How Do Bird Migrations Propagate the West Nile virus

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HOW DO BIRD MIGRATIONS PROPAGATE THE WEST NILE VIRUS

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The rapid spread of the West Nile virus from New York City (USA) in 1999 to the West Coast of North America by 2003 is related to several avian species. The propagation of this virus follows the migratory routes of these birds.

1. INTRODUCTION

The West Nile virus (WNV) disease appeared for the first time in New York City in the summer of 1999 and then infected 200 species. The WNV is an arthropod-borne flavivirus. The primary vectors of the WNV are *Culex spp* mosquitoes (Campbell et al., 2002).

The transmission to humans depends on the abundance and feeding patterns of infected mosquitoes and on human exposure to mosquitoes (Harrington et al., 2005). Mammals do not develop sufficiently high bloodstream titers to play a significant role in the transmission (Hayes, 1989; DeBiasi and Tyler, 2006), which is a reason to consider the mosquito–bird cycle.

Wonham et al. (2004), Kenkre et al. (2005), Cruz-Pacheco et al. (2005), and Bowman et al. (2005) studied the dynamic without space. Lewis et al. (2006) and Maidana and Yang (2009) incorporated the homogeneous space according to Wonham et al. (2004) and Cruz-Pacheco et al. (2005).

We study the geographic propagation of WNV using the same method applied to describe the dissemination of rabies among foxes by Murray et al. (1986), Murray and Seward (1992), Milner and Zhao (2008) for directly transmitted disease, and Maidana and Yang (2009) for indirectly transmitted diseases.

We consider several avian populations and look for the traveling waves connecting the disease-free state and the endemic equilibrium. We determine the

speed of propagation of the WNV disease. We study the importance of diffusion and migratory movements of different bird species.

2. MODEL

2.1. Spatial WNV Propagation

The WNV disease first appeared in North America in summer 1999, with the simultaneous occurrence of an unusual total number of deaths of exotic birds and crows in New York City (DeBiasi and Tyler, 2006). The WNV propagated across the United States until 2003.

The population sizes are denoted by $\overline{N}_j(t)$ and $\overline{N}_v(t)$, where $j = 1, \ldots, n$, describes an avian species. Each avian population is divided into susceptible, infective, and recovered subpopulations, named $\overline{S}_j$, $\overline{I}_j$, and $\overline{R}_j$, while for the vector population, the susceptible and infected subpopulations are $\overline{S}_v$ and $\overline{I}_v$.

The population densities of the avian species vary; Λ_j is a constant recruitment rate due to birth and migration, and the death rate including emigration is $\overline{\mu}_j$. Each bird population varies, irrespective of the WNV infection, according to:

$$\frac{d\overline{N}_j(t)}{dt} = \Lambda_j - \overline{\mu}_j \overline{N}(t)_j, \quad j = 1, \ldots, n, \tag{1}$$

resulting in $\overline{N}_j = \Lambda_j / \overline{\mu}_j$ as total population size at equilibrium. Birth and death rates of mosquitoes populations are equal to $\overline{\mu}_v$, resulting in a constant mosquito population size $\overline{N}_v$.

The WNV is transmitted when an infected mosquito bites a susceptible bird. The transmission rate is denoted by $\overline{\beta}_j$, for $j = 1, \ldots, n$. Conversely, a susceptible mosquito is infected when it bites infected birds, denoted by $\overline{\beta}_{vj}$. The biting rate of one mosquito is assumed to be the same for all bird species and is equal to b. The proportions of each population of birds at the steady state disregarding the WNV infection are denoted by $\overline{q}_j$, $j = 1, \ldots, n$. They are used to approximate the varying populations considering the dissemination of WNV by:

$$\overline{q}_j = \frac{\frac{\Lambda_j}{\overline{\mu}_j}}{\sum_{k=1}^n \frac{\Lambda_k}{\overline{\mu}_k}} \approx \frac{\overline{N}_j}{\sum_{k=1}^n \overline{N}_k}. \tag{2}$$

The per-head infection rates in birds become:

$$b\overline{\beta}_j \frac{\overline{I}_v}{\sum_{k=1}^n \overline{N}_k} \frac{\overline{N}_j}{\overline{N}_j} = b \frac{\overline{\beta}_j}{\overline{N}_j} \frac{\overline{N}_j}{\sum_{k=1}^n \overline{N}_k} \overline{I}_v \approx b\overline{q}_j \frac{\overline{\beta}_j}{\overline{N}_j} \overline{I}_v. \tag{3}$$

Analogously, the rate of transmission in mosquito population is:

$$\sum_{j=1}^n b\overline{q}_j \overline{\beta}_{vj} \frac{\overline{I}_j}{\overline{N}_j}. \tag{4}$$

The infected mosquitoes transmit the WNV during their entire life spans, but infected birds recover at rate $\overline{\gamma}_j$. The specific death rate associated with the WNV

in the avian population is $\overline{\alpha}_j$, with $\overline{\alpha}_j \leq \overline{\gamma}_j$ (Cruz-Pacheco et al., 2005). Another assumption is that mosquitoes can transmit the WNV vertically, and the fraction of the progeny of infected mosquitoes is p.

The populations $\overline{N}_j(t,x)$ and $\overline{N}_v(t,x)$ and their subpopulations depend on each other. These quantities become now densities with respect to space. The diffusion among birds is considered constant and denoted by $\overline{D}_j$. The mosquitoes are considered as a nondiffusive population: the mean dispersal distance for *Aedes aegypti* ranges from 28 to 199 meters (Harrington et al., 2005; Ferreira et al., 2006).

The advection coefficients for avian species are denoted by $\overline{\nu}_j$, $j = 1, \ldots, n$. The infected subpopulations have the same diffusion and advection coefficients assuming that the WNV disease does not affect their movements. The parameters are presented in Table 1.

The model is:

$$\begin{cases} \frac{\partial \overline{S}_j(t,x)}{\partial t} = \overline{D}_j \frac{\partial^2 \overline{S}_j(t,x)}{\partial x^2} - \overline{\nu}_j \frac{\partial \overline{S}_j(t,x)}{\partial x} + \Lambda_j - \frac{b\overline{q}_j\overline{\beta}_j}{\overline{N}_j(t,x)}\overline{I}_v(t,x)\overline{S}_j(t,x) - \overline{\mu}_j\overline{S}_j(t,x) \\ \frac{\partial \overline{I}_j(t,x)}{\partial t} = \overline{D}_j \frac{\partial^2 \overline{I}_j(t,x)}{\partial x^2} - \overline{\nu}_j \frac{\partial \overline{I}_j(t,x)}{\partial x} + \frac{b\overline{q}_j\overline{\beta}_j}{\overline{N}_j(t,x)}\overline{I}_v(t,x)\overline{S}_j(t,x) - (\overline{\gamma}_j + \overline{\mu}_j + \overline{\alpha}_j)\overline{I}_j(t,x) \\ \frac{\partial \overline{R}_j(t,x)}{\partial t} = \overline{D}_j \frac{\partial^2 \overline{R}_j(t,x)}{\partial x^2} - \overline{\nu}_j \frac{\partial \overline{R}_j(t,x)}{\partial x} + \overline{\gamma}_j\overline{I}_j(t,x) - \overline{\mu}_j\overline{R}_j(t,x) \\ \frac{\partial \overline{S}_v(t,x)}{\partial t} = (1-p)\overline{\mu}_v\overline{I}_v(t,x) - \sum_{j=1}^{n}\frac{b\overline{q}_j\overline{\beta}_{vj}}{\overline{N}_j(t,x)}\overline{I}_j(t,x)\overline{S}_v(t,x) \\ \frac{\partial \overline{I}_v(t,x)}{\partial t} = p\overline{\mu}_v\overline{I}_v(t,x) + \sum_{j=1}^{n}\frac{b\overline{q}_j\overline{\beta}_{vj}}{\overline{N}_j(t,x)}\overline{I}_j(t,x)\overline{S}_v(t,x) - \overline{\mu}_v\overline{I}_v(t,x), \end{cases} \quad (5)$$

for $j = 1, \ldots, n$. For susceptible mosquitoes, the recruitment and mortality rates are similar, which explains the absence of the mortality rate. In the simulations, the initial and boundary conditions are:

$$\overline{I}_1(0,x) = \begin{cases} 1, & |x| \leq 1/2 \\ 0 & |x| > 1/2, \end{cases} \quad (6)$$

Table 1. Notations

	Vector (v)	Reservoirs ($j = 1, \ldots, n$)
State variables		
Susceptible	$\overline{S}_v$	$\overline{S}_j$
Infectious	$\overline{I}_v$	$\overline{I}_j$
Recovered	—	$\overline{R}_j$
Total	$\overline{N}_v$	$\overline{N}_j$
Parameters		
Birth	$\overline{\mu}_v$	Λ_j
Death (natural)	$\overline{\mu}_v$	$\overline{\mu}_j$
Death (due to disease)	—	$\overline{\alpha}_j$
Recovery (from disease)	—	$\overline{\gamma}_j$
Virus transmission (to)	$\overline{\beta}_{vj}$	$\overline{\beta}_j$
Vertical transmission	p	—
Diffusion	—	$\overline{D}_j$
Advection	—	$\overline{\nu}_j$

and

$$\overline{S}_j(0, x) = N_j^0, \quad \overline{R}_j(0, x) = 0, \quad \overline{N}_j(0, x) = N_j^0, \quad \overline{S}_v(0, x) = N_v^0, \quad \overline{I}_v = 0, \quad (7)$$

where $N_j^0 = \overline{N}_j = \Lambda_j/\overline{\mu}_j$ and $N_v^0 = \overline{N}_v$. These conditions describe a local introduction of infectious birds of species 1 in a disease free region. At the boundaries, the homogeneous Neumann boundary conditions are:

$$\frac{\partial \overline{S}_j}{\partial x}(t, L) = \frac{\partial \overline{I}_j}{\partial x}(t, L) = \frac{\partial \overline{R}_j}{\partial x}(t, L) = \frac{\partial \overline{N}_j}{\partial x}(t, L) = 0$$

$$\frac{\partial \overline{S}_v}{\partial x}(t, L) = \frac{\partial \overline{I}_v}{\partial x}(t, L) = 0, \quad t > 0. \tag{8}$$

The initial population counts 100 mosquitoes and 20 birds per km for each species: $m_j = N_v^0/N_j^0 = 100/20 = 5$.

The ratio between the size of vector populations and the disease free equilibrium of the jth bird population is denoted $\overline{m}_j = \frac{\overline{N}_v}{\Lambda_j/\overline{\mu}_j}$. The time is scaled with respect to $b\overline{q}_1\overline{m}_1$, where b is the biting rate of mosquitoes. The first species is taken as the fastest one: $D_1 \geq D_j, j = 1, \ldots, n$. The spatial variable is scaled with respect to $\left(\frac{D_1}{b\overline{q}_1\overline{m}_1}\right)^{1/2}$. The remaining parameters, which are dimensionless, are:

$$S_j = \frac{\overline{S}_j}{\Lambda_j/\overline{\mu}_j}, \quad I_j = \frac{\overline{I}_j}{\Lambda_j/\overline{\mu}_j}, \quad R_j = \frac{\overline{R}_j}{\Lambda_j/\overline{\mu}_j}, \quad N_j = \frac{\overline{N}_j}{\Lambda_j/\overline{\mu}_j}, \quad S_v = \frac{\overline{S}_v}{\overline{N}_v}, \quad I_v = \frac{\overline{I}_v}{\overline{N}_v}, \tag{9}$$

$$D_j = \frac{\overline{D}_j}{\overline{D}_1}, \quad \nu_j = \frac{\overline{\nu}_j}{b\overline{q}_1\overline{m}_1}\left(\frac{b\overline{q}_1\overline{m}_1}{D_1}\right)^{1/2}, \quad \nu_v = \frac{\overline{\nu}_v}{b\overline{q}_1\overline{m}_1}\left(\frac{b\overline{q}_1 m_1}{D_1}\right)^{1/2}, \tag{10}$$

$$\mu_j = \frac{\overline{\mu}_j}{b\overline{q}_1\overline{m}_1}, \quad \gamma_j = \frac{\overline{\gamma}_j}{b\overline{q}_1\overline{m}_1}, \quad \alpha_j = \frac{\overline{\alpha}_j}{b\overline{q}_1\overline{m}_1}, \quad \mu_v = \frac{\overline{\mu}_v}{b\overline{q}_1\overline{m}_1}, \tag{11}$$

$$\beta_j = \overline{\beta}_j, \quad \beta_{vj} = \frac{\overline{\beta}_{vj}}{\overline{m}_1}, \quad m_j = \frac{\overline{m}_j}{\overline{m}_1}, \quad q_j = \frac{\overline{q}_j}{\overline{q}_1}. \tag{12}$$

With $N_j = S_j + I_j + R_j$ and $S_v + I_v = 1$, System (5) becomes:

$$\begin{cases} \frac{\partial S_j}{\partial t} = D_j \frac{\partial^2 S_j}{\partial x^2} - \nu_j \frac{\partial S_j}{\partial x} + \mu_j - q_j m_j \frac{\beta_j}{N_j} I_v S_j - \mu_j S_j \\ \frac{\partial I_j}{\partial t} = \frac{\partial^2 I_j}{\partial x^2} - \nu_j \frac{\partial I_j}{\partial x} + q_j m_j \frac{\beta_j}{N_j} I_v S_j - (\gamma_j + \mu_j + \alpha_j) I_j \\ \frac{\partial N_j}{\partial t} = \frac{\partial^2 N_j}{\partial x^2} - \nu_j \frac{\partial N_j}{\partial x} + \mu_j - \mu_j N_j - \alpha_j I_j \\ \frac{\partial I_v}{\partial t} = \left(\sum_{j=1}^{n} q_j \frac{\beta_v}{N_j} I_j\right)(1 - I_v) - (1 - p)\mu_v I_v. \end{cases} \tag{13}$$

We determine the velocity of the propagation of the WNV through space.

3. ANALYSIS

3.1. Spatially Homogeneous Dynamics of the WNV

System (13) homogeneous with respect to space becomes:

$$
\begin{cases}
\frac{dS_j(t)}{dt} = \mu_j - q_j m_j \frac{\beta_j}{N_j(t)} I_v(t) S_j(t) - \mu_j S_j(t) \\
\frac{dI_j(t)}{dt} = q_j m_j \frac{\beta_j}{N_j(t)} I_v(t) S_j(t) - (\gamma_j + \mu_j + \alpha_j) I_j(t) \\
\frac{dN_j(t)}{dt} = \mu_j - \mu_j N_j(t) - \alpha_j I_j(t) \\
\frac{dI_v(t)}{dt} = \left(\sum_{j=1}^{n} q_j \frac{\beta_{vj}}{N_j(t)} I_j(t) \right)(1 - I_v(t)) - (1-p)\mu_v I_v(t),
\end{cases}
\tag{14}
$$

for $j = 1, \ldots, n$. From the product of the thresholds of the transmission coefficients β_j and β_{vj}, the basic reproduction ratio R_0 is:

$$
R_0 = \sum_{j=1}^{n} \frac{q_j^2 m_j \beta_j \beta_{vj}}{(1-p)\mu_v(\gamma_j + \mu_j + \alpha_j)}.
\tag{15}
$$

The stability of the disease-free point is determined by a polynomial of $3n+1$ degree whose coefficient of the term of degree zero depends on R_0. For $R_0 > 1$, the equilibrium point is unstable because the latter coefficient is negative implying the existence of a positive real root (Raimundo and Yang, 2006). The stability for $R_0 < 1$ is checked using the Routh-Hurwitz criterion (Norman and Bowers, 2007). The threshold is an average of the thresholds with respect to the single model for isolated species living in the region. The threshold is then an average of the fitness of the bird species in a region. The proof is in Maidana and Yang (2009).

3.2. Traveling Wave Solution

We determine the minimum wave speed connecting the disease-free equilibrium to the endemic state. The solution corresponding to the minimum wave speed of System (13) describes the biological waves (Volpert and Volpert, 1994; Sandstede, 2002).

The travelling waves solution, when it exists Murray (2002), is:

$$
(s_1(t,x), i_1(t,x), n_1(t,x), \ldots, i_v(t,x)) = (s_1(z), i_1(z), n_1(z), \ldots, i_v(z))),
\tag{16}
$$

where $z = x - ct$. System (13) becomes:

$$
\begin{cases}
-c \frac{ds_j(z)}{dz} = D_j \frac{d^2 s_j(z)}{dz^2} - \nu_j \frac{ds_j(z)}{dz} + \mu_j - q_j m_j \frac{\beta_j i_v(z)}{n_j(z)} s_j(z) - \mu_j s_j(z) \\
-c \frac{di_j(z)}{dz} = D_j \frac{d^2 i_j(z)}{dz^2} - \nu_j \frac{di_j(z)}{dz} + q_j m_j \frac{\beta_j i_v(z)}{n_j(z)} s_j(z) - (\mu_j + \alpha_j + \gamma_j) i_j(z) \\
-c \frac{dn_j(z)}{dz} = D_j \frac{d^2 n_j(z)}{dz^2} - \nu_j \frac{dn_j(z)}{dz} + \mu_j - \mu_j n_j(z) - \alpha_j i_j(z) \\
-c \frac{di_v(z)}{dz} = \sum_{j=1}^{n} q_j \beta_v i_j(z) \frac{(1 - i_v(z))}{n_j(z)} - (1-p)\mu_v i_v(z)
\end{cases}
\tag{17}
$$

for $j = 1, \ldots, n$.

Defining the variables $u_j := \frac{ds_j}{dz}$, $y_j := \frac{di_j}{dz}$, and $w_j := \frac{dn_j}{dz}$, $j = 1, \ldots, n$, the differentials with respect to z are:

$$\begin{cases} \frac{ds_a(z)}{dz} = u_j(z) \\ \frac{du_j(z)}{dz} = \frac{1}{D_j}\left((-c+\nu_j)u_j(z) - \mu_j + \frac{q_j m_j \beta_j i_v(z)}{n_j(z)}s_j(z) + \mu_j s_j(z)\right) \\ \frac{di_j(z)}{dz} = y_j(z) \\ \frac{dy_j(z)}{dz} = \frac{1}{D_j}\left((-c+\nu_j)y_j(z) - \frac{q_j m_j \beta_j i_v(z)}{n_j(z)}s_j(z) + (\gamma_j + \mu_j + \alpha_j)i_j(z)\right) \\ \frac{dn_j(z)}{dz} = w_j(z) \\ \frac{dw_j(z)}{dz} = \frac{1}{D_j}((-c+\nu_j)w_j(z) - \mu_j + \mu_j n_j(z) + \alpha_j i_j(z)) \\ \frac{di_v(z)}{dz} = \frac{1}{c}\left(-\sum_{j=1}^{n} q_j \beta_v i_j(z)\frac{(1-i_v(z))}{n_j(z)} + (1-p)\mu_v i_v(z)\right) \end{cases} \quad (18)$$

for $j = 1, \ldots, n$, where the boundary conditions are:

$$\lim_{z \to -\infty}(s_1(z), u_1(z), i_1(z), y_1(z), n_1(z), w_1(z), \ldots, i_v(z)) = (1, 0, 0, 0, 1, 0, \ldots, 0) \quad (19)$$

and

$$\lim_{z \to \infty}(s_1(z), u_1(z), i_1(z), y_1(z), n_1(z), w_1(z), \ldots, i_v(z)) = (S_1^*, 0, I_1^*, 0, N_1^*, 0, \ldots, I_v^*). \quad (20)$$

All zeros in the second equilibrium correspond to the derivatives of the subpopulations s_j, i_j, and n_j, for $j = 1, \ldots, n$. However, the first equilibrium has more zeros corresponding to infectious populations of birds ($i_j = 0$, $j = 1, \ldots, n$) and mosquitoes ($i_v = 0$), which must not be negative. The linear solutions must not oscillate, that is, the eigenvalues corresponding to this trivial equilibrium point must always be real. The roots of the characteristic polynomial of the linear system at the equilibrium:

$$(s_1, u_1, i_1, y_1, n_1, w_1, \ldots, i_v) = (1, 0, 0, 0, 1, 0, \ldots, 0) \quad (21)$$

are the roots of the polynomials $Q_j(\lambda)$, $j = 1, \ldots, n$, and $P(\lambda)$, where:

$$Q_j(\lambda) = \left(D_j\lambda^2 + (c - \nu_j)\lambda - \mu_j\right)^2 \quad (22)$$

and

$$P(\lambda) = a_{2n+1}\lambda^{2n+1} + a_{2n}\lambda^{2n} + \cdots + a_1\lambda + a_0, \quad (23)$$

where the coefficients depend on the parameters. The polynomials $Q_j(\lambda)$, $j = 1, \ldots, n$, have always real roots.

The polynomial $P(\lambda)$ shows if all the roots of the characteristic polynomial are real. The coefficient a_0, which depends of R_0 determines this fact.

The term a_0 is:

$$a_0 = \frac{(1-p)\mu_v(-1)^{(n+1)}\prod_{j=1}^{n}(\gamma_j + \mu_j + \alpha_j)}{c}(1 - R_0). \tag{24}$$

4. DISSEMINATION OF THE WNV

The WNV was identified in New York City in the year 1999 and spread rapidly from north to south and from east to west. In 2000, the front of disease traveled approximately 187 km to the north and 1100 km to the south. In 2001, the wave front traveled 312 km to the north, reaching the ocean and traveled 1100 km to the west. In 2002, the wave front travelled 1300 km to the west. In 2003, the wave front traveled 1200 km. Figure 1 shows the propagation of the WNV from New York to California (DeBiasi and Tyler, 2006). In the southern and the western directions the range of the wave speed is approximately 3.5 km/day.

We consider the blue jay population because together with the common grackle, it is the most efficient in the dissemination. The blue jay has specific migratory patterns (Stewart, 1982). We describe a unique bird species transmitting the WNV. We ignore long-range movement and focus on diffusion.
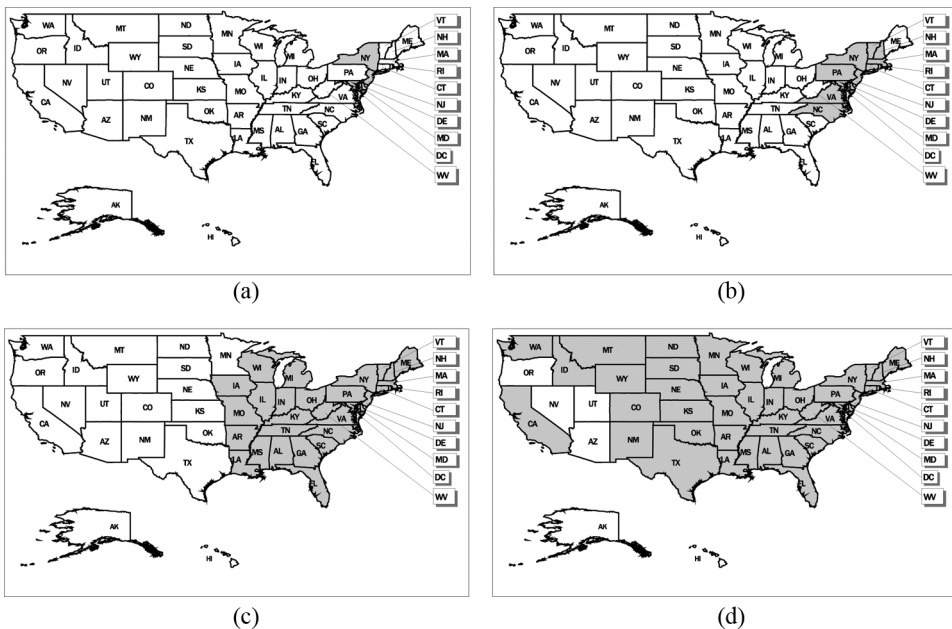

Figure 1. Spread of the West Nile virus (WNV) from 1999 to 2003 in the United States. In 2003, the WNV spread throughout the United States.

4.1. One Bird Species

The wave speed is obtained from the polynomial of Eq. (23) $n = 1$. For a single species transmitting the WNV, the polynomial $P(\lambda)$ is:

$$P(\lambda) = \lambda^3 + a_2 \lambda^2 + a_1 \lambda + a_0, \tag{25}$$

where the coefficients are:

$$a_2 = -c + \nu_1 + \frac{\mu_v(1-p)}{c} \tag{26}$$

$$a_1 = -(\alpha_1 + \gamma_1 + \mu_1) - \frac{\mu_v(c - \nu_1)(1-p)}{c} \tag{27}$$

$$a_0 = \frac{(1-p)\mu_v(\gamma_1 + \mu_1 + \alpha_1)}{c}(1 - R_0), \tag{28}$$

with R_0, obtained from Eq. (15) for one species ($n = 1$), being:

$$R_0 = \frac{q_1^2 m_1 \beta_1 \beta_{v1}}{(1-p)\mu_v(\gamma_1 + \mu_1 + \alpha_1)}. \tag{29}$$

The minimum velocity is determined by the condition that the polynomial evaluated at the unique local maximum, λ_-, must be zero, that is, $P(\lambda_-) = 0$, where:

$$\lambda_- = \frac{1}{3}\left(-a_2 - (a_2^2 - 3a_1)^{1/2}\right). \tag{30}$$

The minimum velocity satisfying $P(\lambda_-) = 0$ is called the critical value c_{min} (Figure 2). When $c > c_{min}$, all the roots are real, while for $c < c_{min}$, the roots are complex.
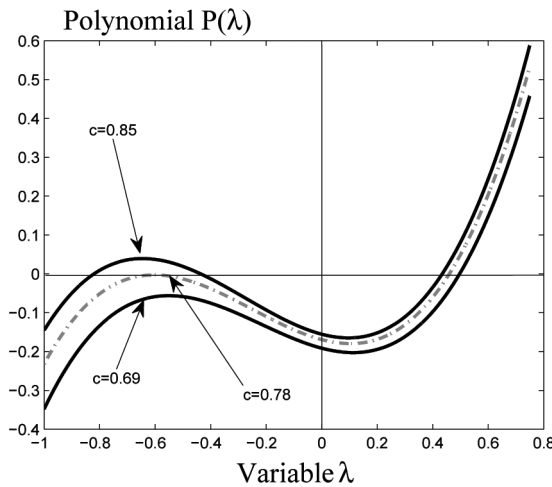

Figure 2. The critical value c_{min}. For $c < c_{min}$, the polynomial has complex roots. However, for $c > c_{min}$ the polynomial increase, and always has real roots. At $c = c_{min}$ the root is double. The parameters associated to the blue jay are taken from Table 2, with $p = 0.007$. Advection is ignored ($\nu_1 = 0$).

If the blue jay were the single species transmitting WNV and if all mosquitoes would bite only this species, then $b\overline{q}_1 = 0.5 \times 1$. The diffusion rates of various population of birds, estimated by Okubo (1998), range from 0 to $14 \, km^2$ per day. With a diffusion rate of blue jay of $D_1 = 6 \, km^2$ per day (Lewis et al., 2006; Maidana and Yang, 2009) in the dimensional parameters for blue jay (Table 2), the disease propagates at a speed of 3.03 km per day (Maidana and Yang, 2009). This velocity was obtained using the values given in Table 2, taking into account the polynomial of Eq. (25). Figure 3 represents the results of the simulated propagation, under the assumption that the starting points were concentrated in a small region.

If the blue jay represents 50% of the total bird population, and in contrast to the previous case where all the birds are bitten by mosquitoes, the biting rate becomes $b\overline{q}_1 = 0.5 \times 0.5$. The wave travel 1.65 km per day, less than 3.03 km per day in the previous case.

Figure 4 represents the simulated propagation of the disease for the northern flicker, under the assumption that infected birds are initially concentrated in a small region. In this case the wave travel is 0.16 km per day, less than 3.03 km per day which characterizes the blue jay.

If the blue jay is 50% of the total bird population and coexists with other species, then the wave speed has the upper bound of 3.03 km per day and the lower bound of 1.65 km per day. Table 2 presents the wave speed for two values of $\overline{q}_1$, 1 (isolated species) and 0.5 (unique transmitter of the WNV comprising 50% of the population of the birds).

4.2. Dissemination With Two Avian Species

We consider the blue jay coexisting with another avian species. Blue jay and common grackle are the most efficient birds transmitting the WNV (Komar et al.,

Table 2. The range of the wave speed obtained for a unique bird species transmitting the WNV, with $\overline{q}_1 = 0.5$ and 1. The epidemiological and demographic parameters are given in Komar et al. (2003) and Cruz-Pacheco et al. (2005). $p = 0.007$, Turell et al. (2001), Dohm et al. (2002), Goddard et al. (2002), $m_1 = 5$, $b = 0.5$, $\overline{\beta}_1 = 1$, Cruz-Pacheco et al. (2005)

| Common name	$\overline{\beta}_{v1}$	$\overline{\gamma}_1$ (day^{-1})	$\overline{\alpha}_1$ (day^{-1})	$\overline{\mu}_{a \times 10^{-4}}$ (day^{-1})	$\overline{\mu}_{v \times 10^{-2}}$ (day^{-1})	R_0^1	$\overline{c}_{min}$ km (day^{-1})
Common grackle	0.68	0.33	0.07	1	6	35.64	[1.67, 3.05]
Blue jay	0.68	0.26	0.15	2	6	34.76	[1.65, 3.03]
House sparrow	0.53	0.33	0.10	2	6	25.84	[1.39, 2.73]
American robin	0.36	0.33	0.00	2	6	22.84	[1.29, 2.51]
American crow	0.50	0.31	0.19	2	6	20.96	[1.20, 2.51]
House Finch	0.32	0.18	0.14	3	6	20.96	[1.20, 2.41]
Ring-billed gull	0.28	0.22	0.1	3	6	18.32	[1.12, 2.29]
Black-billed magpie	0.36	0.33	0.16	1	6	15.40	[0.96, 2.21]
Fish crow	0.26	0.36	0.06	2	6	12.96	[0.85, 2.02]
Mallard	0.16	0.33	0.00	2	6	10.16	[0.70, 1.76]
Morning dove	0.11	0.59	0.00	2	6	3.92	[0.00, 0.96]
Northern flicker	0.06	1.00	0.00	2	6	1.24	[0.00, 0.16]
Canada goose	0.10	3.33	0.00	2	6	0.64	[0.00, 0.00]
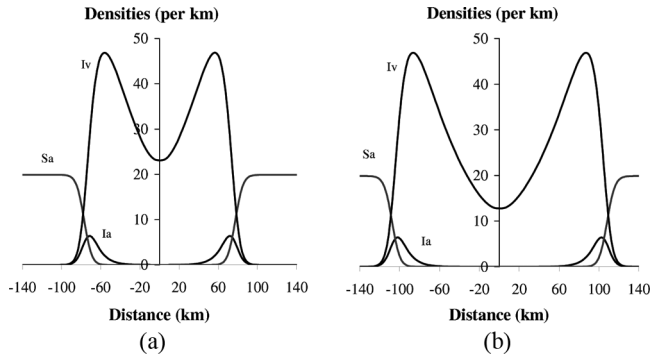
Figure 3. Propagation of the disease for blue jay. Solutions of susceptible (in total number $S_a(t, x)$) and infective (in total number $I_a(t, x)$) birds, assuming that the mosquitoes ($I_v(t, x)$) bite only this species ($q_1 = 1$), are shown at, (a) $t = 33$ and (b) $t = 43$ days. The wave speed is 3.03 km per day.

2003). They live in the region of New York. We consider that the blue jay and the common grackle represent 50% of the total bird population, which corresponds to $n = 2$, $\overline{q}_j = 0.5$, $j = 1, 2$, leading to $q_1 = q_2 = 1$. We consider $\Lambda_1 = \Lambda_2$ and $\mu_1 = \mu_2$, which gives $m_1 = m_2 = 1$. To compute the wave speed, the polynomial of Eq. (23) for $n = 2$ becomes:

$$P(\lambda) = a_5 \lambda^5 + a_4 \lambda^4 + a_3 \lambda^3 + a_2 \lambda^2 + a_1 \lambda^1 + a_0, \tag{31}$$

where:

$$a_0 = -\frac{(\gamma_1 + \mu_1 + \alpha_1)(\gamma_2 + \mu_2 \alpha_2)\mu_v(1 - p)\left(1 - \left(R_0^1 + R_0^2\right)\right)}{c}. \tag{32}$$

The coefficient a_0 depends on R_0. With this polynomial we compute the critical value c_{min} (Figure 5).
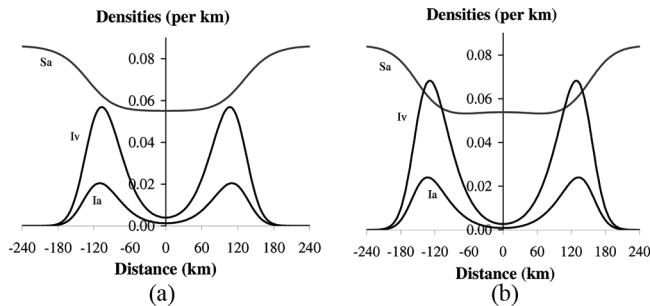

Figure 4. The propagation of the disease for the northern flicker. Solutions of susceptible (in total number $S_a(t, x)$) and infective (in total number $I_a(t, x)$) birds, assuming that mosquitoes (in total number $I_v(t, x)$) bite only this species ($q_1 = 1$), are shown at (a) $t = 965$ and (b) $t = 1,065$ days. The wave is very slow, 0.16 km per day. The susceptible avian population ($S_a(t, x)$) is divided by 200.
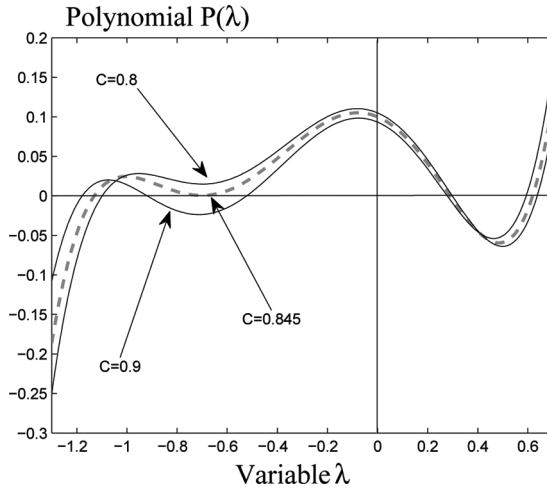
Figure 5. The critical value $c_{min} = 0.845$. For $c = 0.8 < c_{min}$, the polynomial has two complex roots. For $c = 0.9 > c_{min}$, the polynomial has real roots. At $c = c_{min} = 0.845$ the root is double. The parameters corresponding to the blue jay and to the common grackle are taken from (Table 2) with $p = 0.007$, and advection is ignored ($\nu_1 = \nu_2 = 0$).

For the blue jay and the common grackle, we obtain $c_{min} = 0.845$. Maidana and Yang (2009) and Lewis et al. (2006) considered a single bird species with diffusive coefficient of $6 \, km^2$ per day. This diffusive value is assumed here to both the blue jay and the common grackle, that is, $D_1 = D_2 = 6 \, km^2$ per day. The wave speed of disease dissemination is:

$$\overline{c}_{min} = (0.25 \times 5 \times 6)^{1/2} \times 0.845 = 2.31 \text{ km per day.} \tag{33}$$

The wave speed $\overline{c}_{min} = 2.31$ lies in the interval [1.65, 3.03] as expected from Table 2. When we consider only the blue jay and when we assume that mosquitoes bite only this bird, the wave is faster than when the blue jay coexists with the efficient common grackle. The reason is that the total avian population varies while the mosquito population is constant. The probability of one mosquito biting an infected bird is then lower.

Figure 6a shows the initial propagation of the WNV under the assumption that infected blue jays (in total number $I_a(t, x)$) are initially concentrated in a small region. Initially, the infected population of common grackle (in number $I_b(t, x)$) is less numerous, but the infected densities of blue jay and common grackle become similar (Figures 6b and 6c). This is a consequence of the same R_0 for both species (Table 2). Figures 6b and 6c show the wavefront traveling 23 km in 10 days or a wave speed of:

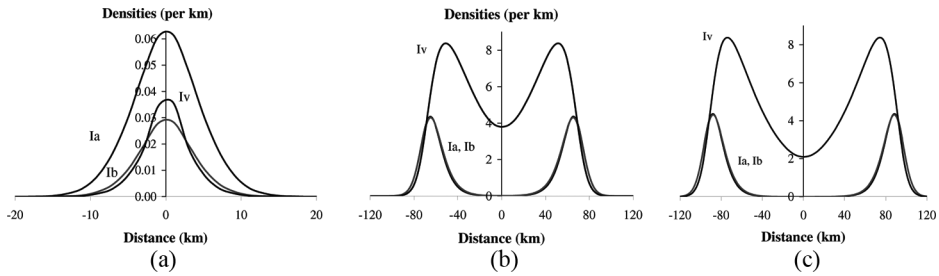$$V = \frac{123 - 100}{54 - 44} = 2.3 \text{ km per day.} \tag{34}$$

Figure 6. Propagation of the disease for the blue jay ($I_a(t, x)$) coexisting with the common grackle ($I_b(t, x)$) and mosquitoes ($I_v(t, x)$) Initial time, (a) $t = 2$, then (b) $t = 44$ and (c) $t = 54$ days. The population density $I_v(t, x)$ of the infected mosquito population is divided by 5.

If we consider other bird species, the wave speed is upper bounded by 3.03 km per day. The fastest wave for blue jay is when this bird coexists with the common grackle, which is the most efficient species. In this case, the wave speed is 2.31 km per day only. When we consider less efficient species coexisting with the blue jay, the speed drops to 1.65 km per day. For the blue jay coexisting with the fish crow, the speed is 1.94 km per day; when the blue jay coexists with the northern flicker, the wave speed is 1.68 km per day (Figure 7).

The resident bird house sparrow for example does not migrate. If this behavior affects the diffusion movement, we assume $D_2 = 2$ km^2 per day. In this case, the coexistence with the blue jay yields a wave speed of 1.94 km per day. However, if $D_2 = 6$ km^2 per day, a value used by Okubo (1998), then the wave speed is 2.19 km per day. A threefold increase in the diffusion coefficient changes the wave speed only little. The diffusion of the house sparrow then does not influence the wave speed.

4.3. Dissemination of the WNV With Three Avian Species

The wave slows down with three species. Again the probability of bites decrease, because the total population increases.
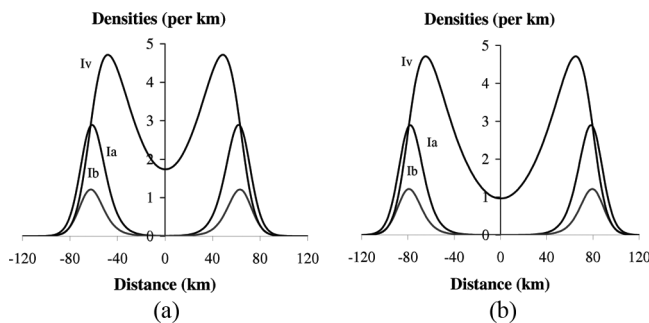

Figure 7. Propagation of the disease for the blue jay ($I_a(t, x)$) and northern flicker ($I_b(t, x)$) and mosquitoes ($I_v(t, x)$), (a) $t = 60$ and (b) $t = 70$ days. The wave speed 1.68 km per day is close the lower limit for the blue jay, because the northern flicker is not very efficient in transmitting the West Nile virus when it is the only species, $R_0^1 = 1.24$ (Table 2). The density of the infected mosquito population ($I_v(t, x)$) is divided by 5.

When we consider the blue jay, the common grackle and the northern flicker, the wave speed is 1.49 km per day. Figure 8a shows the initial time of the propagation. At the beginning, the infected blue jay birds are more numerous than infected common grackles, because the disease affects only the blue jays. Later, the infected blue jay is as numerous as the common grackle because both have similar R_0^1 (Figures 8b and 8c). Infected northern flickers are always less numerous because they are less efficient in the transmission, and because they have a smaller reproduction rate (R_0^1) as a single species than the blue jay and the common grackle.

Figures 8b and 8c represent the wave front at $t = 65$ and $t = 75$ days. The wave speed is 1.49 km per day. With the blue jay only, the wave speed is 3.03 km per day. The coexistence with the common grackle reduces the wave speed to 2.31 km per day. The coexistence of these two bird species with the northern flicker, which is less efficient in transmitting WNV, drops the wave speed to 1.49 km per day.

The blue jay and the common grackle live in the eastern United States. The most efficient transmitters of WNV in the East are the house sparrow and the American robin. The coexistence with the norther flicker yields a wave speed of 1.24 km per day.

The presence of two and three species reduce the wave speed. To explain the observed WNV dissemination in the United States, we need to incorporate the long-reach movement of birds, (Rappole et al., 2000; Reed et al., 2002). The birds transmit the disease during migration because of different stop-over strategies (Erni et al., 2002).

4.4. Migration of Birds

Migration can explain the observed data for dissemination of the WNV. Including migration of two avian populations, for instance the blue jay and the common grackle, the wave travels faster. In Figure 9, $\overline{\nu}_1 = \overline{\nu}_2 = 2$ km per day, and the speed increases from 2.31 to 3.64 km per day.

Migration may exceed diffusion. From simulations the density at the peak of infected subpopulation is 10% of the total population in the direction of migrations and 30% in the opposite direction. This come from the existence of isolated cases in the direction of migration. We expect a faster dissemination but a lower density of infected birds.
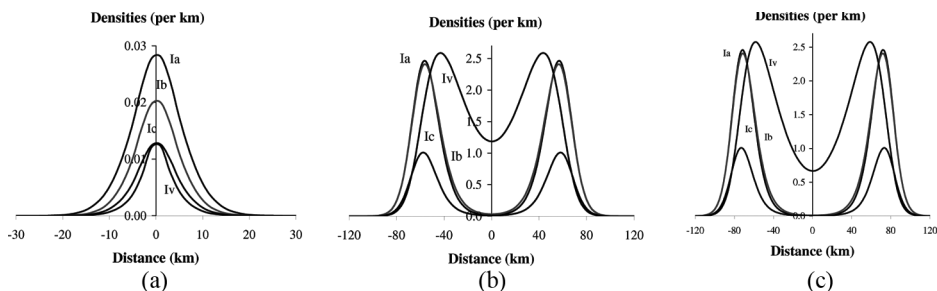

Figure 8. Propagation of the disease for the blue jay ($I_a(t, x)$), the common grackle ($I_b(t, x)$), the northern flicker ($I_c(t, x)$) and mosquitoes ($I_v(t, x)$). Initial time, (a) $t = 4$, (b) $t = 65$ and (c) $t = 75$ days. The density of the infected mosquito population ($I_v(t, x)$) is divided by 10.
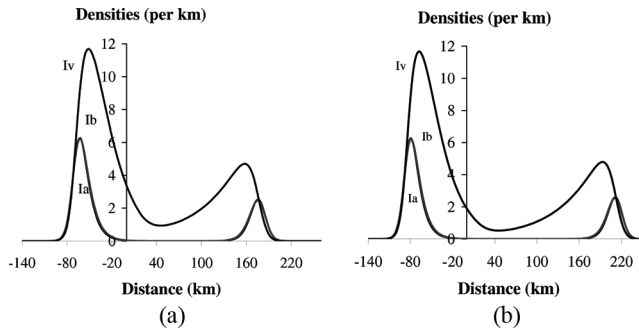
Figure 9. Propagation of the disease for the blue jay ($I_a(t, x)$) and the common grackle ($I_b(t, x)$) and mosquitoes ($I_v(t, x)$), (a) $t = 63$ and (b) $t = 73$ days. Considering the advection movements, the observed wave speed is close to the observed one, but infected populations have lower density, which can explain the isolated cases in migratory directions. The density of infected mosquito population ($I_v(t, x)$) is divided by 5.

When we consider the blue jay coexisting with a resident species, such as the house sparrow, $\nu_2 = 0$. If $\nu_1 = 0$ the wave speed is 2.19 km per day. If we consider the advection movement of the blue jay $\nu_1 = 2$ km per day, the wave speed is 3.12 km per day, under the 3.64 km per day obtained for two migratory species, the blue jay and the common grackle. Although house sparrows do not migrate, the presence of the blue jay migration accelerates the wave.

5. CONCLUSION

From the traveling waves solution and their associated wave speed front, we showed that the coexistence of several bird species reduces the wave speed. This is a consequence of the increase of the total avian population in comparison with the case of one species. The mosquito population is kept constant. The probability of a mosquito biting an infected bird is lower. The observed wave speed is then influenced by migrations of birds. By incorporating long range migration, the wave travels faster, which could explain the dissemination of the WNV in the United States.

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