

ASSESSING THE SPATIAL PROPAGATION OF WEST NILE VIRUS

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In this work we study a spatial model for the West Nile Virus (WNV) propagation across the USA from the east to the west. WNV is an arthropod-borne flavivirus that appeared at first time in New York city in the summer of 1999 and then spread prolifically within birds. Mammals, as human and horse, do not develop sufficiently high bloodstream titers to play a significant role in transmission, which is the reason to consider the mosquito-bird cycle. The proposed model aims to study this propagation in a system of partial differential reaction-diffusion equations considering the mosquito and the avian populations. The diffusion is allowed to both populations, being greater in avian than in the mosquito. When a threshold value R_0 , depending on the model's parameters, is greater than one, the disease remains endemic and could propagate to regions previously free of disease. The travelling wave solutions of the model are studied to determine the speed of the disease propagation. This wave speed is obtained as a function of the model's parameters, for instance, vertical transmission rate and avian diffusion coefficient.

Keywords: *Aedes aegypti*; avian diffusion; travelling waves.

1. Introduction

West Nile Virus (WNV) is an arthropod-borne flavivirus. The primary vectors of WNV are *Culex spp* mosquitoes, although the virus has been isolated from at least 29 more species of ten genera, see Campbell *et al.*¹ When an infected mosquito bites a bird, the virus is transmitted. A mosquito is infected when bites an infected bird. Also, the virus can be passed via vertical transmission, from a mosquito to its offspring.

One major feature of WNV spatial dissemination is the high velocity of geographic invasion and colonization. This is due to long distance flying of birds, and ubiquitous presence of mosquitoes. For instance, WNV was introduced in New York City in 1999, and then propagates across the USA. After five years, WNV was detected among birds in California, west side of USA. Some studies about the non spatial dynamic was developed by Kenkre *et al.*,² wonham *et al.*,³ Cruz-Pacheco *et al.*⁴ and Bowman *et al.*⁵

The models proposed consider different aspects of the WNV disease and determine threshold conditions to assess control strategies. Kenkre *et al.*² study the periodicity of the infection considering vertical transmission, mortality increase due to infection and time scale disparity. In the Wonham *et al.*³ model is considered all the mosquito life cycle. Cruz-Pacheco *et al.*⁴ analyze the mathematical model and use experimental data for several species of birds. In the Bowman *et al.*⁵ model is considered the human population to assess preventive strategies.

A spatial model was studied by Lewis *et al.*⁶ considering for the non spatial dynamic the Wonham *et al.*³ model. They study the WNV propagation using travelling wave solution for a simplified model which does not consider vertical transmission, WNV death rate and the avian recover subpopulation. Aiming to determine the biological invasion of WNV from east to west coast of USA, we develop a spatio-temporal model to study this propagation as a consequence of the zoonotic characteristic of WNV.

In the modeling for the spatial dynamics of WNV the diffusion is considered in avian and mosquito populations, taking into account the fact that the diffusion coefficient in the avian population is greater than the diffusion in the mosquitoes population. From the model we seek for the travelling waves connecting the two steady states, from which we determine the wave speed of propagation of the WNV disease. The dependence of this wave speed on the vertical transmission and on the avian diffusion is obtained. Okubo⁷ estimated the diffusion coefficient of birds situating between 0 and 14 km²/day. Choosing a coefficient of avian diffusion equal to 6 km²/day, and considering parameters regarded to two birds species, named Blue jay and Common grackle, we obtain for the velocity of the disease propagation approximately 3 km/day, which agrees with that observed from field data.

The paper is structured as follows. In section 2 the WNV spatial propagation model is presented, which is preceded by a brief description of the corresponding spatial homogeneous model. In section 3 the minimum speed of the travelling wave is determined, and conclusion is given in Section 4.

2. Model for the West Nile Virus

Let us describe with some details the spatially homogeneous dynamics and the descriptions of the parameters of the model proposed in Cruz-Pacheco *et al.*⁴ From this model we derive the WNV geographic propagation model.

2.1. Model for the spatially homogeneous WNV propagation dynamics

The model proposed in Cruz-Pacheco *et al.*⁴ includes cross-infection between the avian and the vector populations, which sizes are denoted by $N_a(t)$ and $N_v(t)$, respectively. The avian population was divided into susceptible, infective and recovered subpopulations, S_a , I_a and R_a , respectively, while for the vector population, the susceptible and infected subpopulations, S_v and I_v .

The mosquito population is taken constant, assuming that the birth and death rates are equal to μ_v . For the avian population, however, the total population size is allowed to vary, where Λ_a is a constant recruitment rate due to birth and migration, and death rate is μ_a . The differential equation for birds population is, then,

$$\frac{dN_a}{dt} = \Lambda_a - \mu_a N_a.$$

The biting rate b of mosquitoes is defined as the average number of bites per mosquito per day. β_a and β_v are the transmission probabilities from vector to birds and from birds to vector, respectively. Hence the infection rates per susceptible birds and susceptible vector are given by:

$$b\beta_a \frac{N_v}{N_a} \frac{I_v}{N_v} = b \frac{\beta_a}{N_a} I_v$$

and

$$b\beta_v \frac{I_a}{N_a}.$$

The birds are recovered at rate γ_a . The specific death rate associated with WNV in the avian population is α_a , with $\alpha_a \leq \gamma_a$. Another assumption is that mosquitoes can transmit WNV vertically. The fraction of progeny of infectious mosquitoes that is infectious is denoted by p , with $0 \leq p \leq 1$.

Based on the above parameters, the model is the following:

$$\frac{dS_a}{dt} = \Lambda_a - \frac{b\beta_a}{N_a} I_v S_a - \mu_a S_a \tag{4}$$

$$\frac{dI_a}{dt} = \frac{b\beta_a}{N_a} I_v S_a - (\gamma_a + \mu_a + \alpha_a) I_a \tag{5}$$

$$\frac{dR_a}{dt} = \gamma_a I_a - \mu_a R_a \tag{6}$$

$$\frac{dS_v}{dt} = \mu_v S_v + (1 - p)\mu_v I_v - \frac{b\beta_v}{N_a} I_a S_v - \mu_v S_v \tag{7}$$

$$\frac{dI_v}{dt} = p\mu_v I_v + \frac{b\beta_v}{N_a} I_a S_v - \mu_v I_v \tag{8}$$

$$\frac{dN_a}{dt} = \Lambda_a - \mu_a N_a - \alpha_a I_a. \tag{9}$$

The model has the disease free equilibrium and one endemic state, see Cruz-Pacheco *et al.*,⁴ which exists if:

$$R_0 = \frac{mb^2\beta_a\beta_v}{(1 - p)\mu_v(\gamma_a + \mu_a + \alpha_a)} > 1.$$

In Table 1 we show the Basic Reproductive Number for three avian species, Blue jay, Common grackle and Fish crow.

Table 1. Basic Reproductive Number calculated from the epidemiological and demographic parameters.

Common name	β_a	β_v	γ_a (day ⁻¹)	α_a (day ⁻¹)	μ_a (day ⁻¹)	μ_v (day ⁻¹)	$\sqrt{R_0}$
Blue jay	1.0	0.68	0.26	0.15	0.0002	0.06	5.89
Common grackle	1.0	0.68	0.33	0.07	0.0001	0.06	5.97
Fish crow	1.0	0.26	0.36	0.06	0.0002	0.06	3.60

2.2. Model for the spatial dynamics of WNV

WNV disease first appeared in North America in summer of 1999, with the simultaneous occurrence of an unusual number of deaths of exotic birds and crows in the New York City, see DeBiasi *et al.*⁸ We propose a model to study the propagation of WNV across the USA.

The diffusion among avians is denoted by D_a and D_v is regarded to the diffusion of mosquito population. We are not taking into account the long migratory movement of birds. The mosquitoes are considered as a sessible population, then $D_v \ll D_a$. For instance, the mean dispersal distance for *Aedes aegypty* was ranged from 28 to 199 meters, Harrington *et al.*⁹ From now on we consider the spatio-temporal dependence on the populations, e.g. $N_a(x, t)$ and $N_v(x, t)$, and their respective subpopulations. The model is the following:

$$\frac{\partial S_a}{\partial t} = D_a \frac{\partial^2 S_a}{\partial x^2} + \Lambda_a - \frac{b\beta_a}{N_a} I_v S_a - \mu_a S_a \tag{11}$$

$$\frac{\partial I_a}{\partial t} = D_a \frac{\partial^2 I_a}{\partial x^2} + \frac{b\beta_a}{N_a} I_v S_a - (\gamma_a + \mu_a + \alpha_a) I_a \tag{12}$$

$$\frac{\partial R_a}{\partial t} = D_a \frac{\partial^2 R_a}{\partial x^2} + \gamma_a I_a - \mu_a R_a \tag{13}$$

$$\frac{\partial S_v}{\partial t} = D_v \frac{\partial^2 S_v}{\partial x^2} + \mu_v S_v + (1 - p)\mu_v I_v - \frac{b\beta_v}{N_a} I_a S_v - \mu_v S_v \tag{14}$$

$$\frac{\partial I_v}{\partial t} = D_v \frac{\partial^2 I_v}{\partial x^2} + p\mu_v I_v + \frac{b\beta_v}{N_a} I_a S_v - \mu_v I_v \tag{15}$$

$$\frac{\partial N_a}{\partial t} = D_a \frac{\partial^2 N_a}{\partial x^2} + \Lambda_a - \mu_a N_a - \alpha_a I_a. \tag{16}$$

Let us introduce the non dimensional parameters to the system (11) - (16). The time is scaled with respect to bm , where b is the biting rate of mosquitoes and $m = \frac{N_v}{\Lambda/\mu_a}$, the ratio between the vector population and the disease free equilibrium bird population. The spatial variable is scaled considering the bird's diffusion coefficient, according to $\sqrt{\frac{D_a}{bm}}$. Then non dimensional parameters are:

$$\tilde{S}_a = \frac{S_a}{\Lambda/\mu_a}, \tilde{I}_a = \frac{I_a}{\Lambda/\mu_a}, \tilde{R}_a = \frac{R_a}{\Lambda/\mu_a}, \tilde{N}_a = \frac{N_a}{\Lambda/\mu_a}, \tilde{S}_v = \frac{S_v}{N_v}, \tilde{I}_v = \frac{I_v}{N_v}$$

$$D = \frac{D_v}{D_a}, \quad \tilde{\mu}_a = \frac{\mu_a}{bm}, \quad \tilde{\gamma}_a = \frac{\gamma_a}{bm}, \quad \tilde{\alpha}_a = \frac{\alpha}{bm} \quad \tilde{\mu}_v = \frac{\mu_v}{bm}$$

$$\tilde{\beta}_a = \beta_a, \quad \tilde{\beta}_v = \frac{\beta_v}{m}.$$

Therefore, omitting \tilde{R}_a and \tilde{S}_v (both are decoupled form the system), see Cruz-Pacheco *et al.*,⁴ the dimensionless model obtained is:

$$\frac{\partial \tilde{S}_a}{\partial t} = \frac{\partial^2 \tilde{S}_a}{\partial x^2} + \tilde{\mu}_a - \frac{\tilde{\beta}_a}{\tilde{N}_a} \tilde{I}_v \tilde{S}_a - \tilde{\mu}_a \tilde{S}_a \tag{17}$$

$$\frac{\partial \tilde{I}_a}{\partial t} = \frac{\partial^2 \tilde{I}_a}{\partial x^2} + \frac{\tilde{\beta}_a}{\tilde{N}_a} \tilde{I}_v \tilde{S}_a - (\tilde{\gamma}_a + \tilde{\mu}_a + \tilde{\alpha}_a) \tilde{I}_a \tag{18}$$

$$\frac{\partial \tilde{I}_v}{\partial t} = D \frac{\partial^2 \tilde{I}_v}{\partial x^2} + \frac{\tilde{\beta}_v}{\tilde{N}_a} \tilde{I}_a (1 - \tilde{I}_v) - (1 - p) \tilde{\mu}_v \tilde{I}_v \tag{19}$$

$$\frac{\partial \tilde{N}_a}{\partial t} = \frac{\partial^2 \tilde{N}_a}{\partial x^2} + \tilde{\mu}_a - \tilde{\mu}_a \tilde{N}_a - \tilde{\alpha}_a \tilde{I}_a. \tag{20}$$

The system of equations (17-20) has two steady states. The first is the disease free equilibrium point, given by:

$$P_0 = (1, 0, 0, 1).$$

The second is the endemic state:

$$P_1 = (S_a^*, I_a^*, I_v^*, N_a^*),$$

where S_a^* , I_v^* and N_a^* are given by:

$$S_a^* = \frac{\mu_a - (\gamma_a + \mu_a + \alpha_a) I_a^*}{\mu_a},$$

$$I_v^* = \frac{\mu_a \beta_v I_a^*}{(\beta_v \mu_a - \alpha_a (1 - p) \mu_v) I_a^* + (1 - p) \mu_v \mu_a}$$

and

$$N_a^* = \frac{\mu_a - \alpha_a I_a^*}{\mu_a},$$

where I_a^* is the positive root of the second degree polynomial

$$r(I_a) = EI_a^2 + FI_a + G,$$

with the coefficients

$$E = [\tilde{\beta}_v \tilde{\mu}_a - \tilde{\alpha}_a (1 - p) \tilde{\mu}_v] \frac{\tilde{\alpha}_a}{\tilde{\mu}_a}$$

$$F = 2\tilde{\alpha}_a (1 - p) \tilde{\mu}_v - \tilde{\beta}_v \tilde{\mu}_a - (1 - p) \tilde{\mu}_v (\tilde{\gamma}_a + \tilde{\mu}_a + \tilde{\alpha}_a) \tilde{R}_0$$

$$G = \tilde{\mu}_a (1 - p) \tilde{\mu}_v (\tilde{R}_0 - 1).$$

Notice that a positive solution always exists for $\tilde{R}_0 > 1$, where

$$\tilde{R}_0 = \frac{\tilde{\beta}_a \tilde{\beta}_v}{(1 - p) \tilde{\mu}_v (\tilde{\gamma}_a + \tilde{\mu}_a + \tilde{\alpha}_a)}. \tag{23}$$

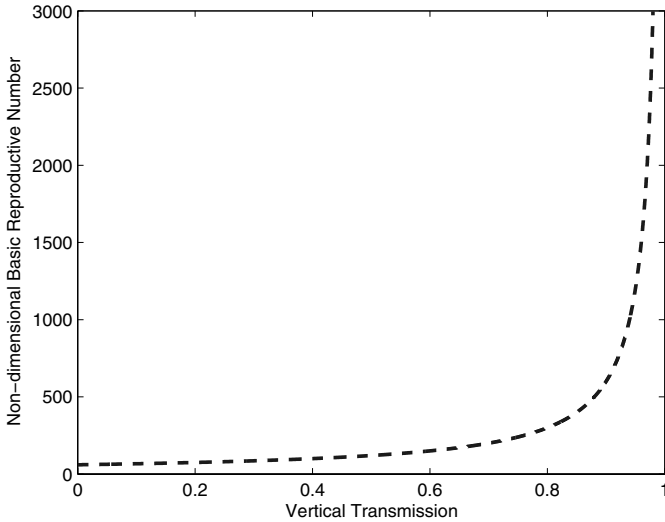


Fig. 1. Graph of the variation of \tilde{R}_0 as a function of the vertical transmission p , for the parameters related to Blue jay given in Table 2. The Basic Reproductive Number increases to infinity with p . This reflects that the vertical transmission is an important factor in the homogeneous situation.

The original system has the equilibrium values given in Cruz-Pacheco *et al.*,⁴ which has positive solution when $R_0 > 1$.

In Figure 1 we show the variation of the basic reproductive number \tilde{R}_0 as a function of the vertical transmission. When p increases to 1, \tilde{R}_0 increases to infinity. The vertical transmission is an important fact on the spatially homogeneous situation.

The following Theorem, equivalent to that in Cruz-Pacheco *et al.*,⁴ regarded to two equilibrium points, is established:

Theorem 2.1. *If $0 \leq p < 1$, then the disease free equilibrium P_0 is unique and locally and asymptotically stable for $\tilde{R}_0 < 1$. When $\tilde{R}_0 > 1$, P_0 becomes unstable, and there appears a new endemic equilibrium P_1 which is locally and asymptotically stable. If $p = 1$, P_0 is always unstable, and P_1 is locally and asymptotically stable.*

3. Travelling Waves Solution

In this section we study the WNV geographic propagation, Murray *et al.*,¹⁰ determining the minimum wave speed connecting the disease free equilibrium point to the endemic state. The solution corresponding to minimum wave speed describes the observed dynamics of the system, see Sandstede,¹¹ Volpert and Volpert.¹²

The travelling waves solution, when exists, can be set in the usual form, see Murray¹³:

$$(s_a(x, t), i_a(x, t), i_v(x, t), n_a(x, t)) = (s_a(z), i_a(z), i_v(z), n_a(z)),$$

where $z = x + ct$. Considering that the diffusion of the avian population is greater than the mosquito population, we assume that $D = 0$. The corresponding first order ordinary differential equations with respect to variable z is:

$$\frac{ds_a}{dz} = u_1,$$

$$\frac{du_1}{dz} = cu_1 - \tilde{\mu}_a + \frac{\tilde{\beta}_a i_v}{n_a} s_a + \tilde{\mu}_a s_a,$$

$$\frac{di_a}{dz} = u_2,$$

$$\frac{du_2}{dz} = cu_2 - \frac{\tilde{\beta}_a i_v}{n_a} s_a + (\tilde{\gamma}_a + \tilde{\mu}_a + \tilde{\alpha}_a) i_a,$$

$$\frac{di_v}{dz} = (1/c) (\tilde{\beta}_v i_a \frac{(1 - i_v)}{n_a} - (1 - p) \tilde{\mu}_v i_v),$$

$$\frac{dn_a}{dz} = u_3,$$

$$\frac{du_3}{dz} = cu_3 - \tilde{\mu}_a + \tilde{\mu}_a \eta_a + \tilde{\alpha}_a i_a,$$

where the boundary conditions are:

$$\lim_{z \rightarrow -\infty} (s_a(z), u_1(z), i_a(z), u_2(z), i_v(z), n_a(z), u_3(z)) = (1, 0, 0, 0, 0, 1, 0)$$

and

$$\lim_{z \rightarrow \infty} (s_a(z), u_1(z), i_a(z), u_2(z), i_v(z), n_a(z), u_3(z)) = (S_a^*, 0, I_a^*, 0, I_v^*, N_a^*, 0).$$

The zeros in both equilibrium points deserve some words. The three zeros in the second equilibrium point correspond to derivatives of the subpopulations s_a , i_a and n_a . However, the first equilibrium point has two more zeros corresponding to infectious populations regarded to avians and mosquitoes, which must not be negative numbers. Due to this constraint, we impose to the linear system solutions that must not oscillate, i.e., the eigenvalues corresponding to this equilibrium point must assume real values.

The characteristic polynomial regarded to the linear system at the equilibrium point $(1, 0, 0, 0, 0, 1, 0)$ is $Q(\lambda) \times P(\lambda)$, where:

$$Q(\lambda) = (\lambda^2 - c\lambda - \tilde{\mu}_a)^2$$

and

$$P(\lambda) = \lambda^3 + A\lambda^2 + B\lambda + C,$$

where the coefficients are

$$\begin{aligned} A &= c - \frac{\tilde{\mu}_v(1-p)}{c} \\ B &= -c(\tilde{\alpha}_a + \tilde{\gamma}_a + \tilde{\mu}_a) - \tilde{\mu}_v c(1-p) \\ C &= (1-p)\tilde{\mu}_v(\tilde{\gamma}_a + \tilde{\mu}_a + \tilde{\alpha}_a) \left(\tilde{R}_0 - 1 \right), \end{aligned}$$

with \tilde{R}_0 being given by (23). The polynomial $Q(\lambda)$ has always real roots. Then the polynomial $P(\lambda)$ must carry on the conditions for the existence of the minimum speed. First, the existence of the endemic state implies that $\tilde{R}_0 > 1$, then we have that:

$$P(0) = (1-p)\tilde{\mu}_v(\tilde{\gamma}_a + \tilde{\mu}_a + \tilde{\alpha}_a)[\tilde{R}_0 - 1] > 0,$$

moreover, it is easy to verify that

$$\lim_{\lambda \rightarrow \pm\infty} P(\lambda) = \pm\infty, \quad \left. \frac{dP(\lambda)}{d\lambda} \right|_{\lambda=0} = -c(\tilde{\alpha}_a + \tilde{\gamma}_a + \tilde{\mu}_a) - \tilde{\mu}_v c(1-p) < 0,$$

which imply that $P(\lambda)$ always has one negative real root. Second, the remaining two roots can be either real positives or complex numbers. In order to obtain the minimum wave speed, we determine the condition that the imaginary part of the complex root must be zero (or, the roots must be real numbers). This condition is satisfied when the positive real roots are equal, from which we determine the wave speed, see Figure 2. The condition to obtain the double roots follows easy calculations: The polynomial evaluated at the unique local minimum, λ_+ , is zero, that is, $P(\lambda_+) = 0$, where:

$$\lambda_+ = \frac{1}{3} \{-A + \sqrt{A^2 - 3B}\}.$$

We calculate the non dimensional wave speed and the corresponding $\sqrt{\tilde{R}_0}$ for three species of birds, which are given in Table 2. We assume, as in Cruz-Pacheco *et al.*,⁴ the typical value of the biting rate, once every two days, $b = 0.5$ and the ratio $m = \frac{N_v}{\Lambda_a/\mu_a} = 5$. For Common grackle and Blue jay, $\sqrt{\tilde{R}_0}$ are different but the wave speeds are close. These species have the same importance in the spatial propagation, but they behave epidemiologically different. Figure 3 shows the wave speed as a function of the vertical transmission. For instance, letting $D_a = 6 \text{ km}^2/\text{day}$: (1) for $p = 0$, we have $V_{min} = 3.03 \text{ km/day}$, and (2) for $p = 1$, we have $V_{min} = 3.09 \text{ km/day}$.

The vertical transmission is not an important factor for the spatial dynamics, see Figure 3, due to the fact that mosquitoes movement is negligible compared with the avian movement, but it is important for the endemics level, as a local factor of the disease dissemination, see Figure 1. For Blue jay the wave speed increases from 0.784 to 0.798, when p increases from 0 to 1.

Figure 4 shows the wave speed as a function of the diffusion coefficient, for three birds species: Blue jay, Common grackle and Fish crow. The wave speeds for Blue jay and Common grackle are the same, although \tilde{R}_0 are different. The Fish

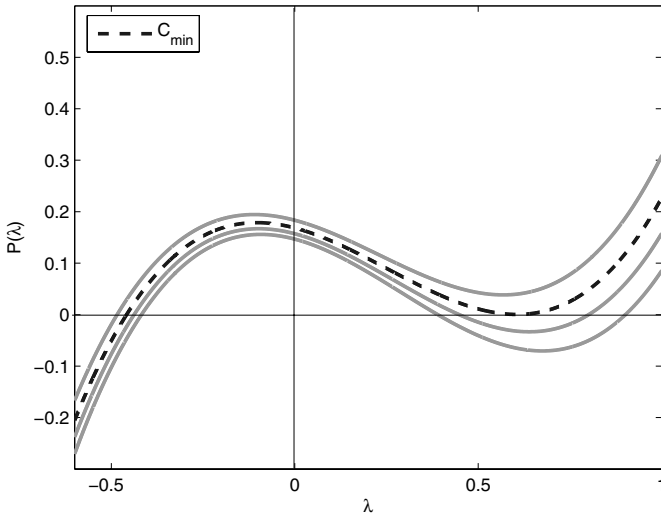


Fig. 2. Polynomial graphics for $c = 0.72$, $c_{min} = 0.78$, $c = 0.84$ and $c = 0.9$, taking into account the non dimensional parameters corresponding to those given in Table 2 for the Blue jay, with $p = 0.007$.

Table 2. Values of the non dimensional parameters used to calculate the non dimensional minimum wave speeds.

Common name	$\tilde{\beta}_a$	$\tilde{\beta}_v$	$\tilde{\gamma}_a$	$\tilde{\alpha}_a$	$\tilde{\mu}_a$	$\tilde{\mu}_v$	$\sqrt{\tilde{R}_0}$	c_{min}
Blue jay	1.0	0.136	0.104	0.06	0.00008	0.024	5.89	0.784
Common grackle	1.0	0.136	0.132	0.028	0.00004	0.024	5.97	0.789
Fish crow	1.0	0.052	0.144	0.024	0.00008	0.024	3.60	0.522

crow has \tilde{R}_0 less than the other two species, and the wave speed is considerably lower. Okubo⁷ estimates an interval for this diffusion between 0 and 14 km²/day. Considering $p = 0.007$ and $D_a = 6$ km²/day, we obtain 3.04 km/day as the velocity of the disease propagation, near to the 3 km/day observed from the field data, see maps in DeBiasi *et al.*⁸ and the bounded above velocity estimated by Lewis *et al.*⁶ assuming arbitrary values for some parameters.

From Figure 5 we can see the first peak of infection in the classes of infected mosquitoes and infected birds, for two values of the vertical transmission, $p = 0$ and $p = 0.8$. The wave speeds are close between them, but we arise an increasing in the proportion of the infected mosquitoes. This fact is due to the importance of p to the corresponding spatially homogeneous modeling.

In Figure 6 we show the numerical travelling waves solution for the first order system. We can observe the first peak of infection in the four classes.

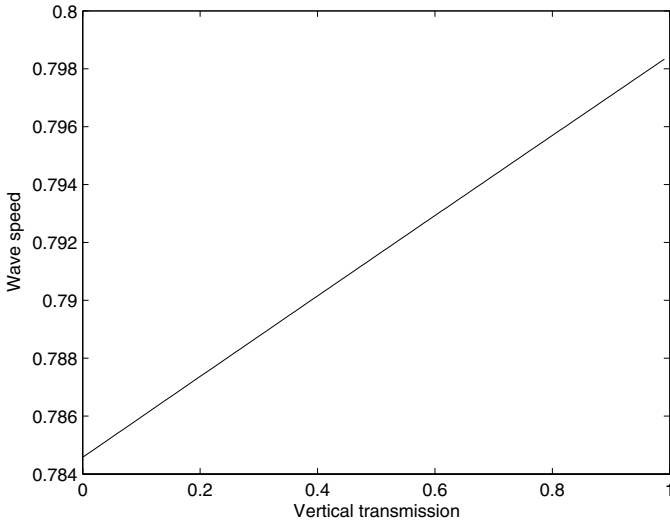


Fig. 3. Graphic of the non dimensional speed wave as a function of p , the vertical transmission, for the Blue jays parameters listed in Table 2.

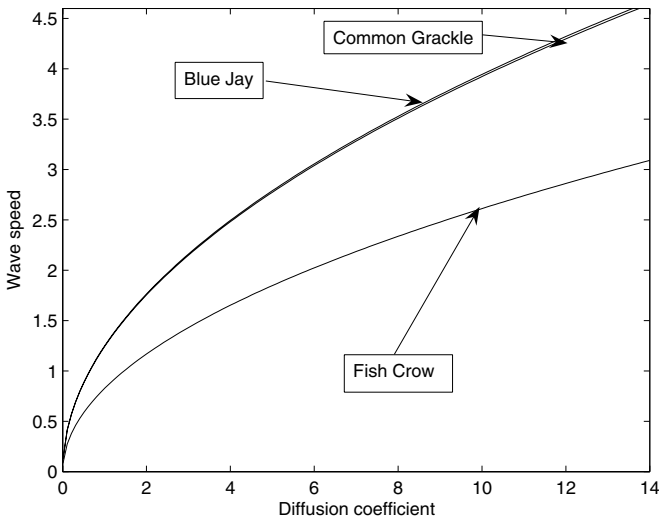


Fig. 4. Graphic of the dimensional speed wave as a function of the diffusion coefficient of the avian population D_a , considering $p = 0.007$.

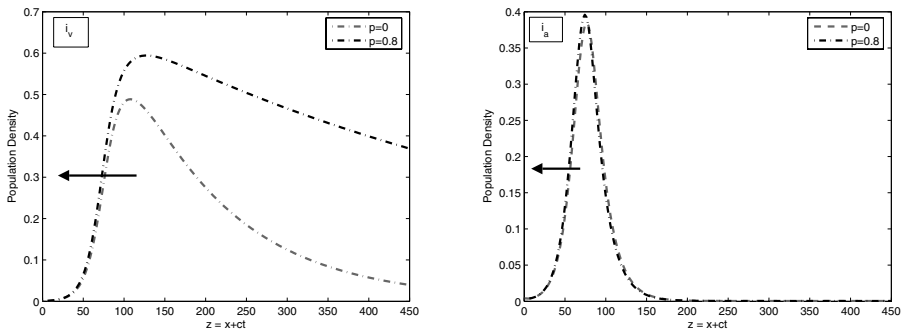


Fig. 5. Graphics for the infected mosquitoes (left) and infected avian (right) population densities, for the parameters for the Blue jay listed in Table 2, considering $p = 0.8$ and absence of the vertical transmission ($p = 0$). The effect of vertical transmission is perceptible in the mosquitoes population, although the wave speed do not increase so much: $c_{min} = 0.785$ for $p = 0$ and $c_{min} = 0.796$ for $p = 0.8$.

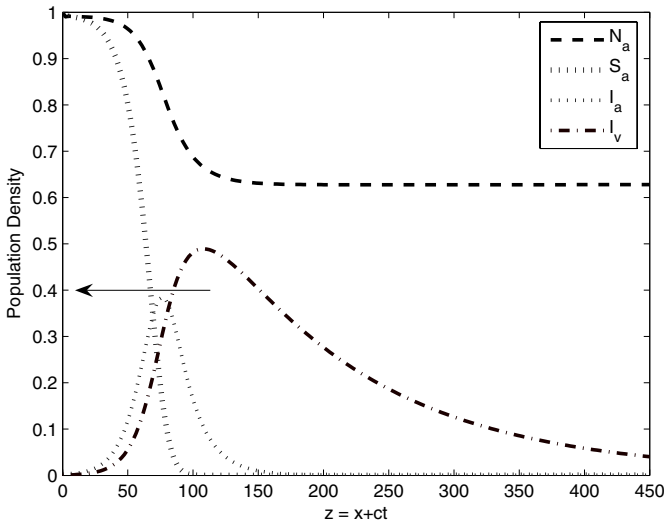


Fig. 6. Travelling wave solution for WNV model, using the parameters related to the Blue jay bird listed in Table 2.

4. Conclusion

In this paper we develop and analyze a spatial propagation model in order to describe the spreading out of the WNV. For the spatially homogeneous dynamics we considered the non spatial model studied by Cruz-Pacheco *et al.* We determine, in non dimensional parameters, as the same way as in Cruz-Pacheco *et al.*,⁴ the

threshold value:

$$\tilde{R}_0 = \frac{\tilde{\beta}_a \tilde{\beta}_v}{(1-p)\tilde{\mu}_v(\tilde{\gamma}_a + \tilde{\mu}_a + \tilde{\alpha}_a)}.$$

When \tilde{R}_0 is greater than one, the endemic state of the disease exists. We study the conditions for the travelling waves solution connecting this endemic point with the disease free equilibrium point. An equation with respect to the minimum speed was determined as a function of the parameters of the model and the threshold \tilde{R}_0 .

The depending of the wave speed on the vertical transmission was studied. As the mosquito movement is less than birds movement, we obtain that the vertical transmission is not an important factor in the spatial propagation, but it plays an important role as a local risk with respect to the incidence of disease.

Finally the wave speed was studied as a function of the avian diffusion. Choosing a value on the range estimated by Okubo,⁷ for the avian diffusion, we obtain the wave speed (3.03 km per day) which is very close to that observed from the field data. For instance, see maps in DeBiasi *et al.*,⁸ which is quite the same obtained by Lewis *et al.*⁶ who studied a simplified model, which does not consider vertical transmission, WNV death rate and the avian recover subpopulation.

In future paper we will analyze the effects of other parameters than the vertical transmission and avian diffusion coefficient in order to determine the efficacy of control strategies, as well as the advection movements in birds and mosquitoes in the modeling.

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