



Dynamic of West Nile Virus transmission considering several coexisting avian populations

Norberto Aníbal Maidana^{a,*}, Hyun Mo Yang^b

^a Centro de Matemática, Computação e Cognição, Universidade Federal do ABC., Rua Catequese 242, 09090-400, Santo André, SP, Brazil

^b UNICAMP – IMECC / DMA, Caixa Postal 6065, CEP: 13083-859, Campinas, SP, Brazil

ARTICLE INFO

Article history:

Received 15 December 2009

Received in revised form 4 December 2010

Accepted 4 December 2010

Keywords:

West Nile Virus

Epidemiological model

Control

Avian populations

Mosquito

ABSTRACT

West Nile Virus is an arthropod-borne flavivirus that appeared for the first time in New York City in the summer of 1999 and then spread prolifically within birds, with over 200 species having been infected. Mammals, such as humans and horses, do not develop sufficiently high bloodstream titers to play a significant role in transmission, which is a reason for considering the mosquito–bird cycle. In this paper we propose a model to study bird involvement in transmitting West Nile Virus using a system of ordinary differential equations considering the mosquito and several avian populations. A threshold value R_0 , depending on the model's parameters, is obtained that determines the disease level and allows us to propose possible control strategies. We determine the effects regarding the disease transmission considering the coexistence of two bird species, and then generalize this taking into account several bird species. We conclude that knowledge of the relative abundance of several bird species allows us to estimate with accuracy the risk for overall West Nile Virus transmission. Also, the establishment of the disease at an endemic level can be explained by the interaction between responsible populations of birds and mosquitoes.

© 2010 Elsevier Ltd. All rights reserved.

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 other species of ten genera [1]. When an infected mosquito bites a bird, the virus is transmitted. A mosquito is infected when it 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 the long flight range of birds, and the ubiquitous presence of mosquitoes. For instance, WNV was introduced into New York City in 1999, and then propagated across the USA. WNV disease first appeared in North America in the summer of 1999, with the simultaneous occurrence of an unusual number of deaths of exotic birds and crows in New York City, as reported by DeBiasi and Tyler [2]. After five years, WNV was detected among birds in California, on the western side of the USA.

Mathematical models, which did not encompass spatial dynamics, were developed by Kenkre et al. [3], Wonham et al. [4], Cruz-Pacheco et al. [5], Bowman et al. [6] and Foppa et al. [7]. Those models considered different aspects of WNV and determined threshold conditions regarding control strategies. Kenkre et al. [3] studied the periodicity of the infection by considering vertical transmission, an increase in the mortality due to infection and a disparity in the time scale. Wonham et al. [4] considered the full life cycle of the mosquito. Cruz-Pacheco et al. [5] took into account experimental data from the literature to estimate threshold values relating to several bird species. The effects of vertical transmission on the dynamic

* Corresponding author. Tel.: +55 11 4437 8403.

E-mail addresses: norberto.maidana@ufabc.edu.br, norbertomaidana@gmail.com (N.A. Maidana), hyunyang@ime.unicamp.br (H.M. Yang).

were also studied, as well as a consideration of different recovery rates for different bird species. The corresponding discrete-time model was studied by Jang [8]. In Bowman et al. [6], the authors coupled the human population to assess preventive strategies. Foppa and Spilerman [7] studied the effect of the host mortality on incidence of the disease.

With respect to spatial models, Lewis et al. [9] considered the corresponding spatially homogeneous modeling proposed by Wonham et al. [4]. They studied WNV propagation using traveling wave solutions as a simplified model, in which they did not consider the vertical transmission, WNV death rate or a recovering avian subpopulation. The effects of vertical transmission in the spatial propagation of the disease for different bird species were studied in Maidana and Yang [10].

We present a model to describe the dynamics of WNV, considering two and more avian populations interacting with a mosquito population, since all cited papers dealt with just one species of bird. In recent experiments to evaluate the transmission dynamics, Komar et al. [11] studied 25 birds species exposed to WNV by infectious mosquito *Culex tritaeniorhynchus* bites. We apply their estimation in our model, choosing the species that are more effective for WNV transmission, determining the role of coexistence of birds in the disease propagation, and in the epidemic level.

The paper is structured as follows. In Section 2 a WNV model with two populations of birds is presented, which is then analyzed in the steady state with stability analysis, and for which numerical results are provided. In Section 3 we generalize the results for several bird species. Our conclusions are given in Section 4.

2. Model for the transmission of WNV in two avian populations

We propose a model which includes cross-infection between two avian populations and a vector population. The densities are here denoted by $\bar{N}_i(t)$ and $\bar{N}_v(t)$, where the subindexes, $i = a, b$, correspond to different avian populations. Each avian population is divided into susceptible, infective and recovered subpopulations, named \bar{S}_i , \bar{I}_i and \bar{R}_i , respectively, while for the vector population, we consider susceptible and infected subpopulations, \bar{S}_v and \bar{I}_v .

We assume that for the avian populations the total population densities are allowed to vary, where Λ_i , for $i = a, b$, is a constant recruitment rate due to birth and migration, and the death rate including emigration is μ_i . The bird population varies, irrespective of WNV infection, according to

$$\frac{d\bar{N}_i}{dt} = \Lambda_i - \mu_i \bar{N}_i, \quad i = a, b, \quad (1)$$

resulting in $\bar{N}_i = \Lambda_i/\mu_i$ as a total population at equilibrium. With respect to the mosquito population, we assume that the birth and death rates are equal to μ_v , resulting in a constant mosquito population \bar{N}_v .

WNV is transmitted when an infected mosquito bites a susceptible bird, and, conversely, a susceptible mosquito is infected when it bites infected birds. Let us define r_i , $i = a, b$, as the rate of biting given by one mosquito in the i bird species. Let us assign as r_{vi} the rate of biting received by a bird species i when coexisting with the other species, in such a way that the total number of bites given by mosquitoes and the total number of bites received by each species of bird in coexistence with the other is $r_a \frac{\bar{N}_a}{\bar{N}_a + \bar{N}_b} \bar{N}_v + r_b \frac{\bar{N}_b}{\bar{N}_a + \bar{N}_b} \bar{N}_v = r_{va} \bar{N}_a + r_{vb} \bar{N}_b$, resulting in

$$r_{vi} = r_i \frac{\bar{N}_v}{\bar{N}_a + \bar{N}_b},$$

for $i = a, b$.

The transmission of WNV depends on the parameters related to the biting of mosquitoes r_{vi} and r_i , $i = a, b$, and on the WNV transmission probabilities from vector to birds and from birds to vector, respectively, β_i and β_{vi} . We assume that the mosquito population is homogeneously distributed in a region. The same assumption is used for two populations of birds, which, additionally, do not compete among themselves for space or resources. Hence the infection rate per susceptible bird for species $i = a$ or b is given by:

$$\beta_i r_i \frac{\bar{N}_v}{\bar{N}_a + \bar{N}_b} \frac{\bar{I}_v}{\bar{N}_v} = r_i \frac{\beta_i}{\bar{N}_a + \bar{N}_b} \bar{I}_v,$$

and the overall infection rate per susceptible vector is given by

$$r_a \beta_{va} \frac{\bar{I}_a}{\bar{N}_a + \bar{N}_b} + r_b \beta_{vb} \frac{\bar{I}_b}{\bar{N}_a + \bar{N}_b}. \quad (2)$$

Let us define the fractions of each population of birds in the steady state, disregarding WNV infection, to be assigned by q_i , $i = a, b$, and approximate them with the actual population considering the dissemination of WNV by

$$q_i = \frac{\Lambda_i/\mu_i}{\Lambda_a/\mu_a + \Lambda_b/\mu_b} \approx \frac{\bar{N}_i}{\bar{N}_a + \bar{N}_b}.$$

By using this approximation, the per-capita infection rates in birds become

$$r_i \frac{\beta_i}{\bar{N}_a + \bar{N}_b} \frac{\bar{N}_i}{\bar{N}_i} \bar{I}_v = r_i \frac{\beta_i}{\bar{N}_i} \frac{\bar{N}_i}{\bar{N}_a + \bar{N}_b} \bar{I}_v \approx r_i q_i \frac{\beta_i}{\bar{N}_i} \bar{I}_v,$$

and, analogously, the rate in the mosquito population becomes

$$r_a \beta_{va} \frac{\bar{I}_a}{\bar{N}_a} \frac{\bar{N}_a}{\bar{N}_a + \bar{N}_b} + r_b \beta_{vb} \frac{\bar{I}_b}{\bar{N}_b} \frac{\bar{N}_b}{\bar{N}_a + \bar{N}_b} \approx r_a q_a \beta_{va} \frac{\bar{I}_a}{\bar{N}_a} + r_b q_b \beta_{vb} \frac{\bar{I}_b}{\bar{N}_b}.$$

We assume that the infected mosquitoes transmit WNV during their entire life-span, but that the infected birds recover at a rate γ_i . The specific death rate associated with WNV in the avian population is α_i , with $\alpha_i \leq \gamma_i$, according to Cruz-Pacheco et al. [5]. Another assumption is that mosquitoes can transmit WNV vertically, and the fraction of progeny of infectious mosquitoes that is infectious is denoted by p , with $0 \leq p < 1$.

Based on the above assumptions and definitions of the parameters, the WNV model is the following:

$$\frac{d\bar{S}_i}{dt} = \Lambda_i - \frac{r_i q_i \beta_i}{\bar{N}_i} \bar{I}_v \bar{S}_i - \mu_i \bar{S}_i \tag{3}$$

$$\frac{d\bar{I}_i}{dt} = \frac{r_i q_i \beta_i}{\bar{N}_i} \bar{I}_v \bar{S}_i - (\gamma_i + \mu_i + \alpha_i) \bar{I}_i \tag{4}$$

$$\frac{d\bar{R}_i}{dt} = \gamma_i \bar{I}_i - \mu_i \bar{R}_i \tag{5}$$

$$\frac{d\bar{N}_i}{dt} = \Lambda_i - \mu_i \bar{N}_i - \alpha_i \bar{I}_i \tag{6}$$

$$\frac{d\bar{S}_v}{dt} = \mu_v \bar{S}_v + (1 - p) \mu_v \bar{I}_v - \frac{r_a q_a \beta_{va}}{\bar{N}_a} \bar{I}_a \bar{S}_v - \frac{r_b q_b \beta_{vb}}{\bar{N}_b} \bar{I}_b \bar{S}_v - \mu_v \bar{S}_v \tag{7}$$

$$\frac{d\bar{I}_v}{dt} = p \mu_v \bar{I}_v + \frac{r_a q_a \beta_{va}}{\bar{N}_a} \bar{I}_a \bar{S}_v + \frac{r_b q_b \beta_{vb}}{\bar{N}_b} \bar{I}_b \bar{S}_v - \mu_v \bar{I}_v, \tag{8}$$

with the conditions $\bar{S}_i + \bar{I}_i + \bar{R}_i = \bar{N}_i$, for $i = a, b$, and $\bar{S}_v + \bar{I}_v = \bar{N}_v$. The region:

$$\bar{\Omega} = \left\{ 0 \leq \bar{S}_i, 0 \leq \bar{I}_i, \bar{S}_i + \bar{I}_i \leq \bar{N}_i \leq \frac{\Lambda_i}{\mu_i}, 0 \leq \bar{I}_v \leq \bar{N}_v \right\}$$

is positively invariant.

Let us introduce into the system (3)–(8) the following dimensionless variables:

$$S_i = \frac{\bar{S}_i}{\Lambda_i / \mu_i}, \quad I_i = \frac{\bar{I}_i}{\Lambda_i / \mu_i}, \quad R_i = \frac{\bar{R}_i}{\Lambda_i / \mu_i}, \quad N_i = \frac{\bar{N}_i}{\Lambda_i / \mu_i}, \quad i = a, b, \tag{9}$$

for avian populations, and

$$S_v = \frac{\bar{S}_v}{\bar{N}_v}, \quad I_v = \frac{\bar{I}_v}{\bar{N}_v},$$

for the vector population. Therefore, omitting R_i and S_v (both are decoupled from the system), the dimensionless system of equations is:

$$\frac{dS_i}{dt} = \mu_i - r_i q_i m_i \frac{\beta_i}{N_i} I_v S_i - \mu_i S_i \tag{10}$$

$$\frac{dI_i}{dt} = r_i q_i m_i \frac{\beta_i}{N_i} I_v S_i - (\gamma_i + \mu_i + \alpha_i) I_i \tag{11}$$

$$\frac{dN_i}{dt} = \mu_i - \mu_i N_i - \alpha_i I_i \tag{12}$$

$$\frac{dI_v}{dt} = \left(r_a q_a \frac{\beta_{va}}{N_a} I_a + r_b q_b \frac{\beta_{vb}}{N_b} I_b \right) (1 - I_v) - (1 - p) \mu_v I_v, \tag{13}$$

for $i = a, b$, where the relative abundance of mosquito population with respect to one bird species m_i is

$$m_i = \frac{\bar{N}_v}{\Lambda_i / \mu_i}. \tag{14}$$

The invariant region is the subset $\Omega = \{0 \leq S_i, 0 \leq I_i, S_i + I_i \leq N_i \leq 1, 0 \leq I_v \leq 1\}$.

We can take into account the total population size $(\Lambda_a/\mu_a + \Lambda_b/\mu_b)$ in Eq. (9) instead of the individual avian sub-population (Λ_i/μ_i) in order to obtain another dimensionless variable. In this case, a second dimensionless system depends on the relative abundance of mosquitoes with respect to the total number of birds, m_{total} , given by

$$m_{total} = \frac{\bar{N}_v}{\Lambda_a/\mu_a + \Lambda_b/\mu_b}, \tag{15}$$

instead of the Eq. (14) for m_i , and μ_i is changed to $q_i\mu_i$. Notice that m_{total} and m_i , $i = a, b$, are related by

$$m_{total} = q_i m_i.$$

We will determine the equilibrium points and assess their stability.

2.1. Steady states of the model

The dimensionless system of Eqs. (10)–(13) has two steady states. The first one is the disease free equilibrium point given by:

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

The second is the endemic state:

$$P^* = (S_a^*, I_a^*, N_a^*, S_b^*, I_b^*, N_b^*, I_v^*),$$

where S_i^*, N_i^* ($i = a, b$) and I_v^* are given by

$$S_i^* = \frac{\mu_i - (\gamma_i + \mu_i + \alpha_i) I_i^*}{\mu_i}, \quad N_i^* = \frac{\mu_i - \alpha_i I_i^*}{\mu_i}, \tag{16}$$

and

$$I_v^* = \frac{\frac{r_a q_a \beta_{va} I_a^*}{N_a^*} + \frac{r_b q_b \beta_{vb} I_b^*}{N_b^*}}{r_a q_a \beta_{va} I_a^* N_b^* + r_b q_b \beta_{vb} I_b^* N_a^* + \mu_v (1 - p) N_a^* N_b^*}, \tag{17}$$

with $I_i^* < \frac{\mu_i}{\gamma_i + \mu_i + \alpha_i}$. The values of I_a^* and I_b^* are given by the intersection of the curves:

$$\begin{cases} I_a = \Gamma_a(I_b) \\ I_b = \Gamma_b(I_a), \end{cases}$$

where

$$\Gamma_a(I_b) = \frac{I_b [A_b I_b^2 + B_b I_b + C_b]}{E_b I_b^3 + F_b I_b^2 + G_b I_b + H_b},$$

and

$$\Gamma_b(I_a) = \frac{I_a [A_a I_a^2 + B_a I_a + C_a]}{E_a I_a^3 + F_a I_a^2 + G_a I_a + H_a},$$

with the coefficients A_i, B_i and C_i being given by

$$\begin{cases} A_i = [\beta_{vi} \mu_i r_i q_i - \alpha_i (1 - p) \mu_v] \frac{\alpha_i}{\mu_i} \\ B_i = 2\alpha_i (1 - p) \mu_v - \beta_{vi} \mu_i r_i q_i - (1 - p) \mu_v (\gamma_i + \mu_i + \alpha_i) R_0^i \\ C_i = \mu_i (1 - p) \mu_v (R_0^i - 1), \end{cases} \tag{18}$$

which are the same as obtained by Cruz-Pacheco et al. [5] and Maidana and Yang [10], and R_0^i is the contribution of the i -th bird species for the basic reproduction number R_0 (see below) given by

$$R_0^i = \frac{(r_i q_i)^2 m_i \beta_i \beta_{vi}}{(1 - p) \mu_v (\gamma_i + \mu_i + \alpha_i)} = \frac{(r_i^{ef})^2 m_i \beta_i \beta_{vi}}{(1 - p) \mu_v (\gamma_i + \mu_i + \alpha_i)}, \tag{19}$$

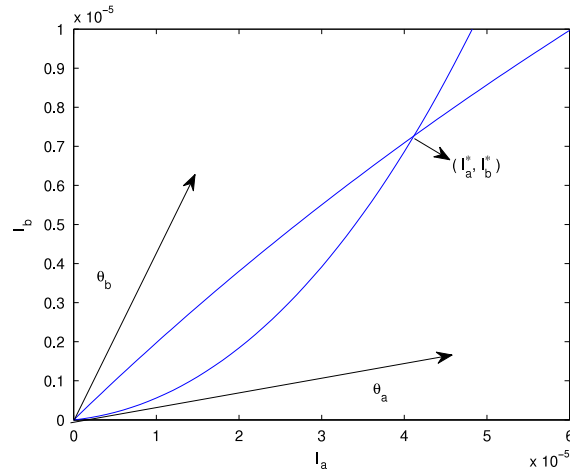


Fig. 1. The curves Γ_a and Γ_b are obtained using the values of parameters for Morning dove and Canada goose, respectively.

with $r_i^{ef} = r_i q_i$ being the effective rate of biting by one mosquito in the i -th bird species. Finally, the coefficients E_i, F_i, G_i and H_i are functions of A_i, B_i and C_i :

$$\begin{cases} E_i = \frac{\alpha_k}{\mu_k} A_i + \frac{\alpha_i^2}{\mu_i} \beta_{vk} r_k q_k \\ F_i = \frac{\alpha_k}{\mu_k} B_i - 2\alpha_i \beta_{vk} r_k q_k - \frac{\alpha_i \beta_i \beta_{vk} m_i r_i q_i r_k q_k}{\mu_i} \\ G_i = \frac{\alpha_k}{\mu_k} C_i + \beta_{vk} r_k q_k (\mu_i + \alpha_i \beta_i m_i r_i q_i + \beta_i m_i r_i q_i) \\ H_i = -\mu_i \frac{\beta_i \beta_{vk} m_i r_i q_i r_k q_k}{(\gamma_i + \mu_i + \alpha_i)}, \quad i \neq k, i, k = a, b. \end{cases} \tag{20}$$

When two bird species are living in same region, a positive solution given by (16) and (17) always exists for $R_0^a > 1$ or $R_0^b > 1$. In other words, one bird species (for instance, $R_0^a > 1$) could maintain WNV infection even when the other bird species is not effective in transmitting WNV alone (due to $R_0^b < 1$). This is a consequence of the WNV transmitting effectiveness of the species and the relative number of birds in the region, with $q_a + q_b = 1$. When both species are not so effective, that is, $R_0^a < 1$ and $R_0^b < 1$, a positive solution always exists if $R_0 = R_0^a + R_0^b > 1$, where the basic reproduction number encompassing the coexistence of two bird species is given by

$$R_0 = R_0^a + R_0^b. \tag{21}$$

The condition $R_0 > 1$ states that the sum of angles from Γ_a to the I_a -axis, denoted by θ_a , and from Γ_b to the I_b -axis, denoted by θ_b , is less than $\pi/2$ (see Fig. 1).

To prove both assertions, let us write

$$\Gamma_i(I_k) = \frac{I_k P_i(I_k)}{Q_i(I_k)},$$

where the polynomials are

$$P_i(I_k) = A_k I_k^2 + B_k I_k + C_k$$

and

$$Q_i(I_k) = E_k I_k^3 + F_k I_k^2 + G_k I_k + H_k,$$

for $i \neq k$, and $i, k \in \{a, b\}$, where the coefficient are given by Eqs. (18) and (20).

We have two cases:

(1) Let us suppose that $R_0^a > 1$ or $R_0^b > 1$. Let us assume that $R_0^a > 1$ (the equations are symmetric with respect to a, b). If $r_b = 0$, from Eq. (17), we have $I_b = 0$ and $P_b(I_a^*) = 0$. Hence, the solution is the same as for a single species and, according to Cruz-Pacheco et al. [5] and Maidana and Yang [10], we have $I_a^* < \frac{\mu_a}{\gamma_a + \mu_a + \alpha_a}$. I_a^* increases with r_b and in the limit case ($r_b \rightarrow \infty$), using Eq. (11), we have I_a^* and I_b^* satisfying the equations:

$$\begin{cases} \alpha_a (\gamma_a + \mu_a + \alpha_a) I_a^2 - (r_a q_a m_a \beta_a + \mu_a) (\gamma_a + \mu_a + \alpha_a) I_a + r_a q_a m_a \beta_a \mu_a = 0 \\ \beta_b m_b \left(1 - \frac{\gamma_b + \mu_b + \alpha_b}{\mu_b} I_b \right) = 0, \end{cases} \tag{22}$$

from which we obtain $I_a^* < \frac{\mu_a}{\gamma_a + \mu_a + \alpha_a}$, as the case $p = 1$ in Cruz-Pacheco et al. [5], and the asymptote $I_b^* = \frac{\mu_b}{\gamma_b + \mu_b + \alpha_b}$. As in the case of a single species, the solution of the i infected subpopulation of bird species is bounded by $\frac{\mu_i}{\gamma_i + \mu_i + \alpha_i}$.

(2) If $R_0^a < 1$ and $R_0^b < 1$, the curves Γ_a and Γ_b intersect if the sum of their angles at the origin is less than $\pi/2$ (see Fig. 1). Now, we show that this condition is equivalent to $R_0^a + R_0^b > 1$.

Let us write

$$Q_a(I_b) = I_b P_a(I_b) \frac{\alpha_a}{\mu_a} + T_a(I_b),$$

where

$$T_a(I_b) = r_a q_a \beta_{va} I_b \left[\frac{\alpha_b}{\mu_b} I_b^2 - \left(2\alpha_b + \frac{\alpha_b \beta_b m_b r_b q_b}{\mu_b} \right) I_b + \mu_b + \beta_b m_b r_b q_b (\alpha_b + 1) \right] + H_b.$$

Observe that $T'_a(I_b) > 0$, and, since $H_b < 0$, we have $T_a(I_b) < 0$, for $I_b \ll 1$. Similarly, $P_a(I_b) < 0$ and $P'_a < 0$, then we have:

$$\Gamma'_a = \frac{P_a T_a + I_b (P'_a T_a - P_a T'_a)}{Q_a^2} > 0. \tag{23}$$

Hence, Γ_a and Γ_b (by the symmetry between indices a and b) are increasing functions, and they intersect if the sum of the angles with respect to the corresponding axis is less than $\pi/2$ (see Fig. 1), in other words

$$\theta_a + \theta_b < \pi/2 \Rightarrow \theta_a < \pi/2 - \theta_b.$$

Applying the tangent function (tan) on both sides of inequality, which is an increasing function, we have

$$\tan(\theta_a) < \tan(\pi/2 - \theta_b) = \cot(\theta_b) = \frac{1}{\tan(\theta_b)}.$$

By Eq. (23) we have $\Gamma'_a(0) > 0$ and $\Gamma'_b(0) > 0$, then:

$$\begin{aligned} \tan(\theta_a) < \frac{1}{\tan(\theta_b)} &\Leftrightarrow \Gamma'_a(0) < \frac{1}{\Gamma'_b(0)} \Leftrightarrow \Gamma'_a(0) \Gamma'_b(0) < 1 \Leftrightarrow \\ &\Leftrightarrow \frac{C_b}{H_b} \frac{C_a}{H_a} = \frac{r_b q_b \beta_{vb}}{r_a q_a \beta_{va}} \left(-1 + \frac{1}{R_0^b} \right) \frac{r_a q_a \beta_{va}}{r_b q_b \beta_{vb}} \left(-1 + \frac{1}{R_0^a} \right) < 1 \Leftrightarrow \\ &\Leftrightarrow \frac{(1 - R_0^b)(1 - R_0^a)}{R_0^b R_0^a} < 1 \Leftrightarrow \\ &\Leftrightarrow 1 < R_0^a + R_0^b. \quad \square \end{aligned}$$

Notice that when $R_0^a + R_0^b < 1$, then $\theta_a + \theta_b > \pi/2$, and there is no intersection between the curves. Let us discuss R_0 given by Eq. (21). Recall that in the case of a single bird species, we have

$$\mathcal{R}_0 = \frac{r^2 m \beta \beta_v}{(1 - p) \mu_v (\gamma + \mu + \alpha)},$$

and that a positive solution for infective birds (I) exists whenever $\mathcal{R}_0 > 1$. Both results were obtained by Cruz-Pacheco et al. [5] and Maidana and Yang [10], and the model describes WNV infection is effective in one species and other bird species are refractory to WNV infection, or, those species located in different regions that are not crossing. Hence, in each region, we must have $\mathcal{R}_0 > 1$ for WNV being prevalent.

Let us consider two different coexisting bird species, each one contributing R_0^i to the overall R_0 . For bird species a , when isolated, we must have

$$\mathcal{R}_0^a = \frac{r_a^2 m_a \beta_a \beta_{va}}{(1 - p) \mu_v (\gamma_a + \mu_a + \alpha_a)},$$

where $m_a = \bar{N}_v / (\Lambda_a / \mu_a)$. When species a coexists with species b and consists of a fraction q_a of the total population, it contributes to the overall R_0 as

$$R_0^a = (q_a)^2 \mathcal{R}_0^a,$$

according to Eq. (19), and the overall reproduction number is calculated using the equation

$$R_0 = (q_a)^2 \mathcal{R}_0^a + (q_b)^2 \mathcal{R}_0^b. \tag{24}$$

If we suppose two identical populations, $b = a$ and $q_a = 0.5$, we have $R_0 = \mathcal{R}_0^a/2$, instead of $R_0 = \mathcal{R}_0^a$. This result shows that when a population of birds is doubled while the vector population is unchanged, the reproduction number must be diminished by half, as expected, because the number of bitings among birds is decreased by half.

Table 1

The basic reproduction number obtained for one bird species only using the epidemiological and demographical parameters given in [5,11]. We assumed $p = 0.007$, Dohm et al. [12], Goddard et al. [13] and Turell et al. [14], $m_a = 5$, $r_a = 0.5$, Pacheco et al. [5], $q_a = 0.5$ and $q_b = 0$. We evaluate $R_0^a = (q_a)^2 \mathcal{R}_0^a$.

Common name	β_a	β_{va}	$\gamma_a(\text{day}^{-1})$	$\alpha_a(\text{day}^{-1})$	$\mu_a(\text{day}^{-1})$	$\mu_v(\text{day}^{-1})$	R_0^a
Common grackle	1.0	0.68	0.33	0.07	0.0001	0.06	8.91
Blue jay	1.0	0.68	0.26	0.15	0.0002	0.06	8.69
House sparrow	1.0	0.53	0.33	0.1	0.0002	0.06	6.46
American robin	1.0	0.36	0.33	0.0	0.0002	0.06	5.71
House finch	1.0	0.32	0.18	0.14	0.0003	0.06	5.24
American crow	1.0	0.5	0.31	0.19	0.0002	0.06	5.24
Ring-billed gull	1.0	0.28	0.22	0.1	0.0003	0.06	4.58
Black-billed magpie	1.0	0.36	0.33	0.16	0.0001	0.06	3.85
Fish crow	1.0	0.26	0.36	0.06	0.0002	0.06	3.24
Mallard	1.0	0.16	0.33	0.0	0.0002	0.06	2.54
Morning dove	1.0	0.11	0.59	0.0	0.0002	0.06	0.98
Northern flicker	1.0	0.06	1	0.0	0.0002	0.06	0.31
Canada goose	1.0	0.1	3.33	0.0	0.0002	0.06	0.16

In the case of the total population size $(\Lambda_a/\mu_a + \Lambda_b/\mu_b)$ being used in order to obtain a dimensionless system, we obtain for R_0^i the expression

$$R_0^i = \frac{(r_i q_i)^2 m_{total} \beta_i \beta_{vi}}{(1-p)\mu_v(\gamma_i + \mu_i + \alpha_i)} = \frac{(r_i^{ef})^2 m_{total} \beta_i \beta_{vi}}{(1-p)\mu_v(\gamma_i + \mu_i + \alpha_i)},$$

where m_{total} is given by Eq. (15). Using the relation $m_{total} = q_a m_a$, we can define $\hat{\mathcal{R}}_0^a$, in terms of the total number of birds m_{total} , as

$$\hat{\mathcal{R}}_0^a = q_a \mathcal{R}_0^a = \frac{r_a^2 m_{total} \beta_a \beta_{va}}{(1-p)\mu_v(\gamma_a + \mu_a + \alpha_a)},$$

and the contribution of species a to the overall reproduction number is given by

$$R_0^a = q_a \hat{\mathcal{R}}_0^a,$$

resulting in

$$R_0 = q_a \hat{\mathcal{R}}_0^a + q_b \hat{\mathcal{R}}_0^b. \tag{25}$$

Now for two identical populations, $b = a$ and $q_a = 0.5$, we have $R_0 = \hat{\mathcal{R}}_0^a$. We stress the fact that $\hat{\mathcal{R}}_0^a$ is not the reproduction number of isolated species a , while \mathcal{R}_0^a is. The reason is that $\hat{\mathcal{R}}_0^a$ is expressed in terms of the relative abundance of mosquitoes with respect to the total population of birds m_{total} instead of m_a . When we increase the total population, we expect that R_0 decreases proportionally due to the increase in the denominator of m_{total} in $\hat{\mathcal{R}}_0^i$, because we have:

$$m_{total} = \frac{\bar{N}_v}{\Lambda_a/\mu_a + \Lambda_b/\mu_b} < \frac{\bar{N}_v}{\Lambda_i/\mu_i} = m_i, \quad i = a, b.$$

In general, the basic reproduction number of WNV in an isolated population of birds (from models dealing with one bird species) is calculated by considering the abundance of mosquitoes with respect to this species, that is, \mathcal{R}_0^a . When in coexistence with another species (we are supposing that there is no kind of interaction between the two populations of birds, which implies that their numbers are not altered when they coexist), there is a decrease in the biting rates among birds by the factor q_i due to the increase in the total population of birds. A second dimensionless system allows us to take into account the total population size $\Lambda_a/\mu_a + \Lambda_b/\mu_b$, yielding $\hat{\mathcal{R}}_0^i$, which is not the reproduction rate of isolated species.

In the model, the vector population is constant \bar{N}_v , but also is fixed when in interaction with two bird species. Conversely, bird species vary according to Eq. (1), but their populations are summed, increasing the total size in comparison with isolated bird species. If we modify the model by allowing the size of vector population to be dependent on the bird populations, then mosquitoes can increase in number when coupling with two bird species. As a consequence, the relative abundance of mosquitoes with respect to birds is not altered, for instance,

$$m = \frac{\bar{N}_{va} + \bar{N}_{vb}}{\Lambda_a/\mu_a + \Lambda_b/\mu_b},$$

and R_0 can then be the sum of the isolated reproduction number multiplied by the relative abundance of the species, the factor q_i .

We illustrate our findings. In Table 1 we present the values of the model parameters and the basic reproduction number \mathcal{R}_0^a of each isolated bird species with respect to the transmission of WNV. All values are fixed, except when explicitly stated. We are not considering the effects of bites in the other population of birds, letting $q_b = 0$.

Table 2

Basic reproduction number $R_0 = R_0^a + R_0^b$ for two coexisting bird species calculated using the epidemiological and demographic parameters given in [5,11], with $r_a^{ef} = r_b^{ef} = 0.25$.

$R_0 = R_0^a + R_0^b$	Blue jay	Common grackle	Fish crow	Morning dove	Northern flicker	Canada goose
Blue jay	17.38	17.6	11.93	9.67	9	8.85
Canada goose	8.85	9.07	3.4	1.14	0.47	0.32

In Fig. 1 we show the curves Γ_a and Γ_b , taking into account the values of parameters for Morning dove (a) and Canada goose (b), considering equal biting rates, $r_a^{ef} = r_b^{ef} = 0.25$ (two per day), which result in $R_0^a = 0.98$ and $R_0^b = 0.16$. As isolated species, they do not transmit the virus, however when they are allowed to coexist (for instance, one species invades the habitat of the other species), then the transmission of the virus persists, and an endemic point exists. Note that R_0^b is smaller than R_0^a , so I_b^* is smaller than I_a^* .

Table 2 shows the variation of R_0 for Blue jay and Canada goose coexisting with other species. The value of R_0 for two coexisting bird species is calculated using the basic reproduction number of each isolated species, given in Table 1, assuming that $m_a = m_b = 0.5$, and considering that the two species are 50% of the total bird population we assigned $q_a = q_b = 0.5$. The per capita rate is constant for all species, $r_a = r_b = 0.5$, one every two days Cruz-Pacheco et al. [5].

For Blue jay (assigned to R_0^a) coexisting with other species, the increment in R_0 from other species is proportionally very low, since their contribution R_0^b is very small. Blue jay increases at least the double of the value of R_0^a . For Canada goose (assigned to R_0^b), in some cases, the disease does not occur, but when we consider coexistence with other species with high R_0^b , then the disease could be transmitted, and R_0 could increase considerably. For example, Canada goose has $R_0^a = 0.16$, but when coexisting with Blue jay, the transmission of WNV increases considerably to $R_0 = 8.85$.

The Morning dove, as a single species, does not transmit WNV disease ($R_0 = 0.98$), but it transmits WNV when considering its coexistence with any other species. The different bird species that inhabit a certain region play an essential role in WNV transmission.

Another important fact we observe is that when two populations of birds are coexisting, R_0 is less than half of the greatest \mathcal{R}_0^i calculated for one isolated species, taking into account $q_i = 1$ (all mosquitoes biting this species). This means that the greatest \mathcal{R}_0^i for one isolated species overestimates R_0 for the coexistence. This is a consequence of number of the total bird population, which decreases the value of R_0 . This result agrees with that obtained for the model of one bird species: if the number of a single bird population increases, \mathcal{R}_0 decreases in the same proportion. For example, if we consider Blue jay as a single species, we have $\mathcal{R}_0 = 34.69$, see Maidana and Yang [10], and when we consider Common grackle with $\mathcal{R}_0 = 35.64$, which is of the same order, for the coexistence we obtain $R_0 = 17.6$ (Table 2) due to a doubled total bird population.

2.2. Stability of the trivial equilibrium point

The following Theorem, concerning the trivial equilibrium point, is established:

Theorem 2.1. *If $0 \leq p < 1$, then the disease free equilibrium point P_0 is unique and is locally asymptotically stable for $R_0^a + R_0^b < 1$. When $R_0^a + R_0^b > 1$, P_0 becomes unstable.*

Proof. The characteristic polynomial of the Jacobian matrix evaluated at the trivial equilibrium point of the system (10)–(13) is written as $p(x) = -p_1(x)p_2(x)p_3(x)$, where we have two second order polynomials

$$p_1(x) = (x + \mu_a)^2,$$

$$p_2(x) = (x + \mu_b)^2,$$

both having two double negative roots, and a third degree polynomial

$$p_3(x) = x^3 + a_2x^2 + a_1x + a_0,$$

with coefficients

$$a_2 = \gamma_a + \mu_a + \alpha_a + \gamma_b + \mu_b + \alpha_b + (1 - p)\mu_v > 0$$

$$a_1 = (\gamma_a + \mu_a + \alpha_a)(\gamma_b + \mu_b + \alpha_b) + (1 - p)\mu_v [(\gamma_a + \mu_a + \alpha_a)(1 - R_0^a) + (\gamma_b + \mu_b + \alpha_b)(1 - R_0^b)]$$

$$a_0 = (1 - p)\mu_v (\gamma_a + \mu_a + \alpha_a)(\gamma_b + \mu_b + \alpha_b) [1 - R_0^a - R_0^b].$$

If $R_0^a + R_0^b < 1$, then the stability of P_0 follows directly from Routh–Hurwitz criteria, since $a_0 > 0$, $a_2 > 0$ and

$$a_2a_1 > (\gamma_b + \mu_b + \alpha_b)(1 - p)\mu_v [(\gamma_a + \mu_a + \alpha_a)(1 - R_0^a)]$$

$$+ (\gamma_a + \mu_a + \alpha_a)(1 - p)\mu_v [(\gamma_b + \mu_b + \alpha_b)(1 - R_0^b)]$$

$$> (1 - p)\mu_v (\gamma_a + \mu_a + \alpha_a)(\gamma_b + \mu_b + \alpha_b)(1 - R_0^a - R_0^b) = a_0.$$

If $R_0^a + R_0^b > 1$, the condition $a_0 < 0$ implies that $p_3(0) < 0$, and p_3 always has a positive root.

The stability of the nontrivial equilibrium point P^* for $R_0^a + R_0^b > 1$ is assessed numerically, because the eigenvalues are roots of a fifth degree polynomial.

Considering $\alpha_a = \alpha_b = 0$, then $N_a \rightarrow 1$ and $N_b \rightarrow 1$. The global stability in Ω , of the trivial equilibrium point P_0 , can be proved using the LaSalle–Lyapunov Theorem [15], considering the following Lyapunov function:

$$V = (\gamma_b + \mu_b) \beta_{va} r_a q_a I_a + (\gamma_a + \mu_a) \beta_{vb} r_b q_b I_b + \left[\frac{(\gamma_b + \mu_b) \beta_a \beta_{va} r_a^2 q_a^2 m_a + (\gamma_a + \mu_a) \beta_b \beta_{vb} r_b^2 q_b^2 m_b}{(1-p)\mu_v} \right] I_v.$$

The orbital derivative of V is given by:

$$\begin{aligned} \dot{V} &= -(\gamma_b + \mu_b) \beta_a \beta_{va} r_a^2 q_a^2 m_a I_v (1 - S_a) - (\gamma_a + \mu_a) \beta_b \beta_{vb} r_b^2 q_b^2 m_b I_v (1 - S_b) \\ &\quad - (\gamma_a + \mu_a) (\gamma_b + \mu_b) \beta_{vb} r_b q_b I_b [1 - (R_0^a + R_0^b) (1 - I_v)] \\ &\quad - (\gamma_a + \mu_a) (\gamma_b + \mu_b) \beta_{va} r_a q_a I_a [1 - (R_0^a + R_0^b) (1 - I_v)] \\ &= -(\gamma_b + \mu_b) \beta_a \beta_{va} r_a^2 q_a^2 m_a I_v (1 - S_a) - (\gamma_a + \mu_a) \beta_b \beta_{vb} r_b^2 q_b^2 m_b I_v (1 - S_b) \\ &\quad - (\gamma_a + \mu_a) (\gamma_b + \mu_b) \beta_{vb} r_b q_b I_b [1 - (R_0^a + R_0^b) + (R_0^a + R_0^b) I_v] \\ &\quad - (\gamma_a + \mu_a) (\gamma_b + \mu_b) \beta_{va} r_a q_a I_a [1 - (R_0^a + R_0^b) + (R_0^a + R_0^b) I_v], \end{aligned}$$

which is less than zero for $R_0^a + R_0^b < 1$. The maximal invariant sets are determined by $\dot{V} = 0$, and we have two situations:

(1) When $I_a = I_b = I_v = 0$, we are dealing with the (S_a, S_b) -plane. From Eqs. (10)–(13) we have:

$$\begin{aligned} \frac{dS_a}{dt} &= \mu_a - \mu_a S_a \\ \frac{dS_b}{dt} &= \mu_b - \mu_b S_b, \end{aligned}$$

which results in $S_a \rightarrow 1$ and $S_b \rightarrow 1$, when $t \rightarrow \infty$.

(2) When $S_a = S_b = 1$ and $I_a = I_b = 0$ we have

$$\frac{dI_v}{dt} = -(1-p)\mu_v I_v,$$

which results in $I_v \rightarrow 0$, when $t \rightarrow \infty$. \square

2.3. Numerical results

In this section we study the effects in the WNV dynamics when we deal with the coexistence of two avian species. Numerical results are obtained using values given in Table 1.

Let us first simulate a single bird species and two bird species, in which one is not a WNV transmitter. If we consider $q_a = 1$ and $q_b = 0$, our model reproduces that considered by Cruz-Pacheco et al. [5] for a single bird population, where the second bird population has no influence in the dynamic. Assuming mosquitoes bite once every two days, we have a biting rate $r_a = 0.5$, the same as considered by Cruz-Pacheco et al. [5], and hence we have $r_a^{ef} = 0.5 \times 1 = 0.5$. For the values of parameters related to the American crow, we can observe in Fig. 2(a) that the peak of the infected bird population is 0.29, as was obtained by Cruz-Pacheco et al. [5]. In this case we are considering only the American crow population, and all the mosquitoes are biting this bird species. This kind of assumption resulted in higher value for the reproduction number, which resulted in $R_0^a = 20.9718$, using Eq. (19).

Another approach was given in Wonham et al. [4]. That is, mosquitoes bite other bird populations but their contributions are not taken into account. Assuming that crows are 20% of the total population of birds, then we have $q_{crow} = 0.2$, that is $r_a^{ef} = 0.5 \times 0.2 = 0.1$. All other bird species compound $q_b = 0.8$, but by the fact that their bitings are not being measured, we are tacitly letting $r_b = 0$, hence $r_b^{ef} = 0$. Using these parameter values in the simulation of the model, we observe in Fig. 2 (b) that the peak of infected birds is less than 0.01, a considerable difference from the peak of 0.29 obtained for a biting rate $r_a^{ef} = 0.5$. The relative abundance of one species with respect to others reduced the effective biting rate $r_a^{ef} = 0.1$, and the disease does not remain endemic because $R_0 = R_0^a = 0.838872 < 1$.

When we are not considering mosquitoes biting other bird species, but a single species only (Fig. 2(b), with biting rate $r_a^{ef} = 0.1$), we are also assuming that the other species are not allowed to be infected. This fact must decrease the number of infected mosquitoes and, consequently, decrease the infected american crows when compared with two coexisting bird species. These features can be assessed by the model for two populations of birds. We study two cases.

American crow and Blue jay

The Blue jay inhabits the east and center of the USA, and the American crow is in greater numbers in the east than in the center of the USA, and does not inhabit the west. In the east, these two species coexist [16].

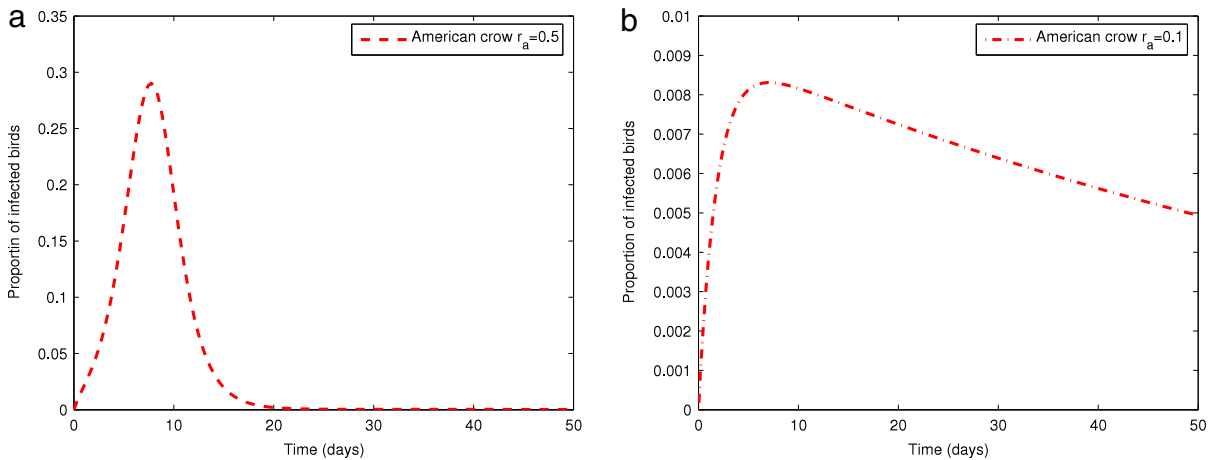


Fig. 2. Graphs of the proportion of infected American crow population. (a) Considering only the American crow population, i.e., 100% of the population and $r_a^{ef} = 0.5$. (b) Considering only the American crow population being measured with respect to WNV transmission, and taking into account that it is 20% of the total bird population, i.e., $r_a^{ef} = 0.1$, and $r_b^{ef} = 0$. The initial values are $S_a^0 = 1, I_a^0 = 0, N_a^0 = 1$ and $I_v^0 = 0.01$.

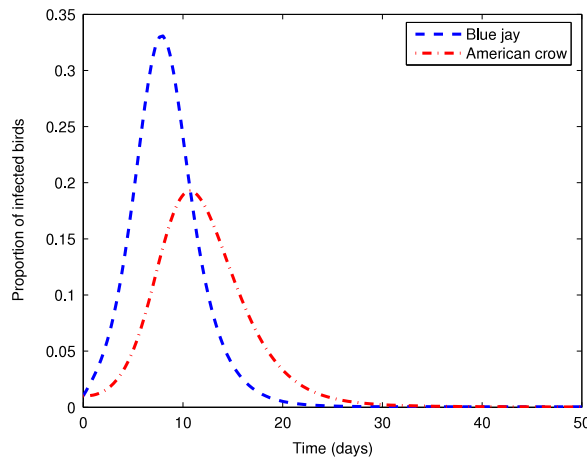


Fig. 3. Graph of the infected bird proportions considering coexistence between Blue jay and American crow. Blue jay is 80% of the total population ($r_b^{ef} = 0.4$) and American crow, 20% ($r_a^{ef} = 0.1$). The initial values are $S_i^0 = 1, I_i^0 = 0, N_i^0 = 1$ and $I_v^0 = 0.01$.

We can consider that the American crow population is 20% of the total population of birds, and the Blue jay population is 80%. Hence, the biting rates are $r_a^{ef} = 0.5 \times 0.2 = 0.1$ and $r_b^{ef} = 0.5 \times 0.8 = 0.4$ for American crow and Blue jay, respectively.

We can observe in Fig. 3 that the peak of the infected American crow subpopulation increases from 0.0084 to 0.19, when we consider the Blue jay population together with the American crow population. This is due to the fact that infected Blue jay birds produce many new infected mosquitoes, which in turn are able to infect American crow birds at an endemic level even though the reproduction number is lower than unity when isolated.

If we consider that mosquitoes are biting only the American crow population ($r_a^{ef} = 0.1$ and $r_b^{ef} = 0$), the peak of infected birds is underestimated in comparison with the peak for the American crow population in coexistence with the Blue jay population. Furthermore, R_0 for American crow increases greatly: for $r_a^{ef} = 0.1$ and $r_b^{ef} = 0$, we have $R_0 = 0.838872$, but for $r_a^{ef} = 0.1$ and $r_b^{ef} = 0.4$, we have $R_0 = 23.0977$, an increase of around 30 times due to Blue jay.

If we consider that 100% of the bird population is American crow ($r_a^{ef} = 0.5$) the peak is overestimated. This is due to some mosquitoes biting Blue jay, instead of biting only American crow, therefore, decreasing the infected American crow subpopulation. The peak of the proportion of infected birds decreases from 0.3 (Fig. 2(a)) to 0.2 (Fig. 3). In Fig. 3 we can see the infected American crow and Blue jay subpopulations.

With respect to the mosquito population, we can observe in Fig. 4 that the model for a single bird species, for the pair $r_a^{ef} = 0.5$ and $r_b^{ef} = 0$, underestimates the peak of the proportion of infected mosquitoes obtained when two species are considered, $r_a^{ef} = 0.1$ and $r_b^{ef} = 0.4$.

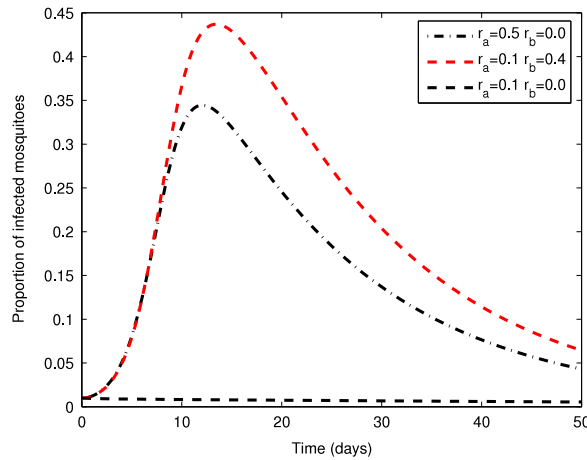


Fig. 4. Graph of the proportion of infected mosquitoes. The initial values are $S_i^0 = 1, I_i^0 = 0, N_i^0 = 1$ and $I_v^0 = 0.01$.

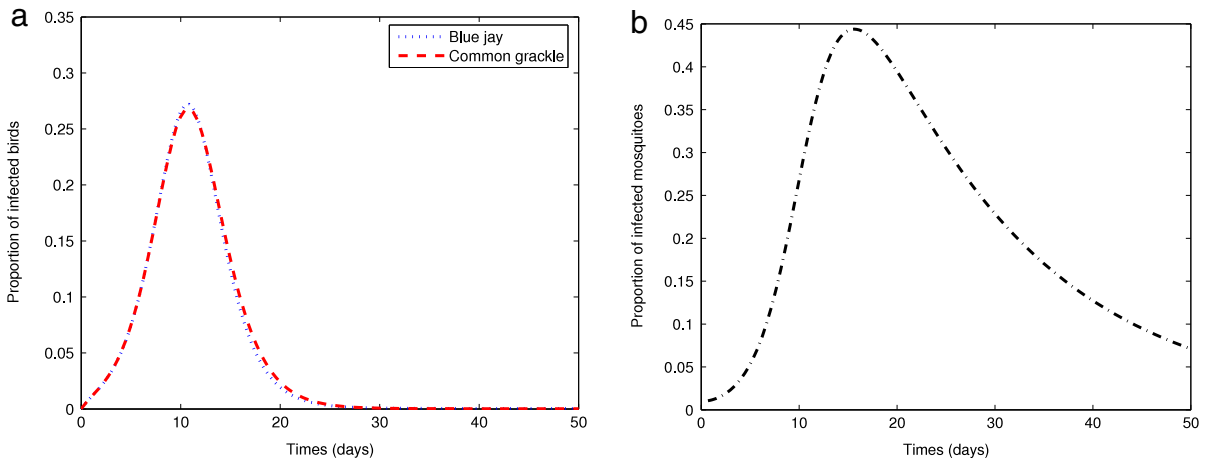


Fig. 5. Graph of the proportion of infected subpopulation for coexisting Blue jay and Common grackle, considering that each species is 50% of the total population ($r_a^{ef} = r_b^{ef} = 0.25$). (a) graph of the proportion of infected birds. (b) graph of the proportion of infected mosquitoes. The initial values are $S_i^0 = 1, I_i^0 = 0, N_i^0 = 1$ and $I_v^0 = 0.01$.

This is due to the fact that mosquitoes that bite American crow also bite Blue jay, which is one of the most effective birds at transmitting WNV. Hence, this increases the proportion of infected mosquitoes. For the pair $r_a^{ef} = 0.1$ and $r_b^{ef} = 0$, the peak of infected mosquitoes does not exist. The curve of infected mosquitoes when considering two populations is closer to the curve obtained with a single biting rate $r_a^{ef} = 0.5$ than for $r_a^{ef} = 0.1$. For $r_a^{ef} = 0.1$, the curve of infected mosquitoes decreases slowly (Fig. 4). Determining the incidence of WNV in mosquitoes is important because they transmit the disease to the human population.

Blue jay and Common grackle

Blue jay is a bird that inhabits the east of the USA, with some birds accounted for in the center but none in the west. Common grackle inhabits the east of USA as well. These two species are encountered in New York, and hence can be a major factor in WNV transmission. We assume in the model $r_a^{ef} = r_b^{ef} = 0.25$, i.e., 50% of each population in the east.

In Fig. 5(a) we see the peak of the infected bird proportion for the pair of species Blue jay and Common grackle. We can observe that the peak for infected Blue jay in this pair of species is 0.28, less than 0.33, which is the peak observed in the pair Blue jay and American crow. This is a consequence of our considering in the pair Blue jay and American crow that Blue jay is 80% of the total population.

If we consider the total infected subpopulation, i.e., the sum of the peaks of coexisting infected birds, we have for the pair Blue jay and Common grackle a peak $0.28 + 0.28 = 0.56$, and for the pair Blue jay and American crow, $0.33 + 0.19 = 0.52$. This is a consequence of Blue jay and Common grackle being the most effective species in WNV transmission. The peak of infected Blue jay when coexisting with Common grackle decreases, but the total infected peak increases. In Fig. 5(b) we observe the peak of infected mosquitoes. The proportion of infected mosquitoes is similar for the pair Blue jay and Common grackle and for the pair Blue jay and American crow.

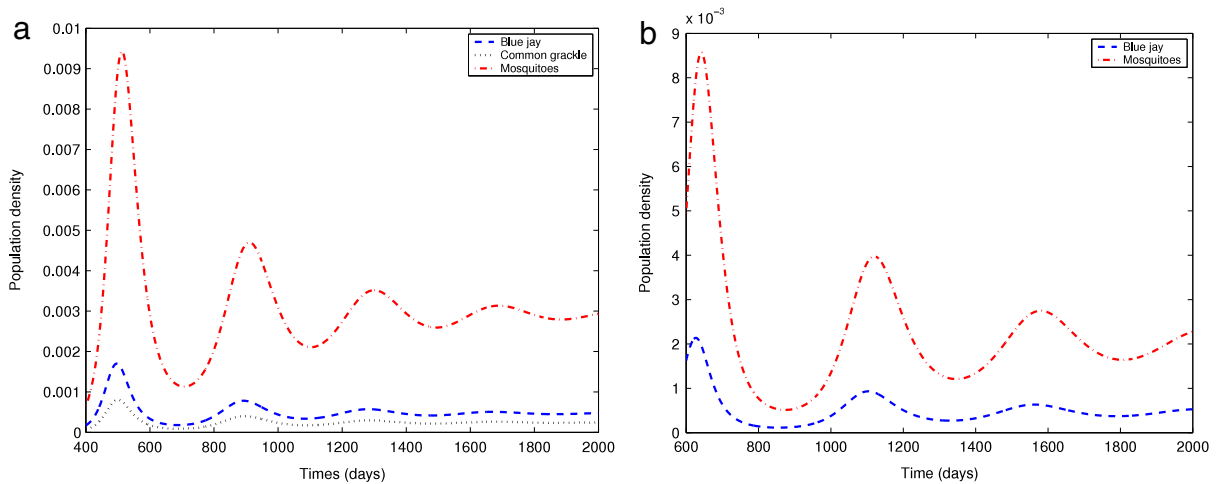


Fig. 6. (a) Cyclic fronts graphic for Blue jay and Common grackle ($r_a^{ef} = r_b^{ef} = 0.25$). (b) Cyclic front graphic for Blue jay ($r_a^{ef} = 0.25, r_b^{ef} = 0$). The initial values are $S_i^0 = 1, I_i^0 = 0, N_i^0 = 1$ and $I_v = 0.01$.

In Fig. 6 is shown the cyclic front of the epidemic. In Fig. 6(a) we show the coexistence between Blue jay and Common grackle ($r_a^{ef} = r_b^{ef} = 0.25$). In Fig. 6(b) we show only the Blue jay population ($r_a^{ef} = 0.25$ and $r_b^{ef} = 0$), i.e., considering another population that does not transmit WNV. When we consider the coexistence of the species, the second peak appears earlier and is higher than for one species. In the mosquito population the same effect is observed. This fact is important when control strategies are considered.

3. Generalization of the model – several bird species

In each region several bird species can coexist, hence we consider now a natural generalization of the model (3)–(8) to n bird species. The dimensionless version is given by:

$$\frac{dS_i}{dt} = \mu_i - r_i q_i m_i \frac{\beta_i}{N_i} I_v S_i - \mu_i S_i \tag{26}$$

$$\frac{dI_i}{dt} = r_i q_i m_i \frac{\beta_i}{N_i} I_v S_i - (\gamma_i + \mu_i + \alpha_i) I_i \tag{27}$$

$$\frac{dN_i}{dt} = \mu_i - \mu_i N_i - \alpha_i I_i \tag{28}$$

$$\frac{dI_v}{dt} = \left(\sum_{i=1}^n r_i q_i \frac{\beta_{vi}}{N_i} I_i \right) (1 - I_v) - (1 - p) \mu_v I_v, \tag{29}$$

for $i = 1, \dots, n$. The threshold value for this model is:

$$R_0 = \sum_{i=1}^n \frac{(r_i q_i)^2 m_i \beta_i \beta_{vi}}{(1 - p) \mu_v (\gamma_i + \mu_i + \alpha_i)},$$

or

$$R_0 = \sum_{i=1}^n \frac{(r_i^{ef})^2 m_i \beta_i \beta_{vi}}{(1 - p) \mu_v (\gamma_i + \mu_i + \alpha_i)},$$

using $r_i^{ef} = r_i q_i$.

The stability of the trivial point (free of disease) is given by the roots of an $n + 1$ degree polynomial whose degree 0 coefficient depends on R_0 , as in the case $n = 2$ shown in previous section. It is easy to check that for $R_0 > 1$ the equilibrium point is unstable, because the independent coefficient is less than zero, and hence a positive real root always exists (as in the case of two species $n = 2$ in previous section). The stability for $R_0 < 1$ can be checked numerically. In the previous section we used the Routh–Hurwitz criterion in order to assess the stability of the trivial equilibrium point of the model with only two bird species. The threshold is an average of the thresholds with respect to the single model for an isolated species that inhabits a region. Hence the threshold is an average of the effectiveness of the bird species in a region.

If we consider the bird species that inhabit the south-east of USA, and the average number of birds of each species in that region [16], we can assume that: the percentage of House sparrow, Common grackle, American robin, Fish crow (only exists in south-east) is 18% each, and American crow and Morning dove is 15% each. For the first four we have $r_i^{ef} = 0.09$ and for the last two, $r_i^{ef} = 0.075$. Hence, we have the following R_0^i 's (using values given in Table 1): House sparrow, $R_0^1 = 0.83$, Common grackle, $R_0^2 = 1.15$, American robin, $R_0^3 = 0.74$, Fish crow, $R_0^4 = 0.42$, American crow, $R_0^5 = 0.47$ and Morning dove, $R_0^6 = 0.08$. Hence we obtain as the total reproduction number:

$$R_0 = \sum_{i=1}^6 R_0^i = 3.69.$$

In the south-west region we have 20% of House sparrow, 17% of House finch and Morning dove, and 13% of Ringed-billed gull, Mallard and American crow. We have the effective biting rates $r_i^{ef} = 0.1$, $r_i^{ef} = 0.08$ and $r_i^{ef} = 0.07$, respectively. Hence, we have the following R_0^i 's: House sparrow, $R_0^1 = 0.84$, House finch, $R_0^2 = 0.54$, Morning dove, $R_0^3 = 0.1$, Ringed-billed gull, $R_0^4 = 0.36$, Mallard $R_0^5 = 0.2$ and American crow $R_0^6 = 0.41$. We obtain in this case, as the total reproduction number:

$$R_0 = \sum_{i=1}^6 R_0^i = 2.45.$$

The mosquito *Culex quinquefasciatus* is the most common in the south of USA, and we can consider $\beta_a = 0.52$ [13,10] for all the species, instead of that given in Table 1. For this value we obtain for the south-east, $R_0 = 1.92$ and for south-west, $R_0 = 1.27$, a smaller value. The lower incidence of WNV in the south can be explained as a combination of bird coexistence and the lower effectiveness of the mosquitoes.

4. Conclusion

In this paper we proposed a model to study the coexistence of two avian populations in the transmission dynamics of West Nile Virus. Furthermore the model was generalized for several avian populations.

We analyzed the effects of considering different values for the biting rates as found in the literature. The biting rate can be assigned assuming an isolated species (r_a), or one species coexisting with another species in a certain proportion ($r_a^{ef} = q_a r_a$). According to the assumption for the biting rate, the level of incidence (measured by the peak) and the reproduction number are completely different. The different results come from the manner in which the relative abundance of mosquitoes with respect to the avian populations is considered: in an isolated bird species, we have m_a , while for one species transmitting WNV in coexistence with another that is not a transmitter, we used m_{total} .

Let us assume that in a region infested by mosquitoes (*Culex spp*) there is just one species of bird. Among the mosquitoes, *Culex pipiens* and *Culex tarsalis* are the most effective transmitters of WNV, followed by *C. tritaniorhynchus*, while *C. quinquefasciatus* is the least effective. In the case of an isolated bird species, we obtained

$$R_0 = \mathcal{R}_0 = \frac{r^2 m \beta \beta_v}{(1-p)\mu_v(\gamma + \mu + \alpha)},$$

due to the fact that all mosquitoes bite a single population of birds.

In general different birds species coexist. Let us assume that one species of bird (for instance, species denoted by a) is a transmitter of WNV, while the remaining species of birds are less competent, and are gathered together in a non-transmitting group. The size of the mosquito population is fixed, and at this moment the total population of birds is fixed too (that is, equal to the isolated population, then m is fixed). In this situation we obtained the reproduction number

$$R_0 = \frac{(r_a q_a)^2 m_a \beta_a \beta_{va}}{(1-p)\mu_v(\gamma_a + \mu_a + \alpha_a)} + \frac{(r_b q_b)^2 m_b \beta_b \beta_{vb}}{(1-p)\mu_v(\gamma_b + \mu_b + \alpha_b)},$$

where $q_a + q_b = 1$. For simplicity, let us deal with the non-transmitting species of birds by letting $\beta_b = 0$. In this case, we have, from Eq. (24), a diminished value

$$R_0 = R_0^a = (q_a)^2 \mathcal{R}_0,$$

showing that the relative abundance of bird species plays an important role in WNV transmission. The coexistence of two or more avian populations can result in the maintenance of the disease settling at an endemic level if $R_0 = \sum_{i=1}^n R_0^i > 1$. Hence, knowledge about the relative abundance of several bird species allows us to estimate with accuracy the risk of overall WNV transmission.

Now, the bird populations are allowed to vary, aiming to assess the spread of WNV by migratory movements. As we discussed above, in a region we have several coexisting bird species. Let us assume that this region is free of WNV. Migratory infected birds can disseminate WNV over a long range. If $R_0 = \sum_{i=1}^n R_0^i > 1$, WNV epidemics are triggered along the migratory routes, and the disease settles at an endemic level. Otherwise, the disease fades out. Notice that the contribution of each

species of birds is

$$R_0^i = \frac{(r_i q_i)^2 m_i \beta_i \beta_{vi}}{(1-p)\mu_v (\gamma_i + \mu_i + \alpha_i)},$$

depending on β_i and β_{vi} , the WNV transmission probabilities, respectively, from vector to bird (of species i) and from bird to vector. This fact shows that the effectiveness of mosquitoes to transmit WNV is as important as the effectiveness of birds.

We obtained the estimation of the overall R_0 by considering the six most effective species of birds: House sparrow, Common grackle, American robin, Fish crow, American crow and Morning dove. In the south-east of the USA, we estimated $R_0 = 3.69$, with $R_0 = 2.45$ for the south-west of the USA. Taking into account the mosquito *C. quinquefasciatus*, which is the most common in the south of USA and less effective in transmitting WNV, we estimated $R_0 = 1.92$ and $R_0 = 1.27$ for, respectively, the south-east and south-west of the USA.

In USA there are effective birds (for instance, Blue jay and Common grackle) as well as effective mosquitoes (for instance, *C. pipiens* and *C. tarsalis*) at transmitting WNV. The north-south migratory routes of birds in the USA spread WNV cases along this movement. However, the establishment of the disease at an endemic level can be explained by the interaction between effective populations of birds and mosquitoes. The migratory route of birds also reach Mexico. However, in Mexico WNV was not established. Even though WNV could be spread by infected birds, due to less effective mosquitoes (*C. quinquefasciatus* [17]) at transmitting this virus, Mexico is free of this disease ($R_0 = \sum_{i=1}^n R_0^i < 1$). The long range migratory routes of birds can spread WNV, but the complete establishment at an endemic level is strongly influenced by the capacity of mosquitoes to transmit the virus (for instance, the role played by *C. tarsalis* in the east-west dissemination of WNV in the USA [18]).

For this reason, a field study is necessary to determine, in each region, the effectiveness of the avian and mosquito populations to transmit WNV in order to estimate the risk of the disease. In places where more effective avian populations are present, the infected level are high, having implications on the adopted mosquito reduction strategies to result in $R_0 < 1$, Bowman et al. [6]. Another way of controlling WNV transmission consists in importing and releasing refractory, or very inefficient, WNV transmitter bird species, but with a high affinity to receive bites from mosquitoes. By doing this, the overall R_0 can be diminished below unity, and WNV disease fades out.

In a future work we will study traveling waves of WNV infection promoted by the migration of an effective avian population into a region where avian populations are very inefficient transmitters of WNV.

Acknowledgements

We thank the anonymous referees for providing comments and suggestions that contributed to improving this paper. The first author acknowledges a grant from FAPESP. The second author acknowledges a CNPq Fellowship.

References

- [1] L.G. Campbell, A.A. Martin, R.S. Lanciotti, D.J. Gubler, West Nile Virus, *The Lancet Infectious Diseases* 2 (2002) 519–529.
- [2] R.L. DeBiasi, K. Tyler, West Nile Virus meningoencephalitis, *Nature Clinical Practice Neurology* 3 (5) (2006) 264–275.
- [3] V.M. Kenkre, R.R. Parmenter, I.D. Peixoto, L. Sadasiv, A theoretical framework for the analysis of the West Nile Virus epidemic, *Computer and Mathematics with Applications* 42 (2005) 313–324.
- [4] M.J. Wonham, T. De-camino-Beck, M.A. Lewis, An epidemiological model for West Nile Virus: invasion analysis and control applications, *Proceedings of the Royal Society of London B* 271 (2004) 501–507.
- [5] G. Cruz-Pacheco, L. Esteve, J.A. Montañó-Hirose, C. Vargas, Modelling the dynamics of the West Nile Virus, *Bulletin of Mathematical Biology* 67 (2005) 1157–1172.
- [6] C. Bowman, A.B. Gumel, P. Van den Driessche, J. Wu, H. Zhu, A mathematical model for assessing control strategies against West Nile virus, *Bulletin of Mathematical Biology* 67 (2005) 1107–1133.
- [7] I.M. Foppa, A. Spielman, Does reservoir host mortality enhance transmission of West Nile Virus? *Theoretical Biology and Medical Modelling* 4:7 (2007).
- [8] S.R.-J. Jang, On a discrete West Nile Virus epidemic model, *Computational and Applied Mathematics* 26 (3) (2007) 397–414.
- [9] M. Lewis, J. Renclawowicz, P. Van den Driessche, Travelling waves and spread rate for a West Nile virus model, *Bulletin of Mathematical Biology* 68 (2006) 3–23.
- [10] N.A. Maidana, H.M. Yang, Spatial spreading of West Nile virus described by traveling waves, *Journal of Theoretical Biology* (2009) 403–417.
- [11] N. Komar, S. Langevin, S. Hinten, Nicole Nemeth, E. Edwards, D. Hettler, B. Davis, R. Bowen, M. Bunning, Experimental infection of north American birds with the New York 1999 strain of West Nile virus, *Emerging Infectious Diseases* 9 (3) (2003) 311–322.
- [12] D.J. Dohm, M.R. Sardelis, J. Turell, Experimental vertical transmission of West Nile virus by *Culex pipiens* (Diptera: culicidae), *Journal of Medical Entomology* 39 (4) (2002) 640–644.
- [13] L.B. Goddard, A.E. Roth, W.K. Reisen, T.W. Scott, Vector Competence of California Mosquitoes for West Nile Virus, *Emerging Infectious Diseases* 8 (12) (2002) 1385–1391.
- [14] M.J. Turell, M.L. O'Guinn, D.J. Dohm, J.W. Jones, Vector competence of North American mosquitoes (Diptera: culicidae) for west nile virus, *Journal of Medical Entomology* 38 (2) (2001) 130–134.
- [15] J.K. Hale, *Ordinary Differential Equation*, John Wiley and Sons, New York, 1969.
- [16] Breeding bird survey summary and analysis. <http://www.mbr-pwrc.usgs.gov/bbs/bbs.html> (July 2009).
- [17] <http://www.smsl.co.nz/Services/New+Zealand+BioSecure/Exotic+Mosquitoes.html>.
- [18] T.L. Goldberg, T.K. Anderson, G.L. Hamer, West Nile virus may have hitched a ride across the western United States on *Culex tarsalis* mosquitoes, *Molecular Ecology* 19 (2010) 1518–1519.