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Research article

Modeling the impact of host heterogeneity on the risk and dynamics of a West Nile virus epidemic

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Abstract: West Nile virus (WNV) is a mosquito-borne arbovirus with significant ecological and public health implications. Its transmission cycle involves avian hosts and mosquito vectors. Many factors, including host diversity and mosquito population dynamics are known to shape epidemic patterns. In this study, we extend previous work by incorporating multiple host types, horizontal transmission among hosts, and mosquito feeding preference into a WNV model. Using a system of ordinary differential equations, we analyze the impact of variable host competence, host abundance, host community structure, and mosquito biting preference on epidemic metrics. We derive an expression for the basic reproduction number in multihost systems and qualify the impact of less competent hosts on its value. Numerical simulations explore the impact of structural variations in the model on epidemic metrics and assess the potential for less competent hosts and mosquito feeding preference to dilute the epidemic. Our findings elucidate the influence of host heterogeneity, horizontal transmission in hosts, and mosquito biting preference on the severity and dynamics of a WNV epidemic.

Keywords: multihost models; basic reproduction number; West Nile virus; horizontal transmission; mosquito feeding preference

1. Introduction

West Nile virus (WNV) is a mosquito-borne arbovirus of global concern due to its rapid spread, significant impact on avian populations, and potential for spillover into human and other mammalian hosts [1,2]. Since its discovery in Uganda in 1937, WNV has expanded across continents. Its introduction to North America in 1999 resulted in substantial ecological and public health consequences [3–5]. Transmission occurs primarily through interactions between avian hosts and mosquito vectors, with

birds acting as the main amplifiers of the virus and mosquitoes as the vectors of transmission [6, 7].

Mathematical modeling has been used extensively to study WNV transmission and control. Several papers, including [8, 9], provide helpful summaries of mathematical/theoretical progress in this field. A survey of transmission mechanisms in mathematical models is also available [10], complemented by a recent analysis of factors known to impact WNV transmission [11].

Previously, we studied the problem of WNV control via pesticides using a late-season model with three mosquito life stages, vertical transmission in mosquitoes, and transmission between mosquitoes and birds [12]. This work contributed a dynamic model for adult- and larvae-specific pesticides and explored the impact of objective type on the optimal treatment schedule and course of the epidemic. In this paper, we extend our previous model to include new factors of importance for understanding long-term control and reemergence of WNV, such as bird demographics and host heterogeneity. The importance of differential feeding preference and competence for quantifying WNV risk and incidence is supported by several studies [9, 13, 14].

A considerable amount of research into the impact of host heterogeneity on WNV transmission has already been conducted. Abdelrazec et al. [9] considered the impact of host diversity on WNV dynamics using a model with two competent host classes comprising corvid and noncorvid birds, in addition to dead-end hosts. This model accounted for transmission between birds and mosquitoes as well as vertical transmission in mosquitoes. A basic reproduction number for the model relates host competence, mortality, and abundance to the risk of a WNV outbreak. The model was also shown to exhibit backward bifurcations, which can help support the maintenance of endemic WNV. Further analysis of host heterogeneity in WNV transmission was provided in [15]. This work developed an n-host model for the disease and derived an n-host basic reproduction number which depends on a weighted average of the one-host basic reproduction numbers and showed that in the multihost case, the basic reproduction number is nonmonotone in host abundance. In contrast, for one-host models, the basic reproduction number is monotone increasing in the mosquito-to-host ratio and hence monotone decreasing in host abundance. While both papers provide useful insights into the impact of host heterogeneity on WNV transmission, much of the analysis in these papers focuses on the case of two competent host classes representing either two broad families of birds [9] or two select bird species [15].

Subsequent work explored more ecologically detailed assessments of WNV risk. For example, using eBird data, Kain et al. [13] provided a tremendously detailed account of host diversity in different ecoregions of Texas. A discrete time model which included feeding preference was used to study the impact of diversity on the basic reproduction number, classify specific host species as diluters or amplifiers, and investigate the impact of uncertainty, model simplifications, and seasonal variability on the epidemic. Other works focused on estimating the basic reproduction number of specific habitats according to the composition of the local community and environmental factors [16, 17]. However, unlike [13], these papers consider only a single bird species (house sparrows and magpies, respectively), selected for high WNV competence.

More recent model-based investigations of WNV dynamics [8, 18–20] characterize the potential for bird migration to result in WNV outbreaks or re-emergence [8, 19], study the impact of environmental disturbance on both WNV risk and long-term dynamics [20], and study the impact of host community composition on the probability of WNV extinction. Like [16, 17], these models include just one or two competent hosts and do not include horizontal transmission in hosts.

Here, we develop a dynamic model of WNV that accounts for varied host demographics, feeding preference, abundance, mortality, and transmission competence, including the capacity for horizontal transmission in hosts. Although early empirical work suggests birds of the family *Corvidae* are competent for horizontal transmission [21], horizontal transmission is rarely considered in mathematical models of WNV [10]. Some exceptions include [22, 23] and [24] which, respectively, explore horizontal transmission between hosts as a mechanism for overwintering of the virus, evaluate the relative impact of horizontal transmission in hosts and vector-host transmission on the virus basic reproduction number, and explore the impact of competition between hosts and feeding preference in the presence of horizontal transmission in birds.

These prior works confirm the importance of horizontal transmission in hosts and feeding preference for quantifying the risk of a WNV epidemic as measured by the model basic reproduction number and maximum prevalence of infectious individuals. The research presented here builds on [23] by investigating the impact of horizontal transmission in hosts on epidemic dynamics and complements [22] by exploring horizontal transmission in hosts during the breeding season, where frequency-dependent transmission may occur between birds in family groups, as opposed to the winter season, where density-dependent transmission occurs in a communal roosting environment. Similarly, our work on the model basic reproduction number for an n-host system with horizontal transmission in hosts extends work in [24] on the single-host case. However, it should be noted that, unlike our model, the model developed in [24] includes competition between hosts. The inclusion of long-term survivorship of vulnerable hosts as an epidemic metric and the complexity and careful parameterization of the host community are other unique features of the model presented here. While previous works, most notably [13], have included highly detailed and painstakingly parameterized representations of the host community, previous investigations employing dynamic models were typically limited to two competent host types. The model presented here includes four distinct types of competent hosts: vulnerable amplifiers with horizontal transmission, vulnerable amplifiers without horizontal transmission, invulnerable amplifiers, and low-competence hosts; as well as dead-end hosts. We provide a recursive formula for computation of the basic reproduction number in the n-host case, carefully parameterize the model to reflect different levels of urbanization in the northern US and Canada, and systematically explore the impact of model structure and parameter values on measures of epidemic severity, including the basic reproduction number, maximum prevalence of infectious mosquitoes, and long-term survivorship of vulnerable birds.

This paper is organized as follows. In Section 2, we present the extended model. In Section 3, we derive an expression for the basic reproduction number in some simple cases and relate these expressions to results from earlier models without horizontal transmission. We also provide for the computation of the basic reproduction number in multihost systems using a block matrix approach and derive a recursive formula for direct computation of the characteristic polynomial of the next-generation matrix. These results are used to show that accounting for the competence of a host type, that is, distinguishing lower-competence hosts from dead-end hosts, can only increase the basic reproduction number. In Section 4 we numerically explore epidemic dynamics and endemic steady-states and characterize the impact of host heterogeneity on a WNV epidemic by varying both the model structure and parameters. Results are summarized in Section 5. Details of the model construction and parameterization, including a discussion of challenges related to modeling mosquito feeding preference are included in the Appendices.

2. Model formulation

This model describes the dynamics of a WNV epidemic in a population consisting of bird hosts and female mosquitoes. The bird population is divided into $J + 1$ host compartments, based on competence and susceptibility. Each competent host compartment is subdivided into three classes according to disease status. These classes are susceptible, $H_{S_j}(t)$, infectious with the WNV, $H_{I_j}(t)$, and recovered, $H_{R_j}(t)$. Hence, the total host population is

$$N_H(t) = N_D + \sum_j N_{H_j}(t), \tag{2.1}$$

where N_D is a parameter representing the density of dead-end hosts which neither transmit nor contract the infection but potentially attract mosquito bites, and

$$N_{H_j}(t) = H_{S_j}(t) + H_{I_j}(t) + H_{R_j}(t). \tag{2.2}$$

The mosquito population is divided into three groups: eggs, aquatic larva and pupae, and adults. These groups are further divided according to infection status. Since WNV can be transmitted vertically in the mosquito population, we separate compartments for eggs laid by susceptible mosquitoes, $E_S(t)$, and eggs laid by infectious mosquitoes, $E_I(t)$. The aquatic population is further divided into susceptible larvae and pupae, $L_S(t)$, and infected larvae and pupae, $L_I(t)$. The adult stage group is divided into susceptible mosquitoes, $M_S(t)$, exposed mosquitoes, $M_E(t)$, and infectious mosquitoes, $M_I(t)$. Because the lifespan of adult mosquitoes is short relative to the duration of infection, we do not consider recovery among the mosquito population in this model. The model dynamics are described by the following system of ordinary differential equations:
For $j = 1 \dots J$

$$\frac{d}{dt}H_{S_j} = \Lambda_j(H_{S_j} + H_{R_j}) - P_{MH_j}\, b\, M_I \frac{H_{S_j}}{N_H} - \omega_j H_{I_j}\frac{H_{S_j}}{N_{H_j}} - \frac{d_{H_j}}{C_{H_j}} N_{H_j} H_{S_j} - \mu_{H_j} H_{S_j} \tag{2.3}$$

$$\frac{d}{dt}H_{I_j} = P_{MH_j}\, b\, M_I \frac{H_{S_j}}{N_H} + \omega_j H_{I_j}\frac{H_{S_j}}{N_{H_j}} - \left(\gamma_{H_j} + g_{I_j} + \mu_{H_j}\right) H_{I_j} - \frac{d_{H_j}}{C_{H_j}} N_{H_j} H_{I_j} \tag{2.4}$$

$$\frac{d}{dt}H_{R_j} = g_{I_j} H_{I_j} - \frac{d_{H_j}}{C_{H_j}} N_{H_j} H_{R_j} - \mu_{H_j} H_{R_j}. \tag{2.5}$$

In addition,

$$\frac{d}{dt}E_S = r_S(M_S + M_E) - m_E\, E_S \tag{2.6}$$

$$\frac{d}{dt}E_I = r_I\, M_I - m_E\, E_I \tag{2.7}$$

$$\frac{d}{dt}L_S = m_E\, q_S\, E_S + m_E\, q_I(1-\phi)E_I - (\mu_L + m_L)L_S - \frac{d_L}{C_L}(L_S + L_I)L_S \tag{2.8}$$

$$\frac{d}{dt}L_I = m_E\, q_I\, \phi\, E_I - (\mu_L + m_L)L_I - \frac{d_L}{C_L}(L_S + L_I)L_I \tag{2.9}$$

$$\frac{d}{dt}M_S = m_L\, L_S - b\, M_S \sum_j \left(P_{H_jM}\frac{H_{I_j}}{N_H}\right) - \mu_M\, M_S \tag{2.10}$$

$$\frac{d}{dt}M_E = b\,M_S\,\sum_j\left(P_{H_jM}\,\frac{H_{I_j}}{N_H}\right) - (k_L + \mu_M)\;M_E \tag{2.11}$$

$$\frac{d}{dt}M_I = m_L\,L_I + k_L\,V_E - \mu_M\,M_I \tag{2.12}$$

where $d_L = \frac{m_L\,r_S\,q_S}{\mu_M} - \mu_L - m_L$ and $d_{H_j} = \Lambda_j - \mu_{H_j}$ so that C_{H_j} is the disease-free carrying capacity for each host compartment and C_L is the disease-free carrying capacity for the larvae.

The above system of equations reflects the following dynamic processes: Healthy susceptible birds acquire infection in two ways. The first is following contact with infected mosquitoes at a per capita rate $P_{MH_j}\,b\,V_I\frac{H_{S_j}}{N_H}$, where P_{MH} is the transmission probability of WNV per mosquito bite. Note that this model assumes no mosquito biting preference so that mosquitoes bite at rate b and the fraction of bites that are on infected hosts of type j is $\frac{H_{I_j}}{N_H}$. The effect of biting preference on this model will be explored in Section 3.2. The second way hosts acquire infection is following contact with other infected birds at a per capita rate $\omega_j\,H_{I_j}\frac{H_{S_j}}{N_{H_j}}$, where ω_j is the maximal horizontal transmission rate of birds in host group j with other birds in this group, assuming frequency-dependent contacts. Frequency-dependent transmission between birds and mosquitoes reflects a mosquito biting rate that is approximately independent of host density. Frequency-dependent transmission between hosts reflects social transmission among birds of a single host type. Infectious birds die due to WNV disease at the per capita rate γ_{H_j} or recover at the per capita rate g_{I_j}. The birth and natural death rates of the birds are Λ_j and μ_{H_j}, respectively. Finally, birds are subject to density-dependent population regulation with carrying capacity C_{H_j}.

A proportion q_S of the susceptible-laid eggs hatch into live larva and a proportion q_I of infectious-laid eggs hatch into live larva. A fraction ϕ of larva descending from infectious mothers are infected. Larva mature into adult mosquitoes at rate m_L. Larva are subject to density-independent natural mortality at per capita rate μ_L and density-dependent mortality with carrying capacity C_L.

Susceptible mosquitoes acquire the infection following contact with the infected birds at the per capita rate $\sum_j\left(b\,P_{H_jM}\,M_S\,\frac{H_{I_j}}{N_H}\right)$. Adult mosquitoes have a natural per capita mortality rate μ_M regardless of their infection status. Exposed mosquitoes progress to the infectious class at the per capita rate k_L.

The model variables and parameters as well as values and ranges are summarized in Appendix A. An explanation of the mathematical derivation of the composite parameters is summarized in Appendix B.

3. Characterization of the model basic reproduction number

We begin by determining the disease-free equilibrium (DFE) of the model. Letting $\mathcal{E}_0$ denote the DFE, we have

$$\mathcal{E}_0 = (H^*_{S_1}, H^*_{I_1}, H^*_{R_1}, \ldots, H^*_{S_j}, H^*_{I_j}, H^*_{R_j}, E^*_S, E^*_I, L^*_S, L^*_I, M^*_S, M^*_E, M^*_I), \tag{3.1}$$

where $H^*_{I_1} = H^*_{R_1} = E^*_{I_1} = \cdots = H^*_{I_j} = H^*_{R_j} = E^*_{I_j} = L^*_I = M^*_E = M^*_I = 0$. Substituting these values into the model and setting the right-hand sides to zero, for $j = 1 \ldots J$ (2.3) yields

$$H^*_{S_i} = C_{H_i}. \tag{3.2}$$

Further substituting $H^*_{S_i} = C_{H_i}$ into (2.6), (2.8), and (2.10) yields

$$\begin{aligned} 0 &= r_S\, M^*_S - m_E\, E^*_S \\ 0 &= m_E\, q_S\, E^*_S - (\mu_L + m_L)\, L^*_S - \frac{d_L}{C_L}\,(L^*_S)^2 \\ 0 &= m_L\, L^*_S - \mu_M\, M^*_S. \end{aligned} \tag{3.3}$$

Hence $E^*_S = \frac{r_S}{m_E}\, M^*_S$, $M^*_S = \frac{m_L}{\mu_M}\, L^*_S$, and

$$0 = \left(\frac{m_L\, r_S\, q_S}{\mu_M} - \mu_L - m_L\right) L^*_S - \frac{d_L}{C_L}(L^*_S)^2, \tag{3.4}$$

By choice of d_L, we find that $L^*_S = C_L$, $E^*_S = \frac{m_L\, r_S}{\mu_M\, m_E}\, C_L$ and $M^*_S = \frac{m_L}{\mu_M}\, C_L$. In summary, the DFE for the model is

$$\mathcal{E}_0 = \left(C_{H_1}, 0, 0, \ldots, C_{H_J}, 0, 0, \frac{m_L\, r_S}{\mu_M\, m_E}\, C_L, 0, C_L, 0, \frac{m_L}{\mu_M}\, C_L, 0, 0\right). \tag{3.5}$$

For convenience, let $s_j = \gamma_{H_j} + g_{I_j} + \mu_{H_j} + d_{H_j}$, $\tau = m_L + \mu_L + d_L$, $N^*_{H_j} = C_{H_j}$, and $N^*_H = N_D + \sum_{j=1}^{J} C_{H_j}$. In an entirely susceptible population (2.4) becomes

$$\frac{d}{dt} H_{I_j} = -s_j\, H_{I_j} + \omega_j\, H_{I_j} + P_{MH_j}\, b\, \frac{N^*_{H_j}}{N^*_H} M_I \tag{3.6}$$

and the infectious vector system is

$$\frac{d}{dt} E_I = -m_E\, E_I + r_I\, M_I \tag{3.7}$$

$$\frac{d}{dt} L_I = m_E\, q_I\, \phi\, E_I - \tau\, L_I \tag{3.8}$$

$$\frac{d}{dt} M_E = \sum_j \frac{b\, P_{H_j M}\, M^*_S}{N^*_H}\, H_{I_j} - (k_L + \mu_M)\; M_E \tag{3.9}$$

$$\frac{d}{dt} M_I = m_L\, L_I + k_L\, M_E - \mu_M\, M_I \tag{3.10}$$

3.1. Characterization of $\mathcal{R}_0$

We compute $\mathcal{R}_0$ as the spectral radius of the next-generation matrix, $-FV^{-1}$ [25], where F captures transmission in an entirely susceptible population the new infections, and V captures movement between infectious compartments. For convenience, we let $W = -V$. F and W can be represented as block matrices:

$$F = \begin{bmatrix} (F_{HH})_{J\times J} & (F_{MH})_{J\times 4} \\ (F_{HM})_{4\times J} & (F_{MM})_{4\times 4} \end{bmatrix} \text{ and } W = \begin{bmatrix} (W_H)_{J\times J} & (0)_{J\times 4} \\ (0)_{4\times J} & (W_M)_{4\times 4} \end{bmatrix}, \tag{3.11}$$

where

$$F_{HH} = \begin{bmatrix} \omega_1 & 0 & 0 & \dots & 0 \\ 0 & \omega_2 & 0 & \dots & \vdots \\ \vdots & 0 & \ddots & & 0 \\ 0 & \dots & \vdots & \dots & 0 \quad \omega_J \end{bmatrix} \qquad F_{MM} = \begin{bmatrix} 0 & 0 & 0 & r_I \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix} \tag{3.12}$$

$$F_{MH} = \begin{bmatrix} 0 & 0 & 0 & \left(b\, P_{MH_1} \frac{N^*_{H_1}}{N^*_H}\right) \\ \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & 0 & \left(b\, P_{MH_J} \frac{N^*_{H_J}}{N^*_H}\right) \end{bmatrix} \quad F_{HM} = \begin{bmatrix} 0 & 0 & \dots & 0 \\ 0 & 0 & \dots & 0 \\ b\, P_{H_1 M} \frac{M^*_S}{N^*_H} & b\, P_{H_2 M} \frac{M^*_S}{N^*_H} & \dots & b\, P_{H_j M} \frac{M^*_S}{N^*_H} \\ 0 & 0 & \dots & 0 \end{bmatrix} \tag{3.13}$$

$$W_H = \begin{bmatrix} s_1 & 0 & 0 & \dots & 0 \\ 0 & s_2 & 0 & \dots & \vdots \\ \vdots & 0 & \ddots & & 0 \\ 0 & \dots & \vdots & \dots & 0 \quad s_J \end{bmatrix} \qquad W_M = \begin{bmatrix} m_E & 0 & 0 & 0 \\ -(m_E\, q_I\, \phi) & \tau & 0 & 0 \\ 0 & 0 & (k_L + \mu_M) & 0 \\ 0 & -m_L & -k_L & \mu_M \end{bmatrix}. \tag{3.14}$$

Because W is a diagonal block matrix, W^{-1} will have W_H^{-1} in the top left corner, W_M^{-1} in the bottom right corner, and zero matrices in the other two corners. This means that the matrix FW^{-1} will take the following block matrix form:

$$FW^{-1} = \begin{bmatrix} \left(F_{HH} W_H^{-1}\right)_{J\times J} & \left(F_{MH} W_M^{-1}\right)_{J\times 4} \\ \left(F_{HM} W_H^{-1}\right)_{4\times J} & \left(F_{MM} W_M^{-1}\right)_{4\times 4} \end{bmatrix}. \tag{3.15}$$

The characteristic polynomial of FW^{-1} is

$$\begin{aligned} \mathcal{P}_J(\lambda) = \det\left[FW^{-1} - \lambda I\right] &= \det\left[FW^{-1} - \lambda WW^{-1}\right] \\ &= \det\left[(F - \lambda W)W^{-1}\right] \\ &= \det\left[F - \lambda W\right] \cdot \det\left[W^{-1}\right]. \end{aligned} \tag{3.16}$$

More specifically, for a model with J competent host compartments, $F - \lambda W$ will have the form

$$\begin{bmatrix} F_{HH} - \lambda W_H & F_{MH} \\ F_{HM} & F_{MM} - \lambda W_M \end{bmatrix} =$$

$$\left[\begin{array}{ccccc|cccc}
\omega_1-\lambda s_1 & 0 & 0\ \ldots & 0 & | & 0 & 0 & 0 & b\,P_{MH_1}\frac{N^*_{H_1}}{N^*_H}\\
0 & \omega_2-\lambda s_2 & 0\ \ldots & \vdots & | & 0 & 0 & 0 & b\,P_{MH_2}\frac{N^*_{H_2}}{N^*_H}\\
\vdots & 0 & \ddots & 0 & | & \vdots & \vdots & \vdots & \vdots\\
0 & \ldots\vdots\ldots & \ldots\ 0 & \omega_J-\lambda s_J & | & 0 & 0 & 0 & b\,P_{MH_J}\frac{N^*_{H_J}}{N^*_H}\\
\hline
0 & 0 & \ldots\,0\,\ldots & 0 & | & -\lambda m_E & 0 & 0 & r_I\\
0 & 0 & \ldots\vdots\ldots & 0 & | & \lambda m_E\,q_I\,\phi & -\lambda\tau & 0 & 0\\
b\,P_{H_1M}\frac{M^*_S}{N^*_H} & b\,P_{H_2M}\frac{M^*_S}{N^*_H} & \ldots\,0\,\ldots & b\,P_{H_JM}\frac{M^*_S}{N^*_H} & | & 0 & 0 & -\lambda\,(k_L+\mu_M) & 0\\
0 & 0 & \ldots\,0\,\ldots & 0 & | & 0 & \lambda m_L & \lambda k_L & -\lambda\mu_M
\end{array}\right]. \tag{3.17}$$

By properties of determinants [26],

$$\det\left[F-\lambda W\right]=\det\left[F_{MM}-\lambda W_M\right]\cdot\det\left[F_{HH}-\lambda W_H-F_{MH}\left[F_{MM}-\lambda W_M\right]^{-1}F_{HM}\right]. \tag{3.18}$$

It is helpful to note that $\det\left[F_{MM}-\lambda W_M\right]\det W_M^{-1}$ is the characteristic polynomial of a vector-only model. Since

$$\det\left[F_{MM}-\lambda W_M\right]=-\lambda^3\ m_E\left(\mu_M+k_L\right)A(\lambda), \tag{3.19}$$

where $A(\lambda)=q_I\,\phi\,r_I\,m_L-\lambda\,\tau\,\mu_M$. Hence, the root of $A(\lambda)$ is the basic reproduction number of a vector-only model. We will denote this root as R_M.

3.1.1. Computation of $\mathcal{R}_0$ for one competent host

Now we consider a model with a single competent host type, i.e., $J=1$. In this case, we have the following coefficient matrices:

$$W=\begin{bmatrix}
s & 0 & 0 & 0 & 0\\
0 & m_E & 0 & 0 & 0\\
0 & -(m_E\,q_I\,\phi) & \tau & 0 & 0\\
0 & 0 & 0 & (k_L+\mu_M) & 0\\
0 & 0 & -m_L & -k_L & \mu_M
\end{bmatrix} \tag{3.20}$$

$$F=\begin{bmatrix}
\omega & 0 & 0 & 0 & \left(\dfrac{b\,P_{MH_1}\,N^*_{H_1}}{N^*_H}\right)\\
0 & 0 & 0 & 0 & r_I\\
0 & 0 & 0 & 0 & 0\\
\left(\dfrac{b\,P_{H_1M}\,M^*_S}{N^*_H}\right) & 0 & 0 & 0 & 0\\
0 & 0 & 0 & 0 & 0
\end{bmatrix}. \tag{3.21}$$

The next-generation matrix FW^{-1} is

$$\begin{bmatrix} \left(\frac{\omega}{s}\right) & \left(\frac{b\,P_{MH_1}\,N^*_{H_1}\,q_I\,\phi\,m_L}{N^*_H\,\mu_M\,\tau}\right) & \left(\frac{b\,P_{MH_1}\,N^*_{H_1}\,m_L}{N^*_H\,\mu_M\,\tau}\right) & \left(\frac{b\,P_{MH_1}\,N^*_{H_1}\,k_L}{\mu_M\,[k_L+\mu_M]\,N^*_H}\right) & \left(\frac{b\,P_{MH_1}\,N^*_{H_1}}{\mu_M\,N^*_H}\right) \\ 0 & \left(\frac{m_L\,q_I\,\phi\,r_I}{\mu_M\,\tau}\right) & \left(\frac{m_L\,r_I}{\mu_M\,\tau}\right) & \left(\frac{k_L\,r_I}{\mu_M\,[k_L+\mu_M]}\right) & \left(\frac{r_I}{\mu_M}\right) \\ 0 & 0 & 0 & 0 & 0 \\ \left(\frac{b\,P_{H_1M}\,\frac{M^*_S}{N^*_H}}{s}\right) & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \end{bmatrix}, \tag{3.22}$$

and the characteristic polynomial for FW^{-1} is

$$\begin{aligned} \mathcal{P}_1(\lambda) &= \det\left[F-\lambda\,W\right]\cdot\det\left[W^{-1}\right] \\ &= \det\left[F_{MM}-\lambda\,W_M\right]\cdot\left[\omega-\lambda\,s-\frac{\tau\,k_L\,b^2\,M^*_S}{(k_L+\mu_M)\,A(\lambda)}\cdot\frac{P_{MH_1}\,P_{H_1M}\,N^*_{H_1}}{(N^*_H)^2}\right]\cdot\det\left[W^{-1}\right] \\ &= \left[-\lambda^3\;m_E\,(\mu_M+k_L)\;A(\lambda)\right]\cdot\left[\omega-\lambda\,s-\frac{\tau\,k_L\,b^2\,M^*_S}{(k_L+\mu_M)\,A(\lambda)}\cdot\frac{P_{MH_1}\,P_{H_1M}\,N^*_{H_1}}{(N^*_H)^2}\right]\cdot\det\left[W^{-1}\right] \\ &= \left[-\lambda^3\;m_E\,(\mu_M+k_L)\right]\cdot\left[(\omega-\lambda\,s)\;A(\lambda)-\frac{\tau\,k_L\,b^2\,M^*_S\,P_{MH_1}\,P_{H_1M}\,N^*_{H_1}}{(\mu_M+k_L)\,(N^*_H)^2}\right]\cdot\det\left[W^{-1}\right], \end{aligned} \tag{3.23}$$

where the second line follows from (3.18), noting that the second factor in (3.18), $\det\left[F_{HH}-\lambda\,W_H-F_{MH}\,[F_{MM}-\lambda\,W_M]^{-1}\,F_{HM}\right]$, is a scalar in the one-host case. For additional details, see [27].

The middle factor, which determines the basic reproduction number of the model, can be expanded as

$$(\omega-\lambda\,s)\;A(\lambda)-\frac{\tau\,k_L\,b^2\,M^*_S\,P_{MH_1}\,P_{H_1M}\,N^*_{H_1}}{(\mu_M+k_L)\,(N^*_H)^2}=G_1\,\lambda^2-G_2\,\lambda+G_3 \tag{3.24}$$

where

$$\begin{aligned} G_1 &= s\,\tau\,\mu_M \\ G_2 &= \omega\,\tau\,\mu_M+s\,q_I\,\phi\,r_I\,m_L \\ G_3 &= \omega\,q_I\,\phi\,r_I\,m_L-\frac{\tau\,k_L\,b^2\,M^*_S\,P_{MH_1}\,P_{H_1M}\,N^*_{H_1}}{(\mu_M+k_L)\,(N^*_H)^2}. \end{aligned} \tag{3.25}$$

Then,

$$\lambda=\frac{G_2\pm\sqrt{G_2^2-4\,G_1\,G_3}}{2\,G_1}. \tag{3.26}$$

Taking the positive root, we have

$$\begin{aligned}\mathcal{R}_0 &= \frac{1}{2}\frac{G_2}{G_1} + \frac{1}{2}\frac{1}{G_1}\sqrt{(G_2)^2 - 4\,G_1\,G_3} \\ &= \frac{1}{2}\frac{\omega}{s} + \frac{1}{2}\frac{q_I\,\phi\,r_I\,m_L}{\mu_M\,\tau} + \frac{1}{2}\sqrt{\left(\frac{\omega}{s} - \frac{q_I\,\phi\,r_I\,m_L}{\mu_M\,\tau}\right)^2 + \frac{1}{s}\left(\frac{4\,k_L\,b^2\,M_S^*\,P_{MH}\,P_{HM}\,N_{H_1}^*}{\mu_M\,(\mu_M + k_L)\,(N_H^*)^2}\right)},\end{aligned} \tag{3.27}$$

where $\tau = m_L + \mu_L + \frac{d_L\,L_S^*}{C_L}$ and $s = \gamma_H + g_I + \mu_H + d_H$.

Inspection of (3.27) or (3.24) shows that in case host of type 1 are incompetent for mosquito-host transmission, the basic reproduction number of the model is the maximum of the vector-only basic reproduction number, R_M, and the basic reproduction number corresponding to horizontal transmission in hosts of type 1, $\frac{\omega}{s}$. We also note that, unlike vertical transmission in mosquitoes and horizontal transmission in hosts, mosquito-host transmission always acts to increase the basic reproduction number. Moreover, the presence of mosquito-host transmission alters the dependence of the basic reproduction number on vertical transmission in mosquitoes and horizontal transmission in hosts. Specifically, in the presence of mosquito-host transmission, the basic reproduction number of the model is monotone increasing with respect to the basic reproduction numbers for vertical transmission in mosquitoes and horizontal transmission in hosts.

A simplification of this model which does not include host demographics or horizontal transmission in hosts [12] has a basic reproduction number of

$$\mathcal{R}_0 = \frac{1}{2}\frac{q_I\,\phi\,r_I\,m_L}{\mu_M\,\tau} + \frac{1}{2}\sqrt{\left(\frac{q_I\,\phi\,r_I\,m_L}{\mu_M\,\tau}\right)^2 + \frac{1}{n}\left(\frac{4\,k_L\,b^2\,M_S^*\,P_{MH}\,P_{HM}}{\mu_M\,(\mu_M + k_L)\,N_H^*}\right)}, \tag{3.28}$$

where $n = d_H + g_I = s - (\gamma_H + \mu_H)$. Comparing (3.27) to (3.28) shows that if horizontal transmission in hosts and diversity of hosts are neglected, then the former reduces to the latter.

3.1.2. Further characterization of $\mathcal{R}_0$ for two hosts

In the two-host case,

$$F - \lambda\,W = \left[\begin{array}{cc|cccc} \omega_1 - \lambda\,s_1 & 0 & 0 & 0 & 0 & b\,P_{MH_1}\frac{N_{H_1}^*}{N_H^*} \\ 0 & \omega_2 - \lambda\,s_2 & 0 & 0 & 0 & b\,P_{MH_2}\frac{N_{H_2}^*}{N_H^*} \\ \hline 0 & 0 & -\lambda\,m_E & 0 & 0 & r_I \\ 0 & 0 & \lambda\,m_E\,q_I\,\phi & -\lambda\,\tau & 0 & 0 \\ b\,P_{H_1M}\frac{M_S^*}{N_H^*} & b\,P_{H_2M}\frac{M_S^*}{N_H^*} & 0 & 0 & -\lambda\,(k_L + \mu_M) & 0 \\ 0 & 0 & 0 & \lambda\,m_L & \lambda\,k_L & -\lambda\,\mu_M \end{array}\right]. \tag{3.29}$$

Hence, $F_{HH} - \lambda W_H - F_{MH}\,[F_{MM} - \lambda W_M]^{-1} F_{HM} =$

$$\begin{bmatrix} \omega_1 - \lambda s_1 - \dfrac{\tau k_L b^2 M_S^*}{(k_L+\mu_M)A(\lambda)} \cdot \dfrac{P_{MH_1} P_{H_1M} N_{H_1}^*}{(N_H^*)^2} & \dfrac{\tau k_L b^2 M_S^*}{(k_L+\mu_M)A(\lambda)} \cdot \dfrac{P_{MH_1} P_{H_2M} N_{H_1}^*}{(N_H^*)^2} \\ \dfrac{\tau k_L b^2 M_S^*}{(k_L+\mu_M)A(\lambda)} \cdot \dfrac{P_{MH_2} P_{H_1M} N_{H_2}^*}{(N_H^*)^2} & \omega_2 - \lambda s_2 - \dfrac{\tau k_L b^2 M_S^*}{(k_L+\mu_M)A(\lambda)} \cdot \dfrac{P_{MH_2} P_{H_2M} N_{H_2}^*}{(N_H^*)^2} \end{bmatrix}. \quad (3.30)$$

Note that if host 2 is incompetent for transmission, that is, when either $P_{H_2M} = 0$ or $P_{MH_2M} = 0$ and $\omega_2 = 0$, at least one of the off-diagonal terms in (3.30) is zero. For convenience, set

$$E_j(\lambda) = \omega_j - \lambda s_j - \frac{\tau k_L b^2 M_S^*}{(k_L+\mu_M)A(\lambda)} \cdot \frac{P_{MH_j} P_{H_jM} N_{H_j}^*}{(N_H^*)^2}, \quad (3.31)$$

and let

$$P_j(\lambda) = A(\lambda)E_j(\lambda). \quad (3.32)$$

Comparing to (3.24), we see that P_j is a polynomial factor of the characteristic polynomial for the model with a single competent host of type j, and its largest root, which we denote by R_j, is the basic reproduction number for that model. Hence, in the two-host case, the largest root of P_1 determines the number of secondary infections resulting from transmission chains involving host 1 when host 2 is treated as incompetent for transmission. Similarly, the largest root of P_2 determines the number of secondary infections resulting from transmission chains involving host 2 when host 1 is treated as incompetent for transmission. Assuming $R_M < R_j$ for $j = 1, 2$, and, without loss of generality, that $R_1 < R_2$, we have $A(R_j) < 0$ and $E_j(R_j) = P_j(R_j) = 0$ for $j = 1, 2$.

Let

$$\star_j(\lambda) = \frac{\tau k_L b^2 M_S^*}{(k_L+\mu_M)A(\lambda)} \cdot \frac{P_{MH_j} P_{H_iM} N_{H_j}^*}{(N_H^*)^2}, \quad (3.33)$$

$$\bigstar_j(\lambda) = A(\lambda) \star_j (\lambda), \quad (3.34)$$

and note $\bigstar_j > 0$ for $j = 1, 2$. Up to a constant factor, the determinant (3.18), and hence the characteristic polynomial of the two-host model, is

$$A(\lambda) \cdot \begin{vmatrix} E_1(\lambda) & \star_1(\lambda) \\ \star_2(\lambda) & E_2(\lambda) \end{vmatrix} = A(\lambda)E_1(\lambda)E_2(\lambda) - A(\lambda) \star_1 (\lambda) \star_2 (\lambda). \quad (3.35)$$

Factoring $\frac{1}{A(\lambda)}$ from the expression, we are left with

$$P_1(\lambda)\, P_2(\lambda) - \bigstar_1(\lambda)\, \bigstar_2(\lambda). \quad (3.36)$$

Provided $\bigstar_j \neq 0$ for $j = 1, 2$, i.e., that both hosts are competent for vector-host transmission, (3.36) is negative when evaluated at R_2 since $P_2(R_2) = 0$. Also, since $P_1(\lambda)\, P_2(\lambda)$ is a positive quartic, $\lim_{\lambda\to\infty} P_1(\lambda)\, P_2(\lambda) = \infty$. Thus, by the intermediate value theorem, (3.36) has a root greater than R_2. That is, the basic reproduction number of the two-host model satisfies $\mathcal{R}_0 > R_2 > R_1 > R_M$.

Setting (3.36) equal to zero,

$$P_1(\lambda)\,P_2(\lambda) - \bigstar_1(\lambda)\,\bigstar_2(\lambda) = 0 \Leftrightarrow P_1(\lambda)\,P_2(\lambda) = \bigstar_1(\lambda)\,\bigstar_2(\lambda). \tag{3.37}$$

Thus,

$$\bigstar_1\bigstar_2 = \left[\frac{\tau\,k_L\,b^2\,M_S^*}{(k_L+\mu_M)\,(N_H^*)^2}\right]^2 \cdot \left(P_{H_1M}\,P_{MH_2}\,P_{H_2M}\,P_{MH_1}\,N_{H_1}^*\,N_{H_2}^*\right) \tag{3.38}$$

determines how much greater $\mathcal{R}_0$ is than R_2. Note (3.38) represents a transmission chain of maximal length: hosts of type 1 → mosquitoes → hosts of type 2 → mosquitoes → hosts of type 1. Similar to the one-host case, if one or more hosts is incompetent for mosquito-host transmission, the characteristic polynomial for the two-host model reduces to the product of those for models with a single competent host, and the basic reproduction number is the maximum of those for cases with a single competent host.

In summary, we find that including a second host that is competent for mosquito-host transmission while holding N_H^* constant increases the basic reproduction number of the disease, regardless of the host's competence level. Moreover, if we begin with a model where one or more of two host types is competent for mosquito-host transmission, a reduction that neglects either or both hosts' competence for this type of transmission necessarily reduces the basic reproduction number. Note the latter result relies on the observation that the basic reproduction number for a single-host model without mosquito-host transmission (i.e., with horizontal or no transmission in hosts) increases when mosquito-host transmission is introduced (see 3.28). The above findings are significant from a modeling perspective since hosts with low competence for transmission may be treated as dead-end hosts during model construction to reduce model complexity. The result will be extended to models with more host categories in the following sections.

3.1.3. Further characterization of $\mathcal{R}_0$ for n hosts

To extend the previous result to the case of n hosts, it is helpful to further simplify (3.18). Let

$$Q = \frac{\tau\,k_L\,b^2\,M_S^*}{{N_H^*}^2\,(k_L+\mu_M)}, \tag{3.39}$$

Then,

$$F_{HH} - \lambda\,W_H - F_{MH}\,[F_{MM} - \lambda\,W_M]^{-1}\,F_{HM} =$$

$$\frac{Q}{A(\lambda)} \cdot \begin{bmatrix} \dfrac{P_1(\lambda)}{Q} & P_{MH_1}\,P_{H_2M}\,N_{H_1}^* & \cdots & P_{MH_1}\,P_{H_JM}\,N_{H_1}^* \\ P_{MH_2}\,P_{H_1M}\,N_{H_2}^* & \dfrac{P_2(\lambda)}{Q} & \cdots & P_{MH_2}\,P_{H_JM}\,N_{H_2}^* \\ \vdots & \vdots & \ddots & \vdots \\ P_{MH_J}\,P_{H_1M}\,N_{H_J}^* & P_{MH_J}\,P_{H_2M}\,N_{H_J}^* & \cdots\vdots\cdots & \dfrac{P_J(\lambda)}{Q} \end{bmatrix}. \tag{3.40}$$

In case host k is incompetent for mosquito-host transmission, the off-diagonal elements of the k^{th} row and/or those of the k^{th} column are zero. Hence, $\dfrac{P_k(\lambda)}{Q}$ can be factored from (3.40), meaning the basic

reproduction numbers for hosts which are incompetent for mosquito-host transmission are roots of the characteristic polynomial for the full model. In light of this, in the sequel, we focus on the case where all hosts are competent for mosquito-host transmission.

Factoring P_{H_jM} from the j^{th} column and $P_{MH_j}N_{H_j}$ from the j^{th} row for $j = 1, \dots J$, the determinant can be expressed as

$$\mathrm{L}(\lambda) \cdot \begin{vmatrix} \mathrm{P}_1(\lambda) & 1 & \dots & 1 \\ 1 & \mathrm{P}_2(\lambda) & 1 \dots & 1 \\ \vdots & \vdots & \ddots & \vdots \\ 1 & 1 \dots & \dots \vdots \dots & 1 \quad \mathrm{P}_J(\lambda) \end{vmatrix}, \tag{3.41}$$

where

$$\mathrm{L}(\lambda) = \left(\frac{Q}{A(\lambda)}\right)^j \cdot \prod_{i=1}^{j} \left(P_{H_jM}\, P_{MH_j}\, N^*_{H_j}\right), \tag{3.42}$$

and where we have redefined P_j as

$$\mathrm{P}_j(\lambda) = \frac{P_j(\lambda)}{QP_{MH_j}P_{H_jM}N^*_{H_j}}. \tag{3.43}$$

The special form of the matrix in 3.41, with ones off the diagonal, results from the assumption that there is no horizontal transmission or movement between the host categories, as this makes $F_{HH} - \lambda W_H$ a diagonal matrix. A result of this structure is that (3.41) is invariant with respect to the ordering of the polynomials along the diameter.

To show the basic reproduction number decreases when mosquito-host transmission competence is eliminated for one or more host types, we define a real-valued function D_n of n real variables as

$$D_n(p_1, \dots, p_n) := \begin{vmatrix} p_1 & 1 & \dots & 1 \\ 1 & p_2 & 1 \dots & 1 \\ \vdots & \vdots & \ddots & \vdots \\ 1 & 1 \dots & \dots \vdots \dots & 1 \quad p_n \end{vmatrix}. \tag{3.44}$$

The result is already established for $n = 2$. To prove the result for $n > 2$, we first compute D_{n+1} by cofactor expansion across the final row

$$D_{n+1}(P_1, \dots, P_{n+1})(r) = \begin{vmatrix} P_1(r) & 1 & \dots & \dots & 1 \\ 1 & \ddots & \ddots & & \vdots \\ \vdots & \ddots & P_j(r) & \ddots & \vdots \\ \vdots & & \ddots & \ddots & 1 \\ 1 & \dots & \dots & 1 & P_{n+1}(r) \end{vmatrix} \tag{3.45}$$

$$= P_{n+1}(r) \begin{vmatrix} P_1(r) & 1 & \dots & \dots & 1 \\ 1 & \ddots & \ddots & & \vdots \\ \vdots & \ddots & P_j(r) & \ddots & \vdots \\ \vdots & & \ddots & \ddots & 1 \\ 1 & \dots & \dots & 1 & P_n(r) \end{vmatrix} \tag{3.46}$$

$$-\begin{vmatrix} 1 & 1 & \dots & \dots & 1 \\ 1 & P_2(r) & \ddots & & \vdots \\ \vdots & \ddots & \ddots & \ddots & \vdots \\ \vdots & & \ddots & P_{n-1}(r) & 1 \\ 1 & \dots & \dots & 1 & P_n(r) \end{vmatrix} - \dots - \begin{vmatrix} P_1(r) & 1 & \dots & \dots & 1 \\ 1 & P_2(r) & \ddots & & \vdots \\ \vdots & \ddots & \ddots & \ddots & \vdots \\ \vdots & & \ddots & P_{n-1}(r) & 1 \\ 1 & \dots & \dots & 1 & 1 \end{vmatrix} \tag{3.47}$$

In summary,

$$\begin{aligned} D_{n+1}(p_1, \dots, p_n) &= p_{n+1} D_n(p_1, \dots, p_n) \\ &- D_n(1, p_2, \dots, p_n) - D_n(p_1, 1, \dots, p_n) - \dots - D_n(p_1, \dots, p_{n-1}, 1). \end{aligned} \tag{3.48}$$

The special form of the final terms in (3.47), which represent terms 2 through n of the cofactor expansion of D_{n+1}, is achieved through column swaps. To see how these final terms can be represented in this special form, define the $(n+1) \times (n+1)$ matrix A by $D_{n+1} = |A|$, and consider the process of computing D_{n+1} via cofactor expansion across the final $(n+1)$ row of A from right to left.

When computing the j^{th} term in the expansion for $j > 1$, elimination of the $(n+1) - (j-1)$ column of A leaves only ones in row $(n+1) - (j-1)$ of the resulting matrix, A' and reduces the column indices of entries in column k of A for $n+1 \geq k > (n+1) - (j-1)$ by one, leaving A' with n columns and potentially nonunit entries in the subdiagonal of columns $n-1 \geq k \geq (n+1) - (j-1)$. Then, elimination of the final $(n+1)$ row of A' leaves a matrix M with a final (n^{th}) column of ones.

A sequence of $j-2$ column swaps moves the final (n^{th}) column of ones in M to the $(n+1) - (j-1)$ column, and increases the column indices of entries in columns k of M for $n > k \geq (n+1) - (j-1)$ by one. Hence, these $j-2$ column swaps move all non-unit entries back to the diagonal, leaving only ones in both row and column $(n+1) - (j-1)$ of the resulting matrix N.

Finally, when computing the cofactor expansion of A from right to left across the bottom row, the first term (corresponding to row $n+1$ and column $n+1$) has a cofactor of $1 \cdot P_{n+1}(r)$. Since the other entries in row $n+1$ of A are all ones, the cofactor of the j^{th} term in the expansion is $(-1)^{j-1}$. Since N is obtained via $j-2$ column swaps on M,

$$(-1)^{j-1}|M| = (-1)^{2j+1}|N| = -|N|, \tag{3.49}$$

as desired.

To help the reader visualize the special form of the final terms in the cofactor expansion of A, we illustrate the steps for the first two terms in the co-factor expansion for $n+1 = 5$. Consider

$$D_5(P_1, \dots, P_5)(r) = \begin{vmatrix} P_1(r) & 1 & 1 & 1 & 1 \\ 1 & P_2(r) & 1 & 1 & 1 \\ 1 & 1 & P_3(r) & 1 & 1 \\ 1 & 1 & 1 & P_4(r) & 1 \\ 1 & 1 & 1 & 1 & P_5(r) \end{vmatrix} \tag{3.50}$$

Computing the cofactor expansion across the final row, from right to left, the second term has only ones

off the diagonal:

$$\begin{vmatrix} P_1(r) & 1 & 1 & 1 \\ 1 & P_2(r) & 1 & 1 \\ 1 & 1 & P_3(r) & 1 \\ 1 & 1 & 1 & 1 \end{vmatrix} \tag{3.51}$$

The third term is:

$$\begin{vmatrix} P_1(r) & 1 & 1 & 1 \\ 1 & P_2(r) & 1 & 1 \\ 1 & 1 & 1 & 1 \\ 1 & 1 & P_4(r) & 1 \end{vmatrix} \tag{3.52}$$

Swapping the fourth and third columns yields

$$\begin{vmatrix} P_1(r) & 1 & 1 & 1 \\ 1 & P_2(r) & 1 & 1 \\ 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & P_4(r) \end{vmatrix} \tag{3.53}$$

Note that the special form of the matrices above, namely, the fact that all off-diagonal entries are one, makes D_n invariant with respect to the order of its arguments. Indeed, a sequence of paired row and column swaps can be used to achieve any ordering of the diagonal elements desired without altering the determinant. Because of this invariance, the following claim enables us to evaluate the final $n-1$ terms in (3.47).

Claim 1. *For all $n \in \mathbb{N}$, with $n \geq 2$, $D_n(1, p_2, \ldots, p_n) = \prod_{i=2}^{n}(p_i - 1)$.*

Proof. The proof is by induction.

First, note the claim holds for $n = 2$:

$$D_2(1, p_2)(r) = \begin{vmatrix} 1 & 1 \\ 1 & p_2 \end{vmatrix} = p_2 - 1. \tag{3.54}$$

as desired.

Expanding the determinant $D_n(1, p_2, \ldots, p_n) = |N|$ across the second row of N, we see that terms 3 through n of the cofactor expansion are zero since the first two columns of the corresponding submatrices are identical. Indeed, eliminating row 2 of N leaves an $(n-1) \times n$ matrix, N', with nothing but ones in its first two columns. Thus, eliminating any column $j \geq 3$ of N' leaves a matrix with two identical columns, so the 2, j minor of N is zero for $j \geq 3$.

$$\begin{aligned} D_n(1, p_2, \ldots, p_n) &= -D_{n-1}(1, p_3, \ldots, p_n) + p_2 D_{n-1}(1, p_3, \ldots, p_n) \\ &= (p_2 - 1) D_{n-1}(1, p_3, \ldots, p_n) \\ &= (p_2 - 1) \prod_{i=3}^{n} (p_i - 1) \end{aligned} \tag{3.55}$$

where the first equality follows by inspection, and the final equality follows from application of the inductive hypothesis. □

It is interesting to note that Claim 1 together with (3.48) provides a means of computing the characteristic polynomial for the n-host case.

Now we will show that the basic reproduction number of a model where all n host types are competent for mosquito-host transmission is at least as great as one where competence of a subset of $m \geq 1$ host types are incompetent for mosquito-host transmission. Note that in this scenario, N_H^* is held constant and select hosts are reclassified as dead-end hosts or hosts that only experience horizontal transmission. In short, we consider the impact of neglecting the competence of one or more host types for mosquito-host transmission.

Proof. The proof is by complete mathematical induction. The result is already established for $n = 2$. Suppose the result holds for every model with n host types, where $n \geq 2$. Letting R_0 denote the greatest real root of $D_{n+1}(P_1, \ldots, P_{n+1})$, by the inductive hypothesis, and since the single-host basic reproduction number, determined by P_i is monotone increasing in competence for mosquito-host transmission (see 3.27), it suffices to show that $R_0 \geq r_n$, where

$$r_n := \max\{\operatorname{argmax}\{D_n(p_2, \ldots, p_{n+1}) = 0\}, \operatorname{argmax}\{D_n(p_1, p_3, \ldots, p_{n+1}) = 0\}, \ldots, \operatorname{argmax}\{D_n(p_1 \ldots, p_n)\} = 0\}. \quad (3.56)$$

Without loss of generality, let $r_n = \operatorname{argmax}\{D_n(P_1, \ldots, P_n) = 0\}$. Recall that R_i denotes the greatest root of P_i, which is a quadratic with a positive lead coefficient. Thus, by the inductive hypothesis, for all $i \in \{1, \ldots, n+1\}$, $r_n \geq R_i$, and

$$P_i(r_n) \geq 0. \quad (3.57)$$

Also, for all $i \neq j \in \{1, \ldots, n+1\}$,

$$D_2(P_i(r_n), P_j(r_n)) = \begin{vmatrix} P_i(r_n) & 1 \\ 1 & P_j(r_n) \end{vmatrix} = P_i(r_n)P_j(r_n) - 1 \geq 0. \quad (3.58)$$

That is,

$$P_i(r_n)P_j(r_n) \geq 1. \quad (3.59)$$

Indeed, by the inductive hypothesis, the basic reproduction number of every model where hosts i and j are competent for mosquito-host transmission, is less than or equal to that of every model where n hosts, including hosts i and j, are competent for mosquito-host transmission, which is, by definition, less than or equal to r_n. Hence, since $P_i(x)P_j(x) \to \infty$ as $x \to \infty$, it must be that $P_i(r_n)P_j(r_n) \geq 1$.

By (3.48) and Claim 1

$$D_{n+1}(P_1, \ldots, P_n)(r_n) = -\left[\sum_{i=1}^{n} \prod_{j=1,\ j\neq i}^{n} (P_j(r_n) - 1)\right] \quad (3.60)$$

We see that if $P_i(r_n) \geq 1$ for all $i \in \{1, \ldots, n\}$, then $D_{n+1}(P_1, \ldots, P_n)(r_n) \leq 0$. Since $D_{n+1}(P_1, \ldots, P_n)$ is a polynomial with a positive lead coefficient, $D_{n+1}(P_1, \ldots, P_n)(r) \to \infty$ as $r \to \infty$. Hence, in this case, $D_{n+1}(P_1, \ldots, P_n)$ must have a root at least as great as r_n. That is, $R_0 \geq r_n$, as desired.

Suppose there exists $i \in \{1, \dots, n\}$ so that $P_i(r_n) < 1$. It follows from (3.57) and (3.59) that there exists at most one such i. Without loss of generality, let $P_n(r_n) < 1$. Then, $D_{n+1}(P_1, \dots, P_n)(r_n)$ can be rearranged as

$$D_{n+1}(P_1, \dots, P_{n+1})(r_n) = (1 - P_n(r_n)) \left[\sum_{i=1}^{n-1} \prod_{j=1,\ j\neq i}^{n-1} (P_j(r_n) - 1) \right] - \prod_{j=1}^{n-1} (P_j(r_n) - 1) \tag{3.61}$$

By definition of r_n, $D_n(P_1, \dots, P_n)(r_n) = 0$. Hence, by (3.48), Claim 1, and $P_n(r_n) < 1$

$$\left[\sum_{i=1}^{n-1} \prod_{j=1,\ j\neq i}^{n-1} (P_j(r_n) - 1) \right] = P_n(r_n) D_{n-1}(P_1, \dots, P_{n-1})(r_n) < D_{n-1}(P_1, \dots, P_{n-1}) \tag{3.62}$$

Substituting into (3.61) and applying Claim 1, we have

$$\begin{aligned} D_{n+1}(P_1, \dots, P_{n+1})(r_n) &< (1 - P_n(r_n)) \begin{vmatrix} P_1(r_n) & 1 & \dots & \dots & 1 \\ 1 & \ddots & \ddots & & \vdots \\ \vdots & \ddots & P_j(r_n) & \ddots & \vdots \\ \vdots & & \ddots & \ddots & 1 \\ 1 & \dots & \dots & 1 & P_{n-1}(r_n) \end{vmatrix} - \begin{vmatrix} P_1(r_n) & 1 & \dots & \dots & 1 \\ 1 & \ddots & \ddots & & \vdots \\ \vdots & \ddots & \ddots & \ddots & \vdots \\ \vdots & & \ddots & P_{n-1}(r_n) & 1 \\ 1 & \dots & \dots & 1 & 1 \end{vmatrix} \\ &= (1 - P_n(r_n)) D_{n-1}(P_1, \dots, P_{n-1}) - D_n(P_1, \dots, P_{n-1}, 1) \end{aligned} \tag{3.63}$$

Note $D_{n-1}(P_1, \dots, P_{n-1})$ is the final term in the cofactor expansion of $D_n(P_1, \dots, P_{n-1}, 1)$ along its final row. Hence, combining the two terms in (3.63), we find

$$D_{n+1}(P_1, \dots, P_{n+1})(r_n) < - \begin{vmatrix} P_1(r_n) & 1 & \dots & \dots & 1 \\ 1 & \ddots & \ddots & & \vdots \\ \vdots & \ddots & P_j(r_n) & \ddots & \vdots \\ \vdots & & \ddots & \ddots & 1 \\ 1 & \dots & \dots & 1 & P_n(r_n) \end{vmatrix} = 0. \tag{3.64}$$

As before, since $D_{n+1}(P_1, \dots, P_n)(r) \to \infty$ as $r \to \infty$, we see that $D_{n+1}(P_1, \dots, P_n)$ must have a root at least as great as r_n. That is, $R_0 \geq r_n$, as desired. □

To aid the reader, we illustrate the final steps of the argument beginning at (3.61) for $n + 1 = 3$.

We suppose that $D_2(P_1(r_2)P_2(r_2)) = 0$, and $P_2(r_2) < 1$. Then, (3.61) becomes

$$D_3(P_1(r_2), P_2(r_2), P_3(r_2)) = (1 - P_2(r_2)) - (P_1(r_2) - 1). \tag{3.65}$$

From $D_2(P_1(r_2), P_2(r_2)) = 0$, we have $1 = P_1(r_2)P_2(r_2) < P_1(r_2)$. (For comparison to the general n-host case, note that the factor $\left[\sum_{i=1}^{n-1} \prod_{j=1,\ j\neq i}^{n-1} (P_j(r_n) - 1)\right]$ in (3.61) is 1 when $n + 1 = 3$.) Thus 3.65 yields

$$\begin{aligned} D_3(P_1(r_2), P_2(r_2), P_3(r_2)) &< P_1(r_2)(1 - P_2(r_2)) - (P_1(r_2) - 1) \\ &= P_1(r_2) - P_1(r_2)P_2(r_2) - P_1(r_2) + 1 \\ &= 1 - P_1(r_2)P_2(r_2) \end{aligned} \tag{3.66}$$

$$\begin{aligned} &= -D_2(P_1(r_2), P_2(r_2)) \\ &= 0. \end{aligned}$$

In summary, we have the following theorem.

Theorem 1. *The basic reproduction number of a model where all n host types are competent for mosquito-host transmission is at least as great as one where competence of a subset of $m \geq 1$ host types are incompetent for mosquito-host transmission.*

3.2. Feeding preference

Model (2.3)–(2.12) can be adapted to include feeding preference. In this section, we present the model with feeding preference and investigate how its addition impacts the basic reproduction number.

The model with feeding preference is as follows:
For $j = 1, \ldots, J$

$$\frac{d}{dt}H_{S_j} = \Lambda_j(H_{S_j} + H_{R_j}) - P_{MH_j}\, b\, M_I \frac{\alpha_j H_{S_j}}{\alpha_D N_D + \sum_k \alpha_k N_{H_k}} - \omega_j H_{I_j} \frac{H_{S_j}}{N_{H_j}} - \frac{d_{H_j}}{C_{H_j}} N_{H_j} H_{S_j} - \mu_{H_j} H_{S_j} \quad (3.67)$$

$$\frac{d}{dt}H_{I_j} = P_{MH_j}\, b\, M_I \frac{\alpha_j H_{S_j}}{\alpha_D N_D + \sum_k \alpha_k N_{H_k}} + \omega_j H_{I_j} \frac{H_{S_j}}{N_{H_j}} - \left(\gamma_{H_j} + g_{I_j} + \mu_{H_j}\right) H_{I_j} - \frac{d_{H_j}}{C_{H_j}} N_{H_j} H_{I_j} \quad (3.68)$$

$$\frac{d}{dt}H_{R_j} = g_{I_j} H_{I_j} - \frac{d_{H_j}}{C_{H_j}} N_{H_j} H_{R_j} - \mu_{H_j} H_{R_j} \quad (3.69)$$

In addition,

$$\frac{d}{dt}E_S = r_S(M_S + M_E) - m_E E_S \quad (3.70)$$

$$\frac{d}{dt}E_I = r_I M_I - m_E E_I \quad (3.71)$$

$$\frac{d}{dt}L_S = m_E q_S E_S + m_E q_I(1-\phi)E_I - (\mu_L + m_L)L_S - \frac{d_L}{C_L}(L_S + L_I)L_S \quad (3.72)$$

$$\frac{d}{dt}L_I = m_E q_I \phi E_I - (\mu_L + m_L)L_I - \frac{d_L}{C_L}(L_S + L_I)L_I \quad (3.73)$$

$$\frac{d}{dt}M_S = m_L L_S - b M_S \sum_j \left(P_{H_j M} \frac{\alpha_j H_{I_j}}{\alpha_D N_D + \sum_k \alpha_k N_{H_k}} \right) - \mu_M M_S \quad (3.74)$$

$$\frac{d}{dt}M_E = b M_S \sum_j \left(P_{H_j M} \frac{\alpha_j H_{I_j}}{\alpha_D N_D + \sum_k \alpha_k N_{H_k}} \right) - (k_L + \mu_M) M_E \quad (3.75)$$

$$\frac{d}{dt}M_I = m_L L_I + k_L V_E - \mu_M M_I. \quad (3.76)$$

Changing variables,

$$Y_{S_j} = \alpha_j H_{S_j},$$

$$
\begin{aligned}
Y_{I_j} &= \alpha_j H_{I_j}, \\
Y_{R_j} &= \alpha_j H_{R_j}, \\
Y_j &= Y_{S_j} + Y_{I_j} + Y_{R_j} = \alpha_j N_{H_j}, \\
N_Y &= Y_D + \sum_j Y_j,
\end{aligned}
\tag{3.77}
\tag{3.78}
$$

and defining the composite parameters

$$
\begin{aligned}
C_j &= \alpha_j C_{H_j}, \\
Y_D &= \alpha_D N_D, \\
P_{MY_j} &= \alpha_j P_{MH_j},
\end{aligned}
\tag{3.79}
$$

yields the following system:
For $j = 1, \ldots, J$

$$\frac{d}{dt} Y_{S_j} = \Lambda_j (Y_{S_j} + Y_{R_j}) - P_{MY_j}\, b\, M_I \frac{Y_{S_j}}{N_Y} - \omega_j\, Y_{I_j} \frac{Y_{S_j}}{Y_j} - \frac{d_{H_j}}{C_j} Y_j\, Y_{S_j} - \mu_{H_j}\, Y_{S_j} \tag{3.80}$$

$$\frac{d}{dt} Y_{I_j} = P_{MY_j}\, b\, M_I \frac{Y_{S_j}}{N_Y} + \omega_j\, Y_{I_j} \frac{Y_{S_j}}{Y_j} - \left(\gamma_{H_j} + g_{I_j} + \mu_{H_j}\right) Y_{I_j} - \frac{d_{H_j}}{C_j} Y_j\, Y_{I_j} \tag{3.81}$$

$$\frac{d}{dt} Y_{R_j} = g_{I_j}\, Y_{I_j} - \frac{d_{H_j}}{C_j} Y_j\, Y_{R_j} - \mu_{H_j}\, Y_{R_j}. \tag{3.82}$$

In addition,

$$\frac{d}{dt} E_S = r_S (M_S + M_E) - m_E\, E_S \tag{3.83}$$

$$\frac{d}{dt} E_I = r_I\, M_I - m_E\, E_I \tag{3.84}$$

$$\frac{d}{dt} L_S = m_E\, q_S\, E_S + m_E\, q_I (1 - \phi) E_I - (\mu_L + m_L) L_S - \frac{d_L}{C_L} (L_S + L_I) L_S \tag{3.85}$$

$$\frac{d}{dt} L_I = m_E\, q_I\, \phi\, E_I - (\mu_L + m_L) L_I - \frac{d_L}{C_L} (L_S + L_I) L_I \tag{3.86}$$

$$\frac{d}{dt} M_S = m_L\, L_S - b\, M_S \sum_j \left(P_{H_j M} \frac{Y_{I_j}}{N_Y}\right) - \mu_M\, M_S \tag{3.87}$$

$$\frac{d}{dt} M_E = b\, M_S \sum_j \left(P_{H_j M} \frac{Y_{I_j}}{N_Y}\right) - (k_L + \mu_M)\, M_E \tag{3.88}$$

$$\frac{d}{dt} M_I = m_L\, L_I + k_L\, V_E - \mu_M\, M_I. \tag{3.89}$$

We see that the transformed model has the same structure as the model without feeding preference. Let system (3.67)–(3.76) be represented as $\dot{X} = f(X)$. The transformed variables can be expressed as $Y = AX$, where A is an $m \times m$ block matrix

$$A = \begin{bmatrix} (A_H)_{3J \times 3J} & (0)_{3J \times (m-3J)} \\ (0)_{(m-3J) \times 3J} & (\mathbb{I})_{(m-3J) \times (m-3J)} \end{bmatrix}, \tag{3.90}$$

and

$$A_H = \begin{bmatrix} \alpha_1 (\mathbb{I})_{3\times3} & (0)_{3\times3} & (0)_{3\times3} & \dots & (0)_{3\times3} \\ (0)_{3\times3} & \alpha_2 (\mathbb{I})_{3\times3} & (0)_{3\times3} & \dots & \vdots \\ \vdots & (0)_{3\times3} & & \ddots & (0)_{3\times3} \\ (0)_{3\times3} & \dots \vdots \dots & & \dots (0)_{3\times3} & \alpha_J (\mathbb{I})_{3\times3} \end{bmatrix}. \tag{3.91}$$

Since A is a diagonal matrix, $X = A^{-1}Y$,

$$\dot{Y} = A\dot{X} = A\, f(A^{-1}Y) =: g(Y), \tag{3.92}$$

and X_0 is a steady state of (3.67)–(3.76) if and only if AX_0 is a steady state of (3.80)–(3.89). Moreover, the Jacobian of (3.67)–(3.76) at X_0, $Df(X_0)$, and the Jacobian of (3.80)–(3.89) at AX_0 are similar:

$$Dg(AX_0) = A\, Df(A^{-1}A\, X_0)\, A^{-1} = A\, Df(X_0)\, A^{-1}. \tag{3.93}$$

Hence, these Jacobian matrices have the same eigenvalues, and the linear stability of (3.67)–(3.76) at X_0 is equivalent to that of (3.80)–(3.89) at AX_0. Similarly, letting $\hat{A}$ denote the restriction of the transformation to the infected compartments, the transition and infection matrices for the transformed system at the disease free equilibrium are $\hat{A}V\hat{A}^{-1}$ and $\hat{A}F\hat{A}^{-1}$. Thus, the next-generation matrix for the transformed system is similar to that of the original system, meaning the two systems share the same basic reproduction number. Applying the results of Section 3 to the transformed model, we compute the basic reproduction number of the system with feeding preference. For example, when feeding preference is added to a model with a single competent host type k, we have the following basic reproduction number

$$\mathcal{R}_0 = \frac{1}{2}\frac{\omega}{s} + \frac{1}{2}\frac{q_I\,\phi\, r_I\, m_L}{\mu_M\,\tau} + \frac{1}{2}\sqrt{\left(\frac{\omega}{s} - \frac{q_I\,\phi\, r_I\, m_L}{\mu_M\,\tau}\right)^2 + \frac{1}{s}\left(\frac{4\,k_L\,b^2\,M_S^*\,\alpha_k^2\,P_{MH_K}\,P_{H_KM}\,C_{H_K}}{\mu_M\,(\mu_M + k_L)\,(\alpha_D N_D + \alpha_k C_{H_K})^2}\right)}, \tag{3.94}$$

where $\tau = m_L + \mu_L + d_L$ and $s = \gamma_H + g_I + \mu_H + d_H$. Note that in (3.94), we have replaced $N_{H_K}^*$ with its value, C_{H_K}, and that N_D, the density of dead-end hosts is constant in this model.

4. Numerical experiments

In this section, we explore the impact of model structure and parameters on a WNV epidemic, where impact is quantified by the basic reproduction number, the maximum prevalence in mosquitoes (defined as the ratio of infectious to noninfectious individuals), and the long-term survivorship of vulnerable hosts.

Our baseline model includes five types of hosts categorized by competence for horizontal transmission, competence for mosquito-host transmission, attractiveness to *Culex pipiens* (*C. pipiens*) mosquitoes, and vulnerability to WNV-induced mortality. Type 1 hosts are highly competent for both mosquito-host and horizontal transmission, vulnerable to WNV-induced mortality, and not a preferred source of blood meals for *C. pipiens* mosquitoes. These hosts are intended to model birds in the corvidae family, such as American crows and blue jays. Type 2 hosts are incompetent for horizontal transmission, competent

for mosquito-host transmission, vulnerable to WNV-induced mortality, and not a preferred source of blood meals for *C. pipiens* mosquitoes. These hosts model house sparrows. Type 3 hosts have moderate competence for mosquito-host transmission, are incompetence for horizontal transmission, have low vulnerability to WNV-induced mortality, and are a preferred source of blood meals for *C. pipiens* mosquitoes. These hosts model passerine birds native to North America, such as the American robin. Type 4 hosts are incompetent for horizontal transmission, have very low competence for mosquito-host transmission, are invulnerable to WNV-induced mortality, and are not a preferred source of blood meals for *C. pipiens* mosquitoes. These assumptions are consistent with the characteristics of many urban bird species, including rock pigeons, starlings, and mourning doves. The focal vector, host types, and parameters are selected to reflect urban environments in northern US and Canada.

We consider two baseline community structures aimed at representing varying levels of urbanization. The two communities have identical densities of dead-end hosts (70 indv ha^{-1}) and similar densities of competent hosts (7.25 indv ha^{-1} in the more urban setting vs 7 indv ha^{-1} in the less urban setting). However, the more urban setting includes considerably fewer type 1 hosts (0.25 vs 1 indv ha^{-1}), considerably more type 2 hosts (5 vs 2 indv ha^{-1}), in addition to having fewer hosts of types 3 and 4. See Table 1 for a summary of the two host community structures.

Table 2 provides a summary of community structure as measured by effective and actual mosquito-to-host ratios. The mosquito-to-host ratio of a community is often considered as a indication of outbreak risk. All else being equal, higher mosquito-host ratios result in greater risk since higher ratios indicate more bites per host and hence increased amplification of transmission by infected hosts. Mosquito feeding preference, however, alters the effective mosquito-to-host ratio and the average number of bites per hosts. Mosquito feeding preference together with variable host competence make it difficult to intuit a simple relation between the mosquito-host ratio and risk in a heterogeneous host community.

Table 1. Avian host densities across levels of urbanization and the Shannon diversity index of the avian community. L.U.: less urban, M.U.: more urban. Units for host densities are indv ha^{-1}. The density of dead-end hosts was 70 individuals(indv) ha^{-1} in both communities. Type 1: vulnerable amplifiers with horizontal transmission; Type 2: vulnerable amplifiers without horizontal transmission; Type 3: invulnerable amplifiers; Type 4: low competence hosts. See Appendix B for details of the model parameterization.

Avian Host Community Structure

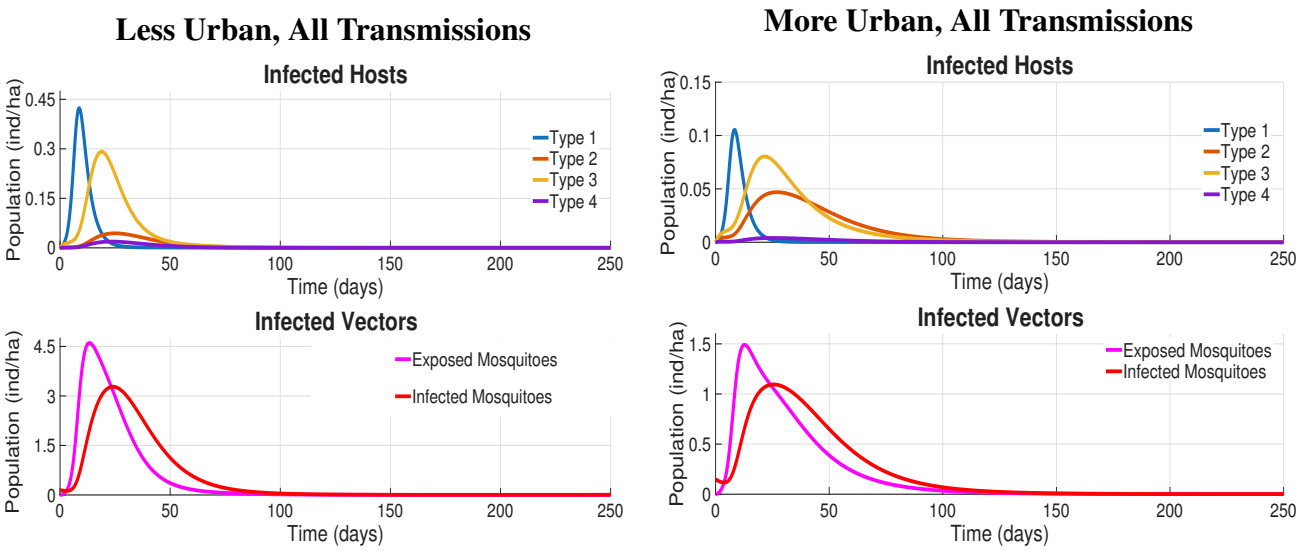
Host yype	L.U. density	M.U. density
Type 1	1	0.25
Type 2	2	5
Type 3	2	1
Type 4	2	1
Shannon diversity index	1.3618	0.9188

Table 2. Mosquito-to-host ratios across levels of urbanization.

Mosquito-host ratios	Less urban	More urban
Effective ratio	21.53	27.77
Actual ratio	1.93	1.92

4.1. Baseline simulations

We begin by simulating an outbreak initiated by the introduction of a small number of infected mosquitoes in both communities (Figure 1). We see that the less urban community experiences higher maximum densities of infected individuals. The larger peak density in infected individuals is mirrored by a greater basic reproduction number for the less urban community. Since the mosquito carrying capacity is the same in both communities, the less urban community also has a much greater maximum prevalence of infection in mosquitoes. In contrast, since the less urban community has four times as many type 1 hosts, the prevalence of infection in type 1 hosts is similar in both communities. On the other hand, since the more urban community has many more type 2 hosts, like the prevalence of infection in mosquitoes, the prevalence of infection in type 2 hosts is much lower in the more urban community. The outbreak is also longer lasting in the more urban community. Overall, the more urban community experiences a milder, more slow-burning epidemic.

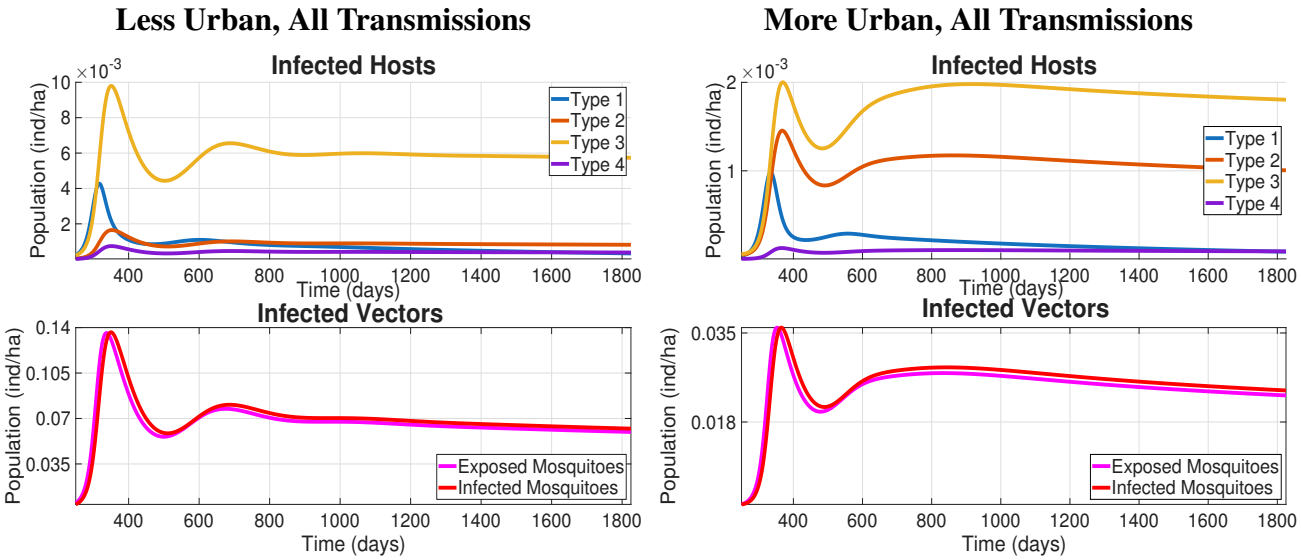


(a) $\mathcal{R}_0 = 3.94$; origin: adult mosquitoes, scenario: L.U.

(b) $\mathcal{R}_0 = 3.69$; origin: adult mosquitoes; scenario: M.U.

Figure 1. Comparison of WNV epidemics in less- and more-urban host communities. Note the difference is the scale of the y-axis between the less- (panel a) and more-urban (panel b) simulations. L.U.: less urban, M.U.: more urban. Type 1: vulnerable amplifiers with horizontal transmission; Type 2: vulnerable amplifiers without horizontal transmission; Type 3: invulnerable amplifiers; Type 4: low-competence hosts. For a list of parameters and initial conditions for the simulations, see Tables A1–A6.

Figure 2 displays the dynamics of the disease compartments in the long term, from day 250 through year 5. As with the short-term simulations, the overall magnitude of the outbreak is lower in the more urban scenario. Both long-term simulations show a second smaller outbreak that resolves into an apparent endemic equilibrium with low density and low prevalence of infected individuals.



(a) $\mathcal{R}_0 = 3.94$; origin: adult mosquitoes; scenario: L.U. **(b)** $\mathcal{R}_0 = 3.69$; origin: adult mosquitoes; scenario: M.U.

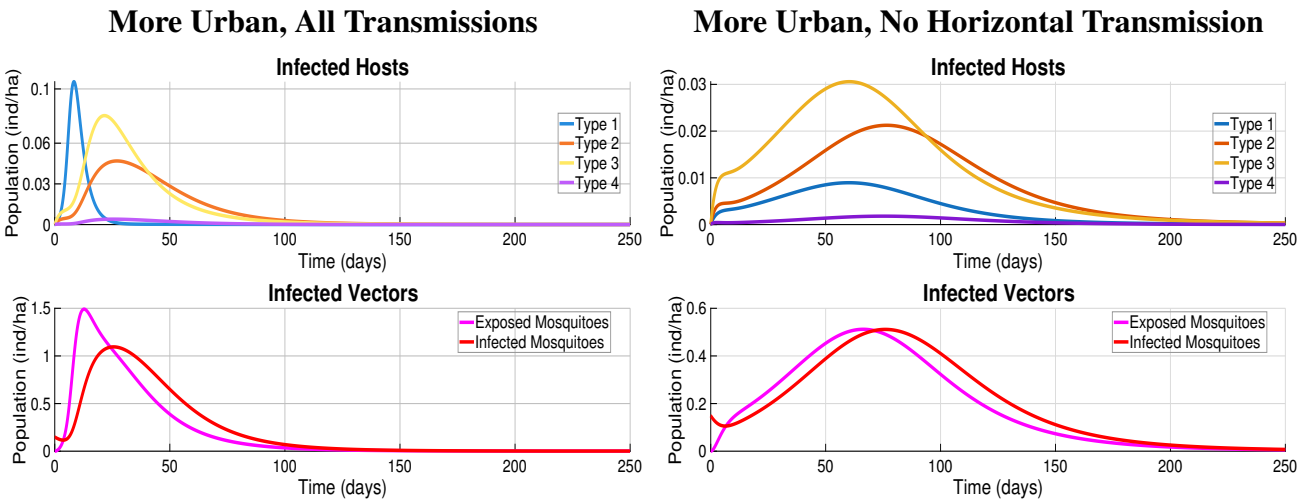
Figure 2. Comparison of long-term dynamics of WNV epidemics in less- and more-urban communities. The simulations span day 250 through year 5 post initial introduction of the virus. Note the difference in the scale of the y-axis between the less- (panel a) and more-urban (panel b) simulations. L.U.: less urban, M.U.: more urban. Type 1: vulnerable amplifiers with horizontal transmission; Type 2: vulnerable amplifiers without horizontal transmission; Type 3: invulnerable amplifiers; Type 4: low-competence hosts. For a list of parameters and initial conditions for the simulations, see Tables A1–A6.

4.2. Exploring the impact of structural perturbations on a WNV epidemic in two ecologically feasible urban communities

Next, we explore the impact of structural model alterations on the model epidemic in the less and more urban communities. Specifically, we explore the impact of neglecting horizontal transmission in type 1 hosts, neglecting mosquito-host transmission in hosts with low competence (i.e., host types 3 and 4), and removing low-competence hosts. Although experimental evidence [21] supports horizontal transmission in several bird species (especially in species of the Corvidae family), horizontal transmission is rarely included in WNV models. Similarly, models frequently focus on hosts of the highest competence, neglecting the transmission and contraction of the virus by low-competence hosts, or neglecting low-competence hosts altogether. Hence, the perturbations considered here represent common modeling simplifications.

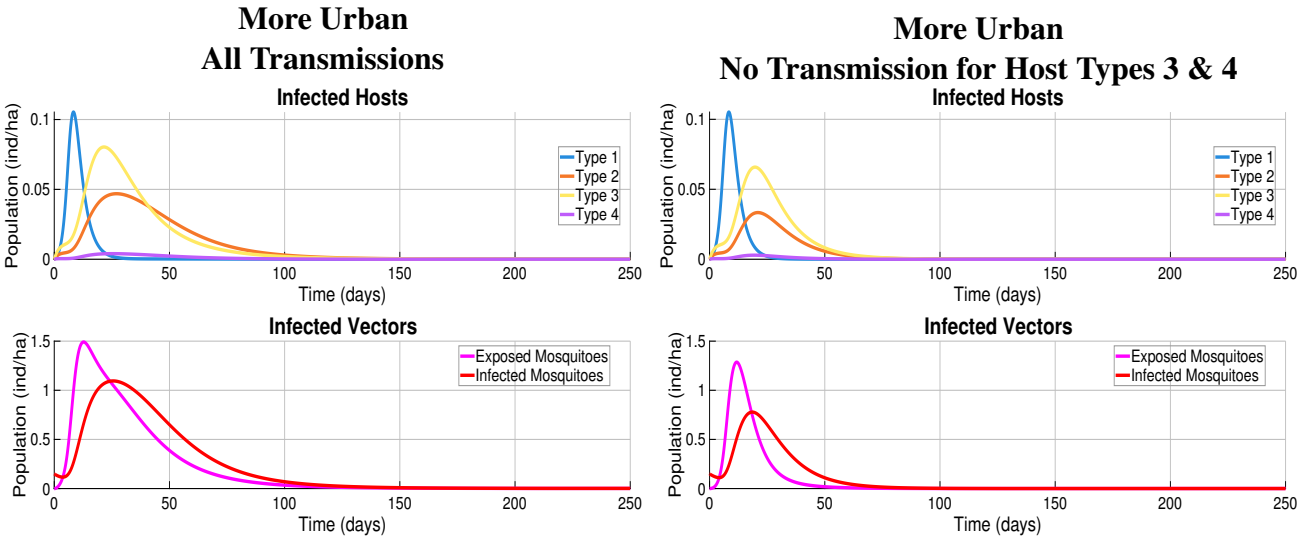
4.2.1. Impact on dynamics

The impact of neglecting select types of transmission on the dynamics of the epidemic in a more urban community are presented in Figures 3–5. We see the impact of eliminating horizontal transmission is to lengthen the outbreak and lower its peak. Meanwhile, eliminating transmission via hosts with moderate or low competence (types 3 and 4 hosts) shortens the epidemic and reduces the peak density of infectious mosquitoes. Eliminating transmission in hosts with low competence (type 4 hosts) has minimal impact on the dynamics of the epidemic.



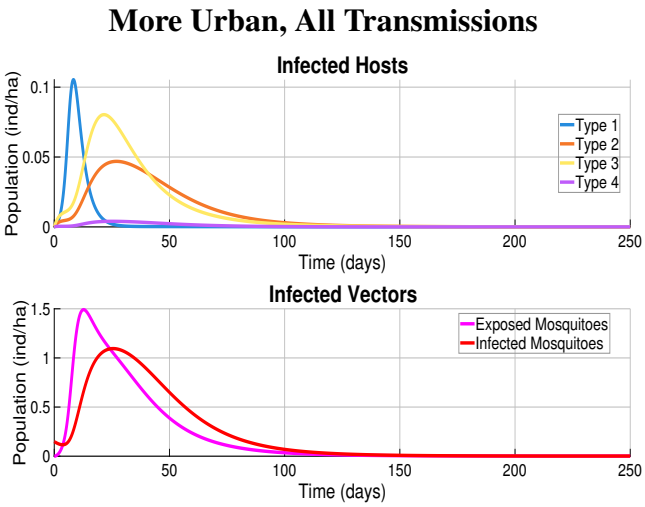
(a) $\mathcal{R}_0 = 3.69$; origin: adult mosquitoes; scenario: M.U. **(b)** $\mathcal{R}_0 = 1.38$; origin: adult mosquitoes; scenario: M.U.

Figure 3. Comparison of WNV epidemics in a more urban host communities with and without horizontal transmission for type 1 hosts. Note the difference is the scale of the y-axis in the panels with horizontal transmission- (panel a) and without horizontal transmission- (panel b). M.U.: more urban. Type 1: vulnerable amplifiers with horizontal transmission; Type 2: vulnerable amplifiers without horizontal transmission; Type 3: invulnerable amplifiers; Type 4: low-competence hosts. For a list of parameters and initial conditions for the simulations, see Tables A1–A6.

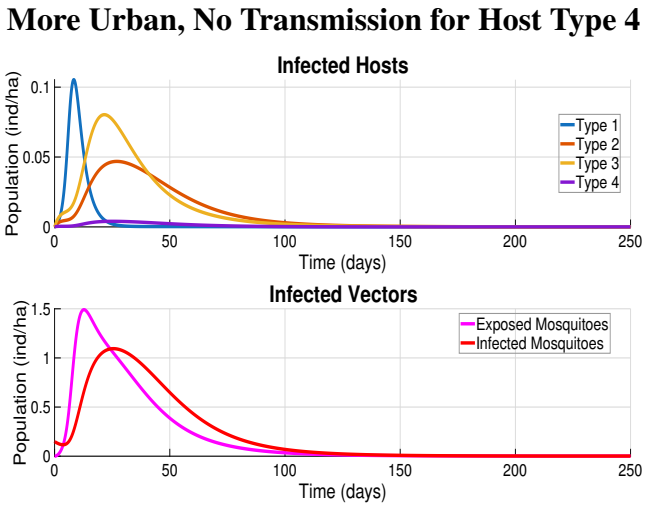


(a) $\mathcal{R}_0 = 3.69$; origin: adult mosquitoes; scenario: M.U. **(b)** $\mathcal{R}_0 = 3.68$; origin: adult mosquitoes; scenario: M.U.

Figure 4. Comparison of WNV epidemics in more urban host communities with and without transmission from hosts types 3 & 4. M.U.: more urban. Type 1: vulnerable amplifiers with horizontal transmission; Type 2: vulnerable amplifiers without horizontal transmission; Type 3: invulnerable amplifiers; Type 4: low-competence hosts. For a list of parameters and initial conditions for the simulations, see Tables A1–A6.

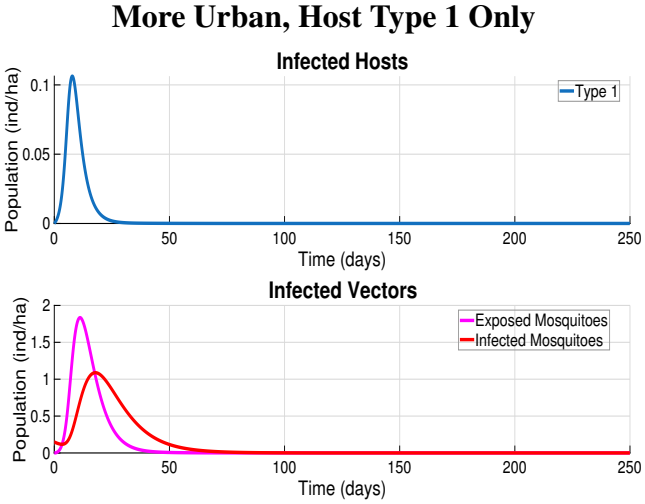


(a) $\mathcal{R}_0 = 3.69$; origin: adult mosquitoes; scenario: M.U.

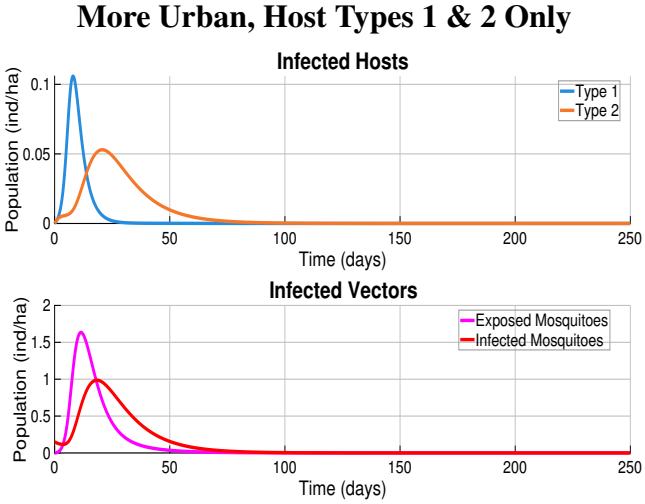


(b) $\mathcal{R}_0 = 3.69$; origin: adult mosquitoes; scenario: M.U.

Figure 5. Comparison of WNV epidemics in more urban host communities with and without transmission from Host 4. M.U.: more urban. Type 1: vulnerable amplifiers with horizontal transmission; Type 2: vulnerable amplifiers without horizontal transmission; Type 3: invulnerable amplifiers; Type 4: low-competence hosts. For a list of parameters and initial conditions for the simulations, see Tables A1–A6.



(a) $\mathcal{R}_0 = 3.85$; origin: adult mosquitoes; scenario: M.U.



(b) $\mathcal{R}_0 = 3.78$; origin: adult mosquitoes; scenario: M.U.

Figure 6. Comparison of WNV epidemics in more urban host communities with only type 1 hosts- (panel a) and with only type 1 and type 2 hosts- (panel b). M.U.: more urban. Type 1: vulnerable amplifiers with horizontal transmission; Type 2: vulnerable amplifiers without horizontal transmission; Type 3: invulnerable amplifiers; Type 4: low-competence hosts. For a list of parameters and initial conditions for the simulations, see Tables A1–A6.

Finally, Figure 6 shows the dynamics of a more urban epidemic that includes only the most competent hosts. Comparing panels (a) and (b), we see that the addition of a second host with lower competence has

little if any impact on the dynamics of the disease in the first host and produces a very small reduction in the maximum density of infectious mosquitoes. In contrast, comparing panel (b) of Figure 6 and panel (a) of Figure 5, we see that the introduction of types 3 and 4 hosts slightly increases the maximal density of infectious mosquitoes while greatly increasing the length of the epidemic.

4.2.2. Impact on the basic reproduction number

Table 3 shows that impact of neglecting various types of transmission on the basic reproduction number. Recall a basic reproduction number greater than 1 indicates a community is at risk of experiencing a WNV epidemic. Comparison across columns shows the basic reproduction number is greater than 1 in every case and consistently higher in the less urban community despite the fact that this community has a lower effective mosquito-to-host ratio. Meanwhile comparison across rows reveals that horizontal transmission in type 1 hosts has the most significant impact on the basic reproduction number, while the impact of neglecting transmission in hosts with lower competence is minimal. The effect of neglecting horizontal transmission is similar in the two communities, producing a reduction to about 44% and 35% in the less and more urban communities, respectively. By comparison, neglecting transmission in host types 3 and 4 results in an approximate 1% reduction in the basic reproduction number of both communities. Finally, we see that the absence of horizontal transmission accentuates community-specific variation in the basic reproduction number. For the baseline parameterization, the ratio of more to less urban basic reproduction numbers is about 0.94, but that value drops to about 0.79 in the absence of horizontal transmission.

Table 3. The impact of neglecting select types of transmission. Scenarios represented in rows 1–4 explore the impact of neglecting horizontal transmission, neglecting transmission in the host with lowest competence (type 4) and neglecting transmission in the hosts with low-competence (types 3 and 4). Comparison across columns reveals the impact of the bird community composition on experimental outcomes. Basic reproduction numbers were computed via the next-generation matrix method.L.U.: less urban, M.U.: more urban.

The impact of neglecting select transmissions on R_0

Scenario	L.U. R_0	M.U. R_0
Baseline	3.94	3.69
No horizontal transmission	1.74	1.38
No transmission for host types 3 & 4	3.90	3.68
No transmission for host type 4	3.94	3.69

Table 4 shows how neglecting host types with lower competence impacts the model basic reproduction number in two communities. Since neglecting hosts with lower competence necessarily increases bites per highly competent host, it is not surprising that neglecting less competent hosts increases the model basic reproduction number. On the other hand, comparison across columns reveals that the impact of neglecting less competent hosts is also community specific. In particular, the more urban basic reproduction number was much more robust to these types of perturbations experiencing a maximum increase of about 4% compared to a maximum increase of about 11% in the less urban model.

Table 4. The impact of neglecting host types on the basic reproduction number. Scenarios represented in rows 1–3 show basic reproduction numbers for models that include all hosts, type one hosts, and types 1 and 2 hosts, respectively. Note that adding or removing host types alters the size of the host population. Comparison across columns reveals the impact of the bird community composition. Basic reproduction numbers were computed via the next-generation matrix method. L.U.: less urban, M.U.: more urban.

The impact of neglecting select host types on R_0		
Hosts included	L.U. R_0	M.U. R_0
All hosts	3.94	3.69
Type 1 & 2 Hosts	4.30	3.78
Type 1 Hosts	4.36	3.85

4.2.3. Impact on the maximum prevalence of infection in mosquitoes

Table 5 shows the impact of neglecting select types of transmission on the maximum prevalence of infection in mosquitoes. We note that maximum prevalence of infection in mosquitoes is a metric of independent interest because it serves as a measure of the risk of spillover infection into the human population. Similar to the basic reproduction number, the maximum prevalence in mosquitoes is consistently higher in the less urban community and most heavily influenced by horizontal transmission, experiencing a reduction to approximately 60% and 46% of its baseline value in the absence of horizontal transmission in less urban and more urban scenarios, respectively. However, unlike the basic reproduction number, maximum prevalence in mosquitoes is also strongly influenced by transmission from type 3 hosts, experiencing a reduction to approximately 72% and 70% of its baseline value in the absence of transmission from types 3 and 4 hosts in less urban and more urban scenarios, respectively.

Table 5. Maximum prevalence of infectious adult mosquitoes across different scenarios and levels of urbanization. Prevalence is computed as the density of infectious mosquitoes divided by the total density of mosquitoes. L.U.: less urban, M.U.: more urban.

The impact of neglecting select transmissions on max prevalence of infectious mosquitoes		
Scenario	L.U.	M.U.
All transmissions	0.0222	0.0074
No horizontal transmission	0.0134	0.0034
No transmission for host types 3 & 4	0.0160	0.0052
No transmission for host type 4	0.0221	0.0074

4.2.4. Impact on the survival of vulnerable hosts

Table 6 shows the impact of neglecting various types of transmission on the five-year survivorship of hosts that are vulnerable to WNV-induced mortality. Not surprisingly, eliminating horizontal transmission for type 1 hosts improves their survival. Eliminating transmission in hosts with moderate or low competence (types 3 and 4) also produces a very small improvement in the survival of vulnerable hosts.

Table 6. Five-year survivorship of vulnerable host populations in the more urban community across different transmission scenarios. Survivorship is computed as the number of hosts remaining after five years divided by the host carrying capacity.

The impact of neglecting select transmissions on five-year host survivorship		
Scenario	Host 1	Host 2
All transmissions	0.25	0.92
No horizontal transmission	0.37	0.92
No transmission for host types 3 & 4	0.26	0.97
No transmission for host type 4	0.25	0.92

4.3. Exploring the impact of systematic parameter variation

In this section, we investigate the sensitivity of epidemic metrics to systematic variations of select parameters. Using the less urban model parameterization as a baseline for comparison, the abundance of less competent hosts and relative feeding preference of mosquitoes for these hosts is varied. These perturbations are designed to determine the potential for hosts with lower competence to lessen the severity of an epidemic. The abundance of hosts with lower competence was controlled by varying the respective carrying capacity. Mosquito feeding preference for host type i was controlled by effectively scaling α_i. Here, however, it is helpful to note that the model is invariant with respect to the magnitude of the vector of feeding preference parameters $(\alpha_1, \ldots, \alpha_J)$. Because of this invariance, we prefer to scale the feeding preference vector so its greatest component is one. Hence, in practice, feeding preference for host type 4 was controlled as follows: (1) Scale α_4 to achieve a new parameter set $(\alpha_1, \alpha_2, \alpha_3, k\alpha_4)$. (2) In case $k\alpha_4 > 1$, rescale to achieve $(\frac{\alpha_1}{k\alpha_4}, \frac{\alpha_2}{k\alpha_4}, \frac{\alpha_3}{k\alpha_4}, 1)$. Note this procedure preserves the relative preference for host i to host j for $i, j \neq 4$. Similarly, for host type 2.

First, we consider the impact of increasing the density of hosts with moderate and low competence for transmission (host types 3 and 4). That is, we investigate the capacity of these hosts to act as epidemic diluters. Biologically, perturbations in host abundance represent ecological variability in the host community structure. Interestingly, despite the fact that type 4 hosts have the lowest competence for infection, increasing the abundance of type 3 hosts is a more effective means of improving the epidemic metrics, especially the maximum prevalence of infection in mosquitoes and the basic reproduction number. The superior capacity of type 3 hosts to act as diluters is likely a result of the fact that these hosts, unlike type 4 hosts, are highly attractive to mosquitoes (*C. pipiens*). An interesting exception to this rule occurs when the metric of interest is survivorship of type 1 hosts and the density of types 3 and 4 hosts is not too large.

Next, we consider the impact of varying mosquito feeding preference by comparing the impact of increasing the feeding preference for high-competence (type 2) hosts to that of increasing the feeding preference for low-competence (type 4) hosts. Biologically, perturbations of feeding preference reflect the influence of the environment (e.g., humidity) and mosquito species on foraging behavior. In this case, increasing the preference of mosquitoes for the less competent host (host type 4) is the most effective means of improving epidemic metrics. In fact, each metric saturates relatively quickly with respect to this parameter value. However, it should be noted that gains in survivorship of type 1 hosts and the basic reproduction number are limited by the presence of horizontal transmission in type 1 hosts.

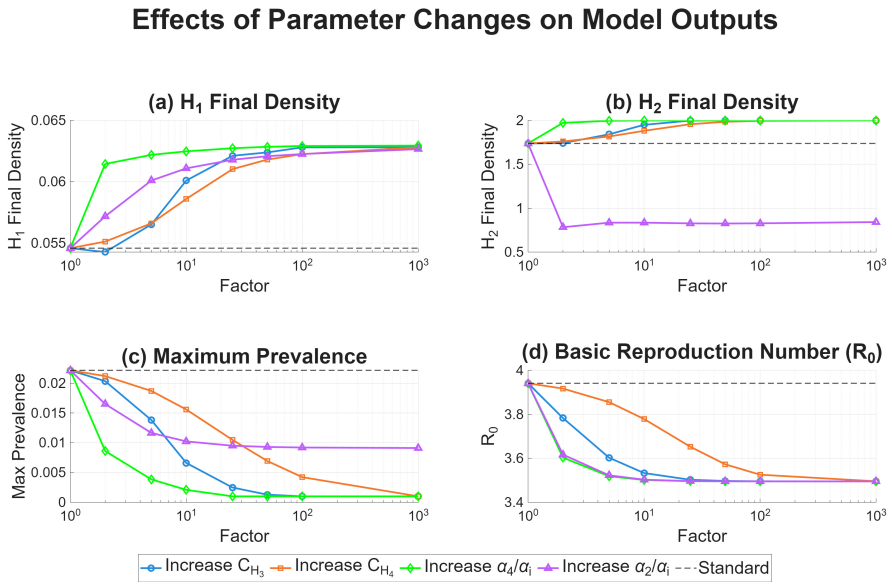


Figure 7. Sensitivity of epidemic metrics to systematic parameter variation. The final density of host types is reported five years after the beginning of the epidemic. The standard metric values (black dashed line) are those for the less urban community. The points represent simulation results. Simulation data points are connected with lines to demonstrate trends.

In summary, these experiments indicate that altering mosquito foraging behavior is the most effective way to improve epidemic metrics. While low-competence hosts have the potential to act as epidemic diluters, their capacity to improve epidemic metrics is context dependent and potentially influenced by mosquito feeding preference and absolute host density in a complex way.

5. Conclusions

This work developed a multihost model structure for WNV which allows for multiple transmission routes (vertical transmission in mosquitoes, horizontal transmission in hosts, and vector-host transmission) and mosquito feeding preference. We began with a characterization of the model basic reproduction number: We provided an explicit formula for the basic reproduction number in the case of a single competent host, thereby extending the results in [9,12,28] and a recursive formula for computing the characteristic polynomial of the next-generation matrix in the n-host case. In addition, we proved that reclassifying dead-end hosts as competent for mosquito-host transmission can only increase the basic reproduction number. The impact of low-competence hosts on the basic reproduction number is of interest from a modeling methodology perspective since low-competence hosts are often neglected or treated as dead-end hosts to reduce model complexity. From a biological perspective, this theoretical result emphasizes that even low-competence hosts can increase the risk of an epidemic.

Next, we considered model parameterization. In Appendices A and B, we provide parameter values and results of our research on parameterization for an urban environment in the northern US or Canada. Data from Clergeua et al. [29] was used to capture variability of the avian host community structure with the level of urbanization. As structured, the less urban community has a Shannon diversity index

of 1.3618. That of the more urban community is lower, 0.9188, owing to the distribution of hosts being heavily weighted toward house sparrows in the more urban setting. This difference in community structure results in a less severe but longer lasting epidemic in the more urban community. The two communities also respond differently to the omission of horizontal transmission in type 1 hosts, with the more urban community experiencing a larger reduction in both the basic reproduction number (about 45% of the baseline value in the more urban community vs. about 60% of the baseline value in the less urban community) and the maximum prevalence of infectious mosquitoes (about 37% of the baseline value in the more urban community vs. about 44% of the baseline value in the less urban community). This suggests that despite the lower absolute abundance and prevalence of type 1 hosts in the more urban community, horizontal transmission accounts for a larger fraction of the WNV epidemic risk in that community as measured by these two metrics.

The appendix also includes a discussion of challenges and resources for parameterizing the model, including mosquito feeding preference. An interesting conclusion of our findings is that while it is difficult, if not impossible, to quantify the relative feeding preference of a mosquito species for two hosts, available data can be useful for ranking hosts according to mosquito feeding preference. Given the challenge of parameterizing mosquito feeding preference, a future direction of research related to model parameterization is to consider model-aided approaches to compensating for incompleteness of the host and vector census data. Model-based methods have been used previously in the context of disease epidemics to study the prevalence of undetected infections [30]. A second outcome of this research is a proposal to stratify competent hosts into four categories: Type 1 hosts represent birds of the family Corvidae, e.g., American crows and blue jays, which are depicted as highly competent for horizontal and mosquito-host WNV transmission, highly vulnerable to WNV-induced mortality, and preferred by mosquitoes. Type 2 hosts represent house sparrows, which are depicted as highly competent for mosquito-host transmission, highly vulnerable to WNV-induced mortality, and avoided by mosquitoes. Type 3 hosts represent native passerine birds, e.g., American robins and cardinals, which are described as moderately competent for mosquito-host transmission, invulnerable to WNV-induced mortality, and preferred by mosquitoes. Finally, type 4 hosts represent other birds of low-competence for WNV transmission, including rock pigeons, starlings, and mourning doves, which are additionally treated as being invulnerable to WNV-induced mortality and avoided by mosquitoes.

Numerical simulations were then used to study the impact of common model variations on the severity of a WNV epidemic for two ecologically feasible parameterizations representing differing levels of urbanization. We found that in both the more and less urban communities, horizontal transmission in type 1 hosts accounted for more than half the value of the basic reproduction number and accentuated community-specific differences in risk. On the other hand, neglecting transmission by hosts with low (type 4) or moderate (type 3) competence had minimal impact on the basic reproduction number. Meanwhile, neglecting these hosts altogether resulted in a moderate increase in the basic reproduction number. Similarly, only horizontal transmission in type 1 hosts had a sizable impact on the five-year survivorship of vulnerable hosts, and that impact was limited to type 1 hosts. In contrast, when assessing the risk of spillover infections via maximum prevalence of infectious mosquitoes, we found transmission from type 3 hosts can have a considerable impact. In summary, these results suggest that horizontal transmission may have a large impact on all epidemic metrics, and hence, should not be excluded from WNV models. Moreover, when limiting model complexity is a priority, neglecting the competence of low-competence and moderate-competence hosts may be preferable to eliminating these hosts from the

model altogether. Finally, if assessing the risk of spillover infections is a modeling objective, it may be important to account for transmissions through preferred hosts (in this case, native passerine birds) regardless of their level of competence.

Lastly, we assessed the sensitivity of epidemic metrics to select parameters in order to determine the potential for (i) hosts with low or moderate competence and (ii) mosquito feeding preference to dilute the epidemic. Despite having higher competence, we found that, likely due to its attractiveness to mosquitoes, increasing the abundance of host type 3 (which encompasses moderately competent native passerine birds like robins) is generally more effective than increasing the abundance of the very low-competence host type 4 at improving epidemic metrics. This result is interesting since birds such as robins and northern cardinals are often treated as WNV amplifiers [13, 19, 31]. The finding that type 3 hosts can act as effective diluters of a WNV epidemic suggests that the impact of a species is determined by many factors, including the relative competence of that species within the host community and mosquito feeding preference. As a result, care should be taken when classifying species as epidemic diluters or amplifiers within a specific community. Nevertheless, driving mosquitoes to feed on low-competence host type 4 by increasing α_4 was by far the most effective means of improving the epidemic metrics, that is, diluting the epidemic. This result confirms and strengthens the conclusions of related works wherein analyses of less complex models [16, 31] also identified mosquito feeding preference as a critical determinant of WNV epidemic risk. The sensitivity of the epidemic metrics to mosquito feeding preference leads to a recommendation that efforts to forecast and control risk should focus on mosquito feeding preference. Because mosquito feeding preference can vary significantly with environmental conditions [32, 33] and in response to seasonal changes in the availability of hosts [34], the sensitivity of metrics to mosquito feeding preference may be a predominant source of uncertainty in WNV risk forecasting. On the other hand, feeding preference presents itself as a high-valued target for WNV risk management, and tactics like barrier zones which limit the access of mosquitoes to highly competent host species are predicted to be highly efficient at limiting WNV risk [35].

Although we have taken care to achieve results that are ecologically relevant and reflective of modeling norms, it is important to consider the limitations of our methods when interpreting our results. For example, we neglected WNV-induced mortality in host types 3 and 4. While this simplification is motivated by data on experimentally infected birds from Komar et al. [21], the authors of that study noted that stress associated with WNV infection likely increases mortality rates in non-captive birds. Similarly, our model does not include inter-group competition or horizontal transmission between host types. In addition, while varying mosquito feeding preference can serve as a proxy for varying environmental conditions or mosquito species, this work focuses on a single mosquito species and does not explicitly link parameters to environmental conditions. Perhaps most importantly, our model is parameterized to describe WNV transmission during the breeding season in the northern US and Canada. As such, the model does not include seasonal forcing in recruitment or death of mosquitoes or hosts, and model simulations are not expected to accurately represent real-world epidemic dynamics beyond the breeding season. Nevertheless, some long-term simulations were included to indicate potential long-term dynamics and characterize the model's asymptotic behavior. Incorporating seasonal forcing into the model is a topic of interest for future work. Despite these limitations, we hope that the findings reported here can benefit model-aided WNV control and management and inform future theoretical work on modeling of vector-borne disease.

Use of AI tools declaration

The authors declare they have not used artificial intelligence (AI) tools in the creation of this article.

Conflict of interest

The authors declare there is no conflict of interest.

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Appendix

A. Parameter values and sources

Table A1. Mosquito parameter values used in the simulations. (adapted from [12]).

Parameter	Description	Value	Reference
b	Mosquito biting rate	$\frac{1}{5}$ day^{-1}	[36]
P_{MH}	Mosquito-to-host transmission probability	1	[7, 13, 36]
-	Eggs per raft	150	[7]
-	Length of *Culex* gonotrophic cycle	8 days	[37]
r_S	Average susceptible/exposed egg-depositing rate	$75/8$ $\frac{\text{eggs}}{\text{mosquito} \cdot \text{day}}$	composite parameter
r_I	Average WNV-infected egg-depositing rate	$50/8$ $\frac{\text{eggs}}{\text{mosquito} \cdot \text{day}}$	composite parameter
m_E	Rate eggs hatch into larvae	$\frac{1}{2}$ day^{-1}	[38, 39]
m_L	Susceptible and infected larvae maturation rate	$\frac{1}{7}$ day^{-1}	[38, 39]
q_S	Fractions of susceptible eggs that hatch	0.56	[7]
q_I	Fraction of exposed eggs that hatch	0.43	[7]
ϕ	Fraction of exposed larva that are infected	0.003	[40]
d	Density dependent larval death rate	7.4971 day^{-1}	composite parameter
C_L	Mosquito larval carrying capacity	100 $\frac{\text{indv}}{\text{ha}}$	[41, 42]
μ_M	Adult mosquito natural mortality rate	$\frac{1}{10.4}$ day^{-1}	[37]
μ_L	Larva natural mortality rate	0.16 day^{-1}	[36, 43]
k_L	Disease progression rate in vectors	$\frac{1}{10}$ day^{-1}	[7]

Table A2. Parameter values for type 1 hosts, vulnerable amplifiers with horizontal transmission, used in the simulations. * See Appendix B for details. ** When parameter values differ between the less and more urban simulations, the value used in the less urban simulation is given first and that for the more urban simulation appears in parentheses.

Parameter	Description	Less (More)** urban value	Reference
P_{H_1M}	Host-to-mosquito transmission probability	0.68	[21]
γ_{H_1}	WNV-induced mortality rate	0.2114 day^{-1}	[21]
g_{I_1}	WNV recovery rate	0.06906 day^{-1}	*
C_{H_1}	Carrying capacity	1 (0.25) indv ha^{-1}	*
d_{H_1}	Density-dependent mortality rate	4.1096×10^{-4} day^{-1}	*
μ_{H_1}	Natural mortality rate	14.00×10^{-4} day^{-1}	[44]
Λ_{H_1}	Per capita birth rate	18.10×10^{-4} day^{-1}	*
α_1	Parameter controlling biting preference	1	*
ω_1	Maximal horizontal transmission rate	0.9864 day^{-1}	*

Table A3. Parameter values for type 2 hosts, vulnerable amplifiers without horizontal transmission, used in the simulations. * See Appendix B for details. ** When parameter values differ between the less and more urban simulations, the value used in the less urban simulation is given first and that for the more urban simulation appears in parentheses.

Parameter	Description	Less (More)** urban value	Reference
P_{H_2M}	Host-to-mosquito transmission probability	0.53	[21]
γ_{H_2}	WNV-induced mortality rate	0.2114 day^{-1}	[21]
g_{I_2}	WNV recovery rate	0.2100 day^{-1}	*
C_{H_2}	Carrying capacity	2 (5) indv ha^{-1}	[29]
d_{H_2}	Density-dependent mortality rate	8.219×10^{-4} day^{-1}	*
μ_{H_2}	Natural mortality rate	14.00×10^{-4} day^{-1}	[44]
Λ_{H_2}	Per capita birth rate	22.21×10^{-4} day^{-1}	*
α_2	Parameter controlling biting preference	0.1	*
ω_2	Maximal horizontal transmission rate	0 day^{-1}	*

Table A4. Parameter values for type 3 hosts, invulnerable amplifiers, used in the simulations. * See Appendix B for details. ** When parameter values differ between the less and more urban simulations, the value used in the less urban simulation is given first and that for the more urban simulation appears in parentheses.

Parameter	Description	Less (More)** urban value	Reference
P_{H_3M}	Host-to-mosquito transmission probability	0.36	[21]
γ_{H_3}	WNV-induced mortality rate	0 day^{-1}	[21]
g_{I_3}	WNV recovery rate	0.3333 day^{-1}	[21]
C_{H_3}	Carrying capacity	2 (1) indv ha^{-1}	[29]
d_{H_3}	Density-dependent mortality rate	4.301×10^{-4} day^{-1}	*
μ_{H_3}	Natural mortality rate	14.00×10^{-4} day^{-1}	[44]
Λ_{H_3}	Per capita birth rate	18.30×10^{-4} day^{-1}	*
α_3	Parameter controlling biting preference	1	*
ω_3	Maximal horizontal transmission rate	0 day^{-1}	[21]

Table A5. Parameter values for type 4 hosts used in the simulations. * See Appendix B for details. ** When parameter values differ between the less and more urban simulations, the value used in the less urban simulation is given first and that for the more urban simulation appears in parentheses.

Parameter	Description	Less (More)** urban value	Reference
P_{H_4M}	Host-to-mosquito transmission probability	0.1	*
γ_{H_4}	WNV-induced mortality rate	0 day^{-1}	*
g_{I_4}	WNV recovery rate	1 day^{-1}	*
C_{H_4}	Carrying capacity	2 (1) indv ha^{-1}	*
d_{H_4}	Density-dependent mortality rate	8.219×10^{-4} day^{-1}	*
μ_{H_4}	Natural mortality rate	14.00×10^{-4} day^{-1}	[44]
Λ_{H_4}	Per capita birth rate	22.21×10^{-4} day^{-1}	*
α_4	Parameter controlling biting preference	0.1	*
ω_4	Maximal horizontal transmission rate	0 day^{-1}	*

Table A6. Parameter values for dead-end hosts used in the simulations. * See Appendix B for details.

Parameter	Description	Value	Reference
N_D	Carrying capacity	70 indv ha^{-1}	*
α_D	Parameter controlling biting preference	0.05	*

B. Parameters explained

Model parameterization can be challenging. First, the model is a simplification of reality; hence, some model parameters do not exactly correspond to any real-world quantity. For example, the model assumes a constant per-capita death rate for hosts and mosquitoes. In reality, the probability of death varies with age. Despite this challenge, many parameters can be reasonably estimated by choosing values that are consistent with measurable scalars. For example, the per capita death rate can be selected to match empirically measured average life expectancies. Second, many parameters, like mosquito larval density and mosquito feeding preference are simply difficult to measure, and available data may be insufficient to confidently determine a quantitative parameter value or range. In such cases, it is sometimes possible to normalize parameters in a way that allows for a rough parameterization based on qualitative comparisons. This approach is adopted to parameterize mosquito feeding preferences below. In the face of parameter uncertainty, empirically verified model outputs like the maximum prevalence of infection in the mosquito population can provide evidence to support or reject a parameterization.

One of the most uncertain parameters in the model is the density of mosquitoes which, by model construction, is determined by the larval environmental carrying capacity. In previous work [12], we provided some estimates and sources for larval carrying capacity. In this work, we use a larval carrying capacity of 100 $\frac{\text{indv}}{\text{ha}}$. This choice yields a mosquito density of about 149 $\frac{\text{indv}}{\text{ha}}$. The mosquito density employed here is somewhat larger than that estimated via trapping in [19]. Figure 3 of [19] gives a maximal mosquito density of about 3750 $\frac{\text{indv}}{4\text{km}^2}$ or just 9 $\frac{\text{indv}}{\text{ha}}$. We believe that the larger mosquito density used here is nevertheless ecologically feasible over a small region with favorable breeding conditions: The study region in [19] was composed primarily of agricultural land, and *C. pipiens* mosquitoes are known to prefer urban environments, for which our model was parameterized. Indeed, a study of the Emilia-Romagna region of Italy [45], which has an average population density consistent with the European Commission's definition of a town [46] and includes the large city of Bologna, estimated the maximum *C. pipiens* mosquito density to be several times higher than the value used here. In summary, the mosquito density used here appears to be moderate and within the range of values measured elsewhere.

A downstream model output, the maximum prevalence of infection in mosquitoes, supports the ecological relevance of our parameter choices and simulations. For example, the maximum prevalence of infection in mosquitoes in our baseline model simulations (more urban: 2.22%, less urban: 0.74%) is similar to, though somewhat higher than, the maximum percent prevalence estimated from data in [45] for the Emilia-Romagna region of Italy (0.8%). Similarly, [47] reports WNV prevalence in *Culex* species ranging from 0% to 0.334% across six collection sites in St Tammany Parish, Louisiana. Note, however, that these WNV percent prevalence values were reported per site using data collected between June and October, not through time, so peak prevalence, which was not reported in that study, would have been higher. Finally, [48] reports WNV prevalence in mosquitoes (measured as the minimum infection rate)

varied widely between collection sites, from 0.07% to 5.7%, during the New York epidemic of 1999. As parameterized, our model yields prevalence of infection values that are relatively high but within the range of empirically measured values. Our baseline simulations can be considered to represent a relatively severe though ecologically feasible WNV epidemic.

The following sections discuss parameterization of the multihost model, including mosquito feeding preference. Please see [12] for a discussion of other mosquito-associated parameters.

B.1. Mosquito feeding preference

In the ecological and entomological literature, mosquito biting preference is often quantified by forage ratios, which give the ratio of the portion of mosquito blood meals taken from a host species to the relative abundance of the host species [34]. Mosquitoes are known to exhibit preferential feeding based on host class (e.g., preference for avian versus mammalian hosts) [31, 49–51]. For instance, a study of *Culex quinquefasciatus* in Yucatan, Mexico, found that these mosquitoes exhibit a clear preference for avian versus mammalian hosts, with the average forage ratio for avian hosts being approximately ten times that of mammals [52]. At the same time, mosquitoes are also known to exhibit opportunistic feeding behavior, wherein availability of host species influences the distribution of blood meals among species. For example, a study of *Culiseta melanura* mosquitoes found that these mosquitoes, which usually remain within their breeding area, will fly as far as 2 km in response to high mosquito densities (presumably due to increased competition for hosts) or favorable weather conditions [35]. Since host abundance varies in space, changes in mosquito dispersal patterns will likely impact forage ratios. In another study, high moisture levels permitted ornithophilic mosquitoes living in wooded areas to access mammalian hosts located in fields [33]. Host behavior can also impact mosquito feeding patterns; some avian and mammalian species are thought to be more tolerant of mosquitoes than others [33, 49, 53].

We assume the proportion of bites falling on a host of type j is

$$p_j = \frac{\alpha_j H_j}{\sum_k \alpha_k H_k}, \tag{A.1}$$

where H_k denotes the absolute number of hosts of type k. Note here that $\alpha_D N_D$ is also incorporated into the sum in the denominator. That is, dead-end hosts are included in this calculation. We set $\max_k \{\alpha_k\} = 1$, so that the most attractive host has an attractiveness of 1. This functional form has been used frequently to model host feeding preference [9, 16, 18].

Estimates of host-specific forage ratios, F_j, relative host abundance, $R_j = \frac{N_{H_j}}{N_H}$, and total density of host species, N_H, enable estimation of α_j. In particular,

$$F_j = \frac{p_j}{R_j} = \frac{\alpha_j}{\sum_k \alpha_k R_k}. \tag{A.2}$$

Note that in this model, as the relative abundance of host j increases to one, the proportion of bites falling on host j approaches one. Similarly, as relative abundance of host j decreases to zero, the proportion of bites falling on host j falls to zero. The forage ratio for a host also varies with relative abundance, but unlike the proportion of bites, the forage ratio for host j is maximized when the population is dominated by the least attractive host (as quantified by α_k), and minimized when the population is dominated by the

most attractive host. The modeled dependence of the forage ratio on relative host abundance, provides a potential explanation for observed variation in forage ratios between studies [34]. In addition, this model implies that in the case of two hosts, the proportion of bites on the preferred hosts is concave down as a function of the relative abundance of that host in the total host population, as in [51]. On the other hand, the pairwise ratio $\frac{F_j}{F_k}$, or host feeding index of host j relative to host k [52], is constant in this model, which is convenient for model parameterization. In fact,

$$\frac{F_j}{F_k} = \frac{\alpha_j}{\alpha_k}. \tag{A.3}$$

As our interest is in modeling WNV transmission in an urban setting, we focus our attention on *C. pipiens* and *C. quinquefasciatus* mosquitoes since these mosquitoes are important vectors for WNV transmission [21, 34] which can be found in urban areas [54]. Whereas *C. pipiens* prefer urban areas of the northern US and Canada, *C. quinquefasciatus* is well-suited for warmer regions of the southern US and Mexico. These mosquitoes may also differ in their feeding behaviors. *C. quinquefasciatus* is regarded as a generalist that readily feeds on mammal and avian hosts while *C.pipiens* is considered to be more ornithophilic. For the purpose of selecting model parameters, we turn our attention to the northern US and Canada and select values that are appropriate for *C. pipiens* mosquitoes. In addition, as *C. pipiens* mosquitoes are present in multiple types and known to hybridize to produce types with intermediate feeding preferences [51], for concreteness, we focus our attention on *C. pipiens* form *pipiens* mosquitoes.

While α values could, in theory, be assigned based on measured forage ratios, for several reasons, data are lacking for the accurate quantitative estimation of α_k for all host categories considered here. First, it is difficult to reliably measure forage ratios: It is challenging to measure the relative abundance of hosts within a given region of interest because detectability varies between species [13]. Moreover, the accessibility of a host is likely subject to distance-dependence and environmental effects that are nonuniform in space and time [34, 35]. While some research supports the idea that the distribution of blood meals among hosts is heavily influenced by host proximity [34, 52], the ability of *Culex* mosquitoes to travel as far as 1 km per day complicates measures of host abundance. Second, because studies of *C. pipiens* biting preference often neglect mammal surveys [55, 56], it is not possible to directly estimate α values from available field studies. Nevertheless, avian forage ratios and mammal feeding counts provide a rough means of comparing host attractiveness. In addition, a controlled study where *C.pipiens* form *pipiens* mosquitoes were provided a choice of feeding on chickens or humans allows us to estimate $\frac{\alpha_D}{\alpha_4} \approx 0.2$ [32]. In general, values of α employed here are selected to qualitatively reflect the relative preference of mosquitoes for hosts.

B.2. Host community composition and urbanization

We consider two scenarios representing WNV epidemics in i) a highly urban residential area where 30% of land cover is vegetative and 40% of land cover is buildings and ii) a less urban residential area where 70% of land cover is vegetative and 15% of land cover is buildings. These scenarios are based on a study of bird abundance and diversity in residential areas of Quebec [29]. Hosts are characterized according to competence, attractiveness, mortality rate, intrinsic growth rate, and the propensity for horizontal transmission.

Hosts with low competence have the potential to dilute WNV transmission. Low competence is often a result of low or short-lived viremia [21]. A study of WNV infection in diverse bird species supports the idea that WNV-induced mortality and the propensity for horizontal transmission are inversely related to competence [21]. For simplicity, we suppose low-competence hosts experience no WNV-induced mortality and no horizontal transmission. Because low-competence hosts do not experience WNV-induced mortality in our model, their carrying capacities and intrinsic growth rates have no impact on the epidemic's dynamics.

Hosts with high competence have the potential to amplify WNV transmission. Because our model focuses on mosquito species which are important for WNV transmission, highly competent hosts tend to be attractive to mosquitoes in this model. We note, however, that some species, such as the American crow, might be an exception to this rule. Similarly, the life history of highly competent hosts varies considerably between species, with urban-adapted birds tend to have higher intrinsic rates of increase than less urban-adapted birds.

In the following paragraphs, we describe each host category and its parameter estimates.

B.3. Vulnerable amplifiers with horizontal transmission

These hosts exhibit high WNV competence, high levels of WNV-induced mortality, and horizontal transmission. Species that might fall into this category include birds in the Corvidae family such as the American crow and the blue jay [21,49,57]. Since multiple studies suggest that American crows are not a preferred source of blood meals for *C. pipiens* complex and *C. pipiens* mosquitoes [34], we focus our attention on blue jays, which might be attractive hosts for *C. pipiens* mosquitoes [55]. Assuming this is the case, we set $\alpha_1 = 1$ for these hosts.

We were unable to find an estimate of the intrinsic rate of increase for a blue jay population in a residential area. However, [44] provides rough estimates of intrinsic growth rates for small altricial birds according to life history. Assuming blue jays reach sexually maturity at 1 year of age, and have one brood of about four eggs per year [58], we set $d = \Lambda - \mu = 0.15$ per year for this host category. The mean average survival rate for adult blue jays was estimated in [59] as 0.54. Since this rate likely includes density-dependent effects, for model parameterization, we use a higher mean annual survival rate of 0.6, which reflects assumed survial rates in [44], and set $\mu = -\ln 0.6 = 0.5108$ per year.

We suppose that this host category is not well-adapted to highly urban environments, and hence, absent in the highly urban simulation. In the less urban simulation, assuming this bird is prevalent, with a density similar in magnitude, but somewhat lower than that of that observed for the American robin in well vegetated areas of Quebec [29], we set the density for this host category to $C = 1$ birds per ha. We set the density of this host class to $C = 0.25$ birds per ha in the highly urban simulation.

Parameters related to competence and mortality for this host category were based on data on the blue jay in [21]. The probability of transmission from mosquito to host is set to 1, $P_{MH} = 1$. The probability of transmission from host to mosquito is $P_{HM} = 0.68$. The mean number of days until death post inoculation for blue jays was 4.7, so $\mu + \gamma = \frac{1}{4.7}$ per day for this host category. The mean duration of infectiousness for blue jays in [21] was 3.75 days. However, this value may be truncated since the majority of blue jays did not survive the infection. For this reason, we select the mean duration of infectiousness, which is equivalent to the mean time to recovery in our model, so that the WNV-induced

mortality rate of blue jays matches that in [21], 75%. That is, $\frac{\gamma}{g+\gamma+\mu} = 0.75$. This gives $g = 0.06906$ per day. In [21], the horizontal transmission rate in blue jays was 100%. Although the sample size in this study was too small to accurately infer a transmission probability ($N = 2$ infected/healthy bird pairings), the result does suggest that horizontal transmission is efficient in select birds. We suppose that an infectious bird in this category will succeed at infecting 70% of its contacts. Since this model describes WNV transmission in a breeding population, the number of contacts per bird is selected to match the average size of a blue jay family group, 6. Therefore, ω is estimated according to: $3.5 = \frac{\omega}{\gamma+\mu+g}$. The resulting value of ω, 0.964 day^{-1}, is somewhat higher than the daily transmission rates used in [22] and [23], approximately 0.3 day^{-1}, but within the range of reported horizontal transmission rates for birds [22].

B.4. Vulnerable amplifiers without horizontal transmission

These hosts exhibit high WNV competence, high levels of WNV-induced mortality, low attractiveness, and no horizontal transmission. This host category is modeled on the house sparrow, which is highly adapted to urban life and present at high densities in urban areas [29]. We selected densities for this host category to be within the range of densities reported in [29] for the house sparrow. The carrying capacity for this host category is taken to be 5 birds per ha in the highly urban simulation and 1 bird per ha in the less urban simulation.

We set the intrinsic rate of increase for house sparrows to $d = \Lambda - \mu = 0.3$ per year [60]. We suppose density-independent death rates for house sparrows are similar to those of blue jays and set $\mu = -\ln 0.6 = 0.5108$ per year.

Data suggest that *C. pipiens* mosquitoes are not attracted to house sparrows [55]. We set $\alpha = 0.1$ for this host category.

Parameters related to competence and mortality for this host category were based on data on the house sparrow in [21]. The probability of transmission from mosquito to host is set to 1, $P_{MH} = 1$. The probability of transmission from host to mosquito is $P_{HM} = 0.53$. We suppose this host is not subject to horizontal transmission ($\omega = 0$). In [21], the mean number of days until death for house sparrows was the same as that for blue jays, 4.7, so we set $\gamma + \mu = \frac{1}{4.7}$. The mean duration of infectiousness for house sparrows in [21] was 3 days. However, this value may be truncated since many house sparrows did not survive the infection. For this reason, we select the mean duration of infectiousness, which is equivalent to the mean time to recovery in our model, so that the WNV-induced mortality rate of house sparrows matches that in [21], 50%. That is, $\frac{\gamma}{g+\gamma+\mu} = 0.5$.

B.5. Invulnerable amplifiers

This category represents native passerine hosts that are fed on preferentially by mosquitoes ($\alpha \approx 1$), have low WNV-induced mortality, high WNV competence, and no horizontal transmission ($\omega = 0$). Species that might fall into this category include American robins, northern cardinals, and northern mockingbirds [21, 49, 57].

We suppose that birds in this category prefer vegetated areas and hence less abundant in highly urban areas. For example, in [29], American robins were mostly found in less built-up residential areas with ample vegetation. We will also suppose that this host category is dominated by a small number of species

with similar abundance to the American robin and set this host category's density to 4 birds per ha in the less urban setting and 1 birds per ha in the more urban setting. In this way, the abundance of invulnerable amplifiers complements that of vulnerable amplifiers along an urbanization gradient in this model.

Birds in this host category are assumed to experience much lower rates of WNV-induced mortality than house sparrows and birds of the Corvidae family [21]. For simplicity, we suppose birds in this category do not experience any WNV-induced mortality ($\gamma = 0$).

The population growth rate for American robins in wild and rural habitats was measured in [61]. In the most favorable habitat considered, the annual population growth rate was 1.17. Although population growth rate estimates from [61] were intended for comparison between habitats and species rather than prediction of population growth, in the absence of a more accurate estimate, we use this value to parameterize our model. Specifically, setting $1.17 = e^{\Lambda-\mu}$, we find $\Lambda - \mu = 0.1570$ per year. Note this value is almost identical to that assumed for blue jays. We suppose the density-independent death rate for invulnerable amplifiers is similar to that of blue jays and set $\mu = -\ln 0.6 = 0.5108$ per year.

We suppose birds in this category and blue jays are similarly attractive to mosquitoes. We set $\alpha = 1$ for this host category.

Parameters related to competence and mortality for this host category were based on data on the American robin [21]. The probability of transmission from mosquito to host is 1, $P_{MH} = 1$, for all host categories. The probability of transmission from host to mosquito is moderate; $P_{HM} = 0.36$. We assume this host is not subject to horizontal transmission ($\omega = 0$) or WNV-induced mortality ($\gamma = 0$). The mean duration of infectiousness for the American robin is [21] was three days, so we set $g = \frac{1}{3}$ per day.

B.6. Low-competence hosts

This category represents birds with very low WNV competence. Low competence is often a result of low or short-lived viremia [21]. Examples of bird species in this host category are rock pigeons, mourning doves, and European starlings [13, 21, 55, 56].

In consideration of reported spring densities of rock pigeons, European starlings, and mourning doves [29], we set $C_H = 2$ birds per ha for this bird category in the less urban simulation and $C_H = 1$ in the highly urban simulation. These densities were chosen to reflect the idea that, taken together, the birds in this category may achieve a population density that is similar in magnitude to that of the American robin, which is supported by bird surveys in [55, 56]. The comparatively higher density in the less urban simulation is motivated by the idea that mourning doves and European starlings will prefer urban areas with ample vegetative land cover. For example, European starlings require open grassy areas to forage [62], and maximal European starlings densities in [29] were observed in a neighborhood with about 53% vegetative land cover. Moreover, while rock pigeons can obtain extremely high densities in areas with little to no vegetation, as described above, evidence suggest these birds have more modest densities in residential areas like those considered here [29, 55, 56]. Hence, rock pigeons are not likely to alter the ratio of bird densities for the two scenarios considered here.

Since rock pigeons and mourning doves have multiple broods per year [63, 64], we expect birds in this category to have high intrinsic rates of increase on average. We set the demographic parameters for birds in this category to match those selected for the house sparrow: $d = \Lambda - \mu = 0.3$ per year and $\mu = -\ln 0.6 = 0.5108$ per year.

Data suggest many birds in this host category are not preferred sources of mosquito blood meals [55, 56]. We suppose these birds are similarly attractive to house sparrows and set $\alpha = 0.1$.

Following [21], we set the probability of transmission from mosquito to host to 1, $P_{MH} = 1$, for all competent host categories. A study of WNV infection in diverse bird species supports the idea that WNV-induced mortality and the propensity for horizontal transmission are inversely related to competence [21]. For simplicity we suppose low-competence hosts experience no WNV-induced mortality ($\gamma = 0$) and no horizontal transmission ($\omega = 0$). Since this composite category represents hosts with very low competence, we suppose the probability of transmission from host to mosquito is very low, $P_{HM} = 0.1$, and the the mean duration of infectiousness is short, lasting only one day, $g = 1$ per day. These values are consistent with ranges in [21] for hosts of low competence. For example, the proportion of mosquitoes infected after feeding on rock pigeons, starlings, and mourning doves ranged from 0 to 0.12 in that work, and the mean duration of infectiousness for these species ranged from 0 to 1.8 days.

B.7. Dead-end hosts

This host category represents mammals. The extent to which *C. pipiens* mosquitoes utilize mammals as hosts varies between studies, with some studies showing *C. pipiens* mosquitoes readily utilize mammal hosts [55], and others suggesting mammals are only incidental hosts for this mosquito species [56]. We assume this category of hosts is abundant, including humans, companion animals, and ample numbers of small mammals, such as gray squirrels. We set the density of this host category to 70 hosts per ha in both the less urban and highly urban simulations. For comparison, see [65] for estimates of gray squirrel densities and [66] for a sample human density in one of the neighborhoods surveyed in [56].

Although utilization of mammalian hosts by *C. pipiens* mosquitoes varies between studies, these mosquitoes are ornithophilic. For example, in [55], avian blood meals were almost five times as numerous as mammalian blood meals, and in [56], mammals were only incidental hosts for *C. pipiens*. Since residential areas dominated capture sites in the aforementioned studies, it seems likely that mammals would have been at least as prevalent as birds. Hence, data suggest that mammals are not attractive hosts to *C. pipiens* mosquitoes. For these reasons, we set $\alpha = 0.05$ for this category of hosts, meaning mammals are about half as attractive as the least attractive avian host in this model.

Following [21], we set the probability of transmission from mosquito to host to 1 for all host categories, $P_{MH} = 1$. Since this composite category represents hosts with very low competence, we suppose the probability of transmission from host to mosquito is very low and set $P_{HM} = 0.05$. For the same reason, we suppose the mean duration of infectiousness is short and set $g = 1$ per day. See [21] for sample competence-related parameter values in avian hosts with very low competence.