenvalues of the linearization at E_3 have a negative real part.

At the equilibrium E_2 when $\tau \neq 0$, we have the following characteristic equation:

$$(1 - C_0(\tau) - \lambda)\left(-d_S + b'(M_{\max}^\tau)e^{-d_Y\tau}e^{-\lambda\tau} - \beta M_{\max}^\tau \lambda\right) = 0. \tag{4.15}$$

It can be shown easily that there exists a constant τ_2 so that equilibrium E_2 is hyperbolic for $C(\tau) < 1$ and $\tau \in [0, \tau_2)$, where τ_2 is the first positive number satisfying

$$|b'(M_{\max}^{\tau_2})e^{-dy\tau_2}| > |d_S|, \quad \text{and} \quad \tau_2 = \frac{\pi - \arccos \frac{d_s}{|b'(M_{\max}^{\tau_2})e^{-d_y\tau_2}|}}{\sqrt{(b'(M_{\max}^{\tau_2})e^{-d_y\tau_2})^2 - d_s^2}}. \tag{4.16}$$

We should mention that formula (4.16) can be obtained by the well-known Hopf bifurcation theory, and that if there is no τ_2 satisfying (4.16), then we assume that $\tau_2 = \infty$.

With the above preparation, we are now ready to prove a theorem concerning the heteroclinic connection for (4.9) when $\tau \neq 0$. To present our result, we first introduce some notation.

- For a vector $x \in R^2$, we denote $||x|| = ||x||_{R^2}$.
- Let $X(R, R^2)$ be the space of continuous and bounded functions from R to R^2 equipped with the standard norm $||\phi|| = \sup\{||\phi(t)||,\, t \in R\}$.
- Let $X^1 = X^1(R, R^2) = \{\phi \in X : \phi' \in X\}$.
- Let $X_0 = \{\phi \in X : \lim_{t\to\pm\infty} \phi = 0\}$ and $X_0^1 = \{\phi \in X_0 : \phi' \in X_0\}$.

Under the conditions in Theorem 3.1, we have the following result.

THEOREM 4.2. *Assume that* $C_0(\tau) < 1$. *Then there exists a positive constant* δ *so that for* $0 \le \tau \le \delta$, *equation* (4.9) *has a heteroclinic orbit* $(J(t), M(t))$ *which connects* E_2 *and* E_3.

Proof. We first introduce the transformation

$$U = \frac{J(t)}{J_*^\tau}, \quad V = \frac{M_{\max}^\tau - M}{M_{\max}^\tau - M_*^\tau}$$

to get rid of the τ-dependence of E_2 and E_3. Substituting this into (4.9), we have the following system for U and V:

$$\begin{cases} \frac{dU}{dt} = \beta(M_{\max}^\tau - V(M_{\max}^\tau - M_*^\tau))U - d_I U \\ \qquad + \beta U \int_0^\tau \bar{b}(V(t-a)e^{\int_0^a -(d_Y + \beta J_*^\tau U(t-s))ds}da, \\ \\ \frac{dV}{dt} = \frac{\beta J_*^\tau (M_{\max}^\tau - V(M_{\max}^\tau - M_*^\tau))U}{M_{\max}^\tau - M_*^\tau} + \frac{d_S(M_{\max}^\tau - V(M_{\max}^\tau - M_*^\tau))}{M_{\max}^\tau - M_*^\tau} \\ \qquad - \frac{\bar{b}(V(t-\tau)}{M_{\max}^\tau - M_*^\tau} e^{\int_{t-\tau}^t -(d_Y + \beta J_*^\tau U(s))ds}, \end{cases} \tag{4.17}$$

where $\bar{b}(V(t-\tau)) = b(M^\tau_{\max} - V(M^\tau_{\max} - M^\tau_*))$. Equation (4.17) has two equilibria $E_2 := (0,0)$ and $E_3 := (1,1)$. In particular when $\tau = 0$, we know from Theorem 4.1 that there exists a heteroclinic solution $(U_0(t), V_0(t))$ that connects two points E_2 and E_3 and satisfies

$$\text{(4.18)} \quad \begin{cases} \frac{dU_0}{dt} = F_1(u,v)|_{u=U_0,v=V_0} = \beta(M^0_{\max} - V_0(M^0_{\max} - M^0_*))U_0 - d_I U_0, \\ \frac{dV_0}{dt} = F_2(u,v)|_{u=U_0,v=V_0} = \frac{\beta J^0_*(M^0_{\max} - V_0(M^0_{\max} - M^0_*))V_0}{M^0_{\max} - M^0_*} + \frac{d_S(M^0_{\max} - V(M^0_{\max} - M^0_*))}{M^0_{\max} - M^0_*} \\ \qquad\qquad - \frac{\bar{b}(V_0(t))}{M^0_{\max} - M^0_*}. \end{cases}$$

Note that the relation between $M^\tau_{\max}$ and $M^0_{\max}$, M^τ_* and M^0_*, and J^τ_* and J^0_* can be described as

$$\text{(4.19)} \qquad M^\tau_{\max} = M^0_{\max} + O(\tau), \quad M^\tau_* = M^0_* + O(\tau), \quad J^\tau_* = J^0_* + O(\tau).$$

We now show that there exists a constant δ such that (4.17) has a heteroclinic orbit $(U(t), V(t))$ connecting two points E_2 and E_3 provided $\tau < \delta$.

First of all, we let $W_1 = U - U_0$ and $W_2 = V - V_0$ and obtain the following equation for the remainder (W_1, W_2):

$$\text{(4.20)} \qquad \begin{cases} \frac{dW_1}{dt} = \frac{\partial F_1(U_0,V_0)}{\partial u} W_1 + \frac{\partial F_1(U_0,V_0)}{\partial v} W_2 + \Gamma_1(t,\tau,W_1,W_2), \\ \frac{dW_2}{dt} = \frac{\partial F_2(U_0,V_0)}{\partial u} W_1 + \frac{\partial F_2(U_0,V_0)}{\partial v} W_2 + \Gamma_2(t,\tau,W_1,W_2), \end{cases}$$

where

$$\begin{aligned} &\Gamma_1(t,\tau,W_1,W_2) \\ &= \beta(M_{\max} - (V_0 + W_2)(M^\tau_{\max} - M^\tau_*))(U_0 + W_1) - d_I(U_0 + W_1) \\ &\quad + \beta(U_0 + W_1)\int_0^\tau \bar{b}(V_0(t-a) + W_1(t-a)) e^{\int_0^a -(d_Y + \beta J^\tau_*(U_0(t-s) + W(t-s)))ds} da \\ \text{(4.21)} &\quad - F_1(U_0,V_0) - \left(\frac{\partial F_1(U_0,V_0)}{\partial u} W_1 + \frac{\partial F_1(U_0,V_0)}{\partial v} W_2\right) \end{aligned}$$

and

$$\begin{aligned} \Gamma_2(t,\tau,W_1,W_2) = &\frac{\beta J^\tau_*(M^\tau_{\max} - (V_0 + W_2)(M^\tau_{\max} - M^\tau_*))(U_0 + W_1)}{M^\tau_{\max} - M^\tau_*} \\ \text{(4.22)} \qquad &+ \frac{d_S(M^\tau_{\max} - (V_0 + W_2)(M^\tau_{\max} - M^\tau_*))}{M^\tau_{\max} - M^\tau_*} \\ &- \frac{\bar{b}(V_0(t-\tau) + W_2(t-\tau))}{M^\tau_{\max} - M^\tau_*} e^{\int_{t-\tau}^t -(d_Y + \beta J^\tau_*(U_0(s) + W_1(s)))ds} \\ &- F_2(U_0,V_0) - \left(\frac{\partial F_2(U_0,V_0)}{\partial u} W_1 + \frac{\partial F_2(U_0,V_0)}{\partial v} W_2\right). \end{aligned}$$

Define an operator $T : \Psi \in X^1 \to X$ from the homogeneous part of (4.20) as follows:

$$\text{(4.23)} \qquad T\Psi = \Psi' - A(t)\Psi, \ t \in R,$$

where

$$A(t) = \begin{pmatrix} \frac{\partial F_1(U_0(t),V_0(t))}{\partial u} & \frac{\partial F_1(U_0(t),V_0(t))}{\partial v} \\ \frac{\partial F_2(U_0(t),V_0(t))}{\partial u} & \frac{\partial F_2(U_0(t),V_0(t))}{\partial v} \end{pmatrix}.$$

We remark that $(U_0(t), V_0(t))$ tends, respectively, to E_2 and E_3 when $t \to -\infty$ and $t \to \infty$. This means that the linear operator T is asymptotically hyperbolic as $t \to \pm\infty$ in the sense that

$$\Psi' - A(-\infty)\Psi = 0 \quad \text{and} \quad \Psi' - A(\infty)\Psi = 0$$

are hyperbolic due to (4.11) and (4.14). Furthermore, we know that every eigenvalue for the linear equation $\Psi' - A(\infty)\Psi = 0$ has a negative real part. Define the formal adjoint equation of $T\Psi = \Psi' - A(t)\Psi = 0$ as

$$\Phi' + A^T(t)\Phi = 0, \quad t \in R. \tag{4.24}$$

We now divide our proof into five steps.

Step 1. We claim that if $\Phi \in X$ is a solution of (4.24) and Φ is C^1-smooth, then $\Phi = 0$. Moreover, we have $R(T) = X$, where $R(T)$ is the range of T.

Indeed, assuming to the contrary that Φ is not zero at some point t_0, then we can solve (4.24) to obtain

$$\Phi(t) = \Phi(t_0)e^{-\int_{t_0}^{t} A^T(t)dt}.$$

Since when $t \to \infty$, $A^T(t)$ tends to $A^T(\infty)$ whose eigenvalues are negative, we deduce that

$$\lim_{t\to\infty} \Phi(t) = \infty,$$

which contradicts the fact that Φ is bounded.

By the classical Fredholm theory, this claim means further that $R(T) = X$ in the sense that for any $\Theta \in X$, there exists $\Psi \in X^1$ so that

$$T\Psi = \Theta.$$

Step 2. Let $\Theta \in X_0$ be given. If Ψ is a bounded solution of $T\Psi = \Theta$, then $\Psi \in X_0^1$. In fact, we need to show only that

$$\lim_{t\to\pm\infty} \Psi(t) = 0.$$

Actually when $t \to \infty$, equation

$$\Psi' - A(t)\Psi = \Theta \tag{4.25}$$

asymptotically tends to

$$\Psi' - A(\infty)\Psi = 0. \tag{4.26}$$

Note that for (4.26), the ω-limit set of every bounded solution is just the critical point $\Psi = 0$. Using the result from [21] or [18], every bounded solution of (4.25) also satisfies

$$\lim_{t\to\infty} \Psi(t) = 0.$$

When inverting the time from $-t$ to t, we can similarly prove that

$$\lim_{t\to-\infty}\Psi(t)=0.$$

Step 3. We rewrite (4.20) as

$$W'(t)+W=W+A(t)W+\Gamma(t), \tag{4.27}$$

where

$$W=(W_1,W_2)^T,\ \ \Gamma(t)=(\Gamma_1(s,\tau,W_1,W_2),\Gamma_2(s,\tau,W_1,W_2))^T.$$

Changing (4.27) into an integral equation gives

$$W(t)=\int_{-\infty}^{t}e^{-(t-s)I}(W(s)+A(s)W(s)+\Gamma(s))ds, \tag{4.28}$$

where I is the 2×2 identity matrix and $W(t)=(W_1(t),W_2(t))^T$.

Define a linear operator $L:X_0\to X_0$ as follows:

$$L(W)(t)=W(t)-\int_{-\infty}^{t}e^{-(t-s)I}(W(s)+A(s)W(s))ds,\ W\in X_0.$$

Obviously $L(W)\in X_0$ if $W\in X_0$. Now we prove that $R(L)=X_0$, that is, for each $Z\in X_0$, we can have a $W\in X_0$ so that

$$W(t)-\int_{-\infty}^{t}e^{-(t-s)I}(W(s)+A(s)W(s))ds=Z(t).$$

To see this, assuming that $\xi=W-Z$, we obtain an equation for ξ as follows:

$$\xi(t)=\int_{-\infty}^{t}e^{-(t-s)I}(\xi(s)+A(s)\xi(s))ds+\int_{-\infty}^{t}e^{-(t-s)I}(Z(s)+A(s)Z(s))ds.$$

Differentiating both sides yields

$$T(\xi)(t)=\xi'(t)-A(t)\xi(t)=Z(t)+A(t)Z(t). \tag{4.29}$$

Using the results that $R(T)=X$ in Step 2, one can obtain that there exists a solution ξ for (4.29) and $\xi\in X_0^1$. Returning to the variable W, we have $W=\xi+Z\in X_0$.

Step 4. Let $N(L)$ be the null space of the operator L. Define $N^{\perp}(L)=X_0/N(L)$. It is clear that $N^{\perp}(L)$ is a Banach space. If we let $S=L|_{N^{\perp}(L)}$ be the restriction of L on $N^{\perp}(L)$, then $S:N^{\perp}(L)\to X_0$ is one-to-one and onto. By the well-known Banach inverse operator theorem, we have that $S^{-1}:X_0\to X_0/N(L)$ is a linear bound operator.

Step 5. When L is restricted on $N^{\perp}(L)$, equation (4.28) can be written as

$$S(W)(t)=\int_{-\infty}^{t}e^{-(t-s)I}\Gamma(s,W,\tau)ds$$

or

$$W(t)=S^{-1}\left(\int_{-\infty}^{t}e^{-(t-s)I}\Gamma(s,W,\tau)ds\right). \tag{4.30}$$

The term $\int_{-\infty}^{t} e^{-(t-s)I}\Gamma(s)ds$ on the right-hand side can be estimated. Actually when τ is small and $W \in X_0^1$, from (4.19), (4.21), and (4.22), we have the following estimations:

$$\left|\int_{-\infty}^{t} e^{-(t-s)}\Gamma_1(s)ds\right| = O(\tau) + O(\tau||W||_{X_0}) + O(||W||_{X_0}^2) \tag{4.31}$$

and

$$\left|\int_{-\infty}^{t} e^{-(t-s)}\Gamma_2(s)ds\right| = O(\tau) + O(\tau||W||_{X_0}) + O(||W||_{X_0}^2) \tag{4.32}$$

as $\tau \to 0$ and $||W|| \to 0$. To derive (4.31) and (4.32), we have made use of the following result:

$$\int_{-\infty}^{t} e^{-(t-s)}\left(W_i(s-\tau)) - W_i(s)\right)ds = O(\tau||W||), \quad i = 1, 2. \tag{4.33}$$

Actually, if $W \in X_0^1$, by exchanging the order integration and by integration by parts, we have

$$\begin{aligned}
&\left|\int_{-\infty}^{t} e^{-(t-s)}\big(W_i(s-\tau) - W_i(s)\big)ds\right| \\
&= \left|\tau\int_{-\infty}^{t} e^{-(t-s)}\int_0^1 W_i'(s-\tau u)duds\right| \\
&= \left|\tau\int_0^1\int_{-\infty}^{t} e^{-(t-s)}W_i'(s-\tau u)dsdu\right| \\
&= \left|\tau\int_0^1\left(W_i(t-\tau u) - \int_{-\infty}^{t} e^{-(t-s)}W_i(s-\tau u)ds\right)du\right| \\
&= O(\tau||W||), \ i = 1, 2,
\end{aligned}$$

leading to (4.33). Using the fact that X_0^1 is dense in X_0, we conclude that (4.31) and (4.32) hold for any $W \in X_0$.

Let $B(\sigma)$ denote the closed ball in X_0 with radius σ and center at the origin. Since the norm $||S^{-1}||$ is independent of τ, it follows from (4.31) and (4.32) that there exist $\sigma > 0$, $\delta > 0$, and $0 < \rho < 1$ such that for all $\tau \in (0, \delta]$ and $\varphi, \psi, W \in B(\sigma) \subset X_0$,

$$\left|\left|S^{-1}\left(\int_{-\infty}^{t} e^{-(t-s)I}\Gamma(s, W, \tau)ds\right)\right|\right| \le \frac{1}{3}\left(||W|| + \sigma\right)$$

and

$$\left|\left|S^{-1}\left(\int_{-\infty}^{t} e^{-(t-s)I}\Gamma(s, \varphi, \tau)ds\right) - S^{-1}\left(\int_{-\infty}^{t} e^{-(t-s)I}\Gamma(s, \psi, \tau)ds\right)\right|\right| \le \rho||\varphi - \psi||.$$

Hence, $S^{-1}\left(\int_{-\infty}^{t} e^{-(t-s)I}\Gamma(s, W, \tau)ds\right)$ is a uniform contractive mapping of $W \in X_0 \cap B(\sigma)$. By using the classical fixed point theorem, it follows that for $\tau \in [0, \delta]$, (4.30) has a unique solution $W \in X_0/N(L)$. Returning to the original variable, we get that $(W_1 + U_0, W_2 + V_0)$ is a heteroclinic connection between E_2 and E_3. This completes our proof.

REMARK 4.3. *When $\tau \geq \delta$, we can rescale the time variable $t \to t\tau$ to obtain*

$$\begin{cases} \frac{dJ}{dt} = \tau\beta MJ - \tau d_I J + \tau\beta J \int_0^1 b(M(t-a)e^{\int_0^a -(d_Y+\beta J(t-s))ds}da, \\ \frac{dM}{dt} = -\tau\beta MJ - \tau d_s M + \tau b(M(t-1))e^{\int_{t-1}^t -(d_Y+\beta J(s))ds}. \end{cases} \tag{4.34}$$

At $\tau = \delta$, by Theorem 4.2, equation (4.34) has a heteroclinic connection. We can as well show that if $C_0(\tau) < 1$, there exists a constant δ_1, $\delta < \delta_1 < \min\{\tau_1, \tau_2\}$, such that if $\delta \leq \tau \leq \delta_1$, equation (4.9) has a heteroclinic orbit $(J(t), M(t))$ which connects E_2 and E_3. The proof is the same as that of Theorem 4.2. The method is referred as to a homotopy approach (see [5]); namely, we view τ as a varying parameter and start with (4.34), and extend the result from δ to $\delta_1 \in (\delta, \min\{\tau_1, \tau_2\})$ by replacing the arguments in Step 1 to Step 5 by those of the parallel theory in linear delay differential equations. It would be interesting to see how far this homotopy argument can be applied to push the upper bound τ.

4.2.2. Traveling wavefronts with large wave speeds.

We now consider the reaction diffusion system (2.7)–(2.8) for which we will use Theorem 1.1 in [8] to give traveling wavefronts in the case when the wave speed c is large. The main idea of this result is simple: if the nondiffusive equation has a heteroclinic connection between E_2 and E_3, then the diffusive system has a family of traveling wavefronts from E_2 to E_3 with large wave speeds.

THEOREM 4.4. *Assume that $\tau \leq \delta$. Then there exists a $c^* > 0$ such that for any $c \geq c^*$, system (2.7)–(2.8) has a traveling wavefront $(J(t,x), W(t,x)) = (u(ct+x), v(ct+x))$ which connects E_2 and E_3.*

Proof. First we observe that if there is no diffusion, that is, if $D_I = 0$ and $D_Y = 0$, our equations (2.7)–(2.8) reduce to (4.9). When $\tau \leq \delta$, the equilibria E_2 and E_3 are hyperbolic, and, in particular, all the eigenvalues to E_3 have negative real parts. From Theorem 4.2, we know that when $\tau \leq \delta$, equation (4.9) has a heteroclinic connection. So conditions (H_1), (H_2), and (H_3) in [8, Theorem 1.1] are satisfied. Last, for our kernel function $f(x) = \frac{1}{\sqrt{4\pi}}\exp(-\frac{y^2}{4})$, it is easy to see that

$$\frac{1}{\sqrt{4\pi}}\int_{-\infty}^{\infty}\exp\left(-\frac{y^2}{4}\right)|y|dy < \infty.$$

So all conditions in [8, Theorem 1.1] are satisfied. Hence by [8, Theorem 1.1], we conclude that there exists a $c^* > 0$ so that for any $c > c^*$, system (2.7)–(2.8) has a traveling wavefront $(J(t,x), W(t,x)) = (u(ct+x),\ v(ct+x))$ which connects E_2 and E_3.

4.3. Numerical simulations.

In this subsection, we will numerically study the traveling wavefronts of our model (2.7)–(2.8).

We first describe our numerical methods. We give initial data

$$J(s,x) = j_0(s,x),\ M(s,x) = m_0(s,x),\ -\tau \leq s \leq 0,\ x \in [-L, L],$$

and solve (2.7) and (2.8) to obtain $(J(t,x), M(t,x))$ in a sufficiently large interval $[-L, L]$ for $t \geq 0$ and some $L > 0$. As usual, in the process of finding numerical solutions, we take the homogeneous Neumann boundary conditions at the end points $x = \pm L$. Depending on other parameters in our model and the solution patterns, we may adjust the parameter L from 100 to 1000 so as to present a clear view of our graphs. We take a constant h satisfying

$$M_*^\tau < h < M_{\max}^\tau.$$

For any fixed t, we find the first position $x = z(t, h) > -L$ so that

$$M(t, z(t, h)) = h.$$

Choose a sequence $\{t_j\}_{j=1}^{\infty}$, and consider

$$(J(t_j, x + z(t_j, h)), M(t_j, x + z(t_j, h))). \tag{4.35}$$

If the numerical solutions $(J(t_j, x + z(t_j, h)),\ M(t_j, x + z(t_j, h)))$, $j = 1, 2, 3, \ldots,$ converge uniformly to a nonconstant function $(J(\cdot), M(\cdot))$ which satisfies the boundary conditions

$$\lim_{\xi\to-\infty}(J(\xi), M(\xi)) = E_2 \ \text{ and } \ \lim_{\xi\to+\infty}(J(\xi), M(\xi)) = E_3,$$

then the limit $(J(\cdot), M(\cdot))$ is viewed as a traveling wavefront. Theoretically, this process has also been used to prove the existence of traveling wavefronts for certain monotone dynamics; see [4]. The limit

$$\lim_{j\to\infty} \frac{z(t_{j+1}, h) - z(t_j, h)}{t_{j+1} - t_j} \tag{4.36}$$

is correspondingly thought of as the asymptotic wave speed of the traveling wavefront.

We now discuss the parameter values from relevant references [2, 15, 16]. First of all, we note that [16, p. 126] suggests 9 to 12 months for the maturation time, and we will therefore restrict our attention to the range of τ to $[0.5, 0.8]$ (year). The diffusion coefficient $D_I = 60$ km^2/year will be used, based on the value in [15].

For red foxes, the average per capita intrinsic death rate is 0.5 year^{-1} [2], so we take $d_S = 0.5$ year^{-1}. Since it is known that the death rate of juvenile foxes is greater than that of adult foxes, we take $d_Y = 0.8$ year^{-1} [16, p. 127].

An infective fox first goes through an incubation period that can vary from 12 to 110 days. A life expectancy of about 35 days gives d_I as approximately 10 year^{-1}. For the transmission coefficient, we derive $\beta = 10$ km^2/year by using formula (5) in [15]. The number of cubs in a litter ranges from 1 to 10, with a mean of 4.7 in Europe [2, 17, 16, 30, 31]. Sex ratios are in general close to unity at birth, and the pregnancy rate is in the region of 90% [17, 16], with a further 10% of vixens failing to produce offspring [2]. In view of this information, the average per capita birth rate b_0 is taken to be 1.9 year^{-1}.

We now calculate the minimal wave speed $c_{\min}$. The carrying capacity S_0 is assumed to be 2 foxes per km^2, as in Figure 4 of [2], and it is the sum of the population of the immature and the adult foxes when they reach the stable equilibria in the disease-free case, that is,

$$S_0 = M_{\max}^{\tau} + b(M_{\max}^{\tau})\frac{1 - e^{-d_Y\tau}}{d_Y}.$$

We need further information in order to estimate the maturation time, which is related to the parameter $\bar{a}$ in the birth function. By Table 26 in [16], the number of adult foxes per km^2 varies from 0.5 to 1.8, and the number of litters found per km^2 varies from 0.16 to 0.6. Thus we take the mean value of the ratio of the adult foxes to the litter foxes as 1.15 : 0.38. Using the facts $S_0 = M_{\max}^{\tau} + b(M_{\max}^{\tau})\frac{1-e^{-d_Y\tau}}{d_Y} = 2$ and

$$M_{\max}^{\tau} : b(M_{\max}^{\tau})\frac{1 - e^{-d_Y\tau}}{d_Y} = 1.15 : 0.38,$$

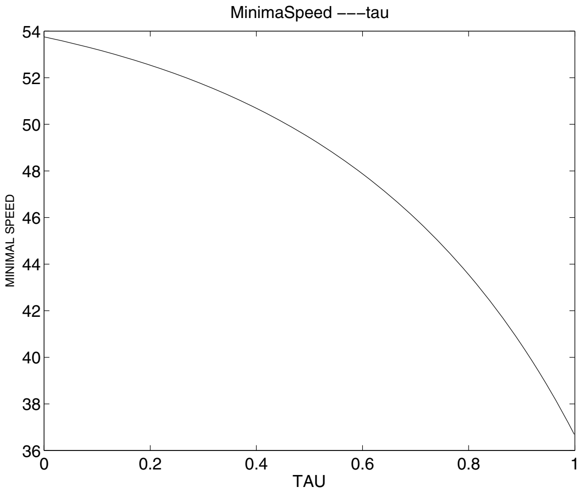

FIG. 1. *Graph of* $c_{min}(\tau)$ *as a decreasing function of* τ.

we calculate that the carrying capacity is 2 when the parameters $\tau = 0.5305$ and

$$\bar{a} = \frac{1}{S_0}\left(1 + \frac{d_S}{d_Y}(e^{d_Y\tau} - 1)\right)\ln\frac{b_0}{d_S e^{d_Y\tau}} = 0.6057.$$

The result calculated in [15] gives the minimal speed $c_{old} = 48.9898$ km/year. In our calculation, $c_{\min}$ is a decreasing function of τ, with $c_{\min} = 53.757$ km/year if $\tau = 0$; and

$$\begin{aligned} c_{\min} &= 2\sqrt{\beta M^{\tau}_{\max} D_I}\sqrt{1 - \frac{d_I}{\beta M^{\tau}_{\max}} + \frac{b(M^{\tau}_{\max})}{M^{\tau}_{\max} d_Y}(1 - e^{-d_Y\tau})} \\ &= 2\sqrt{\beta D_I}\sqrt{M^{\tau}_{\max} + b(M^{\tau}_{\max})\frac{(1 - e^{-d_Y\tau})}{d_Y} - \frac{d_I}{\beta}} \\ &= 43.549 \text{ km/year} \end{aligned}$$

if $\tau = 0.8$. The graph of $c_{\min}$ as a function of τ is given in Figure 1.

To describe numerically the solution patterns, we first scale the variable x by $\sqrt{D_I}x$ so that the diffusion rate for rabid foxes in our simulations becomes constant 1. The length L of the half interval is taken to be 300. We use the the Neumann boundary condition and the initial values

$$M(t,x) = \begin{cases} M^{\tau}_{\max}, & -300 \le x \le 150,\ \tau \le t \le 0, \\ 0.6, & 150 < x \le 300,\ \tau \le t \le 0, \end{cases}$$

and

$$J(t,x) = \begin{cases} 0, & -300 \le x \le 150,\ \tau \le t \le 0, \\ 0.05, & 150 < x \le 300,\ \tau \le t \le 0. \end{cases}$$

A finite difference method coupled with iterative techniques is used in our numerical approximation via the software MATLAB, and the numerical result when $D_Y = 0$

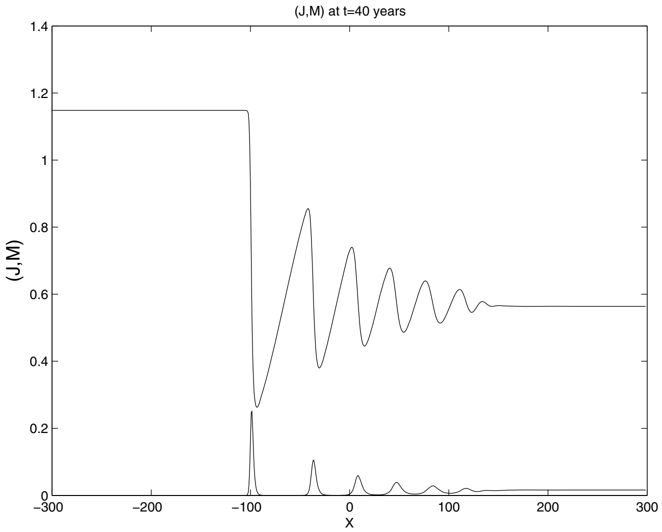

FIG. 2. *Graph of solutions M (upper) and J (lower) at $t = 40$ years, here $\tau = 0.8$, $d_I = 10$, $d_S = 0.5$, $d_Y = 0.8$, $S_0 = 2$, $b_0 = 2$, and $\beta = 10$. There exist long wave tails for both J and M.*

and $\tau = 0.8$ shows that the solution stabilizes to a traveling wavefront with minimal speed 43.549 km/year. The numerical result when $t = 40$ years is shown in Figure 2.

Fixing other parameters, we carry out simulations in the cases when $D_Y = 0.25D_I$ and $D_Y = D_I$. It is found that in both cases, the spreading speeds stabilize to the same minimal wave speed 43.549 km/year and the change of the diffusion rate D_Y has impact only on the amplitudes and frequencies of oscillation for the long tail in the traveling wave, and its impact on the shape of the solution is less apparent if we confine the value D_Y/D_I to the interval $[0, 1]$. This result is what we should expect because the maturation time τ is relatively small that the contribution of D_Y to the pattern of solutions is limited. See Figure 3 for the comparison of M up to $t = 40$ years between the case $D_Y/D_I = 0$ and the case $D_Y/D_I = 1$.

Our simulations agree with the theoretical analysis in the above sections that the minimal wave speed of rabies depends on the maturation time τ, while the amplitude and frequencies of oscillations of the long tail are influenced also by the diffusion rate of juvenile foxes.

We conclude with a remark about the limitation of this work. We assumed two age classes and homogeneity within each age class. Namely, many parameters in the model such as death and diffusion rates and force of infection are all assumed to be constants that depend on the age class but are independent of the precise age. This is certainly only an approximation to the biological reality, and parameter values should be thought of as some sort of averages during the whole juvenile or adult period. For example, newborn susceptible juveniles would not be moving at all and the search for new territories by juveniles must happen only during a particular phase of childhood. In [16], it was noted that breeding season varies from region to region but usually begins early in the year, then in the autumn following birth the pups of the litter will disperse to their own territories. Ideally, we should use age-dependent coefficients and parameters, and hence the model would become an age-structured reaction diffusion equation that cannot be reduced to a system of reaction diffusion equations with delayed nonlocal nonlinearities.

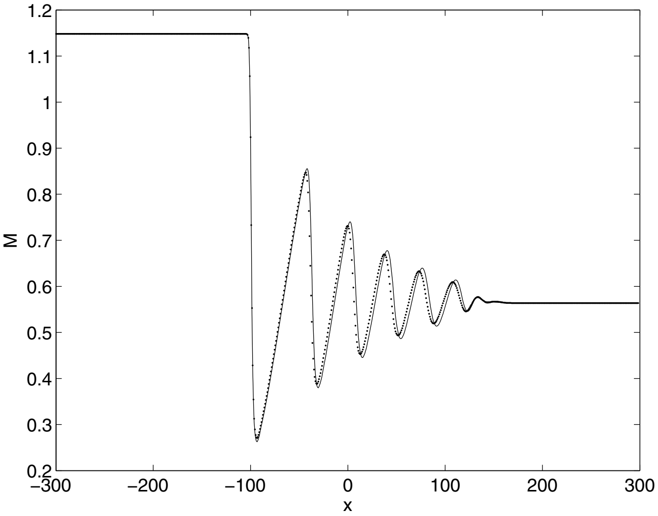

FIG. 3. *Graph of solutions M for $D_Y/D_I = 0$ (solid line) and $D_Y/D_I = 1$ (dashed line) where $t = 40$ years.*

REFERENCES

[1] L. J. S. Allen, D. A. Flores, R. K. Ratnayake, and J. R. Herbold, *Discrete-time deterministic and stochastic models for the spread of rabies*, Appl. Math. Comput., 132 (2002), pp. 271–292.

[2] R. M. Anderson, H. C. Jackson, R. M. May, and A. M. Smith, *Population dynamics of fox rabies in Europe*, Nature, 289 (1981), pp. 765–771.

[3] N. F. Britton, *Spatial structures and periodic travelling waves in an integro-differential reaction-diffusion population model*, SIAM J. Appl. Math., 50 (1990), pp. 1663–1688.

[4] X. Chen, *Existence, uniqueness, and asymptotic stability of traveling waves in nonlocal evolution equations*, Adv. Differential Equations, 2 (1997), pp. 125–160.

[5] S.-N. Chow, X.-B. Lin, and J. Mallet-Paret, *Transition layers for singularly perturbed delay differential equations with monotone nonlinearities*, J. Dynam. Differential Equations, 1 (1989), pp. 3–43.

[6] P. Daszak, A. A. Cunningham, and A. D. Hyatt, *Wildlife ecology—Emerging infectious diseases of wildlife—Threats to biodiversity and human health*, Science, 287 (2000), pp. 443–449.

[7] S. R. Dunbar, *Travelling wave solutions of diffusive Lotka-Volterra equations*, J. Math. Biol., 17 (1983), pp. 11–32.

[8] T. Faria, W. Huang, and J. Wu, *Traveling waves for delayed reaction-diffusion equations with non-local response*, Proc. Roy. Soc. London Ser. A, 462 (2006), pp. 229–261.

[9] S. A. Gourley and N. F. Britton, *A predator prey reaction diffusion system with nonlocal effects*, J. Math. Biol., 34 (1996), pp. 297–333.

[10] S. A. Gourley, J. W.-H. So, and J. Wu, *Non-locality of reaction-diffusion equations induced by delay: Biological modeling and nonlinear dynamics*, J. Math. Sci. (N.Y.), 124 (2004), pp. 5119–5153.

[11] S. A. Gourley and J. Wu, *Delayed reaction diffusion equations: Theory and applications to biological invasion and disease spread*, in Nonlinear Dynamics and Evolution Equations, H. Brunner, X. Zhao, and X. Zou, eds., AMS, Providence, RI, 2006, pp. 137–200.

[12] W. S. C. Gurney, S. P. Blythe, and R. M. Nisbet, *Nicholson's blowflies revisited*, Nature, 287 (1980), pp. 17–21.

[13] J. K. Hale and X.-B. Lin, *Heteroclinic orbits for retarded functional-differential equations*, J. Differential Equations, 65 (1986), pp. 175–202.

[14] A. Kallen, *Thresholds and travelling waves in an epidemic model for rabies*, Nonlinear Anal., 8 (1984), pp. 851–856.

[15] A. Kallen, P. Arcuri, and J. D. Murray, *A simple model for the spatial spread and control of rabies*, J. Theoret. Biol., 116 (1985), pp. 377–393.

[16] H. G. Lloyd, *The Red Fox*, B. T. Batsford Ltd., London, 1980.

[17] D. W. MacDonald, *Rabies and Wildlife. A Biologist's Perspective*, Oxford University Press, Oxford, UK, 1980.

[18] L. Markus, *Asymptotically autonomous differential systems*, in Contributions to the Theory of Nonlinear Oscillations, Vol. 3, Ann. of Math. Stud. 36, Princeton University Press, Princeton, NJ, 1956, pp. 17–29.

[19] R. H. Martin, Jr., and H. L. Smith, *Abstract functional-differential equations and reaction-diffusion systems*, Trans. Amer. Math. Soc., 321 (1990), pp. 1–44.

[20] J. A. J. Metz and O. Diekmann, eds., *The Dynamics of Physiologically Structured Populations*, papers from the colloquium held in Amsterdam, 1983, Lecture Notes in Biomath. 68, Springer-Verlag, Berlin, 1986.

[21] K. Mischaikow, H. Smith, and H. R. Thieme, *Asymptotically autonomous semiflows: Chain recurrence and Lyapunov functions*, Trans. Amer. Math. Soc., 347 (1995), pp. 1669–1685.

[22] J. D. Murray, E. A. Stanley, and D. L. Brown, *On the spatial spread of rabies among foxes*, Proc. Roy. Soc. London Ser. B, 229 (1986), pp. 111–150.

[23] R. E. O'Malley, Jr., *Singular Perturbation Methods for Ordinary Differential Equations*, Appl. Math. Sci. 89, Springer-Verlag, New York, 1991.

[24] M. A. Pozio, *Behaviour of solutions of some abstract functional differential equations and application to predator-prey dynamics*, Nonlinear Anal., 4 (1980), pp. 917–938.

[25] M. A. Pozio, *Some conditions for global asymptotic stability of equilibria of integro-differential equations*, J. Math. Anal. Appl., 95 (1983), pp. 501–527.

[26] R. Redlinger, *Existence theorems for semilinear parabolic systems with functionals*, Nonlinear Anal., 8 (1984), pp. 667–682.

[27] R. Redlinger, *On Volterra's population equation with diffusion*, SIAM J. Math. Anal., 16 (1985), pp. 135–142.

[28] H. L. Smith and H. R. Thieme, *Strongly order preserving semiflows generated by functional-differential equations*, J. Differential Equations, 93 (1991), pp. 332–363.

[29] J. W.-H. So, J. Wu, and X. Zou, *A reaction diffusion model for a single species with age structure,* I. *Travelling wave fronts on unbounded domains*, Proc. Roy. Soc. London Ser. A, 457 (2001), pp. 1841–1853.

[30] A. Wandeler, G. Wachendorfer, U. Forster, H. Krekel, W. Schale, J. Muller, and F. Steck, *Rabies in wild carnivores in central Europe.* 1. *Epidemiological studies*, Zbl. Veter. Med. B, 21 (1974), pp. 735–756.

[31] A. Wandeler, G. Muller, G. Wachendorfer, W. Schale, U. Forster, and F. Steck, *Rabies in wild carnivores in central Europe.* 3. *Ecology and biology of the fox in relation to control operations*, Zbl. Veter. Med. B, 21 (1974), pp. 765–773.

[32] G. F. Webb, *Theory of Nonlinear Age-Dependent Population Dynamics*, Monogr. Textbooks Pure Appl. Math. 89, Marcel Dekker, New York, 1985.

[33] J. Wu, *Theory and Applications of Partial Functional-Differential Equations*, Appl. Math. Sci. 119, Springer-Verlag, New York, 1996.

[34] Y. Yamada, *Asymptotic stability for some systems of semilinear Volterra diffusion equations*, J. Differential Equations, 52 (1984), pp. 295–326.