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Multi-species interactions in West Nile virus infection

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In this paper, we analyse the interaction of different species of birds and mosquitoes on the dynamics of West Nile virus (WNV) infection. We study the different transmission efficiencies of the vectors and birds and the impact on the possible outbreaks. We show that the basic reproductive number is the weighted mean of the basic reproductive number of each species, weighted by the relative abundance of its population in the location. These results suggest a possible explanation of why there are no outbreaks of WNV in Mexico.

Keywords: West Nile virus; multiple species; endemic equilibrium; basic reproduction number

1. Introduction

West Nile virus (WNV) is an arbovirus disease transmitted by the bite of mosquitoes to different species of birds and mammals, including humans. Infected mammals cannot transmit the disease; therefore, the disease cycles only between birds and mosquitoes [4].

The disease has been observed in Africa, Europe, and the Middle East for several decades. It was first detected in the Western Hemisphere in 1999 during an outbreak in New York. Since then, it has spread to most of the USA. The impact of WNV has been much greater in North America than in the Eastern Hemisphere. More than 2500 cases of WNV fever are reported each year in the USA, and many mild cases are probably not diagnosed [34]. In Canada, outbreaks of WNV has been reported in Alberta, Quebec, Ontario, Manitoba, and Saskatchewan [14].

The virus was first detected in 2001 in Jamaica and the Cayman Islands where 17 WNV seropositive birds were reported in a sample of 348. In 2002, WNV continued to spread in the Caribbean Basin. Guadeloupe Island reported numerous subclinical infections in horses and chickens, determined serologically by neutralization; however, subsequent surveillance in 2003 and 2004 failed to detect any transmission in this region. In 2002, seropositive horses were reported from six states (Chihuahua, Coahuila, Tamaulipas, Veracruz, Tabasco, and Yucatán) of México [11,22]. In the same country, seropositive birds were rare and were first detected in the early

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winter months of 2003 [12,33]. The widespread WNV seropositivity among horses observed in Mexico in 2003 was also present in El Salvador and Guatemala [6]. However, anecdotal reports of fatal or life-threatening neurological disease in Mexican and Central American horses have rarely been confirmed as being due to WNV. In 2004, the first serological evidence of WNV activity in South American ecosystems was found in Colombia, where WNV neutralizing antibodies were found circulating in domestic animals [25]. All these data indicate the presence of WNV in Latin America and the Caribbean since at least 2001, but the incidence has remain very low and no outbreaks have been reported.

Taking into account the ecological conditions of Latin America and the Caribbean Islands which favour some arbovirus transmissions such as dengue, the low incidence of WNV activity reported in these regions is surprising [14]. Several explanations have been given for this fact, all of them related to the virus. One hypothesis is that the wide circulation of other flavivirus (like dengue) in Latin America and the Caribbean have created cross-immunization against WNV. Another hypothesis is that the virus has mutated into a more benign strain in its way down south [14].

The role of different mosquitoes and birds species in the spread of WNV is an important problem that has been studied, for example, in [1,14–16,31]. Laboratory and field studies show that some species are more competent at transmitting the disease [1,14–16,26,31,32]. These studies found that transmission efficiency, species abundance, and biting behaviour of mosquitoes are among the most important parameters for the risk of an outbreak. For instance, in [32], it was concluded that although *Culex pipiens* is only a moderately competent laboratory vector, it is a very efficient enzootic vector in regions where it is abundant, because it feeds primarily on avian hosts. In the same paper, it was suggested that since *Aedes albopictus* feeds on a variety of hosts, it could be a bridge vector between the enzootic avian cycle and mammals. All of these studies suggest that the development of outbreaks in a particular location depends strongly on the epidemiological characteristics and on the abundance of the local bird and mosquito species of the region. In particular, we hypothesize that a possible explanation for the absence of outbreaks of WNV in some countries such as Mexico is the lack of sufficiently large populations of good transmitters (birds or vectors) of the disease.

Several mathematical models have been developed explaining a variety of features on the transmission of WNV disease. In [36], the authors used a core model that summarized the biological assumptions common to several of these models to compare the different R_0 obtained for each model. Some of the cited models include the exposed class in the vector population to account for the viral incubation time in the mosquitoes [21,35]. Others assume vertical transmission in the vector population [7,30]. Some models incorporate the aquatic life stage of the mosquitoes (eggs, larval and pupal stages) [35]. For the avian population, most of the models include a recovered class [2,7,21,30,35]. Spatial diffusion of WNV is modelled in [19,20,23,24], and seasonal effects on new outbreaks starting from an endemic situation are studied in [8]. Most of the above models deal with only one species of birds and one species of mosquitoes, although in [3] the authors divide the susceptible birds into two groups: the crow family birds and the remaining birds under consideration to show that the non-crow family birds susceptible to WNV are one of the key factors responsible for the endemicity of the virus in the region of study.

In this work, we consider that epidemiological heterogeneity is an important factor in the transmission of WNV, and therefore we formulate a mathematical model to study the effect of the interaction between different species of birds and mosquitoes living in the same locality on the emergence and prevalence of the disease. Our model is based on [7]. The exposed class is not considered as in [21,35], since this class just introduces a time delay in the outbreak. Neither the initial stages of the vector are considered as in [35], since our interest is the dynamics of vector–host interactions, and not the control of the vector.

We find an expression for the basic reproductive number which reflects the relative importance of each of the species in the emergence of epidemics and endemicity of the disease. This expression

indicates that the abundance of a competent species leads to the possibility of an outbreak in species which are not good transmitters by themselves. We illustrate this behaviour using data from birds and mosquito species with different transmission competence and population sizes.

This paper is structured as follows: in Section 2, we formulate and analyse a model for the transmission of WNV considering that there are several species of birds and only one species of mosquitoes. Further, we make a sensitivity analysis and numerical simulations of the model. In Section 3, we treat the problem of several kinds of mosquitoes and only one species of birds. The general model considering several species of birds and mosquitoes is formulated in Section 4, and we obtain an estimation of the basic reproduction number for some numerical examples. Finally, in Section 5, we present our conclusions.

2. *N* species of birds

2.1. *Formulation of the model*

The following system of nonlinear differential equations was proposed in [7] to explore the temporal mosquito–bird cycle transmission of WNV.

$$\begin{aligned}
\frac{\mathrm{d}S_\mathrm{a}}{\mathrm{d}t} &= \Lambda_\mathrm{a} - \frac{b\beta_\mathrm{a}}{N_\mathrm{a}} I_\mathrm{v} S_\mathrm{a} - \mu_\mathrm{a} S_\mathrm{a} \\
\frac{\mathrm{d}I_\mathrm{a}}{\mathrm{d}t} &= \frac{b\beta_\mathrm{a}}{N_\mathrm{a}} I_\mathrm{v} S_\mathrm{a} - (\gamma_\mathrm{a} + \mu_\mathrm{a} + \alpha_\mathrm{a}) I_\mathrm{a} \\
\frac{\mathrm{d}R_\mathrm{a}}{\mathrm{d}t} &= \gamma_\mathrm{a} I_\mathrm{a} - \mu_\mathrm{a} R_\mathrm{a} \\
\frac{\mathrm{d}S_\mathrm{v}}{\mathrm{d}t} &= \mu_\mathrm{v} S_\mathrm{v} + (1-p)\mu_\mathrm{v} I_\mathrm{v} - \frac{b\beta_\mathrm{v}}{N_\mathrm{a}} I_\mathrm{a} S_\mathrm{v} - \mu_\mathrm{v} S_\mathrm{v} \\
\frac{\mathrm{d}I_\mathrm{v}}{\mathrm{d}t} &= p\mu_\mathrm{v} I_\mathrm{v} + \frac{b\beta_\mathrm{v}}{N_\mathrm{a}} I_\mathrm{a} S_\mathrm{v} - \mu_\mathrm{v} I_\mathrm{v} \\
\frac{\mathrm{d}N_\mathrm{a}}{\mathrm{d}t} &= \Lambda_\mathrm{a} - \mu_\mathrm{a} N_\mathrm{a} - \alpha_\mathrm{a} I_\mathrm{a},
\end{aligned} \tag{1}$$

where S_a, I_a, and R_a denote the susceptibles, infectives, and recovered of the bird population with $N_\mathrm{a} = S_\mathrm{a} + I_\mathrm{a} + R_\mathrm{a}$ the total bird population, and S_v, I_v denote the susceptibles and infectives of the vector population with $N_\mathrm{v} = S_\mathrm{v} + I_\mathrm{v}$ the total mosquito population.

The parameters of the model are the recruitment rate Λ_a, the natural mortality rate μ_a of the bird population, the mortality rate of mosquitoes μ_v, the biting rate of mosquitoes b, β_a, and β_v the transmission probabilities, γ_a the recovery rate, α_a the disease-related death in the avian population, and finally p the proportion of vertical transmission in mosquitoes.

Based on the above equations, we formulate a model to study the interaction of several avian species with one species of mosquitoes. The population size of the ith bird species is denoted by N_i, with N_i divided into epidemiological compartments: S_i, I_i, and R_i.

The dynamics of the different species in the absence of the disease is given by

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = \Lambda_i - \mu_i N_i, \tag{2}$$

where Λ_i is the recruitment rate and μ_i is the bird mortality rate of the ith species. We assume zero vertical transmission for all species of birds. The vector population is constant with value N_v and mortality rate μ_v.

The model considers the interaction among susceptible and infective individuals of each of the n species of birds with the mosquito population and assumes that the transmission of the disease is only through mosquito bites. The infection rate for the ith bird species depends on the mosquito biting rate, the transmission probabilities and on the number of infective and susceptible individuals of each species.

The average number of vectors per bird is given by $N_v/(N_1 + \cdots + N_n)$, a particular bird receives on average, $bN_v/(N_1 + \cdots + N_n)$ bites per unit of time.

The transmission probability is the probability that an infectious bite produces a new case in a susceptible member of the other species. For the ith bird species, β_i and β_{v_i} are the transmission probabilities from mosquito to bird and bird to mosquito, respectively. Then, the infection rates per susceptible bird of the ith bird species and susceptible vector are given by

$$\frac{b\beta_i}{N_1 + \cdots + N_n} I_v, \quad \frac{b\beta_{v_i}}{N_1 + \cdots + N_n} I_i.$$

We assume that infected birds of the ith bird species recover at a constant rate γ_i, and we denote by α_i the corresponding specific death rate associated with WNV in the mentioned bird population.

Since $R_i = N_i - S_i - I_i$, it is enough to consider the system in the variables S_i, I_i, N_i, and I_v. According to the assumptions above, we modify the basic system (1) to include several bird species:

$$\begin{aligned}
\frac{dS_i}{dt} &= \Lambda_i - \frac{b\beta_i}{N_1 + \cdots + N_n} S_i I_v - \mu_i S_i \\
\frac{dI_i}{dt} &= \frac{b\beta_i}{N_1 + \cdots + N_n} S_i I_v - (\gamma_i + \mu_i + \alpha_i) I_i \\
\frac{dI_v}{dt} &= \sum_{i=1}^{n} \frac{b\beta_{v_i} I_i}{N_1 + \cdots + N_n} (N_v - I_v) - \mu_v I_v \\
\frac{dN_i}{dt} &= \Lambda_i - \mu_i N_i - \alpha_i I_i
\end{aligned} \tag{3}$$

with $i = 1, \ldots, n$.

System (3) leaves invariant the first orthant in R^{3n+1} since the vector field on the boundary points inward. Furthermore, since $dN_i/dt < 0$ for $N_i > \Lambda_i/\mu_i$, $i = 1, \ldots, n$, all trajectories in the first orthant enter or stay inside the region

$$\Omega = \left\{ S_i + I_i \le N_i \le \frac{\Lambda_i}{\mu_i}, i = 1, \ldots, n, 0 \le I_v \le N_v \right\}.$$

The continuity of the right-hand side of Equation (3) implies that given an initial condition in Ω, a unique solution exists. Since the orbits approach, enter, or stay in Ω, they eventually are bounded and hence exist for $t > 0$. Therefore, the initial value problem for system (3) is mathematically well posed as biologically reasonable since all variables remain non-negative.

2.2. *Disease-free equilibrium*

We denote the disease-free equilibrium by E_0, whose coordinates are $N_i = S_i = \Lambda_i/\mu_i$; $I_i = 0$; $i = 1, \ldots, n$, and $I_v = 0$. Using the next generation operator approach [9,10], we compute the *basic reproduction number* R_0 associated with the disease-free equilibrium. The non-negative

matrix, K, of the infection terms, and the non-singular M-matrix, T, of the transition terms are given by

$$K = \begin{pmatrix} 0 & 0 & \cdots & 0 & \dfrac{b\beta_1 \bar{N}_1}{\bar{N}} \\ 0 & 0 & \cdots & 0 & \dfrac{b\beta_2 \bar{N}_2}{\bar{N}} \\ \cdot & \cdots & \cdots & \cdot & \cdot \\ \cdot & \cdot & \cdots & \cdot & \dfrac{b\beta_n \bar{N}_n}{\bar{N}} \\ \dfrac{b\beta_{v_1} N_{\mathrm{v}}}{\bar{N}} & \dfrac{b\beta_{v_2} N_{\mathrm{v}}}{\bar{N}} & \cdots & \dfrac{b\beta_{v_n} N_{\mathrm{v}}}{\bar{N}} & 0 \end{pmatrix},$$

and

$$T = \begin{pmatrix} \gamma_1 + \mu_1 + \alpha_1 & 0 & \cdot & \cdot & 0 \\ 0 & \gamma_2 + \mu_2 + \alpha_2 & \cdot & \cdot & 0 \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ 0 & 0 & 0 & \gamma_n + \mu_n + \alpha_n & 0 \\ 0 & \cdot & \cdot & 0 & \mu_{\mathrm{v}} \end{pmatrix},$$

where $\bar{N}_i = \Lambda_i/\mu_i$, $i = 1, \ldots, n$, and $\bar{N} = \sum_{i=1}^{n} \bar{N}_i$.

It is known that $R_0 = \rho(KT^{-1})$, where ρ denotes the spectral radius [9]. In the following theorem, we find an expression for R_0.

THEOREM 1 *The basic reproduction number associated with the disease-free equilibrium of model* (3) *is given by*

$$R_0^a = \sqrt{\sum\nolimits_{i=1}^{n} (R_{0_i}^a)^2 \left(\frac{\bar{N}_i}{\bar{N}}\right)}, \tag{4}$$

where

$$R_{0_i}^a = \sqrt{\frac{b^2 \beta_i \beta_{v_i}}{\mu_{\mathrm{v}}(\gamma_i + \mu_i + \alpha_i)} \left(\frac{N_{\mathrm{v}}}{\bar{N}}\right)} \tag{5}$$

is the basic reproductive number corresponding to ith *species,* $i = 1, \ldots, n$.

Proof KT^{-1} is a $(n+1) \times (n+1)$ matrix of the form

$$A = \begin{pmatrix} \mathbf{0} & \bar{u}^{\mathrm{T}} \\ \bar{v} & 0 \end{pmatrix},$$

with

$$\bar{u} = \left(\frac{b\beta_1 \bar{N}_1}{\mu_{\mathrm{v}} \bar{N}}, \ldots, \frac{b\beta_n \bar{N}_n}{\mu_{\mathrm{v}} \bar{N}}\right) \quad \text{and} \quad \bar{v} = \left(\frac{b\beta_{v_1} N_{\mathrm{v}}}{(\gamma_1 + \mu_1 + \alpha_1)\bar{N}}, \ldots, \frac{b\beta_{v_n} N_{\mathrm{v}}}{(\gamma_n + \mu_n + \alpha_n)\bar{N}}\right)$$

n-dimensional row vectors and $\mathbf{0}$ is the $n \times n$ null matrix.

The matrix A has $n-1$ eigenvectors associated with the eigenvalue zero of the form $(\bar{w}, 0)$, where $\bar{w}$ is an n-dimensional row vector such that $\bar{v} \cdot \bar{w} = 0$. The other two eigenvectors are $(\bar{u}, \pm\sqrt{\bar{u} \cdot \bar{v}})$ with eigenvalues $\pm\sqrt{\bar{u} \cdot \bar{v}}$. It is straightforward to see that $\sqrt{\bar{u} \cdot \bar{v}} = R_0^a$. ■

Using Theorem 2 of [10], the following result is established.

THEOREM 2 *The disease-free equilibrium, E_0, of model* (3) *is locally asymptotically stable if $R_0^a < 1$ and unstable if $R_0^a > 1$.*

The above theorem shows that WNV infection disappears if the initial conditions of model (3) are sufficiently close to the disease-free equilibrium. To ensure the elimination of the disease regardless of the initial population sizes, a global stability result is needed. For the case when the disease-related mortalities are zero, we prove that the disease-free equilibrium is globally asymptotically stable. This is done below using a comparison theorem.

THEOREM 3 *Assume $\alpha_i = 0$, for $i = 1, \ldots, n$. If $R_0^a < 1$, the disease-free-equilibrium, E_0, of model* (3) *is globally asymptotically stable in the region Ω, whenever $R_0^a < 1$.*

Proof The conditions $\alpha_i = 0$ imply $N_i \to \bar{N}_i$ for $i = 1, \ldots, n$. Therefore, the equations for I_i and I_v in Equation (3) can be written as

$$\begin{aligned}
\frac{\mathrm{d}I_1}{\mathrm{d}t} &= \frac{b\beta_1}{\bar{N}} S_1 I_\mathrm{v} - (\gamma_1 + \mu_1) I_1 \\
&\vdots \\
\frac{\mathrm{d}I_n}{\mathrm{d}t} &= \frac{b\beta_n}{\bar{N}} S_n I_\mathrm{v} - (\gamma_n + \mu_n) I_n \\
\frac{\mathrm{d}I_\mathrm{v}}{\mathrm{d}t} &= \sum_{i=1}^{n} \frac{b\beta_{v_i} I_i}{\bar{N}} (N_\mathrm{v} - I_\mathrm{v}) - \mu_\mathrm{v} I_\mathrm{v}.
\end{aligned} \tag{6}$$

Since $S_i \leq \bar{N}_i$, the following vectorial inequality holds

$$\frac{\mathrm{d}}{\mathrm{d}t} \begin{pmatrix} I_1(t) \\ \vdots \\ I_n(t) \\ I_\mathrm{v}(t) \end{pmatrix} \leq (K - T) \begin{pmatrix} I_1(t) \\ \vdots \\ I_n(t) \\ I_\mathrm{v}(t) \end{pmatrix}, \tag{7}$$

where the matrices K and T are defined as above.

Now, consider the system in the variables Z_i, $i = 1, \ldots, n$, and Z_v given by

$$\frac{\mathrm{d}}{\mathrm{d}t} \begin{pmatrix} Z_1(t) \\ \vdots \\ Z_n(t) \\ Z_\mathrm{v}(t) \end{pmatrix} = (K - T) \begin{pmatrix} Z_1(t) \\ \vdots \\ Z_n(t) \\ Z_\mathrm{v}(t) \end{pmatrix}. \tag{8}$$

If $R_0^a < 1$, then $\rho(KT^{-1}) < 1$, which is equivalent to $K - T$ has all of its eigenvalues in the left half-plane [9]. It follows that the ODE linear system (8) is stable if $R_0^a < 1$. Consequently, $(Z_1(t), \ldots, Z_n(t), Z_\mathrm{v}(t)) \to (0, \ldots, 0, 0)$ as $t \to \infty$. Then, from Equation (7), using a standard comparison theorem [18, p. 31], $(I_1(t), \ldots, I_n(t), I_\mathrm{v}(t)) \to (0, \ldots, 0, 0)$. This in turn implies that $S_i(t) \to \bar{N}_i$ for $i = 1, \ldots, n$; therefore, the disease-free equilibrium, E_0, is globally asymptotically stable in Ω whenever $R_0^a < 1$. ■

2.3. *Endemic equilibrium*

An endemic equilibrium is given by the solution of the algebraic system obtained setting the derivatives of Equation (3) equal to zero.

$$\begin{aligned}
0 &= \Lambda_i - \frac{b\beta_i}{N_1^* + \cdots + N_n^*} S_i^* I_{\mathrm{v}}^* - \mu_i S_i^* \\
0 &= \frac{b\beta_i}{N_1^* + \cdots + N_n^*} S_i^* I_{\mathrm{v}}^* - (\gamma_i + \mu_i + \alpha_i) I_i^* \\
0 &= \sum_{i=1}^{n} \frac{b\beta_{v_i} I_i^*}{N_1^* + \cdots + N_n^*} (N_{\mathrm{v}} - I_{\mathrm{v}}^*) - \mu_{\mathrm{v}} I_{\mathrm{v}}^* \\
0 &= \Lambda_i - \mu_i N_i^* - \alpha_i I_i^*
\end{aligned} \tag{9}$$

with $i = 1, \ldots, n$.

Solving for I_{v}^* and S_i^* in terms of N_i^* and I_i^*, we obtain

$$\begin{aligned}
I_{\mathrm{v}}^* &= \frac{\sum_{j=1}^{n} b\beta_{v_j} I_j^* N_{\mathrm{v}}}{\sum_{j=1}^{n} b\beta_{v_j} I_j^* + \mu_{\mathrm{v}} \sum_{j=1}^{n} N_j^*} \\
S_i^* &= \frac{\Lambda_i (\sum_{j=1}^{n} b\beta_{v_j} I_j^* + \mu_{\mathrm{v}} \sum_{j=1}^{n} N_j^*) \sum_{j=1}^{n} N_j^*}{(b\beta_i N_{\mathrm{v}} + \mu_i) \sum_{j=1}^{n} b\beta_{v_j} I_j^* + \mu_i \mu_{\mathrm{v}} (\sum_{j=1}^{n} N_j^*)^2}
\end{aligned} \tag{10}$$

with $i = 1, \ldots, n$.

Let $\mathbf{I} = (I_1^*, \ldots, I_n^*)$, $\mathbf{N} = (N_1^*, \ldots, N_n^*)$, and $\mathbf{a} = (\alpha_1, \ldots, \alpha_n)$.

Substituting I_{v}^* and S_i^* in the equations for I_i^*, we obtain that $\mathbf{I}$ and $\mathbf{N}$ are solutions of the algebraic system

$$\begin{aligned}
F_i(\mathbf{I}, \mathbf{N}; \mathbf{a}) &= 0, \\
G_i(\mathbf{I}, \mathbf{N}; \mathbf{a}) &= 0,
\end{aligned} \tag{11}$$

where

$$\begin{aligned}
F_i(\mathbf{I}, \mathbf{N}; \mathbf{a}) &= \frac{b\beta_i \Lambda_i N_{\mathrm{v}} \sum_{j=1}^{n} b\beta_{v_j} I_j^*}{(b\beta_i N_{\mathrm{v}} + \mu_i) \sum_{j=1}^{n} b\beta_{v_j} I_j^* + \mu_i \mu_{\mathrm{v}} (\sum_{j=1}^{n} N_j^*)^2} \\
&\quad - (\alpha_i + \mu_i + \gamma_i) I_i^* \\
G_i(\mathbf{I}, \mathbf{N}, \mathbf{a}) &= \Lambda_i - \mu_i N_i^* - \alpha_i I_i^*
\end{aligned} \tag{12}$$

with $\mathbf{a}$ fixed and $i = 1, \ldots, n$.

We first analyse the case $\mathbf{a} = \mathbf{0}$. For this value of $\mathbf{a}$, N_i^* becomes $\bar{N}_i = \Lambda_i / \mu_i$, $i = 1, \ldots, n$, and we denote by $\bar{I}_i$ the corresponding coordinates of the infective birds at equilibrium.

We define the new variable

$$Y = \sum_{j=1}^{n} b\beta_{v_j} \bar{I}_j. \tag{13}$$

In terms of Y and $\bar{N}_i$, system (11) can be solved for $\bar{I}_i$,

$$\bar{I}_i = \frac{b\beta_i \Lambda_i N_{\mathrm{v}} Y}{((b\beta_i N_{\mathrm{v}} + \mu_i) Y + \mu_i \mu_{\mathrm{v}} \bar{N}^2)(\mu_i + \gamma_i)}, \tag{14}$$

with $i = 1, \ldots, n$.

Multiplying $\bar{I}_i$ by $b\beta_i$, $i = 1, \ldots, n$, and adding, the algebraic system (14) reduces to a single equation for the variable Y,

$$Y = Y \sum_{i=1}^{n} \frac{b^2 \beta_i \beta_{v_i} \Lambda_i N_v}{((b\beta_i N_v + \mu_i)Y + \mu_i \mu_v \bar{N}^2)(\mu_i + \gamma_i)}. \tag{15}$$

Eliminating the trivial solution $Y = 0$ (which corresponds to the disease-free equilibrium) and substituting $R^a_{0_i}$ given by Equation (5) in Equation (15), we get that the non-trivial solutions Y satisfy the equation

$$H(Y) = 1, \tag{16}$$

where

$$H(Y) = \sum_{i=1}^{n} \frac{\mu_v \mu_i (R^a_{0_i})^2 \bar{N} \bar{N}_i}{(b\beta_i N_v + \mu_i)Y + \mu_i \mu_v \bar{N}^2}. \tag{17}$$

Since $H(Y)$ decreases monotonically to zero when Y tends to infinity, and $H(0) = (R^a_0)^2$, it follows that a necessary and sufficient condition for the existence of a unique root Y^* of Equation (16) is $R^a_0 > 1$. Therefore, in the case $\mathbf{a} = \mathbf{0}$, there exists a unique endemic equilibrium if and only if $R^a_0 > 1$.

Now we proceed to analyse the case $\mathbf{a} \neq \mathbf{0}$ and $\mathbf{a}$ sufficiently small. From the implicit function theorem, it follows that system (13) has a unique solution $(\mathbf{I}, \mathbf{N}; \mathbf{a})$ for $\mathbf{a}$ in the neighbourhood of $\mathbf{0}$ if the Jacobian determinant

$$J = \frac{\partial(F_1, \ldots, F_n, G_1, \ldots, G_n)}{\partial(I_1, \ldots, I_n, N_1, \ldots, N_n)}$$

evaluated at $(\mathbf{I},\mathbf{N};\mathbf{0})$ is different from zero. This determinant can be simplified to obtain

$$J = (-1)^n \prod_{i=1}^{n} \mu_i \left(\frac{\partial(F_1, \ldots, F_n)}{\partial(I_1, \ldots, I_n)} \right). \tag{18}$$

We summarize the above results in the following theorem.

THEOREM 4 *Assume $\alpha_i = 0$ for all i, then system* (3) *has a unique endemic equilibrium if and only if $R^a_0 > 1$. If the Jacobian given by Equation* (18) *is different from zero, the result can be extended for* $\mathbf{a}$ *in the neighborhood of* $\mathbf{0}$.

For two species of birds ($n = 2$), the Jacobian J has the form

$$-A \left[\left(\frac{\mu_1 \mu_v \bar{N}_1 \bar{N} R^a_{0_1}}{(b\beta_1 N_v + \mu_1)Y^* + \mu_1 \mu_v \bar{N}^2} \right)^2 + \left(\frac{\mu_2 \mu_v \bar{N}_2 \bar{N} R^a_{0_2}}{(b\beta_2 N_v + \mu_2)Y^* + \mu_2 \mu_v \bar{N}^2} \right)^2 - 1 \right],$$

with $A = \mu_1 \mu_2 (\mu_1 + \gamma_1)(\mu_2 + \gamma_2)$. Substituting $H(Y^*) = 1$ in the last expression, J becomes

$$A \left[\frac{\mu_1 \mu_v \bar{N}_1^2 (R^a_{0_1})^2 Y^* (b\beta_1 N_v + \mu_1)}{(b\beta_1 N_v + \mu_1)Y^* + \mu_1 \mu_v \bar{N}^2} + \frac{\mu_2 \mu_v \bar{N}_2^2 (R^a_{0_2})^2 Y^* (b\beta_2 N_v + \mu_2)}{(b\beta_2 N_v + \mu_2)Y^* + \mu_2 \mu_v \bar{N}^2} \right]. \tag{19}$$

Clearly, $J \neq 0$, and therefore the following result has been proved.

COROLLARY 1 *Assume* $n = 2$. *For* $R_0^a > 1$, *system* (3) *has a unique endemic equilibrium*, *for* (α_1, α_2) *in the neighborhood of* $(0, 0)$.

The global stability of the endemic equilibrium in the interior of Ω can be proved in the case $\alpha_i = 0$ for $i = 1, \ldots, n$ using the Lyapunov function

$$\begin{aligned} V(S_1, \ldots, S_n, I_1, \ldots, I_n, S_v, I_v) = &\sum_{i=1}^{n} A_i \left(S_i - \bar{S}_i - \bar{S}_i \ln \frac{S_i}{\bar{S}_i} \right) \\ &+ \sum_{i=1}^{n} A_i \left(I_i - \bar{I}_i - \bar{I}_i \ln \frac{I_i}{\bar{I}_i} \right) \\ &+ \left(S_v - \bar{S}_v - \bar{S}_v \ln \frac{S_v}{\bar{S}_v} \right) \\ &+ \left(I_v - \bar{I}_v - \bar{I}_v \ln \frac{I_v}{\bar{I}_v} \right). \end{aligned} \tag{20}$$

with $\bar{S}_v = N_v - \bar{I}_v$. The constants A_i, $i = 1, \ldots, n$, are given by

$$A_i = \frac{\beta_{v_i} \bar{S}_v \bar{I}_i}{\beta_i \bar{S}_i \bar{I}_v}. \tag{21}$$

The orbital derivative of Equation (20) is given by

$$\begin{aligned} \dot{V} = &\sum_{i=1}^{n} A_i \left(1 - \frac{\bar{S}_i}{S_i} \right) \left(\Lambda_i - \frac{b\beta_i}{\bar{N}} S_i I_v - \mu_i S_i \right) \\ &+ \sum_{i=1}^{n} A_i \left(1 - \frac{\bar{I}_i}{I_i} \right) \left(\frac{b\beta_i}{\bar{N}} S_i I_v - (\gamma_i + \mu_i) I_i \right) \\ &+ \left(1 - \frac{\bar{S}_v}{S_v} \right) \left(\mu_v N_v - \sum_{i=1}^{n} \frac{b\beta_{v_i}}{\bar{N}} S_v I_i - \mu_v S_v \right) \\ &+ \left(1 - \frac{\bar{I}_v}{I_v} \right) \left(\sum_{i=1}^{n} \frac{b\beta_{v_i}}{\bar{N}} S_v I_i - \mu_v I_v \right). \end{aligned} \tag{22}$$

Substituting the following relations obtained from system (9) at equilibrium,

$$\begin{aligned} \Lambda_i &= \frac{b\beta_i}{\bar{N}} \bar{S}_i \bar{I}_v + \mu_i \bar{S}_i, \\ \gamma_i + \mu_i &= \frac{b\beta_i}{\bar{N}} \frac{\bar{S}_i \bar{I}_v}{\bar{I}_i}, \\ \mu_v N_v &= \sum_{i=1}^{n} \frac{b\beta_{v_i}}{\bar{N}} \bar{S}_v \bar{I}_i + \mu_v \bar{S}_v, \\ \mu_v &= \sum_{i=1}^{n} \frac{b\beta_{v_i}}{\bar{N}} \frac{\bar{S}_v \bar{I}_i}{\bar{I}_i}, \end{aligned}$$

and the expressions for A_i above, into the expression for the Lyapunov derivative in Equation (21) and simplifying, we obtain

$$\begin{aligned}\dot{V} = &-\sum_{i=1}^{n}\mu_i A_i\frac{(S_i-\bar{S}_i)^2}{S_i}-\mu_{\mathrm{v}}\frac{(S_{\mathrm{v}}-\bar{S}_{\mathrm{v}})^2}{S_{\mathrm{v}}}\\ &-2\sum_{i=1}^{n}A_i\frac{b\beta_i}{\bar{N}}S_i I_{\mathrm{v}}-2\sum_{i=1}^{n}A_i\frac{b\beta_i}{\bar{N}}\frac{\bar{S}_i\bar{I}_{\mathrm{v}}}{\bar{S}_{\mathrm{v}}\bar{I}_i}S_{\mathrm{v}}I_i\\ &-\sum_{i=1}^{n}A_i\frac{b\beta_i}{\bar{N}}\bar{S}_i\bar{I}_{\mathrm{v}}\left[\frac{\bar{S}_i}{S_i}+\frac{\bar{S}_{\mathrm{v}}}{S_{\mathrm{v}}}+\frac{S_i\bar{I}_i I_{\mathrm{v}}}{\bar{S}_i I_i\bar{I}_{\mathrm{v}}}+\frac{S_{\mathrm{v}}I_i\bar{I}_{\mathrm{v}}}{\bar{S}_{\mathrm{v}}\bar{I}_i I_{\mathrm{v}}}-4\right].\end{aligned}\tag{23}$$

Let

$$x_{i_1}=\frac{\bar{S}_i}{S_i},\quad x_{i_2}=\frac{S_{\mathrm{v}}}{\bar{S}_{\mathrm{v}}},\quad\text{and}\quad x_{i_3}=\frac{\bar{I}_i I_{\mathrm{v}}}{I_i\bar{I}_{\mathrm{v}}}.$$

It follows that for $i=1,\ldots,n$, the expression inside the square parenthesis of the last term of Equation (23) can be re-written as

$$f_i(x_{i_1},x_{i_2},x_{i_3})=x_{i_1}+\frac{1}{x_{i_2}}+\frac{x_{i_3}}{x_{i_1}}+\frac{x_{i_2}}{x_{i_3}}-4.$$

It is easy to see that the minimum of the functions f_i in $\mathbb{R}^n_+$ is zero, and it is attained when $x_{i_i}=x_{i_2}=x_{i_3}=1$ $(i=1,\ldots,n)$. Hence, it follows that $\dot{V}\leq 0$ and $\dot{V}=0$ if and only if $S_i=\bar{S}_i$, $I_i=\bar{I}_i$, $S_{\mathrm{v}}=\bar{S}_{\mathrm{v}}$, and $I_{\mathrm{v}}=\bar{I}_{\mathrm{v}}$. This implies that all trajectories in the interior of Ω approach the endemic equilibrium as $t\to\infty$, proving the global stability.

It is interesting to notice that R_0^a given in Equation (5) is the average of the basic reproductive numbers of the bird species weighted by their corresponding population proportion with respect to the total number of birds. Then, the balance among the competence of the birds species to transmit the disease and their corresponding population density will determine the evolution of the disease. To illustrate this point, we consider two species of birds, Common Grackle and Northern Flicker, whose epidemiological and demographic parameters are shown in Table 1. As can be appreciated, the first species is more competent than the second one transmitting the disease, since for the first species $\beta_{\mathrm{v}}=0.68$ and for the second $\beta_{\mathrm{v}}=0.06$. Moreover, the population sizes of two species range from hundreds to thousands in the USA. For our example, we assume that the Northern Flicker and Common Grackle populations are $N_1=1000$ and $N_2=100$, respectively. We use the values in Table 1 for the bird populations and the values in Table 2 that correspond

Table 1. Epidemiological and demographic parameters in the numerical simulations of WN models.

Bird	β_{v}	γ_{a}	α_{a}	μ_{a}	Sources
Common Grackle	0.68	0.33	0.07	0.0001	[16,29]
Northern Flicker	0.06	1.0	0.0	0.0003	[16,29]

Table 2. Epidemiological and demographic parameters in the numerical simulations of WN models.

Vector	b	β_{a}	μ_{v}	Sources
A. albopictus	0.1	0.86	0.07	[27,31,36]
C. pipiens	0.5	0.88	0.07	[31,36]

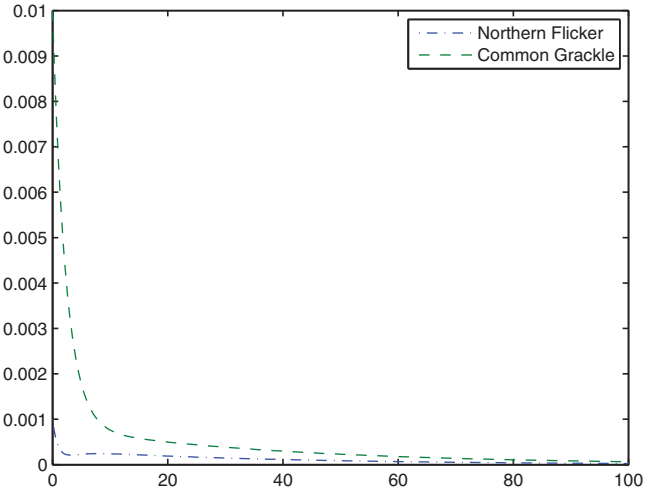

Figure 1. Temporal course of the proportion of infected birds. For Northern Flicker $R_{0_1} = 0.41$ and $\bar{N}_1 = 1000$. For Common Grackle, $R_{0_2} = 2.2$ and $\bar{N}_2 = 100$. In this case, $R_0 = 0.76$.

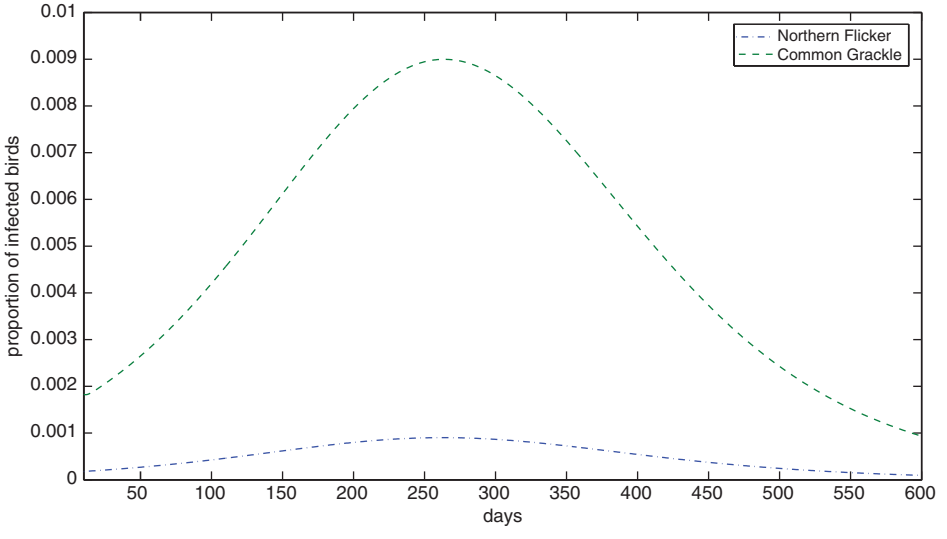

Figure 2. Temporal course of the proportion of infected birds. For Northern Flicker, $R_{0_1} = 0.37$ and $\bar{N}_1 = 1000$. For Common Grackle, $R_{0_2} = 1.95$ and $\bar{N}_2 = 400$. In this case, $R_0 = 1.2$.

to *C. pipiens*. We assume $N_v = 1000$, which is a very low estimate for the mosquito population. The basic reproductive number for Northern Flicker is $R^a_{0_1} = 0.41$, while for Common Grackle it is $R^a_{0_2} = 2.2$, which gives $R^a_0 = 0.76$. Figure 1 shows the temporal course of the infected proportions of the two species for this case. We observe that the infected proportion of Common Grackle decreases monotonically, in spite of being a very competitive species. Now, increasing the population of Common Grackle to $N_2 = 400$ gives $R^a_{0_1} = 0.37$, $R^a_{0_2} = 1.95$, and $R^a_0 = 1.2$. Figure 2 shows that in this case there is an epidemic involving both populations, and the infected proportion of Northern Flicker is slightly lower than the infected proportion of Common Grackle. This shows that a highly competent species can start an outbreak even in an habitat shared with other species less competent.

2.4. *Sensitivity analysis*

We are interested in how the spread of the WNV infection is affected by (i) the susceptibility and transmission rates of each bird species and (ii) the population size of birds and vector species. A way to answer these questions is by calculating the derivative of the basic reproduction number, R_0^a, with respect to the parameters. To answer (i), we observe from expression (5) that R_0^a depends linearly on the transmission rates β_i, $\beta_{\mathrm{v}i}$, and N_{v}. Then, increasing the susceptibility and transmission rate of the ith bird species or increasing the vector population increases R_0^a linearly. To answer (ii), we calculate the derivative of R_0^a with respect to N_i:

$$\frac{\partial (R_0^a)^2}{\partial N_i} = \frac{1}{N}(-2(R_0^a)^2 + (R_{0_i}^a)^2). \tag{24}$$

We observe that the derivative of R_0^a with respect to the population size of the ith bird species depends on the ratio $\rho_i = R_{0_i}/R_0$, then R_0 increases or decreases depending on whether ρ_i is greater or less than $\sqrt{2}$. Returning to the example illustrated in Figure 1, $R_{0_1}^a = 0.41$ and $R_0^a = 0.76$, which give $\rho_1 = 0.53 < \sqrt{2}$. If we increment the population of Northern Flicker to $N_1 = 2000$, we obtain $R_0^a = 0.44$ which is less than the previous value of R_0^a. On the other side, in the example of Figure 2, $R_{0_2}^a = 1.95$, $R_0^a = 1.2$, and $\rho_2 = 1.62 > \sqrt{2}$ for a population of Common Grackle $N_2 = 400$. Now, if we increment N_2 to 800, $R_0^a = 1.38$ which is greater than the previous value of R_0^a. However, for $N_2 = 800$, the basic reproductive number $R_{0_2}^a$ decreases to 1.72, and $\rho_2 = 1.24 < \sqrt{2}$. Therefore, R_0^a decreases when N_2 increases beyond 800. Indeed, calculating the basic reproductive number when $N_2 = 1600$, we obtain $R_0^a = 1.13$. This effect is due to the fact that increasing the bird population decreases $R_{0_i}^a$.

3. *N* species of vectors

In this section, we consider the relation between n species of mosquitoes and one species of birds. For each vector species, we denote by N_{v_i} and μ_{v_i} the constant population size and *per capita* mortality rate, respectively, $i = 1, \ldots, n$. We assume also that there is just one species of birds, and we denote by N_{a} its total population size. The susceptible, infected, and removed avian populations are denoted by S_{a}, I_{a}, and R_{a}, respectively, with $N_{\mathrm{a}} = S_{\mathrm{a}} + I_{\mathrm{a}} + R_{\mathrm{a}}$. As in the previous section, the bird population size changes according to the limited growth model:

$$\frac{\mathrm{d}N_{\mathrm{a}}}{\mathrm{d}t} = \Lambda_{\mathrm{a}} - \mu_{\mathrm{a}} N_{\mathrm{a}}, \tag{25}$$

where Λ_{a} is the recruitment rate and μ_{a} is the bird mortality rate.

We denoted by b_i the biting rate of mosquitos of species i. Assuming the probability that a given bird will be bitten by a vector of species i given by $N_{v_i}/(N_{v_1} + N_{v_2} + \cdots + N_{v_n})$, the transmission rates from vectors of species i to birds become

$$\frac{N_{v_i}}{N_{v_1} + N_{v_2} + \cdots + N_{v_n}} \frac{b_i \beta_{a_i}}{N_{\mathrm{a}}} S_{\mathrm{a}} I_{v_i}, \tag{26}$$

$i = 1, \ldots, n$. With this assumption, the model is given by

$$\frac{\mathrm{d}S_{\mathrm{a}}}{\mathrm{d}t} = \Lambda_{\mathrm{a}} - \sum_{i=1}^{n} \frac{N_{v_i}}{N_{v_1} + N_{v_2} + \cdots + N_{v_n}} \frac{b_i \beta_{a_i}}{N_{\mathrm{a}}} S_{\mathrm{a}} I_{v_i} - \mu_a S_{\mathrm{a}},$$

$$\frac{\mathrm{d}I_{\mathrm{a}}}{\mathrm{d}t} = \sum_{i=1}^{n} \frac{N_{v_i}}{N_{v_1} + N_{v_2} + \cdots + N_{v_n}} \frac{b_i \beta_{a_i}}{N_{\mathrm{a}}} S_{\mathrm{a}} I_{v_i} - (\gamma_{\mathrm{a}} + \mu_{\mathrm{a}} + \alpha_{\mathrm{a}}) I_{\mathrm{a}},$$

$$\frac{\mathrm{d}I_{v_i}}{\mathrm{d}t} = \frac{b_i\beta_{v_i}I_{\mathrm{a}}}{N_{\mathrm{a}}}(N_{v_i} - I_{v_i}) - \mu_{v_i}I_{v_i},$$
$$\frac{\mathrm{d}N_{\mathrm{a}}}{\mathrm{d}t} = \Lambda_{\mathrm{a}} - \mu_{\mathrm{a}}N_{\mathrm{a}} - \alpha_{\mathrm{a}}I_{\mathrm{a}}, \tag{27}$$

where $i = 1, \ldots, n$.

Analogous to Section 2, it can be proved that the basic reproductive number R_0^v associated with the disease-free equilibrium E_0^v is given by

$$R_0^v = \sqrt{\sum\nolimits_{i=1}^{n} (R_{0_i}^v)^2 \frac{N_{v_i}}{N_{\mathrm{v}}}}, \tag{28}$$

where

$$R_{0_i}^v = \sqrt{\frac{b_i^2\beta_{a_i}\beta_{v_i}}{\mu_{v_i}(\gamma_{\mathrm{a}} + \mu_{\mathrm{a}} + \alpha_{\mathrm{a}})}\frac{N_{v_i}}{N_{\mathrm{a}}}} \tag{29}$$

is the basic reproductive number corresponding to species $i, i = 1, \ldots, n$. Then, the following result is established.

THEOREM 5 *The disease-free equilibrium, E_0^v, of model* (27) *is locally asymptotically stable for $R_0^v < 1$. When $R_0^v > 1$, the disease-free equilibrium becomes unstable, and it emerges as a unique endemic equilibrium which is globally asymptotically stable.*

Reasoning along the lines of the previous section, it can be shown that the behaviour of R_0^v has a threshold which can be derived from the formula

$$\frac{\partial (R_0^v)^2}{\partial N_{v_i}} = \frac{1}{N_{\mathrm{v}}}(-(R_0^v)^2 + 2(R_{0_i}^v)^2). \tag{30}$$

R_0^v increases or decreases if $\sigma = R_{0_i}^v / R_0^v$ is greater or less than $1/\sqrt{2}$. Furthermore, once $\sigma_i > 1/\sqrt{2}$, R_0^v will keep increasing when the mosquito population increases, since $R_{0_i}^v$ becomes greater.

4. General case

In this section, we generalize the previous models by taking into account interactions of n species of birds with m species of mosquitoes. Using the notation of the first section, the model is given by

$$\frac{\mathrm{d}S_i}{\mathrm{d}t} = \Lambda_i - \sum_{j=1}^{m} \frac{N_{v_j}}{(N_{v_1} + \cdots N_{v_m})} \frac{b_j\beta_{ij}}{(N_1 + \cdots + N_n)} S_i I_{v_j} - \mu_i S_i$$
$$\frac{\mathrm{d}I_i}{\mathrm{d}t} = \sum_{j=1}^{m} \frac{N_{v_j}}{(N_{v_1} + \cdots N_{v_m})} \frac{b_j\beta_{ij}}{(N_1 + \cdots + N_n)} S_i I_{v_j} - (\gamma_i + \mu_i + \alpha_i)I_i$$
$$\frac{\mathrm{d}I_{v_j}}{\mathrm{d}t} = \sum_{i=1}^{n} \frac{b_j\beta_{v_{ji}}}{N_1 + \cdots + N_n}(N_{v_j} - I_{v_j})I_i - \mu_{v_j}I_{v_j} \tag{31}$$
$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = \Lambda_i - \mu_i N_i - \alpha_i I_i$$

with $i = 1, \ldots, n$, $j = 1, \ldots, m$

The next generation operator associated with the disease-free equilibrium $S_i = \bar{N}_i$, $I_i = 0$, $i = 1, \ldots, n$, and $I_{v_j} = 0$, $j = 1, \ldots, m$ is a $(n+m) \times (n+m)$ matrix of the form

$$\Phi = \begin{pmatrix} 0 & G_1 \\ G_2 & 0 \end{pmatrix},$$

where G_1 and G_2 are $n \times m$ and $m \times n$ matrices, respectively, given by

$$G_1 = \frac{1}{\bar{N} N_{\mathrm{v}}} \begin{pmatrix} \dfrac{b_1 \beta_{11} N_{v_1} \bar{N}_1}{\gamma_1 + \mu_1 + \alpha_1} & \cdots & \dfrac{b_m \beta_{1m} N_{v_m} \bar{N}_1}{\gamma_1 + \mu_1 + \alpha_1} \\ \dfrac{b_1 \beta_{21} N_{v_1} \bar{N}_2}{\gamma_2 + \mu_2 + \alpha_2} & \cdots & \dfrac{b_m \beta_{2m} N_{v_m} \bar{N}_2}{\gamma_2 + \mu_2 + \alpha_2} \\ \cdot & \cdots & \cdot \\ \cdot & \cdots & \cdot \\ \cdot & \cdots & \cdot \\ \dfrac{b_1 \beta_{n1} N_{v_1} \bar{N}_n}{\gamma_n + \mu_n + \alpha_n} & \cdots & \dfrac{b_m \beta_{nm} N_{v_m} \bar{N}_n}{\gamma_n + \mu_n + \alpha_n} \end{pmatrix},$$

$$G_2 = \frac{1}{\bar{N}} \begin{pmatrix} \dfrac{b_1 \beta_{v_{11}} N_{v_1}}{\mu_{v_1}} & \cdots & \dfrac{b_1 \beta_{v_{1n}} N_{v_1}}{\mu_{v_1}} \\ \dfrac{b_2 \beta_{v_{21}} N_{v_2}}{\mu_{v_2}} & \cdots & \dfrac{b_2 \beta_{v_{2n}} N_{v_2}}{\mu_{v_2}} \\ \cdot & \cdots & \cdot \\ \cdot & \cdots & \cdot \\ \cdot & \cdots & \cdot \\ \dfrac{b_m \beta_{v_{m1}} N_{v_m}}{\mu_{v_m}} & \cdots & \dfrac{b_m \beta_{v_{mn}} N_{v_m}}{\mu_{v_m}} \end{pmatrix},$$

with $\bar{N} = \bar{N}_1 + \cdots \bar{N}_n$, $\bar{N}_i = \Lambda_i / \mu_i$, and $N_{\mathrm{v}} = N_{v_1} + \cdots + N_{v_m}$.

The basic reproductive number, R_0, is equal to the spectral radius of Φ. In this general case, it is difficult to obtain a closed expression, even for two species of birds and two species of mosquitoes.

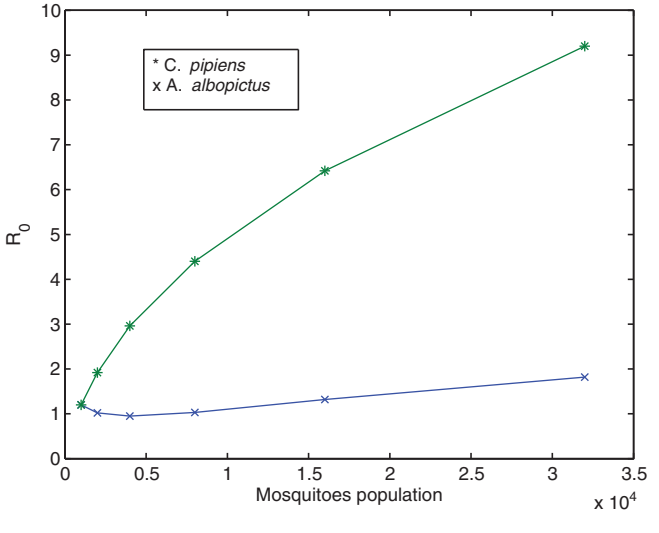

Figure 3. R_0^v for different mosquito population sizes.

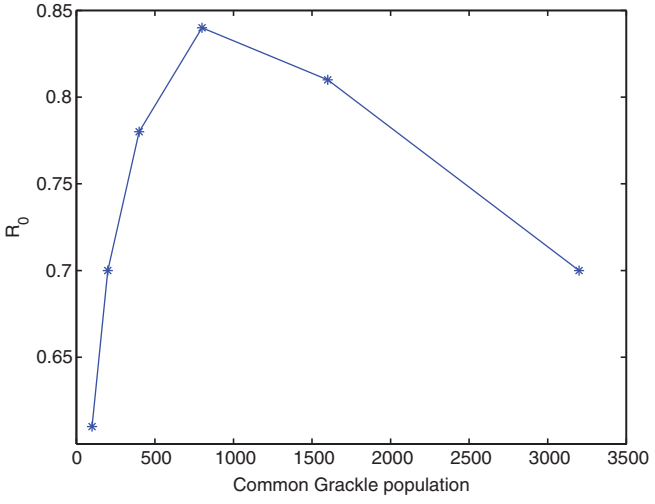

Figure 4. R_0 for different population sizes of Common Grackle species.

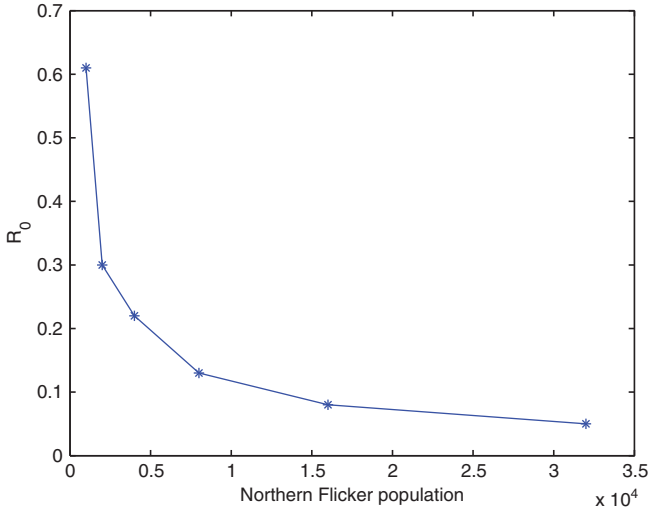

Figure 5. R_0 for different population sizes of Northern Flicker species.

It is clear that R_0 must depend on the competence of each species as well as on its population density like in the cases previously analysed. We study numerically how the value of R_0 changes with respect of the population size *C. pipiens* and *A. albopictus* when they interact with two species of birds (Common Grackle and Northern Flicker). The values of the parameters used in the simulations are given in Tables 1 and 2. According to [31], the two species of mosquitoes have nearly the same transmission efficiency for WNV in the laboratory, but *C. pipiens* feeds primarily on avian host, while *A. albopictus* is an opportunistic vector, since it feeds on a variety of hosts [27]. For a biting rate of 0.5 for *C. pipiens* and 0.1 for *A. albopictus*, we obtain the results illustrated in Figure 3. From this figure, we observe that in the long run, the basic reproduction number of each species increases, although not at the same speed, that is, the basic reproduction number of *C. pipiens* increases much more than that of *A. albopictus*. This result is in accordance with the idea that feeding preferences of mosquitoes are a major factor in disease transmission.

Now, we want to study the behaviour of R_0 when we increase the population of one of the bird species. We consider again the example discussed in Sections 2.3 and 2.4. Figures 4 and 5 illustrate the dependence of R_0 when we increase the population of Common Grackle and Northern Flicker, respectively. We see in Figure 4 that R_0 reaches a maximum value when the population is equal to 800 and then decreases. This is consistent with the result obtained when we consider only one species of mosquitoes, that is, there is a threshold condition on the bird population and according to that R_0 increases or decreases. Figure 5 shows that, for the Northern Flicker, R_0 decreases all the time since ρ_2 never reaches the threshold value.

5. Conclusions

In this work, we formulated mathematical models to study the interactions of several species of birds and mosquitoes in the transmission of WNV. When we considered several species of birds (mosquitoes) and only one of mosquitoes (birds), we found that the basic reproductive number in each case is the mean of the basic reproductive numbers of each species, weighted by the relative abundance of its population in the location. The basic reproductive numbers R_0^a, and R_0^v given in Equations (4) and (28) measure the relative importance of a specific bird and mosquito species, respectively, in the prevalence of WNV. Thus, the competence of a species, as well as its relative abundance determines its role in the spread of the disease. One interesting result is that species that would not be affected by the disease if isolated can suffer outbreaks when they share the same habitat with a sufficiently abundant species with a high basic reproductive number. This is shown in Figure 2 for Northern Flicker and Common Grackle. We observe that the outbreak initiated by the Common Grackle is transmitted to the Northern Flicker which has a basic reproduction number less than one.

Our results indicate that the probability of invasion of WNV is sensitive to the variations of the population densities. The sensitivity analysis of the basic reproductive number with respect to the population size of a bird species indicates that R_0^a is an increasing function of the population size if $R_{0_i}^a / R_0^a > \sqrt{2}$, and R_0^a is a decreasing function when $R_{0_i}^a / R_0^a < \sqrt{2}$. This last result can be explained by the fact that many mosquito bites are wasted in bird species that are not very effective in the transmission of the disease. It is interesting to observe that R_0^a is proportional to

Figure 6. Distribution of *C. pipiens* in North America. Data taken from [28].

$\sqrt{N_v/\bar{N}}$. This implies that if the mosquito population is small compared with the bird population, then the probability of an outbreak is low, independently of the transmission competence of the birds. A similar threshold behaviour is obtained when we consider the model for the interaction of several species of mosquitoes and only one species of birds, with threshold value equal to $1/\sqrt{2}$.

Turell *et al.* [32] show that some *Culex* species can be a very efficient enzootic vectors in regions where they are abundant, because they feed primarily on avian hosts. In particular, *C. pipiens* has been recognized as a very competent vector in Canada and the northern part of the USA, while *Culex qinquefaciatus* is only a moderate one [32]. In contrast, the same authors show that *Aedes* species are not good enzootic vectors, but can be bridge vectors between birds and humans.

Culex pipiens has a distribution that roughly includes the northern half of the USA. The range of this species begins just north of Maine, along the Atlantic seaboard, and extends to the state of Washington in the west with some extension into southern British Columbia. The range along the Pacific coast extends into northern California and then east on a relatively straight line to North Carolina (Figure 6) [5]. On the other hand, *C. quinquefasciatus* is distributed from the southern of USA all the way down to the middle of Argentina, with large variations in the population density [17]. In contrast, the relative abundance of *C. pipiens*, and *C. quinquefaciatus* is quite small compared with mosquitoes of the *Aedes* family, specially *Aedes aegypty*, which is the principal vector of dengue disease [13]. Since the main vectors of WNV are not common in Mexico, this suggest that a plausible explanation for the absence of outbreaks of WNV in this country is the absence of efficient enzootic vectors. However, more entomological studies have to be done, taking into account the geographical and climatological conditions, in order to measure the transmission efficiency of the local species.

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