Epidemic Waves: A Diffusion Model for Fox Rabies

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Abstract

In this paper we formulate a simple model for the spread of vulpine rabies based on fox ecology. This model is also an approximation to the one introduced by J. D. Murray *et al* [MSB]. We prove that a heteroclinic spiral connection exists between the disease free and endemic equilibria of the travelling wave ODE (TWODE). The local analysis and simulation results in [MSB] motivated our proof. We hope that these results will be of interest to researchers investigating outbreaks of raccoon rabies in the United States and fox rabies in Europe as well as to epidemiologists in general.

Key Words: rabies, epidemic models, travelling Fisher waves, prey-predator models, Wazewski principle.

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1 Introduction

This paper was motivated by the research of Murray *et al* [MSB] and the data of MacDonald [Mac].

Our objective is to prove the existence of a spiral heteroclinic connection between the disease free and endemic equilibria associated with travelling waves for a model of the spread of fox rabies. Such a wave has been termed a "wave of invasion" for a related Lotka-Volterra model in [D1] and [CT]. Simulations and local analysis in [MSB] indicate that such a connection exists.

Our model is an approximation of the diffusion model in [MSB] which is a generalization of a spatially homogeneous model of Anderson et al [AJMS]. A precursor of the model in [MSB] can be found in [KAM].

Our method is motivated by that of Dunbar [D1] who found spiral and nodal heteroclinic connections in a diffusive generalization of a prey-predator model introduced by Hirsch and Smale [HS]. An attempt to apply the techniques of [D2] directly to the model of [MSB] is not transparent but the results of this paper are valid for an approximation (based on the shape similarity hypothesis described below) to the full model of [MSB].

We will model the rabies epizootic by the following system.

$$\begin{aligned} S_T &= (a-b)\left(1-\frac{N}{K}\right)S-\beta RS \\ I &= \left(\frac{\gamma+b}{\sigma}\right)R \\ R_T &= \frac{\sigma}{\gamma}\beta RS-\sigma R-(a-b)\frac{NR}{K}+DR_{XX} \\ N &= S+\left(\frac{\gamma+b}{\sigma}+1\right)R \\ X,T &\geq 0. \end{aligned} \tag{1.1}$$

The state variables S, I, R denote (respectively) susceptible, infected, and rabid population densities. The linear relation between I and R (referred to as the shape similarity hypothesis) is based on the simulation and singular perturbation results of [MSB] (see the following figure).

Fig.1.1 Simulation results of [MSB] for a wave speed of 50 km/year.

(From [MSB] p. 113, Fig. 1.)

The meaning and typical values of the model parameters are given in the following table:

Parameter	Parameter Meaning	Parameter Value
a	average birth rate	1 fox/year
b	average death rate	.5 foxes/year
$1/\gamma$	average disease duration	5 days
$1/\sigma$	average incubation time	28 days
β	disease transmission rate	80 km^2/year
K	average carrying capacity	.25-4 foxes/km^2
D	diffusion coefficient	200 /km^2/year

Table 1-1

The lack of a diffusion term in the first equation of (1.1) is based on observations that healthy foxes are territorial. The first term in each equation is a standard logistic term for susceptible foxes where $\frac{1}{K}$ is the constraint on the growth of the total population N imposed by the environmental carrying capacity.

The second term in the first equation of (1.1) represents the loss of susceptible foxes due to infection resulting from the interaction with rabid foxes. The second equation gives the shape similarity hypothesis based on [MSB]. The first term in the third equation of (1.1) represents the density $\frac{\sigma\beta}{\gamma}$ of infected foxes that become rabid (one could also introduce a delay into this term related to the incubation time). The second term in the third equation of (1.1) represents the loss of rabid foxes due to rabies deaths. The third term in the third equation gives the death of rabid foxes due to natural causes. The fourth term in the third equation is the decay term of a logistic function. The growth term in equation (1.1) is absent because rabid foxes do not reproduce.

Since the death rate b due to natural causes is small compared to the death rate σ due to rabies during the height of an epidemic (see Table 1-1), we can approximate the previous system by setting $b = 0$ to obtain

$$\begin{aligned} S_T &= a\left(1 - \frac{N}{K}\right) S - \beta RS \\ I &= \frac{\gamma}{\sigma} R \\ R_T &= \frac{\sigma}{\gamma}(\beta RS) - \sigma R - \frac{aNR}{K} + DR_{XX} \\ N &= S + \left(1 + \frac{\gamma}{\sigma}\right) R \end{aligned} \tag{1.2}$$

We will analyze the dynamics of (1.2) in the next section.

2 Local Analysis and a Lyapunov Function

In this section we obtain necessary conditions for the existence of heteroclinic spiral biological connections between susceptible and endemic equilibria. We also compute a Lyapunov function for the travelling wave ODE (TWODE).

Define the following transformation:

$$\begin{array}{lll} s = s/K & \epsilon = a/\beta K & x = (\beta K/D)^{1/2} X \\ q = I/K & \mu = \sigma/\beta K & t = \beta K T \\ r = R/K & d = \gamma/\beta K & \end{array} \tag{2.1}$$

To reduce the number of parameters apply (2.1) to place (1.2) into the following nondimensional form:

$$
\begin{aligned}
s_t &= \epsilon s[1 - s - (\alpha + \epsilon^{-1})r] \\
r_t &= \frac{\mu}{d} rs - r[\mu + \epsilon(s + \alpha r)] + r_{xx} \\
\alpha &= 1 + \frac{d}{\mu} \\
t, x &\geq 0
\end{aligned} \tag{2.2}
$$

The values of the scaled parameters computed from Table 1-1 using (2.1) are

Parameter	Value
μ	.08
d	.46
ϵ	.003

Table 2-1

The spatially homogeneous system corresponding to (2.2) is obtained by setting $D = 0$ in (1.2) and applying (2.1)(without the space scaling transformation) to obtain

$$
\begin{aligned}
\dot{s} &= \epsilon s[1 - s - (\alpha + \epsilon^{-1})r] \\
\dot{r} &= \frac{\mu}{d} rs - r[\mu + \epsilon(s + \alpha r)] \\
r, s &\geq 0 \\
t &\geq 0
\end{aligned} \tag{2.3}
$$

The equilibria of (2.3) are $E_{00} = (0, 0)$, $E_{+0} = (1, 0)$, and $E_{++} = (s^*, r^*)$ where

$$
\begin{aligned}
s^* &= k^{-1}[\mu(\epsilon^{-1} + \alpha) + \epsilon\alpha] \\
r^* &= k^{-1}\left[\mu(\frac{1}{d} - 1) - \epsilon\right] \\
k &= (\mu/d - \epsilon)(\epsilon^{-1} + \alpha) + \epsilon\alpha, \qquad \alpha = 1 + \frac{d}{\mu}
\end{aligned} \tag{2.4}
$$

The components of E_{++} are positive, if

$$
\mu(\frac{1}{d} - 1) > \epsilon.
$$

For the parameter values in Table 2-1 the positive equilibrium (rounded to the fourth significant digit) is given by $(s^*, r^*) = (.4679, .0016)$.

The stability of the equilibria are: E_{00} is a saddle, E_{+0} is a saddle since $\mu(\frac{1}{d} - 1) > \epsilon$, and E_{++} is a clockwise stable spiral, a stable or unstable node depending on the parameters ϵ, μ, d. For the parameter values in Table 2-1 the characteristic polynomial of E_{++} is $.0022 + .0271x + x^2$(where the coefficients are rounded to the fourth decimal place) and the endemic equilibrium is a stable spiral. A simulation of this system with initial condition (1,0) is provided in figure A-1 of the appendix.

Proposition 2.1 *For an open set in the parameter space (μ, ϵ, d)containing the values in Table 2-1 there exists a spiral heteroclinic orbit connecting E_{+0} to E_{++}.*

Proof. Apply the Bendixson criterion to the region defined by

$$\begin{aligned} & r > \frac{\epsilon - \mu}{3\epsilon\alpha + 1} + \left(\frac{\left[\frac{\mu}{d} - 3\epsilon\right]}{3\epsilon\alpha + 1} \right) s, \mu > max(\epsilon, 3\epsilon d) \\ & s > 0 \end{aligned}$$

followed by the Poincare-Bendixson theorem. One can also apply LaSalle's invariance principle by using the Lyapunov function to be determined later in this section. □

To obtain travelling waves for the spatially dependent system replace (x, t) in (2.2) by $\xi = x + ct$, $c > 0$ to obtain

$$\begin{aligned} x_1' &= \frac{\epsilon}{c} x_1[1 - x_1 + (\alpha + \epsilon_{-1})x_2)] \\ x_2' &= x_3 \\ x_3' &= cx_3 + x_2[\mu + (\epsilon - \mu/d)x_1 + \epsilon\alpha x_2)] \\ \frac{d}{d\xi} &= \prime, \qquad -\infty < \xi < \infty \end{aligned} \tag{2.5}$$

A trajectory of TWODE (i.e., (2.5)) will connect the disease free equilibrium (E_{+00}) to the endemic equilibrium (E_{++0}) if it satisfies the following boundary conditions:

$$\begin{aligned}\lim_{\xi\to+\infty}(x_1,x_2,x_3) &= (s^*,r^*,0)=E_{++0}\\ \lim_{\xi\to-\infty}(x_1,x_2,x_3) &= (1,0,0)=E_{+00}\end{aligned}\tag{2.6}$$

where s^* and r^* are defined in (2.4).

The Jacobian matrix of the vector field of TWODE is:

$$\begin{bmatrix}\frac{\epsilon}{c}(1-2x_1)-\frac{x_2}{c}(1+\epsilon\alpha) & \frac{-(1+\epsilon\alpha)x_1}{c} & 0\\ 0 & 0 & 1\\ \left(\epsilon-\frac{\mu}{d}\right)x_2 & \mu+\left(\epsilon-\frac{\mu}{d}\right)x_1+2\alpha\epsilon x_2 & 0\end{bmatrix}$$

The characteristic polynomial of E_{+00} is

$$p(\lambda)=\det[DF(E_{+00})-\lambda I]=\left(\lambda+\frac{\epsilon}{c}\right)\left[\lambda(c-\lambda)+\left\{\mu\left(\frac{1}{d}-1\right)-\epsilon\right\}\right].$$

The eigenvalues at $(1,0,0)$ are:

$$\begin{aligned}\lambda &= -\epsilon/c\\ \lambda^{\pm} &= \frac{1}{2}\left[c\pm\sqrt{c^2-4\left[\mu\left(\frac{1}{d}-1\right)-\epsilon\right]}\right]\end{aligned}\tag{2.7}$$

If $c^2\geq 4\left[\mu\left(\frac{1}{d}-1\right)-\epsilon\right]$(assuming $\mu\left(\frac{1}{d}-1\right)-\epsilon>0$) then $\lambda^{\pm}$ are both positive and real. If $c^2<4\left[\mu\left(\frac{1}{d}-1\right)-\epsilon\right]$ there is a complex conjugate pair of eigenvalues and no biological connection of E_{+00} to E_{++0} is possible. The case $\mu\left(\frac{1}{d}-1\right)-\epsilon<0$ is not of biological interest. If $d<1$ and $\mu\left(\frac{1}{d}-1\right)-\epsilon>0$ a two dimensional unstable manifold exists at (1,0,0).

The linear components (v_1,v_2,v_3) of the weak E^{wu} and strong E^{su} unstable manifolds at $(1,0,0)$ corresponding to (respectively) λ^- and λ^+ satisfy

$$\begin{aligned}v_2 &= -\left(\frac{\epsilon+c\lambda^{\pm}}{1+\epsilon\alpha}\right)v_1\\ v_3 &= \lambda^{\pm}v_2\end{aligned}\tag{2.8}$$

where $\lambda^{\pm}$ is defined in (2.7).

The characteristic polynomial for the eigenvalues at E_{++0} is

$$\begin{aligned} q(\lambda) &= \left[\frac{\epsilon}{c}(1-2s^*) - \left(\frac{1+\epsilon\alpha}{c}\right) r^* - \lambda\right] \left[\lambda(\lambda - c) - (\mu + s^* \left(\epsilon - \frac{\mu}{d}\right) + 2\alpha\epsilon r^*)\right] \\ & - \left(\frac{1+\epsilon\alpha}{c}\right) s^* \left(\epsilon - \frac{\mu}{d}\right) r^*. \end{aligned}$$

We introduce the following notation to simplify the form of $q(\lambda)$:

$$\begin{aligned} K_1 &= \frac{\epsilon}{c}(1-2s^*) - \left(\frac{1+\epsilon\alpha}{c}\right) r^* \approx \frac{-r^*}{c} \\ K_2 &= \mu + s^* \left(\epsilon - \frac{\mu}{d}\right) + 2\alpha\epsilon r^* \approx \mu + s^* \left(\epsilon - \frac{\mu}{d}\right) \\ K_3 &= -\left(\frac{1+\epsilon\alpha}{c}\right)\left(\epsilon - \frac{\mu}{d}\right) r^* s^* \approx \frac{\mu}{cd} r^* s^* \end{aligned} \tag{2.9}$$

To the right in (2.9) we have written approximations to K_i, $i = 1, 2, 3$ valid to first order in ϵ assuming $d, \mu \gg \epsilon$ where $\epsilon \sim \mu^2$. In the new notation $q(\lambda)$ can be written as

$$q(\lambda) = -\lambda^3 + (c + K_1)\lambda^2 + (K_2 - cK_1)\lambda + K_3 - K_1 K_2. \tag{2.10}$$

Since the formula (2.10) is rather unwieldy we resort to working with $q_0(\lambda)$ which approximates $q(\lambda)$ to first order in ϵ. From (2.9) we have $K_2 - cK_1 \cong \mu + s^*\epsilon - \frac{s^*\mu}{d} + r^*$ and $K_3 - K_1 K_2 \sim \frac{\mu r^*}{c}$, $c + K_1 \sim c - \frac{r^*}{c}$. To first order in ϵ,

$$q_0(\lambda) = -\lambda^3 + \left(c - \frac{r^*}{c}\right)\lambda^2 + \left[\mu\left(1 - \frac{s^*}{d}\right) + s^*\epsilon + r^*\right]\lambda + \frac{\mu r^*}{c}$$

. Now $q_0'(\lambda) = -3\lambda^2 + 2\left(c - \frac{r^*}{c}\right)\lambda + \mu\left(1 - \frac{s^*}{d}\right) + r^* + s^*\epsilon$. The solutions of $q_0'(\lambda) = 0$ are

$$\lambda = \frac{1}{3}\left(c - \frac{r^*}{c}\right) \pm \sqrt{\left[\frac{1}{3}\left(c - \frac{r^*}{c}\right)\right]^2 + \frac{1}{3}\left[\mu\left(1 - \frac{s^*}{d}\right) + r^* + s^*\epsilon\right]} \tag{2.11}$$

If $c^2 > r^*$ and the following inequality holds then the roots of q_0' have opposite sign.

$$\mu\left(1 - \frac{s^*}{d}\right) + r^* + s^*\epsilon > 0 \tag{2.12}$$

Otherwise both roots of $q_0'(\lambda)$ are positive and there is no heteroclinic connection. If (2.12) holds there are two subcases to consider:

$$\begin{aligned} &\text{(a)} \qquad \mu > \frac{-(r^* + s^*\epsilon)}{1 - \frac{s^*}{d}}, \qquad \frac{s^*}{d} < 1 \\ &\text{(b)} \qquad \mu < \frac{-(r^* + s^*\epsilon)}{1 - \frac{s^*}{d}}, \qquad \frac{s^*}{d} > 1 \end{aligned} \tag{2.13}$$

The left inequality of (2.13)(a) holds for all parameter values because $\mu > 0$. In case (b) there is a local bifurcation at E_{++0} as μ increases above $\mu = \frac{-(r^*+s^*\epsilon)}{1-\frac{s^*}{d}}$ from roots of opposite sign to roots of the same sign.

When q_0' has roots of opposite sign, $q_0(\lambda)$ increases between negative and positive extrema. Therefore the graph of $q_0(\lambda)$ can have any one of the three possible forms shown below:

Fig. 2.1 Shapes of $q_0(\lambda)$.

In case a) the connection is a stable spiral while in cases b) and c) the connection is a stable node.

To obtain a lower bound for the wave speed c we consider the case when $p(\lambda)$ has a double root. From (2.7) the critical (minimum) value occurs when $c = c^* = 2\sqrt{\mu\,(1/d-1)-\epsilon}$. If $c \geq c^*$ then both roots of p are positive and real indicating a family of biological connections associated with a two dimensional unstable manifold. For the parameter values in Table 2-1,$c^* \approx .603$. Our local analysis is now complete.

We initiate our construction a Lyapunov function for TWODE by first finding one for the spatially homogeneous system (2.3). The reader may verify that

$h(s,r) = -(\mu/d-\epsilon)(s-s^*+logs/s^*)+(1+\epsilon\alpha)(r-r^*)$ is a Lyapunov function for (2.3) on any closed subset of$0 < s \leq 1, r \geq 0, \mu/d > \epsilon$.

Proposition 2.2 *A Lyapunov function H for a travelling wave system of the form*

$$\begin{aligned} \dot{u} &= \frac{1}{c} F_1(u,v) \\ \dot{v} &= w \\ \dot{w} &= cw - F_2(u,v) \end{aligned} \tag{2.14}$$

is given by $H(u,v,w) = c[h(u,v)] - w\frac{\partial h}{\partial v}$ provided $\frac{\partial^2 h}{\partial v^2} \geq 0$ and $\frac{\partial^2 h}{\partial^u \partial^v} = 0$. In (2.14) the parameter c and the states u,v are positive, and h is a Lyapunov function for $\dot{u} = F_1, \dot{v} = F_2$.

The proof of Proposition 2.2 proceeds by direct computation of H'.

Proposition 2.2 applies directly to TWODE because the conditions on the second partials,the parameters and the state variables are satisfied. The region where H is bounded below and has a negative semidefinite time derivative is any closed subset of the open set

$$\begin{aligned} 0 &< x_1 \leq 1 \\ 0 &< x_2 < \infty \\ -\infty &< x_3 < \infty \\ \epsilon &< \mu(\frac{1}{d} - 1) \\ 0 &< \mu, \epsilon, d \\ 0 &< \mu(1 - \frac{s^*}{d}) + r^* + s^*\epsilon \\ d &< 1 \\ r^* &< c^2. \end{aligned} \tag{2.15}$$

3 Existence of travelling waves with oscillatory decay

In this section we will prove the existence of a heteroclinic orbit connecting the equilibrium $(1,0,0)$ to $(s^*, r^*, 0)$ of the following dynamical system:

$$\begin{aligned} x_1' &= \tfrac{\epsilon}{c} x_1 \left\{1 - [x_1 + (\alpha + \epsilon^{-1}) x_2]\right\} \\ x_2' &= x_3 \\ x_3' &= c x_3 - x_2 \left\{\left(\tfrac{\mu}{d} - \epsilon\right) x_1 - \epsilon \alpha x_2 - \mu\right\} \end{aligned} \tag{TWODE}$$

Equivalently we seek solutions of (TWODE) which satisfy the following boundary conditions:

$$\begin{aligned}\lim_{\xi\to+\infty}(x_1,x_2,x_3) &= (s^*,r^*,0)\\ \lim_{\xi\to-\infty}(x_1,x_2,x_3) &= (1,0,0)\end{aligned}\qquad (3.1)$$

The existence proof proceeds in three stages: a shooting argument, a trapping argument, and an application of LaSalle's invariance principle. Let W, W^0, W^-, and $\sum$ denote (respectively) the Wazewski set, the eventual exit set, the immediate exit set and a connected set which we will show contains a point not in W^0.

Definition 3.1 Let $f : R^n \to R^n$ be a C^1 vector field generating a flow $x \cdot t$ on R^n. Let $y \in W^0 \subset R^n$ and let $T(y)$ be the first exit time from W of the trajectory through y. The Wazewski map is defined by $g(y)$ where

$$g(y) = y \cdot T(y) : W^0 \to W^-.$$

Remark 3.1 The Wazewski map is a retract from W^0 to W^-. In particular it is continuous as a map from W^0 to W^-.

Define the sets P, Q, J as follows:

$$P : \begin{cases} 0 < x_1 < s^* \\ r^* < x_2 < \dfrac{\left(\frac{\mu}{d}-\epsilon\right)}{\alpha\epsilon}x_1 \\ 0 < x_3 < \infty \end{cases}$$

$$Q : \begin{cases} s^* < x_1 < \infty \\ 0 < x_2 < r^* \\ -\infty < x_3 < 0 \end{cases}$$

$$J : \begin{cases} s^* \leq x_1 < \infty \\ -\infty < x_2 < 0 \\ x_3 = 0 \end{cases}$$

Note that $W^- = \partial W / [J \cup \{(s^*, r^*, 0)\}]$ is not a connected set, $J \subset \partial Q$ and P, Q are open in R^3.

Sets P, Q are sketched in the following diagram:

Figure 3.1.The immediate exit set of W.

Define the (closed) Wazewski set W to be the complement of $P \cup Q$ in $\{(x_1, x_2, x_3) : x_1, x_2 \geq 0\}$. Recall that the eigenvalues λ at $(1, 0, 0)$ are

$$\begin{aligned} \lambda_1 &= -\frac{\epsilon}{c}, \\ \lambda^{\pm} &= \frac{1}{2}[c \pm \sqrt{c^2 - 4\left[\mu\left(\frac{1}{d} - 1\right) - \epsilon\right]}] \end{aligned}$$

and the eigenvector components (v_1, v_2, v_3) satisfy

$$v_2 = -(\frac{\epsilon + c\lambda}{1 + \epsilon\alpha})v_1, \qquad v_3 = \lambda v_2 \tag{3.2}$$

where $\alpha = 1 + \frac{d}{\mu}$. If $\lambda = \lambda^+$ then (3.2) yields the strong linear unstable manifold (E^{su}) and if $\lambda = \lambda^-$ then (3.2) yields the weak linear unstable manifold (E^{wu}). Corresponding to the linear unstable manifolds $E^u = E^{su} \oplus E^{wu}$ are the local nonlinear unstable manifolds W^u, W^{su}, and W^{wu} of dimension 2, 1, and 1 respectively where $W^* = W^*_{\text{loc}}(1, 0, 0)$ where * denotes any of the three superscripts used in this sentence.

Let $\sum = \widehat{AB}$ be the arc of a small circle ($\sum = \{(x_1 - 1)^2 + x_2^2 + x_3^2 = \rho^2\} \cap W^u$) subtended by $x_3 = 0$ at B and by W^{su} at A. Now $\Gamma = W^u \cap \{x_3 = 0\}$ is a C^1 curve on $x_3 = 0$ intersecting $\sum$ at B. Let $\mathcal{O}_1$ define a subset of the first octant $\{(x_1, x_2, x_3) : 0 \leq x_1 \leq 1, x_2 \geq 0, x_3 \geq 0\}$. The shooting argument proceeds by a series of lemmas which we now prove.

The first lemma gives a lower bound on x_3 in terms of x_2.

Lemma 3.1 *If* $c > \sqrt{4\left[\mu\left(\frac{1}{d}-1\right)-\epsilon\right]}$ *where* $\mu(1/d-1) > \epsilon$ *then* $x_1(0) < 1$, $x_2(0) > 0$, *and* $x_3(0) > \frac{c}{2}x_2(0)$ *imply* $x_2(\xi) > 0$ *and* $x_3(\xi) > \frac{c}{2}x_2(\xi)$ *for all* $\xi > 0$. *In particular this relation holds for the trajectory emerging from* $W^{su} \cap \mathcal{O}_1$.

Proof. Suppose not. Then there exists an infimum ξ_1 of the times ξ such that $x_3(\xi) \leq \frac{c}{2}x_2(\xi)$. For $0 \leq \xi \leq \xi_1$, $x_2'(\xi) = x_3(\xi) \geq \frac{c}{2}x_2(\xi)$ and since $x_2(0) > 0$ we have $x_2(\xi) > 0$. Since $x_3(\xi_1) = \frac{c}{2}x_2(\xi_1)$ and $x_3(\xi) > \frac{c}{2}x_2(\xi)$ for $0 \leq \xi \leq \xi_1$ we have

$$x_3'(\xi_1) - \frac{c}{2}x_2'(\xi_1) \leq 0. \tag{3.3}$$

Insert the expressions for the derivatives from (TWODE) into (3.3) to obtain the following system valid at $\xi = \xi_1$

$$\begin{aligned} &cx_3 - x_2\left\{\left(\frac{\mu}{d}-\epsilon\right)x_1 - \epsilon\alpha x_2 - \mu\right\} - \frac{c}{2}x_3 \leq 0 \\ &x_3 = \frac{c}{2}x_2. \end{aligned} \tag{3.4}$$

Substitute for x_3 in the inequality of (3.4) to obtain

$$\frac{c^2}{2}x_2 - x_2\left\{\left(\frac{\mu}{d}-\epsilon\right)x_1 - \epsilon\alpha x_2 - \mu\right\} - \frac{c^2}{4}x_2 \leq 0. \tag{3.5}$$

Divide (3.5) by $x_2 > 0$ (valid at $\xi = \xi_1$) to obtain:

$$\frac{c^2}{4} \leq \left(\frac{\mu}{d}-\epsilon\right)x_1 - \epsilon\alpha x_2 - \mu. \tag{3.6}$$

Since $x_1(\xi) < 1$ at ξ_1 (3.6) reduces to

$$\frac{c^2}{4} \leq \frac{\mu}{d} - \epsilon - \epsilon\alpha x_2 - \mu.$$

Since $\epsilon\alpha x_2 < \frac{\mu}{d} - \epsilon$ holds in W the following inequality must be satisfied

$$\frac{c^2}{4} + \frac{\mu}{d} - \epsilon \leq \frac{\mu}{d} - \epsilon$$

which proves the lemma by contradiction since $c > 0$. $\square$

The following estimate for the trajectory emerging from $W^{su} \cap \mathcal{O}_1$ is obtained by estimating the inclination of $E^{su} \cap \mathcal{O}_1$ to first order in ϵ by $\frac{(c\sqrt{\delta}+c^2)/2}{1+\epsilon\alpha}$ since

$$\lambda^+ = \frac{c+\sqrt{\delta}}{2}, \delta = c^2 - [4(\frac{\mu}{d} - 1) - \epsilon] > 0$$

.

Lemma 3.2 *If $\mu(1/d-1) > \epsilon$ then the trajectory emerging from $W^{su} \cap \mathcal{O}_1$ satisfies*

$$x_2(\xi) \geq \frac{2\mu(1/d-1)-\epsilon}{1+\epsilon\alpha}[1 - x_1(\xi)] \, , \forall \, \xi \tag{3.7}$$

Proof. Suppose that ξ_1 is the infimum of the ξ for which (3.7) fails. Then, at $\xi = \xi_1$, we have

$$\begin{aligned} x_2' + \frac{2\mu(1/d-1)-\epsilon}{1+\epsilon\alpha} x_1' &\leq 0 \\ x_2 = \frac{2\mu(1/d-1)-\epsilon}{1+\epsilon\alpha}&[1 - (x_1(\xi)] \end{aligned} \tag{3.8}$$

Combining the information in (3.8) we obtain

$$x_3 + \left(\frac{2\mu(1/d-1)-\epsilon}{1+\epsilon\alpha}\right)\left(\frac{\epsilon}{c}\right) x_1(1-x_1)\left[1 - (\alpha+\epsilon^{-1})\left(\frac{2\mu(1/d-1)-\epsilon}{1+\epsilon\alpha}\right)\right] \leq 0 \tag{3.9}$$

From Lemma 3.1 we also have

$$\frac{c}{2}x_2 \leq x_3 \leq \left(\frac{2\mu(1/d-1)-\epsilon}{1+\epsilon\alpha}\right)\left(\frac{\epsilon}{c}\right) x_1(1-x_1)\left[(\alpha+\epsilon^{-1})\left(\frac{2\mu(1/d-1)-\epsilon}{1+\epsilon\alpha}\right) - 1\right] \tag{3.10}$$

The previous inequality reduces to

$$cx_2 \leq x_1(1-x_1)\frac{2\mu(1/d-1)-\epsilon}{1+\epsilon\alpha}\frac{\epsilon}{c}2[1 - \frac{\mu}{\epsilon}(1/d-1)] \tag{3.11}$$

The hypothesis implies that the right side of (3.11) is negative (contradiction). □

The third lemma provides an upper bound on x_3 in terms of x_2.

Lemma 3.3 *Fix $\Delta > \frac{c+\sqrt{c^2+\mu}}{2}$. If $0 < x_1(0) < 1$, $x_2(0) > 0$ and $x_3(0) < \Delta x_2(0)$ then $x_3(\xi) < \Delta x_2(\xi)$ for all $\xi > 0$ such that $x_2(\xi) > 0$. In particular the bound holds for the trajectory emerging from $W^{su} \cap \mathcal{O}_1$.*

Proof. Suppose $x_3(\xi) \geq \Delta x_2(\xi)$ for some ξ and let ξ_1 be the infimum of those ξ's. At $\xi = \xi_1$, $x_3 = \Delta x_2$ and $\Delta x_2' - x_3' \leq 0$. Using (TWODE) we have:

$$\begin{aligned} &\Delta x_3 - \left[c x_3 - x_2 \left\{ \left(\frac{\mu}{d} - \epsilon \right) x_1 - \epsilon \alpha x_2 - \mu \right\} \leq 0 \\ &x_3 = \Delta x_2. \end{aligned} \tag{3.12}$$

Combining the information in (3.12) we have

$$\Delta^2 x_2 - \left[c\Delta x_2 - x_2 \left\{ \left(\frac{\mu}{d} - \epsilon \right) x_1 - \epsilon \alpha x_2 - \mu \right\} \right] \leq 0 \tag{3.13}$$

Dividing (3.13) by $x_2 > 0$ we obtain

$$\Delta^2 - c\Delta + \left(\frac{\mu}{d} - \epsilon \right) x_1 - \epsilon \alpha x_2 - \mu \leq 0 \tag{3.14}$$

Now $\left(\frac{\mu}{d} - \epsilon\right) x_1 - \epsilon\alpha x_2 \geq 0$ since $x_2 \leq \left(\frac{\frac{\mu}{d} - \epsilon}{\epsilon\alpha}\right) x_1$ in the region W of interest (Figure 3.1). For all (x_1, x_2) in W Δ satisfies

$$\Delta^2 - c\Delta - \mu \leq 0. \tag{3.15}$$

To satisfy (3.15) Δ must obey

$$\frac{c - \sqrt{c^2 + \mu}}{2} \leq \Delta \leq \frac{c + \sqrt{c^2 + \mu}}{2}$$

which contradicts our hypothesis. □

The fourth lemma gives an upper bound on $x_2(s)$ in terms of $1 - x_1(s)$.

Lemma 3.4 *A solution of (TWODE) with initial conditions satisfying* $0 < x_1(0) < 1$, $0 < x_2(0) < \left(1 + \frac{c\Delta}{s^*}\right)[1 - x_1(0)]$, *and* $x_3(0) < \Delta x_2(0)$ *will have* $x_2(\xi) < (1 + \frac{c\Delta}{s^*})[1 - x_1(\xi)]$ *for all* $\xi > 0$ *as long as* $x_1(\xi) > s^*$ *and* $x_2(\xi) > 0$. *In particular the previous inequality holds for the trajectory determined by* $W^{su} \cap O_1$.

Proof. Assume $x_2(\xi) > \left(1 + \frac{c\Delta}{s^*}\right)[1 - x_1(\xi)]$ for some $\xi > 0$ and let ξ_1 be the infimum of such ξ. Then, at $\xi = \xi_1$,

$$\left(1 + \frac{c\Delta}{s^*}\right)[1 - x_1(\xi)] = x_2(\xi). \tag{3.16}$$

Differentiating (3.16) yields a decreasing function at $\xi = \xi_1$:

$$-\left(1+\frac{c\Delta}{s^*}\right)x_1' - x_2' \leq 0,$$

or

$$\left(1+\frac{c\Delta}{s^*}\right)\left[\frac{\epsilon}{c}x_1\left\{1-[x_1+(\alpha+\epsilon^{-1})x_2]\right\}\right]+x_3 \geq 0. \tag{3.17}$$

Insert (3.16) into (3.17) and eliminate x_2 to obtain

$$\left(1+\frac{c\Delta}{s^*}\right)\frac{\epsilon}{c}x_1\left\{1-x_1-(\alpha+\epsilon^{-1})\left(1+\frac{c\Delta}{s^*}\right)(1-x_1)\right\}+x_3 \geq 0.$$

By Lemma 3.3 we have

$$\Delta x_2 \geq x_3 \geq -\left(1+\frac{c\Delta}{s^*}\right)\left\{\frac{\epsilon}{c}\,x_1(1-x_1)\left[1-(\alpha+\epsilon^{-1})\left(1+\frac{c\Delta}{s^*}\right)\right]\right\}.$$

The previous inequality reduces to:

$$\Delta x_2 \geq \left(1+\frac{c\Delta}{s^*}\right)\frac{\epsilon}{c}\,x_1(1-x_1)\left[(\alpha+\epsilon^{-1})\left(1+\frac{c\Delta}{s^*}\right)-1\right]. \tag{3.18}$$

Insert (3.16) into (3.18) to obtain (at $\xi = \xi_1$)

$$\Delta\left(1+\frac{c\Delta}{s^*}\right)(1-x_1) \geq \left(1+\frac{c\Delta}{s^*}\right)\frac{\epsilon}{c}x_1(1-x_1)\left[(\alpha+\epsilon^{-1})\left(1+\frac{c\Delta}{s^*}\right)-1\right].$$

Dividing the previous inequality by $(1-x_1)(1+c\Delta/s^*) > 0$ we obtain

$$x_1 \leq \frac{c\Delta}{\epsilon\left[(\alpha+\epsilon^{-1})\left(1+\frac{c\Delta}{s^*}\right)-1\right]}.$$

The condition $x_1 > s^*$ where

$$\frac{c\Delta}{(1+\epsilon\alpha)\left(1+\frac{c\Delta}{s^*}\right)-\epsilon} > s^*$$

leads to the contradiction (using(2.4)) $0 > s^*(1+\epsilon\mu/d)+\epsilon\alpha c\Delta$.

□

Now we develop the shooting argument. Define the following trapping cone:

$$\begin{aligned} C \quad = \quad & \left\{(x_1,x_2,x_3) : s^* < x_1 < 1, \left(1+\frac{\epsilon+c^2}{1+\epsilon\alpha}\right)(1-x_1) \leq x_2, \right. \\ x_2 \leq \quad & \left.\left(1+\frac{c\Delta}{s^*}\right)(1-x_1), \frac{c}{2}x_2 < x_3 < \Delta x_2\right\} \end{aligned} \tag{3.19}$$

with vertex at $(1,0,0)$. Lemmas 3.1 to 3.4 show that the trajectory emerging from $W^{su} \cap \mathcal{O}_1$ is contained in C. The cone C lies in the region $x_1 > 0$, $1 - [x_1 + (\alpha + \epsilon^{-1})x_2] < 0$ so that, for the trajectory of interest, $x_1(\xi)$ decreases until $x_1(\xi_1) = s^*$ for some $\xi_1 < \infty$. Hence the trajectory hits ∂W on the face $x_1 = s^*$, $x_2 > r^*$, $x_3 > 0$ and then enters P.

Proposition 3.1 *There exists a trajectory determined by* $y_1 \in \text{interior}(\widehat{AB})$ *which remains in* W *for all* $\xi > 0$.

Proof. The immediately preceding arguments show that the trajectory determined by A exits W eventually by entering P while the trajectory determined by B exits W immediately by entering $Q - J$ because $x_2 > 0$. Since the flow generated by (TWODE) is continuous in the region of interest, the Wazewski map $g(y)$ is continuous from W^0 to W^-. If $\sum \subset W^0$ then the image of a connected set would be mapped to a disconnected set by g. Thus $y_1 \in \sum$ exists such that $y(\xi, y_1) = y_1(\xi)$ remains in W for all $\xi \geq 0$. □

Our next objective is to show that the trajectory $y_1(\xi)$ remains in a bounded set $\mathcal{D}$ for all $\xi \in R$. Define $\mathcal{D}$ to be the tent shaped trapping region sketched below:

Figure 3.2. The trapping region

The region $\mathcal{D}$ is defined by the following inequalities:

(i) (a) $x_1 < 1$

(b) $x_1 > 0$

(ii) (a) $x_2 < (1 + c\Delta/s^*)(1 - x_1), s^* < x_1 < 1$

(b) $x_2 < (1 + c\Delta/s^*)(1 - s^*), \frac{\alpha\epsilon}{\mu/d-\epsilon}\hat{s} < x_1 < s^*$

(c) $x_2 < \left(\frac{\mu}{d} - \epsilon\right)(\alpha\epsilon)^{-1}x_1, 0 < x_1 < \frac{\alpha\epsilon}{\mu/d-\epsilon}\hat{s}$

(d)$x_2 > 0$

(iii) (a) $x_3 < \Delta x_2$

(b) $x_3 > -\frac{s^*}{c}x_2$

(iv) $\hat{s} = (\mu/d - \epsilon)(1 + c\Delta/s^*)(1 - s^*)$

In fact $y_1(s)$ remains in $D - (P \cup Q)$.

Lemma 3.5 *The trajectory* $y_1(\xi)$ *defined in* Proposition 3.1 *remains in* $\mathcal{D}$ *for all time.*

Proof. Any trajectory determined by y_1 on $\Sigma, y_1 \neq A$ satisfies the same upper bounds which govern the trajectory determined by A. Thus (ii)(a) and (iii)(a) hold.

Denote the components of y_1 by (x_1, x_2, x_3).

(i)(b) The plane defined by $x_1 = 0$ is invariant for the flow. Thus $x_1(0) > 0$ implies $x_1(\xi) > 0$ for all ξ.

(ii)(d)The inequality $x_2 > 0$ holds because,otherwise, the trajectory y_1 enters Q which violates Proposition 3.1.

(i)(a)From (ii)(d) and (ii)(a) it follows that $x_1 < 1$ for all ξ.

(ii)(c) In fact $x_2 < (\mu/d - \epsilon)(\alpha\epsilon)^{-1}x_1$ holds for $0 < x_1 < s^*$.

(ii)(b) Suppose the inequality is false. Then there exists ξ_1 such that $x_2 > (1+\frac{c\Delta}{s^*})(1-s^*)$ with $x_1 < s^*$. Then $x_2 > r^*$ and $x_2' \geq 0$. Hence x_1 lies in P or immediately enters P which contradicts $y_1 \subset P$.

(iii)(b) Suppose, on the contrary, that there exists ξ_1 such that $x_3 < -(s^*/c)x_2(\xi_1)$. Then there must be a later time ξ_2 such that $x_3 = -s^*/cx_2$. Hence $x_3' + s^*/cx_2' \geq 0$. Combining the previous information we have $-s^*x_2 - (s^*/c)^2 x_2 - x_2[(\mu/d - \epsilon)x_1 - \epsilon\alpha x_2] < 0$. Dividing by $x_2 > 0$ yields a contradiction with (ii)(c). □

Proposition 3.2 *The trajectory $y_1(s)$ defined in Proposition 3.1 converges to the endemic equilibrium as $s \to +\infty$.*

Proof. By LaSalle's principle it suffices to show that the largest invariant subset of $\{\dot{H} = 0\}$ is the endemic equilibrium. Now $\dot{H} = 0$ if

$$(\mu/d - \epsilon)(1 + x_1)\epsilon[1 - x_1 - (\alpha + \epsilon^{-1})x_2] + (1 + \epsilon\alpha)x_2[(\mu/d - \epsilon)x_1 - \epsilon_2 - \mu] = 0 \qquad (3.20)$$

Equation (3.20) has the following feasible solutions:$(1, 0, x_3)$ and $1 - x_1 - (\alpha + \epsilon^{-1})x_2 = 0, (\frac{\mu}{d} - \epsilon)x_1 - \epsilon\alpha x_2 - \mu = 0, x_3$.

From the vector field of (TWODE), it follows that $(x_1, x_2, x_3) = (s^*, r^*, 0)$ is the largest invariant subset of (3.20). Since $y_1(\xi)$ is bounded and H exists $y_1(\xi)$ must converge to $(s^*, r^*, 0)$. □

Remark 3.2 Note that the heteroclinic connection may be nodal or spiral near $(s^*, r^*, 0)$.

Appendix A

In the first part of this appendix we relate our model to the one in [MSB]. For further details the reader may refer to [MSB] (pp. 138–146). By applying the same principles of fox ecology, Murray *et al* derive ([MSB], p. 116) the following model for the spatio-temporal evolution of a rabies epizootic:

$$\begin{aligned} S_T &= (a - b)\left(1 - \frac{N}{K}\right) S - \beta R S \\ I_T &= \beta R S - \sigma I + \left[b + (a - b)\frac{N}{K}\right] I \\ R_T &= \sigma I - \alpha R - \left[b + (a - b)\frac{N}{K}\right] R + D R_{xx} \\ N &= S + I + R \end{aligned} \qquad (A.1)$$

where all parameters and variables have the definitions and values given in Table 1-1.

The transformation (2.1) with the additional change of parameters $\delta = \frac{b}{\beta K}$ is used to place (A.1) into the following nondimensional form.

$$\begin{aligned} s_t &= \epsilon(1-n)s - rs \\ q_t &= rs - (\mu + \delta + \epsilon n)q \\ r_t &= \mu q - (d + \epsilon n)r + r_{xx} \\ n &= s + q + r \end{aligned} \tag{A.2}$$

Note that the number of parameters in the model has been reduced from six to four. Insert $\xi = x + ct$ into (A.2) to obtain the travelling wave ODE

$$\begin{aligned} cs' &= \epsilon(1-n)s - rs \\ cq' &= rs - (\mu + \delta + \epsilon n)q \\ cr' &= \mu q - (d + \epsilon n)r + r'' \\ n &= s + q + r \\ -\infty &< \xi < \infty. \end{aligned} \tag{A.3}$$

The travelling waves of interest are associated with the heteroclinic orbits obtained by imposing the following boundary conditions:

$$\lim_{\xi \to -\infty} (s, q, r) = (1, 0, 0)$$

$$\lim_{\xi \to +\infty} (s, q, r) = (s^*, r^*, 0)$$

.

A linear analysis in [MSB] (p. 141) shows that the shape of the infected and rabid waves satisfy $q \sim \frac{rd}{\mu}$ asymptotically as $\xi \to +\infty$. To show that this profile similarity between the infected (q) and rabid (r) foxes extends over the entire domain for parameter values of interest, change the independent variable in (A.1–A.3) from $-\infty < \xi < \infty$ to $0 < s < 1$.

In addition scale the rabid density and make the following assumptions about the parameters

$$
\begin{aligned}
\epsilon &= \mu^2 \epsilon_0 \\
\delta &= \mu^2 \delta_0 \\
r &= r[s(\xi)] \\
r' &= \frac{dr}{ds} s' \\
r(s) &= \mu y(s).
\end{aligned} \tag{A.4}
$$

Apply (A.4) to (A.3) to obtain

$$
\begin{aligned}
[-ys + \mu\epsilon_0 s(1-n)] \frac{dq}{ds} &= ys - q - \mu(\delta_0 + \epsilon_0 n) q \\
q - dy &= \mu[-ys + \mu\epsilon_0 s(1-n)] \frac{dy}{ds} \\
&\quad - \frac{\mu^2}{c^2}[-ys + \mu\epsilon_0 s(1-n)] \Bigg\{ [-ys + \mu\epsilon_0 s(1-n)] \frac{d^2 y}{ds^2} \\
&\quad + \Bigg[-y + \mu\epsilon_0(1-n-s) - \delta(1+\mu^2\epsilon_0) \frac{dy}{ds} \\
&\quad - \mu\epsilon_0 s - \mu\epsilon_0 s \frac{dq}{ds} \Bigg] \frac{dy}{ds} \Bigg\} + \mu^2 \epsilon_0 y n \\
n &= s + q + \mu y.
\end{aligned} \tag{A.5}
$$

The following diagram is based on simulations and approximate local analysis at the endemic and disease free equilibrium. It exhibits the qualitative features of the interaction between the scaled rabid ($y = r/\mu$) and the susceptible (s) fox population densities.

Figure A-1.

The similarity between successive loops of the spiral in Figure A-1 is used to justify an analysis of the connecting orbit by breaking up each loop into four pieces: top, bottom, and left and right lower corners. By using a (different) singular perturbation approximation for each of the four subsystems specified, Murray *et al* show that the profile similarity $q = \frac{d}{\mu} r$ holds for all $0 < s(\xi) < 1$ to first order in μ assuming the parameters satisfy the relations in (A.4).

Thus our model is an approximation of that of Murray *et al* based on the shape similarity hypothesis. Hence, for our approximation, we may conclude that solitary travelling wave pulses exist for the infected as well as for the rabid fox populations.

Now we apply the following change of variables to estimate the maximum amplitude of the initial rabies pulse generated by the first impact with the susceptible population:

$$\begin{aligned} r &= r(\xi) \\ r' &= \frac{dr}{ds} s' \\ r'' &= (s')^2 \frac{d^2 r}{ds^2} + s' \frac{ds'}{ds} \frac{dr}{ds} \end{aligned} \tag{A.6}$$

The transformation (A.6) is applied to

$$
\begin{aligned}
cs' &= \epsilon s[1 - s + (\alpha + \epsilon^{-1})r] \\
cr' &= \frac{\mu}{d} rs - r[\mu + \epsilon(s + \alpha r)] + r''
\end{aligned} \tag{A.7}
$$

to obtain

$$
\begin{aligned}
\frac{dr}{ds}\,\epsilon s[1 - s - (\alpha + \epsilon^{-1})r] &= \frac{\mu}{d} rs - r[\mu + \epsilon(s + \alpha r)] + \left\{\frac{\epsilon s}{c}[1 - s - (\alpha + \epsilon^{-1})r]\right\}^2 \frac{d^2 r}{ds^2} \\
&+ \frac{\epsilon s}{c}[1 - s + (\alpha + \epsilon^{-1})r]\left\{\frac{\epsilon}{c}[1 - s - (\alpha + \epsilon^{-1})r] - \frac{2\epsilon s}{c}\right\}\frac{dr}{ds}
\end{aligned} \tag{A.8}
$$

Now set $r = \mu y$ and divide by $\mu \neq 0$ to obtain

$$
\begin{aligned}
\frac{dy}{ds}\,\epsilon s[1 - s - (\alpha + \epsilon^{-1})\mu y] &= \frac{\mu}{d} ys - y[\mu + \epsilon(s + \alpha\mu y)] \\
&+ \left\{\frac{\epsilon s}{c}[1 - s - (\alpha + \epsilon^{-1})\mu y]\right\}^2 \frac{d^2 y}{ds^2} \\
&+ \frac{\epsilon s}{c}[1 - s - (\alpha + \epsilon^{-1})\mu y]\left\{\frac{\epsilon}{c}[1 - s - (\alpha + \epsilon^{-1})\mu y] - \frac{2\epsilon s}{c}\right\}\frac{dy}{ds}
\end{aligned} \tag{A.9}
$$

Assume $\epsilon = \mu^2$ and approximate (A.9) by removing all terms of order little o epsilon.

$$
-\mu y s\frac{dy}{ds} = \frac{\mu}{d} ys - y\mu + \frac{s^2\mu^2 y^2}{c^2}\frac{d^2 y}{ds^2} + \left(\frac{s\mu y}{c}\right)^2 \frac{dy}{ds}. \tag{A.10}
$$

Divide both sides of the previous equation by μys and remove terms of order epsilon to produce

$$
-\frac{dy}{ds} = \frac{1}{d} - \frac{1}{s}. \tag{A.11}
$$

Integrate from s_0 to s to obtain:

$$
y(s) - y(s_0) = \ln\left(\frac{s}{s_0}\right) + \frac{s_0 - s}{d}. \tag{A.12}
$$

To estimate the first loop insert $s_0 = 1$, $y(s_0) = 0$ into (A.12) to obtain

$$
y(s) = \ln s + \frac{1 - s}{d}, \qquad 0 < s < 1. \tag{A.13}
$$

The maximum value of $y(s)$ on $[0, 1]$ occurs at $s = d$ and is $y(d) = \ln d + \frac{1-d}{d}$ for $\frac{1}{1+lnd} < d < 1$. Thus the maximum amplitude of r in the first loop is approximately $\mu\left[\ln d + \frac{1-d}{d}\right]$.

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References

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

[CT] Chow, P. L., Tam, W. C.: Periodic and travelling wave solutions to Volterra-Lotka equations with diffusion, *Bull. Math. Biol.* **12**, 643–658 (1976).

[D1] Dunbar, S. R.: Travelling wave solutions of diffusive Lotka-Volterra equations, *J. Math. Biol.* **17**, 11–32 (1983).

[D2] Dunbar, S. R.: Travelling wave solutions of diffusive Lotka-Volterra equations: a heteroclinic connection in R^4, *Trans. Amer. Math. Soc.* **268**, 557–594 (1984).

[HS] Hirsch, M., Smale, S.: Differential equations, dynamical systems and linear algebra, *Pure and Applied Mathematics,* vol. 66, New York: Academic Press, (1974).

[KAM] Källén, A., Arcuri, P., Murray, J. D.: A simple model for the spatial spread and control of rabies, *J. Theor. Biol.* **116**, 377–393 (1985).

[KPP] Kolmogorov, A., Petrovsky, I., Piscounoff, N.: Étude de l'équation de la diffusion avec croissance de la quantité de matière et son application à un problème biologique, *Moscow Univ. Bull. Math.* **1**, 1–25 (1937).

[LAW] Ludwig, D., Aronson, D. G., Weinberger, H. F.: Spatial patterning of the spruce budworm, *J. Math. Biol.* **8**, 217–258 (1979).

[Mac] Macdonald, D. W.: *Rabies and Wildlife: A Biologist's Perspective,* Oxford Univ. Press: Oxford, 1980.

[MSB] Murray, J. D., Stanley, E. A., Brown, D. L.: On the spatial spread of rabies among foxes, *Proc. Roy. Soc. (Lond.)* **B229**, 111–150 (1986).

[P] Pauwelussen, J. P.: Heteroclinic waves of the Fitzhugh-Nagumo equations, *Math. Biosci.* **58**, 217–242 (1982).

[TH] Thieme,H.R.:Asymptotic estimates of the solutions of nonlinear integral equations and asymptotic speeds for the spread of populations, *J.Reine Angew.Math.*306, pp.94-121,(1979).

[WH] Hsu, Sze-Bi and Waltman, P.: On a system of reaction-diffusion equations arising from competition in an unstirred chemostat, *SIAM J. Appl. Math.*, vol 53, No. 4, pp. 1026–1044(1993).