Exploration of the Impact of Complex Host Dynamics on a West-Nile Virus Epidemic

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DEDICATION

I would like to dedicate this work to George Stubblefield, my nephew. He began the journey of life just as I was beginning the journey that has lead me here.

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ABSTRACT

In this project, we use mathematical modeling and optimal control to study the implications of variable host competency and host demographics on a West Nile virus epidemic with the primary objective being to determine how horizontal transmission in birds and variable bird competency impacts the model reproduction number and endemic steady-sates(s). The model uses ordinary differential equations to describe the transmission of the virus between birds and mosquitoes, vertical transmission in mosquitoes, horizontal transmission in birds, the mosquito life cycle, and bird demographics. Previous work, which focused on mosquito dynamics, demonstrated the choice of objective functional can significantly impact the optimal control and its impact on the mosquito population. However, due to the simplistic treatment of the bird demographics, these conclusions were limited to the late summer and early fall. Moreover, previous work did not consider the impact of variable host competency on the epidemic and its control. Here, we formulate and parameterize a model including bird recruitment and two bird types which are thought to be important for West Nile virus maintenance and transmission: Corvides (e.g. crows and jays) and Passerides (e.g. sparrows, wrens and buntings). We investigate how the incorporation of multiple bird types impacts the model reproduction number using the next-generation-matrix method and investigate the existence of endemic steady states.

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CHAPTER 1

INTRODUCTION

West Nile virus (WNV) is a mosquito-borne viral infection maintained in a cycle between mosquitoes and hosts. The Culex mosquitoes species are the predominant vector of WNV in North America [15, 16], and birds are the predominant hosts. Indeed a wide variety of bird species are impacted by the disease and species differ widely in competency for WNV transmission and mortality rate. Bird species with limited mobility or that are endangered are especially vulnerable to WNV [14]. After its introduction to North America in 1999, numerous bird species, especially those belonging to the Corvid clade, experienced significant WNV-associated population decline [14, 12]. However, recent evidence suggests that some species, American crows in particular, are in a period of recovery [11, 21]. In light of changing bird demographics and the persistent threat of spill-over infections in humans [5, 8, 7] we explore the impact of bird demography on a WNV epidemic.

Management of mosquito populations is an important tool for controlling WNV outbreaks so as to minimize WNV transmissions. Modeling the dynamics of WNV is necessary to understand how transmission occurs and how WNV can be controlled. Previously [2], we studied the problem of WNV control via pesticides using a model that included three-mosquito life stages, vertical transmission in mosquitoes, and transmission between mosquitoes and birds. The detailed treatment of mosquitoes was motivated by a desire to evaluate the impact of adult- and larvae-specific pesticides on a WNV epidemic. In this paper, we extend the previous model to include multiple host types, host demography, and horizontal transmission in hosts, to evaluate the impact of varying host competency and mortality on the risk, timing, sustainability, and magnitude of a WNV epidemic. Specifically, the model reproduction number is used to predict the likelihood of an outbreak and numerical simulations are used to study the outbreak magnitude and timing. As such, specific goals of this work are to develop a method for computing the model's basic re-

production number, to numerically explore the existence of endemic steady-states, and to characterize the impact of host heterogeneity on a WNV epidemic through variation of host parameters and comparison to the single-host case.

CHAPTER 2

MODEL FORMULATION

This model describes the dynamics of a West Nile virus (WNV) epidemic in a population consisting of bird hosts and female mosquitoes. The bird population is divided into j host compartments, based on competency and susceptibility. Each compartment is subdivided into three classes according to their disease status. These classes are susceptible birds, $H_{S_j}(t)$, birds that are infectious with the WNV, $H_{I_j}(t)$, and birds that have recovered and are no longer susceptible or infectious, $H_{R_j}(t)$. Hence, the total bird population is given as

$$N_H(t) = \sum_j N_{H_j}(t),$$

where

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

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 de-

scribed by the following system of ordinary differential equations.

$$
\begin{aligned}
\frac{d}{dt}H_{S_j} &= \Lambda_j(H_{S_j}+H_{R_j}) - P_{MH_j}\,b\,M_I\frac{H_{S_j}}{N_H} - P_{HH_j}\,\omega_j\,H_{I_j}\frac{H_{S_j}}{N_{H_j}} - \frac{d_{H_j}}{C_{H_j}}N_{H_j}\,H_{S_j} - \mu_{H_j}\,H_{S_j}\\
\frac{d}{dt}H_{I_j} &= P_{MH_j}\,b\,M_I\frac{H_{S_j}}{N_H} + P_{HH_j}\,\omega_j\,H_{I_j}\frac{H_{S_j}}{N_{H_j}} - \left(\gamma_{H_j}+g_{I_j}+\mu_{H_j}\right)\,H_{I_j} - \frac{d_{H_j}}{C_{H_j}}N_{H_j}\,H_{I_j}\\
\frac{d}{dt}H_{R_j} &= g_{I_j}\,H_{I_j} - \frac{d_{H_j}}{C_{H_j}}N_{H_j}\,H_{R_j} - \mu_{H_j}\,H_{R_j}\\
\frac{d}{dt}E_S &= r_S(M_S+M_E) - m_E\,E_S\\
\frac{d}{dt}E_I &= r_I\,M_I - m_E\,E_I\\
\frac{d}{dt}L_S &= m_E\,q_S\,E_S + m_E\,q_I(1-\phi)E_I - (\mu_L+m_L)L_S - \frac{d_L}{C_L}(L_S+L_I)L_S\\
\frac{d}{dt}L_I &= m_E\,q_I\,\phi\,E_I - (\mu_L+m_L)L_I - \frac{d_L}{C_L}(L_S+L_I)L_I\\
\frac{d}{dt}M_S &= m_L\,L_S - b\,M_S\sum_j\left(P_{H_jM}\,\frac{H_{I_j}}{N_H}\right) - \mu_M\,M_S\\
\frac{d}{dt}M_E &= b\,M_S\sum_j\left(P_{H_jM}\,\frac{H_{I_j}}{N_H}\right) - (k_L+\mu_M)\,M_E\\
\frac{d}{dt}M_I &= m_L\,L_I + k_L\,V_E - \mu_M\,M_I
\end{aligned}
\tag{1}
$$

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 bites sec^{-1} and the fraction of bites that are on infected hosts of type j is $\frac{H_{I_j}}{N_H}$. The second way hosts acquire infection is following contact with other infected birds at a per capita rate $P_{HH_j}\,\omega_j\,H_{I_j}\frac{H_{S_j}}{N_{H_j}}$, where ω_j is the contact rate of

birds in host group j with other birds in this group, and P_{HH_j} is the probability of transmission given contact between healthy and susceptible hosts of type j. Note the model assumes frequency-dependent transmission of the infection between hosts and mosquitoes. 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 in a single compartment. 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. In addition, 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 $\sum_j \left(b\, P_{H_j M}\, M_S\, \frac{H_{I_j}}{N_H} \right)$. 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 are summarized in Table 2. Parameter values and ranges are summarized in Tables 3 and 4.

CHAPTER 3

MODEL REPRODUCTION NUMBER

3.1 Disease-Free Equilibrium

A disease free equilibrium (DFE) of a virus-vector model is a steady-state solution where all infectious and recovered compartments (host and virus-vector) are zero. That is, if $\mathcal{E}_0$ denotes the DFE of our model, then

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

where $H^*_{I_1} = H^*_{R_1} = E^*_{I_1} = \cdots = H^*_{I_j} = H^*_{R_j} = E^*_{I_j} = L^*_I = M^*_E = M^*_I = 0$. The steady-state values of the remaining variables are found by substituting zero for the values of the infected variables in (1), setting the right-hand-side of (1) to zero, and solving. The resulting host equations yield

$$H^*_{S_i} = C_{H_i},$$

for $i = 1, \ldots, j$. The resulting vector equations are:

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

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

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

so that by choice of d_L, $L^*_S = C_L$, $E^*_S = \frac{m_L\, r_S}{\mu_M\, m_E}\, C_L$ and $M^*_S = \frac{m_L}{\mu_M}\, C_L$. Thus, the DFE for this system is

$$\mathcal{E}_0 = \left(\sum_j C_{H_j}, 0, 0, \frac{m_L\, r_S}{\mu_M\, m_E}\, C_L, 0, C_L, 0, \frac{m_L}{\mu_M}\, C_L, 0, 0\right). \tag{2}$$

3.2 The Next-Generation Matrix Method

This section relies on theory from linear algebra and matrix modeling. In particular, given a Matrix $A \in \mathbb{R}^{n\times n}$ with eigenvalue λ, the following standard notations are used:

- $\mathcal{P}(\lambda) = \det(A - \lambda I)$ is the characteristic polynomial for A. The roots of the characteristic polynomial are exactly the eigenvalues of A.
- $\sigma(A)$ denotes the spectrum of A, that is, the set of all eigenvalues of A.
- $\rho(A)$ denotes the spectral radius of A, that is, $\rho(A) = \max\{|\lambda| : \lambda \in \sigma(A)\}$.

The basic reproduction number, $\mathcal{R}_0$, represents the expected number of secondary infections caused by the introduction of one infectious individual into an entirely susceptible population. There is much research on the construction and interpretation of the basic reproduction number for ordinary differential equation models [20]. For completeness and for the convenience of the reader, we will provide a detailed account of the construction and theory related to $\mathcal{R}_0$, including some original proofs.

The basic reproduction number can be computed by extracting two models from the original epidemiological model. The first of these models, which we call the transition model, tracks the fate of infected individuals. The second model, which we will call the transmission model, tracks the number of secondary infections that result from infected individuals from the transmission model interacting with an entirely susceptible population. The basic reproduction number is then the asymptotic limit of the magnitude of the solution to the transmission model with respect to time. Note that the effect of assuming that the transmission occurs in an entirely susceptible population is to linearize the model about the disease-free equilibrium. It has been shown that under relatively relaxed conditions the reproduction number described above is greater than one if and only if the disease-free equilibrium is linearly unstable. [20] This procedure for computing the reproduction number is called the Next-Generation Matrix method.

In detail, suppose we have an epidemiological model,

$$\dot{x} = f(x) \tag{3}$$

consisting of m coupled ODEs. We suppose the first n components of x represent infected compartments, that is, compartments representing individuals that can transmit the infection or transition to compartments which can transmit the infection without first passing through a susceptible state. So, for example, exposed compartments are included in the class of infected compartments. On the other hand, strictly recovered compartments, that is, compartments for individuals that are not newly infected, can no longer transmit the infection, and cannot transition to a transmission class without first becoming susceptible, need not be included in the infected compartments. Their inclusion will not impact the basic reproduction number or the stability of the disease-free equilibrium. For $1 \leq i \leq n$ the ith equation can be expressed as

$$\dot{x}_i = f_i(x) = F_i(x) + V_i(x),$$

where $F_i(x)$ is the rate of appearance of new infections in the ith compartment, and $V_i(x)$ is the rate of transfer of individuals into and out of the ith compartment. We may decompose V_i as

$$V_i = V_i^+ - V_i^-,$$

where V_i^+ denotes the transition of infected individuals into compartment i from other infected compartments, and V_i^- denotes the transition of infected individuals out of compartment i. Let A denote the solution to the transition system linearized about the disease-free equilibrium and P denote the solution to the transmission system linearized about the disease free equilibrium so that

$$\dot{A} = (DV)A$$

$$\dot{P} = (DF)A,$$

where DF and DV are the Jacobian matrices of F and V evaluated at the disease-free

equilibrium. Solving the transition and transmission systems yields

$$A(t) = e^{DVt}A_0$$

$$P(t) = (DF)(DV)^{-1}\left(e^{DVt} - 1\right)A_0.$$

Therefore, the number of secondary infections resulting from the initial infected vector A_0 is

$$\lim_{t\to\infty} ||P(t)|| = \lim_{t\to\infty} ||(DF)(DV)^{-1}(e^{DVt} - 1)A_0||.$$

Because the initial infected individuals only transition between compartments or leave the system entirely, it turns out that $e^{DVt} \to 0$ as $t \to \infty$. To see this, first note that (i) the off-diagonal entries of DV are nonnegative (interpretation: $(DV)_{ij}$ represents the rate of transfer of individuals into the ith compartment from the jth compartment), (ii) the column sums of DV are all negative (interpretation: individuals in each infected compartment are lost from the system, due to, for example, death or recovery, so that the net flux of individuals out of compartment i exceeds the net flux of individuals from compartment i to all other compartments). It follows that the eigenvalues of DV have negative real part.

To see this, first note that solutions of

$$\dot{x}(t) = DVx, \tag{4}$$

subject to $x(0) = C$ are unique and global. In case $C > 0$, by continuity, there exists a maximal interval, $I = (t_1, t_2)$, so that $x(t) > 0$ for $t \in I$. Hence, for $t \in I$, and $i = 1, \ldots, n$

$$\dot{x}_i \geq DV_{ii}\, x_i \tag{5}$$

Thus, for $t \in I$, and $i = 1, \ldots, n$,

$$x_i(t) > x_i(0)e^{DV_{ii}t}.$$

In particular, for $i = 1, \ldots, n$,

$$\lim_{t \to t_2^-} x_i(t) \geq x_i(0) e^{DV_{ii} t} > 0.$$

By maximality of I, it must be that $t_2 = \infty$. That is, if $x(0) = C > 0$, then for all $t > 0$, $x(t) > 0$.

Now, letting $(DV)_i$ denote the i^{th} row of DV,

$$\begin{aligned}
\sum_{i=1}^{n} \dot{x}_i &= \sum_{i=1}^{n} (DV)_i \cdot x \\
&= \sum_{i=1}^{n} \sum_{j=1}^{n} DV_{ij} x_j \\
&= \sum_{j=1}^{n} x_j \sum_{i=1}^{n} DV_{ij} \\
&\leq \sum_{j=1}^{n} x_j \max_{j=1,\ldots,n} \left(\sum_{i=1}^{n} DV_{ij} \right) \\
&= \sum_{j=1}^{n} x_j K,
\end{aligned}$$

where $K := \max_{j=1,\ldots,n} \sum_{i=1}^{n} DV_{ij} < 0$. Hence $\sum_{i=1}^{n} x_i \leq e^{Kt} \sum_{i=1}^{n} x_i(0)$, and

$$0 \leq \lim_{t \to \infty} x_i(t) \leq \lim_{t \to \infty} \sum_{i=1}^{n} x_i = 0.$$

Now let $x(t; x(0))$ denote the dependence of the solution of (4) on its initial value. Given a arbitrary initial condition $x(0) = C$, we can express C as $C = C^+ - C^-$, where $C_i^+ > 2C_i$ and $C_i^- > C_i$, in case $C_i > 0$, $C_i^+ > -C_i$ and $C_i^- > -2C_i$, in case $C_i < 0$, and $C_i^+ = C_i^- = 1$, in case $C_i = 0$. By the superposition principle,

$$x(t; C) = x(t; C^+) - x(t; C^-).$$

From the previous, $x(t; C^+)$ and $x(t; C^-)$ both converge to zero as $t \to \infty$. Thus,

$$\lim_{t \to \infty} x(t; C) = 0.$$

Equivalently, it must be that all the eigenvalues of DV have negative real part[18].

Now we will show that the inverse of DV is strictly negative. Recall that if $\lambda \in \sigma(DV)$ then $\mathrm{Re}(\lambda) < 0$. Hence DV is invertible. Also, from the previous proof, if $x_0 > 0$ then $x(t) = e^{DV\,t}\,x_0 > 0$. Now consider the system

$$\dot{y} = x(t) = e^{DV\,t}\,x_0,$$

where $x_0 > 0$ and $y(0) = 0$. Then $\dot{y} > 0$ and

$$y(t) = e^{V\,t}\,V^{-1}\,x_0 - V^{-1}\,x_0.$$

Because the eigenvalues of DV have negative real part

$$\lim_{t\to\infty} e^{DV\,t}\,DV^{-1}\,x_0 = 0.$$

Thus,

$$\lim_{t\to\infty} y(t) = DV^{-1}\,x_0.$$

And, because $\dot{y} > 0$,

$$\lim_{t\to\infty} y(t) > y(0) = 0.$$

That is, $DV^{-1}\,x_0 > 0$. Suppose toward a contradiction that $-DV_{ij}^{-1} < 0$, and construct a vector x as follows. Put $DW = -DV^{-1}$ so that $DW_{ij} < 0$. Then

$$\begin{aligned}
(DWx)_i < 0 \quad &\Leftrightarrow \quad \sum_k x_k\,DW_{ik} \;<\; 0 \\
&\Leftrightarrow \quad x_j\,DW_{ij} \;<\; -\sum_{k\neq j} x_k\,DW_{i_k} \\
&\Leftrightarrow \quad x_j \;>\; -\sum_{k\neq j} \frac{x_k\,DW_{i_k}}{DW_{ij}}.
\end{aligned} \tag{*}$$

Now we consider two cases:

Case 1: If $\sum_{k\neq j} DW_{ik} > 0$, let $x_j = 2$ and for $k = j$ let

$$x_k = \frac{-DW_{ij}}{\sum_{k\neq j} DW_{ik}},$$

so that

$$-\sum_{k\neq j}\frac{x_k\,DW_{ik}}{DW_{ij}}=\frac{\sum\limits_{k\neq j}W_{ik}}{\sum\limits_{k\neq j}DW_{ik}}=1<x_j.$$

Hence, $(*)$ holds, so $(DW\,x)_i<0$ which contradicts $DW\,x>0$ if $x>0$..

Case 2: Alternatively, if $\sum\limits_{k\neq j}DW_{ik}\leq 0$, let $x_j=1$ and $x_k=1$ so that

$$-\sum_{k\neq j}\frac{x_k\,DW_{ik}}{DW_{ij}}=\frac{-\sum\limits_{k\neq j}DW_{ik}}{DW_{ij}}\leq 0<1=x_j.$$

Again, $(*)$ holds. Hence, $(DW\,x)_i<0$ which contradicts $DW\,x>0$ if $x>0$.

Finally, since F_i describes the influx of newly infected individuals into the i^{th} compartment we suppose $F_i\geq 0$ and $F_i=0$, when $x=x_0$. Hence, as the derivative of F with respect to infected variables evaluated at x_0, DF, satisfies $DF\geq 0$.

In summary, $-(DF)(DV)^{-1}\geq 0$. Hence, by the Perron-Frobenius theorem [4] there exists $\lambda\in\sigma(-(DF)(DV)^{-1})$ such that $0<\lambda=\rho((-(DF)(DV)^{-1})$, where $\rho(A)$ denotes the spectral radius of A.

In consideration of the previous results

$$\lim_{t\to\infty}||P(t)||=||-(DF)(DV)^{-1}A_0||.$$

is a finite number representing the number of secondary infections resulting from the introduction of an initial infectious vector A_0 into an entirely susceptible population. And, it is reasonable to define

$$\mathcal{R}_0:=\rho(-(DF)(DV)^{-1}).$$

Moreover, $-(DF)(DV)^{-1}$ is called the next-generation matrix for model (3).

It is known that under fairly general conditions the basic reproduction number determines the linear stability of the disease-free equilibrium. Indeed, linearizing the full system about the disease-free equilibrium, x_0, yields

$$\dot{x}(t)=J\cdot(x-x_0),$$

where the Jacobian matrix evaluated at x_0 has the form

$$J = \begin{bmatrix} DF + DV & 0 \\ J_3 & J_4 \end{bmatrix}. \tag{6}$$

Note that when the n infected components are all zero, the upper right-hand $n \times (m-n)$ matrix is zero since $F \equiv 0, V \equiv 0$, and hence $F+V \equiv 0$ when the infected compartments are empty. Thus, the eigenvalues of J are completely determined by those of $DF + DV$ and J_4, the Jacobian of the disease-free model.

To link the reproduction number to the stability of the disease-free equilibrium we appeal to the theory of Z and M-matrices:
Definition: $A \in \mathbb{R}^{n\times n}$ is a Z-matrix if $\forall\, i \neq j$, $A_{ij} \leq 0$.
Definition: $A \in \mathbb{R}^{n\times n}$ is an M-matrix if A is a Z-matrix and $\exists\, B \in \mathbb{R}^{n\times n}$ with $B \geq 0$ such that $A = s\mathbb{I} - B$ where $s \geq \rho(B)$. Note that in this case, A is nonsingular if and only if $s > \rho(B)$.

Plemmons [13] gives forty equivalent definitions of a nonsingular M-matrix! In particular, if A is a Z-matrix then the following are equivalent:

- A is a nonsingular M-matrix.
- A has a convergent regular splitting i.e. $A = M - N$, $M^{-1} \geq 0$, $N \geq 0$, and $\rho(NM^{-1}) < 1$ (See F17 [13]).
- Every regular splitting of A is convergent (See H24 [13]).
- A is positive stable i.e. $\forall\, \lambda \in \sigma(A)$ then $\mathrm{Re}(\lambda) > 0$ (See J29 [13]).
- A is inverse positive i.e. A^{-1} exists and $A^{-1} \geq 0$ (See F15 [13]).

From the previous, $-DV$ is a nonsingular M-matrix. Put $DW = -DV$ and consider $J_1 = DF + DV = DF - DW$ where $DF \geq 0$ and DW a Z-matrix. Hence, $-J_1$ is a Z-matrix and $-J_1 = DW - DF$ where $(DW)^{-1} \geq 0$ and $DF \geq 0$. That is, $-J_1 = DW - DF$ is a regular splitting of $-J_1$, and the following are equivalent

- J_1 is negative stable.

- $-J_1$ is positive stable.
- $\rho((DF)(DW)^{-1}) = \rho(-(DF)(DV)^{-1}) < 1$.

In summary, the eigenvalues of J_1 all have negative real part if and only if $\rho((DF)(DV)^{-1}) < 1$. Assuming that x_0 is a stable equilibrium of the disease-free model, i.e., the eigenvalues of J_4 have negative real part, x_0 is a stable equilibrium for the full model if and only if $\mathcal{R}_0 = \rho((DF)(DV)^{-1}) < 1$, as desired.

3.3 Characterization of the Model Reproduction Number

Using the Next-Generation Matrix method for our model, infectious host compartments take the form

$$\frac{d}{dt}H_{I_j} = -\left(\gamma_{H_j} + g_{I_j} + \mu_{H_j} + d_{H_j}\right)\ H_{I_j} + \left(P_{HH_j}\,\omega_j\right)\ H_{I_j} + \left(P_{MH_j}\,b\,\frac{N_{H_j}}{N_H}\right) M_I \quad (7)$$

and the infectious vector compartment system is

$$\begin{aligned}
\frac{d}{dt}E_I &= -\left(m_E\right)\ E_I + \left(r_I\right)\ M_I \\
\frac{d}{dt}L_I &= \left(m_E\,q_I\,\phi\right)\ E_I - \left(\mu_L + m_L + \frac{d_L\,L_S^*}{C_L}\right)\ L_I \\
\frac{d}{dt}M_E &= \sum_j \left(\frac{b\,P_{H_jM}\,M_S^*}{N_H}\right)\ H_{I_j} - \left(k_L + \mu_M\right)\ M_E \\
\frac{d}{dt}M_I &= \left(m_L\right)\ L_I + \left(k_L\right)\ M_E - \left(\mu_M\right)\ M_I
\end{aligned} \quad (8)$$

Then $\mathcal{R}_0$ will be the spectral radius of the next-generation matrix for this system.

For a single host compartment system, we will have the following coefficient matrices.

$$V = -\begin{bmatrix}
\left(\gamma_H + g_I + \mu_H + d_H\right) & 0 & 0 & 0 & 0 \\
0 & m_E & 0 & 0 & 0 \\
0 & -\left(m_E\,q_I\,\phi\right) & \left(\mu_L + m_L + \frac{d_L\,L_S^*}{C_L}\right) & 0 & 0 \\
0 & 0 & 0 & \left(k_L + \mu_M\right) & 0 \\
0 & 0 & -m_L & -k_L & \mu_M
\end{bmatrix} \quad (9)$$

$$F = \begin{bmatrix}
\left(P_{HH_j}\,\omega\right) & 0 & 0 & 0 & \left(P_{MH}\,b\right) \\
0 & 0 & 0 & 0 & r_I \\
0 & 0 & 0 & 0 & 0 \\
\left(\frac{b\,P_{HM}\,M_S^*}{N_H}\right) & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0
\end{bmatrix} \quad (10)$$

For convenience, let $s = \gamma_H + g_I + \mu_H + d_H$ and $\tau = m_L + \mu_L + \frac{d_L\, L_S^*}{C_L}$. Putting $W = -V$, the next-generation matrix $-F\,V^{-1} = FW^{-1}$ will be

$$\begin{bmatrix} \left(\frac{P_{HH}\,\omega}{s}\right) & \left(\frac{b\,P_{MH}\,q_I\,\phi\,m_L}{\mu_M\,\tau}\right) & \left(\frac{b\,P_{MH}\,m_L}{\mu_M\,\tau}\right) & \left(\frac{b\,P_{MH}\,k_L}{\mu_M\,[k_L+\mu_M]}\right) & \left(\frac{b\,P_{MH}}{\mu_M}\right) \\ 0 & \left(\frac{m_L\,q_I\,\phi\,r_I}{\mu_M\,\tau}\right) & \left(\frac{m_L\,r_I}{\mu_M\,\tau}\right) & \left(\frac{k_L\,r_I}{\mu_M\,[k_L+\mu_M]}\right) & \left(\frac{r_I}{\mu_M}\right) \\ 0 & 0 & 0 & 0 & 0 \\ \left(\frac{b\,P_{HM}\,\frac{M_S^*}{N_H}}{s}\right) & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \end{bmatrix}. \tag{11}$$

Expanding to j host compartments, with $s_j = \gamma_{H_j} + g_{I_j} + \mu_{H_j} + d_{H_j}$, yields the following coefficient block matrices:

$$F = \begin{bmatrix} (F_{HH})_{j\times j} & (F_{MH})_{j\times 4} \\ (F_{HM})_{4\times j} & (F_{MM})_{4\times 4} \end{bmatrix} \text{ and } W = \begin{bmatrix} (W_H)_{j\times j} & (0)_{j\times 4} \\ (0)_{4\times j} & (W_M)_{4\times 4} \end{bmatrix}, \text{ where} \tag{12}$$

$$F_{HH} = \begin{bmatrix} (P_{H\,H_1}\,\omega_1) & 0 & 0 & \dots & 0 \\ 0 & (P_{H\,H_2}\,\omega_2) & 0 & \dots & \vdots \\ \vdots & 0 & & \ddots & 0 \\ 0 & \dots\vdots\dots & & \dots\ 0 & \left(P_{H\,H_j}\,\omega_j\right) \end{bmatrix} \qquad F_{MM} = \begin{bmatrix} 0 & 0 & 0 & r_I \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}$$

$$F_{MH} = \begin{bmatrix} 0 & 0 & 0 & \left(b\,P_{MH_1}\frac{N_{H_1}}{N_H}\right) \\ \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & 0 & \left(b\,P_{MH_j}\frac{N_{H_j}}{N_H}\right) \end{bmatrix} \quad F_{HM} = \begin{bmatrix} 0 & 0 & \dots & 0 \\ 0 & 0 & \dots & 0 \\ b\,P_{H_1M}\dfrac{M_S^*}{N_H} & b\,P_{H_2M}\dfrac{M_S^*}{N_H} & \dots & b\,P_{H_jM}\dfrac{M_S^*}{N_H} \\ 0 & 0 & \dots & 0 \end{bmatrix}$$

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

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:

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

The characteristic polynomial of FW^{-1} is

$$\begin{aligned} \mathcal{P}_j(\lambda) = \det\left[FW^{-1} - \lambda\, I\right] &= \det\left[FW^{-1} - \lambda\, W W^{-1}\right] \\ &= \det\left[(F - \lambda\, W) W^{-1}\right] \\ &= \det\left[F - \lambda\, W\right] \cdot \det\left[W^{-1}\right]. \end{aligned} \tag{13}$$

Now consider that for the double host compartment model, $F - \lambda\, W$ will have the form

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

$$\left[\begin{array}{cc|cccc} P_{HH_1}\,\omega_1 - \lambda\, s_1 & 0 & 0 & 0 & 0 & b\, P_{MH_1} \frac{N_{H_1}}{N_H} \\ 0 & P_{HH_2}\,\omega_2 - \lambda\, s_2 & 0 & 0 & 0 & b\, P_{MH_2} \frac{N_{H_2}}{N_H} \\ \hline 0 & 0 & -\lambda\, m_E & 0 & 0 & r_I \\ 0 & 0 & \lambda\, m_E\, q_I\, \phi & -\lambda\, \tau & 0 & 0 \\ b\, P_{H_1 M} \frac{M_S^*}{N_H} & b\, P_{H_2 M} \frac{M_S^*}{N_H} & 0 & 0 & -\lambda\,(k_L + \mu_M) & 0 \\ 0 & 0 & 0 & \lambda\, m_L & \lambda\, k_L & -\lambda\, \mu_M \end{array}\right]. \tag{14}$$

By properties of determinants [17],

$$\det\left[F - \lambda\, W\right] = \det\left[F_{MM} - \lambda\, W_M\right] \cdot \det\left[F_{HH} - \lambda\, W_H - F_{MH}\left[F_{MM} - \lambda\, W_M\right]^{-1} F_{HM}\right]. \tag{15}$$

Here 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. Let $A(\lambda)=q_I\,\phi\,r_I\,m_L-\lambda\,\tau\,\mu_M$. Now

$$\left[F_{MM}-\lambda\,W_M\right]^{-1}=\begin{bmatrix}\dfrac{\tau\,\mu_M}{A(\lambda)\,m_E} & \dfrac{r_I\,m_L}{\lambda\,A(\lambda)\,m_E} & \dfrac{\tau\,r_I\,k_L}{\lambda\,\left(k_L+\mu_M\right)A(\lambda)\,m_E} & \dfrac{\tau\,r_I}{\lambda\,A(\lambda)\,m_E}\\ \dfrac{q_I\,\phi\,\mu_M}{A(\lambda)} & \dfrac{\mu_M}{A(\lambda)} & \dfrac{q_I\,\phi\,k_L}{\lambda\,\left(k_L+\mu_M\right)A(\lambda)} & \dfrac{q_I\,\phi\,r_I}{\lambda\,A(\lambda)}\\ 0 & 0 & \dfrac{-1}{\lambda\,\left(k_L+\mu_M\right)} & 0\\ \dfrac{q_I\,\phi\,m_L}{A(\lambda)} & \dfrac{m_L}{A(\lambda)} & \dfrac{\tau\,k_L}{\left(k_L+\mu_M\right)A(\lambda)} & \dfrac{\tau}{A(\lambda)}\end{bmatrix} \tag{16}$$

$$F_{MH}\left[F_{MM}-\lambda\,W_M\right]^{-1}=$$

$$\frac{b}{N_H\,A(\lambda)}\cdot\begin{bmatrix}q_I\,\phi\,m_L\,P_{MH_1}\,N_{H_1} & m_L\,P_{MH_1}\,N_{H_1} & \dfrac{\tau\,k_L\,P_{MH_1}\,N_{H_1}}{k_L+\mu_M} & \tau\,P_{MH_1}\,N_{H_1}\\ q_I\,\phi\,m_L\,P_{MH_2}\,N_{H_2} & m_L\,P_{MH_2}\,N_{H_2} & \dfrac{\tau\,k_L\,P_{MH_2}\,N_{H_2}}{k_L+\mu_M} & \tau\,P_{MH_2}\,N_{H_2}\end{bmatrix} \tag{17}$$

$$F_{MH}\left[F_{MM}-\lambda\,W_M\right]^{-1}F_{HM}=\frac{\tau\,k_L\,b^2\,M_S^*}{N_H\,\left(k_L+\mu_M\right)A(\lambda)}\cdot\begin{bmatrix}\dfrac{P_{MH_1}\,P_{H_1M}\,N_{H_1}}{N_H} & \dfrac{P_{MH_1}\,P_{H_2M}\,N_{H_1}}{N_H}\\ \dfrac{P_{MH_2}\,P_{H_1M}\,N_{H_2}}{N_H} & \dfrac{P_{MH_2}\,P_{H_2M}\,N_{H_2}}{N_H}\end{bmatrix}. \tag{18}$$

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

$$\begin{bmatrix}P_{HH_1}\,\omega_1-\lambda\,s_1-\dfrac{\tau\,k_L\,b^2\,M_S^*}{\left(k_L+\mu_M\right)A(\lambda)}\cdot\dfrac{P_{MH_1}\,P_{H_1M}\,N_{H_1}}{(N_H)^2} & \dfrac{\tau\,k_L\,b^2\,M_S^*}{\left(k_L+\mu_M\right)A(\lambda)}\cdot\dfrac{P_{MH_1}\,P_{H_2M}\,N_{H_1}}{(N_H)^2}\\ \dfrac{\tau\,k_L\,b^2\,M_S^*}{\left(k_L+\mu_M\right)A(\lambda)}\cdot\dfrac{P_{MH_2}\,P_{H_1M}\,N_{H_2}}{(N_H)^2} & P_{HH_2}\,\omega_2-\lambda\,s_2-\dfrac{\tau\,k_L\,b^2\,M_S^*}{\left(k_L+\mu_M\right)A(\lambda)}\cdot\dfrac{P_{MH_2}\,P_{H_2M}\,N_{H_2}}{(N_H)^2}\end{bmatrix}. \tag{19}$$

Now, consider a model where only hosts of type 1 are able to catch and transmit the infection but both types of hosts receive mosquito bites. Then

$$F_{MH}=\begin{bmatrix}0 & 0 & 0 & b\,P_{MH_1}\dfrac{N_{H_1}}{N_H}\end{bmatrix}\qquad F_{HM}=\begin{bmatrix}0\\0\\\dfrac{b\,P_{H_1M}\,M_S^*}{N_H}\end{bmatrix}. \tag{20}$$

Hence

$$F_{MH}\left[F_{MM}-\lambda W_M\right]^{-1}=\frac{N_{H_1}\,b}{N_H\,A(\lambda)}\cdot\left[q_I\,\phi\,m_L\,P_{MH_1}\quad m_L\,P_{MH_1}\quad\frac{\tau\,k_L\,P_{MH_1}}{k_L+\mu_M}\quad\tau\,P_{MH_1}\right] \tag{21}$$

$$F_{MH}\left[F_{MM}-\lambda W_M\right]^{-1}F_{HM}=\frac{\tau\,k_L\,b^2\,M_S^*}{(k_L+\mu_M)\,A(\lambda)}\cdot\left[\frac{P_{MH_1}\,P_{H_1M}\,N_{H_1}}{(N_H)^2}\right] \tag{22}$$

$$F_{HH}-\lambda W_H-F_{MH}\left[F_{MM}-\lambda W_M\right]^{-1}F_{HM}=$$
$$P_{HH_1}\,\omega_1-\lambda\,s_1-\frac{\tau\,k_L\,b^2\,M_S^*}{(k_L+\mu_M)\,A(\lambda)}\cdot\frac{P_{MH_1}\,P_{H_1M}\,N_{H_1}}{(N_H)^2}. \tag{23}$$

Note that (23) is the form of the first diagonal entry in (19). Similarly, the second diagonal entry in (19) corresponds to the second factor of the characteristic polynomial for the model with all hosts of type 2. Hence, assuming the basic reproduction number of the model with all hosts of type j, R_j is greater than that of the vector-only model, so that $A(R_j)\neq 0$ and the j^{th} diagonal entry of (19) is zero when the matrix is evaluated at R_j for $j=1,2$. Also, since the number of host compartments does not affect $F_{MM}-\lambda W_M$ then, regardless of the number of host types,

$$\begin{aligned}\det\left[F_{MM}-\lambda W_M\right]&=(-\lambda\,m_E)\,(-\lambda\,\tau)\left[-\lambda\,(\mu_M+k_L)\,(-\lambda\,\mu_M)\right]\\&\quad-r_I\left[\lambda\,m_E\,q_I\,\phi\left(\lambda^2\,m_L\left[\mu_M+k_L\right]\right)\right]\\&=\lambda^4\,m_E\,\tau\,\mu_M\,(\mu_M+k_L)-\lambda^3\,r_I\,m_E\,q_I\,\phi\,m_L\,(\mu_M+k_L)\\&=m_E\,(\mu_M+k_L)\left[\lambda^4\,\tau\,\mu_M-\lambda^3\,q_I\,\phi\,r_I\,m_L\right]\\&=-\lambda^3\;m_E\,(\mu_M+k_L)\;A(\lambda),\end{aligned} \tag{24}$$

so that the root of $A(\lambda)$ corresponds to the basic reproduction number of a vector-only model. Setting $\lambda = R_1$, the components of the characteristic polynomial for the double-host compartment model can be simplified as:

$$A(R_1) = q_I\,\phi\,r_I\,m_L - R_1\,\tau\,\mu_M \tag{25}$$

$$P_{HH_1}\,\omega_1 - R_1\,s_1 = \frac{\tau\,k_L\,b^2\,M_S^*}{(k_L+\mu_M)\,(N_H)^2}\cdot\frac{P_{MH_1}\,P_{H_1M}\,N_{H_1}}{A(R_1)} \tag{26}$$

$$\begin{aligned}&\det\left[F_{HH} - R_1\,W_H - F_{MH}\left[F_{MM} - R_1\,W_M\right]^{-1}F_{HM}\right] = \\ &-\left[\frac{\tau\,k_L\,b^2\,M_S^*}{(k_L+\mu_M)\,(N_H)^2}\right]^2\cdot\frac{P_{MH_1}\,P_{H_1M}\,P_{MH_2}\,P_{H_2M}\,N_{H_1}\,N_{H_2}}{A^2(R_1)}.\end{aligned} \tag{27}$$

Likewise, when $\lambda = R_2$ in the double host compartment model, we have

$$A(R_2) = q_I\,\phi\,r_I\,m_L - R_2\,\tau\,\mu_M \tag{28}$$

$$P_{HH_2}\,\omega_2 - R_2\,s_2 = \frac{\tau\,k_L\,b^2\,M_S^*}{(k_L+\mu_M)\,(N_H)^2}\cdot\frac{P_{MH_2}\,P_{H_2M}\,N_{H_2}}{A(R_2)} \tag{29}$$

$$\begin{aligned}&\det\left[F_{HH} - R_2\,W_H - F_{MH}\left[F_{MM} - R_2\,W_M\right]^{-1}F_{HM}\right] = \\ &-\left[\frac{\tau\,k_L\,b^2\,M_S^*}{(k_L+\mu_M)\,(N_H)^2}\right]^2\cdot\frac{P_{MH_1}\,P_{H_1M}\,P_{MH_2}\,P_{H_2M}\,N_{H_1}\,N_{H_2}}{A^2(R_2)}.\end{aligned} \tag{30}$$

Note that in both cases,

$$\det\left[F_{HH} - R_j\,W_H - F_{MH}\left[F_{MM} - R_j\,W_M\right]^{-1}F_{HM}\right] < 0. \tag{31}$$

If $R_0 = \dfrac{q_I\,\phi\,r_I\,m_L}{\tau\,\mu_M}$ then $A(R_0) = 0$, that is R_0 is the basic reproduction number for the vector-only model. Since we have assumed that $R_2 > R_1 > R_0$, then $A(R_1) < 0$ and $A(R_2) < 0$. From this (15), (24), and (31), we see that for the two-host model $\det\left[F - \lambda\,W\right]$ is negative when evaluated at $\lambda = R_1$ or $\lambda = R_2$.

Expanding $\det\left[F - \lambda\,W\right]$ for the two-host model recall

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

and

$$\begin{aligned}
&\det\left[F_{HH} - \lambda W_H - F_{MH}\left[F_{MM} - \lambda W_M\right]^{-1} F_{HM}\right] = \\
&= \left(P_{HH_1}\omega_1 - \lambda s_1 - \frac{\tau k_L b^2 M_S^* P_{MH_1} P_{H_1M} N_{H_1}}{A(\lambda)(\mu_M + k_L)(N_H)^2}\right) \cdot \left(P_{HH_2}\omega_2 - \lambda s_2 - \frac{\tau k_L b^2 M_S^* P_{MH_2} P_{H_2M} N_{H_2}}{A(\lambda)(\mu_M + k_L)(N_H)^2}\right) \\
&\qquad - \left(\frac{\tau k_L b^2 M_S^*}{A(\lambda)(\mu_M + k_L)(N_H)^2}\right)^2 \cdot (P_{MH_1} P_{H_1M} P_{MH_2} P_{H_2M} N_{H_1} N_{H_2}) = \\
&= \quad (P_{HH_1}\omega_1 - \lambda s_1)(P_{HH_2}\omega_2 - \lambda s_2) - (P_{HH_2}\omega_2 - \lambda s_2)\left[\frac{\tau k_L b^2 M_S^* P_{MH_1} P_{H_1M} N_{H_1}}{A(\lambda)(\mu_M + k_L)(N_H)^2}\right] \\
&\qquad - (P_{HH_1}\omega_1 - \lambda s_1)\left[\frac{\tau k_L b^2 M_S^* P_{MH_2} P_{H_2M} N_{H_2}}{A(\lambda)(\mu_M + k_L)(N_H)^2}\right]. \qquad (32)
\end{aligned}$$

Expanding, we get

$$\begin{aligned}
\det[F - \lambda W] = \lambda^3 m_E \; [\, &-(\mu_M + k_L)(P_{HH_1}\omega_1 - \lambda s_1)(P_{HH_2}\omega_2 - \lambda s_2)(q_I \phi r_I m_L - \lambda \tau \mu_M) \\
&+ (P_{HH_2}\omega_2 - \lambda s_2)\left(\frac{\tau k_L b^2 M_S^* P_{MH_1} P_{H_1M} N_{H_1}}{(N_H)^2}\right) \\
&+ (P_{HH_1}\omega_1 - \lambda s_1)\left(\frac{\tau k_L b^2 M_S^* P_{MH_2} P_{H_2M} N_{H_2}}{(N_H)^2}\right)\Big]. \qquad (33)
\end{aligned}$$

Now we will let

$$P_1 = P_{HH_1}\omega_1 \qquad P_2 = P_{HH_2}\omega_2$$

$$P_0 = (\mu_M + k_L) q_I \phi r_I m_L \qquad s_0 = (\mu_M + k_L)\tau \mu_M$$

$$C_1 = \frac{\tau k_L b^2 M_S^* P_{MH_1} P_{H_1M} N_{H_1}}{(N_H)^2} \qquad C_2 = \frac{\tau k_L b^2 M_S^* P_{MH_2} P_{H_2M} N_{H_2}}{(N_H)^2}$$

and

$$\begin{aligned}
G(\lambda) = &- (P_0 - \lambda s_0)(P_1 - \lambda s_1)(P_2 - \lambda s_2) + C_2(P_1 - \lambda s_1) + C_1(P_2 - \lambda s_2) \\
= \quad &\lambda^3 (s_0 s_1 s_2) \\
&- \lambda^2 (s_0 s_2 P_1 + s_2 s_1 P_0 + s_0 s_1 P_2) \\
&+ \lambda (P_2 P_1 s_0 + s_1 P_0 P_2 + s_2 P_0 P_1 - C_2 s_1 - C_1 s_2) \\
&- P_0 P_1 P_2 + C_2 P_1 + C_1 P_2. \qquad (34)
\end{aligned}$$

Finally,

$$\det[F-\lambda W] = \lambda^3 m_E\,[-(P_0-\lambda s_0)(P_1-\lambda s_1)(P_2-\lambda s_2)+C_2(P_1-\lambda s_1)+C_1(P_2-\lambda s_2)]$$
$$= \lambda^3 m_E\, G(\lambda). \tag{35}$$

Hence $\det[F-\lambda W] \to \infty$ as $\lambda \to \infty$. Since $\det[F-\lambda W] < 0$ at $\lambda = R_1$ and at $\lambda = R_2$, by the intermediate value theorem, it must be that the reproduction number of the two host model, $\mathcal{R}_0$, is greater than both R_1 and R_2, which are both greater than R_0.

Now, for $i, j = 1, 2$, let

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

Consider that the product of $A(\lambda) = q_I\,\phi\, r_I\, m_L - \lambda\,\tau\,\mu_M$ and determinant of the the right side of (19) will be of the form

$$A(\lambda)\cdot\begin{vmatrix} E_1(\lambda) & \star_{12}(\lambda) \\ \star_{21}(\lambda) & E_2(\lambda)\end{vmatrix} = A(\lambda)E_1(\lambda)E_2(\lambda) - A(\lambda)\,\star_{12}(\lambda)\,\star_{21}(\lambda).$$

Setting the previous expression equal to 0 and multiplying both sides by $A(\lambda)$ we have

$$P_1(\lambda)\,P_2(\lambda) - \bigstar_{12}(\lambda)\,\bigstar_{21}(\lambda) = 0 \Leftrightarrow P_1(\lambda)\,P_2(\lambda) = \bigstar_{12}(\lambda)\,\bigstar_{21}(\lambda),$$

where $P_j(\lambda)$ has exactly the same nontrivial roots as the λ dependent factor of the characteristic polynomial for the single-host model with host type j with $j = 1, 2$. Then $P_1(\lambda)\,P_2(\lambda)$ is a quartic with double root at R_0, and single roots at R_1, and R_2. This quartic also is positive so the magnitude of $\bigstar_{12}(\lambda)\,\bigstar_{21}(\lambda)$, which equals

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

determines how much greater $\mathcal{R}_0$ is compared to R_2.

3.4 Comparison to Previous Model

As surmised in the previous section, if we consider this model with only one homogeneous host i.e. $j \equiv 1$, then $N_{H_1} = N_H$ and the characteristic polynomial for FW^{-1} is

$$\begin{aligned}
\mathcal{P}_1(\lambda) &= \det\left[F - \lambda\, W\right] \cdot \det\left[W^{-1}\right] \\
&= \det\left[F_{MM} - \lambda\, W_M\right] \cdot \left[P_{HH}\,\omega - \lambda\, s - \frac{\tau\, k_L\, b^2\, M_S^*}{(k_L + \mu_M)\, A(\lambda)} \cdot \frac{P_{MH}\, P_{HM}}{N_H}\right] \cdot \det\left[W^{-1}\right] \\
&= \left[-\lambda^3\; m_E\,(\mu_M + k_L)\; A(\lambda)\right] \cdot \left[P_{HH}\,\omega - \lambda\, s - \frac{\tau\, k_L\, b^2\, M_S^*}{(k_L + \mu_M)\, A(\lambda)} \cdot \frac{P_{MH}\, P_{HM}}{N_H}\right] \cdot \det\left[W^{-1}\right] \\
&= \left[-\lambda^3\; m_E\,(\mu_M + k_L)\right] \cdot \left[(P_{HH}\,\omega - \lambda\, s)\; A(\lambda) - \frac{\tau\, k_L\, b^2\, M_S^*\, P_{MH}\, P_{HM}}{(\mu_M + k_L)\, N_H}\right] \cdot \det\left[W^{-1}\right],
\end{aligned}$$

where $A(\lambda) = q_I\,\phi\, r_I\, m_L - \lambda\,\tau\,\mu_M < 0$. Now we will rewrite the middle factor as

$$(P_{HH}\,\omega - \lambda\, s)\; A(\lambda) - \frac{\tau\, k_L\, b^2\, M_S^*\, P_{MH}\, P_{HM}}{(\mu_M + k_L)\, N_H} = G_1\,\lambda^2 - G_2\,\lambda + G_3$$

where

$$\begin{aligned}
G_1 &= s\,\tau\,\mu_M \\
G_2 &= P_{HH}\,\omega\,\tau\,\mu_M + s\, q_I\,\phi\, r_I\, m_L \\
G_3 &= P_{HH}\,\omega\, q_I\,\phi\, r_I\, m_L - \frac{\tau\, k_L\, b^2\, M_S^*\, P_{MH}\, P_{HM}}{(\mu_M + k_L)\, N_H}.
\end{aligned}$$

Then

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

Taking the positive root, we have

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

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

A simplification of this model which does not include host demographics or horizontal transmission [2] has a reproduction number of

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

where $n = d_H + g_I = s - (\gamma_H + \mu_H)$. Comparing these reproduction numbers shows that if horizontal transmission and host complexity are ignored then the former will reduce to the latter.

CHAPTER 4

ENDEMIC EQUILIBRIUM

4.1 Quantitative Analysis Methodology

Endemic equilibrium points (EEP) of a virus-vector model are other steady-state solutions to the system. Because of the non-linearity of this system, solving outright is quite a technical and time-consuming process. However, when simulating this model using MATLAB, we can graphically demonstrate that such a steady-state exists, using parameter data from Tables 3 and 4.

The mosquito-to-bird ratio is widely known to control the risk of a WNV outbreak. Hence, these simulations focus on the Host 1 to Host 2 ratio to see what effects this complexity of hosts has on possible outbreaks. For all of these simulations, Host 1 is a collection of birds with low mortality from WNV and Host 2 is a collection of Birds with high mortality from WNV. We have simulated the model for large t with a variety of different initial infected densities. All simulations were run using parameter data from Tables 3 and 4, Matlab code implementing the main model (1) for $j = 1, 2$, and the *ode45* Matlab solver.

4.2 Reproduction Number Computation Results

All reproduction numbers have been computed for different ratios of host carrying capacity using values from Tables 3 and 4, equations (35) and (34), and the *root* solver in MATLAB. Host 1 consists specifically of birds with zero WNV mortality and Host 2 consists specifically of Birds with 0.50-1.00 WNV mortality.

P_{H_jM}	P_{HH_j}	$C_{H_1} : C_{H_2}$	$\mathcal{R}_0$
$P_{H_1M} = 0.2146$	$P_{HH_1} = 0$	$10 : 1$	1.2881
		$1 : 1$	1.2893
$P_{H_2M} = 0.4067$	$P_{HH_2} = 9.2029$	$1 : 10$	1.2906

Table 1: The first column from the left are the host-mosquito transmission probabilities used for all computations. The second column from the left are the horizontal transmission probabilities used for all computations. The third column are the different Host1 to Host 2 carrying capacity ratios. The final column are the corresponding reproduction numbers for each Host 1 to Host 2 carrying capacity ratio.

4.3 Small Initial Density of Infected Birds with Low WNV Mortality

In each of the three cases in Figures 1, 2, and 3, the model converges to an endemic equilibrium, but said endemic steady state is unlikely to occur due to seasonal effects not included in this model. We observe a dilution effect when the ratio of densities favors type 1 hosts. This suggests that to preserve type 2 hosts, a dilution is necessary. Having a ratio of densities favoring type 2 hosts does not benefit either host. Another observation of note is that the mosquito population sees much less infection when the Host 1 population is dominant.

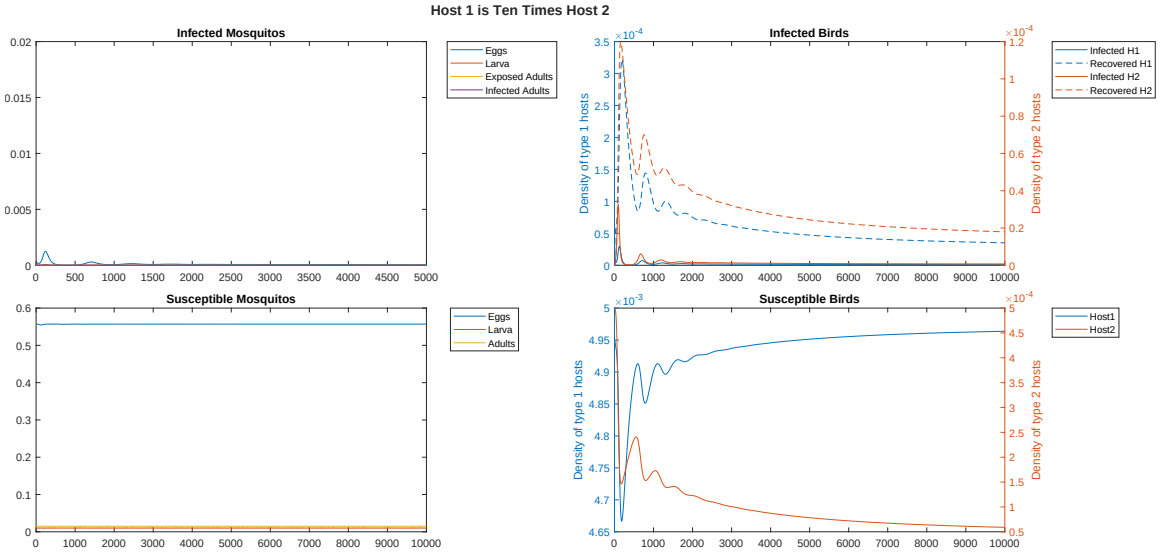

Figure 1: Simulation of the two-host model with infection originating within a small initial density of type 1 hosts (i.e. hosts with low WNV mortality). Specifically, the initial density of $H_{I_1} = 0.01 \times C_{H_1}$. All other initial values are taken from the disease-free steady-state. The carrying capacity of host 1 ($C_{H_1} = 0.005$ birds per m^2) is ten times that of host 2 ($C_{H_2} = 0.0005$ birds per m^2) so that the sum of the two carrying capacities (N_H) is 0.0055 birds per m^2. Other parameters are as in Tables 3 and 4. This yields a reproduction number of $\mathcal{R}_0 = 1.2881$.

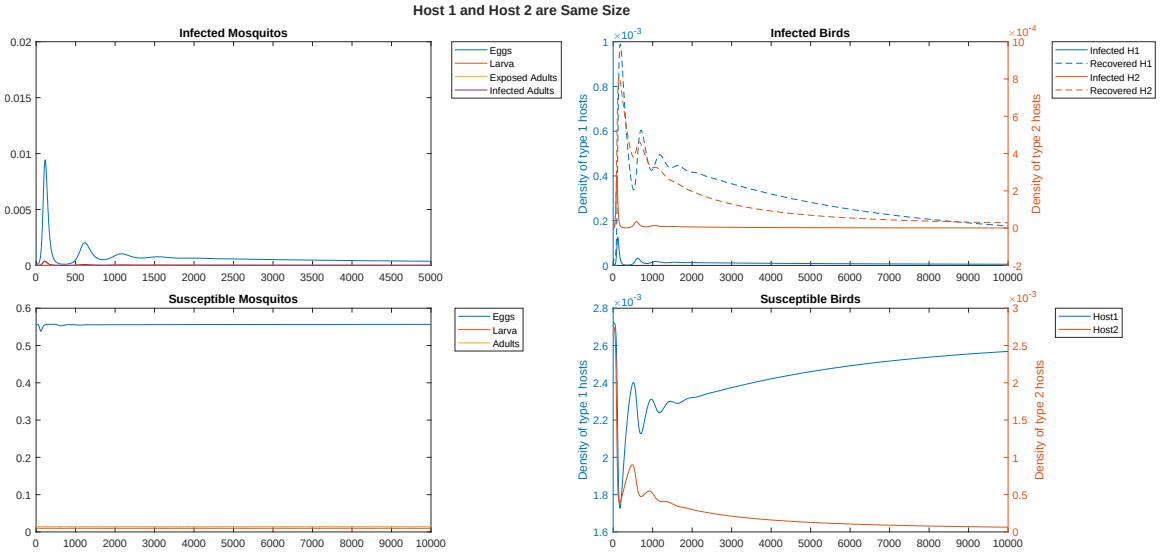

Figure 2: Simulation of the two-host model with infection originating within a small initial density of type 1 hosts (i.e. hosts with low WNV mortality). Specifically, the initial density of $H_{I_1} = 0.01 \times C_{H_1}$. All other initial values are taken from the disease-free steady-state. The carrying capacity of host 1 ($C_{H_1} = 0.0025$ birds per m^2) is equal to that of host 2 ($C_{H_2} = 0.0025$ birds per m^2) so that the sum of the two carrying capacities (N_H) is 0.0055 birds per m^2. Other parameters are as in Tables 3 and 4. This yields a reproduction number of $\mathcal{R}_0 = 1.2893$.

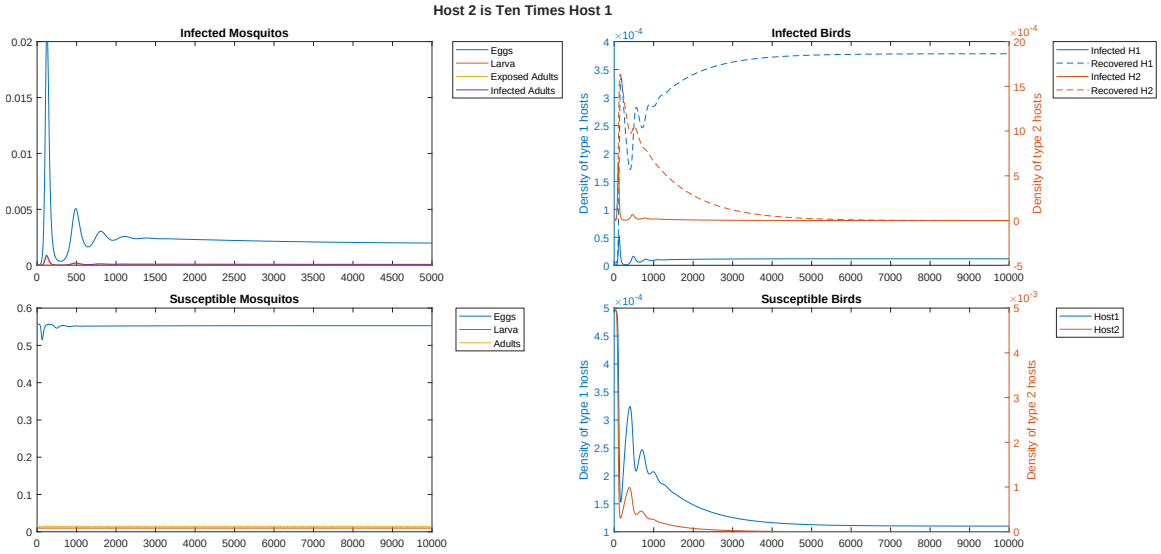

Figure 3: Simulation of the two-host model with infection originating within a small initial density of type 1 hosts (i.e. hosts with low WNV mortality). Specifically, the initial density of $H_{I_1} = 0.01 \times C_{H_1}$. All other initial values are taken from the disease-free steady-state. The carrying capacity of host 1 ($C_{H_1} = 0.0005$ birds per m^2) is one tenth that of host 2 ($C_{H_2} = 0.005$ birds per m^2) so that the sum of the two carrying capacities (N_H) is 0.0055 birds per m^2. Other parameters are as in Tables 3 and 4. This yields a reproduction number of $\mathcal{R}_0 = 1.2906$.

4.4 Small Initial Density of Infected Birds with High WNV Mortality

Just like with the previous simulations, in Figures 4, 5, and 6 the model converges to an endemic equilibrium, but said endemic steady state is unlikely to occur due to seasonal effects not included in this model. We also still observe a dilution effect when the ratio of densities favors type 1 hosts, but this effect here is less pronounced. Because the disease originates within a population of high WNV mortality, there is less of an outbreak within the low WNV mortality population of Host 1, as we would expect. The other major difference here compared to the previous simulations is that the outbreaks for all populations occur faster when the disease originates within Host 2. Also as before, a dominant Host 2 population causes significantly more infection in the mosquito population compared to a dominant Host 1.

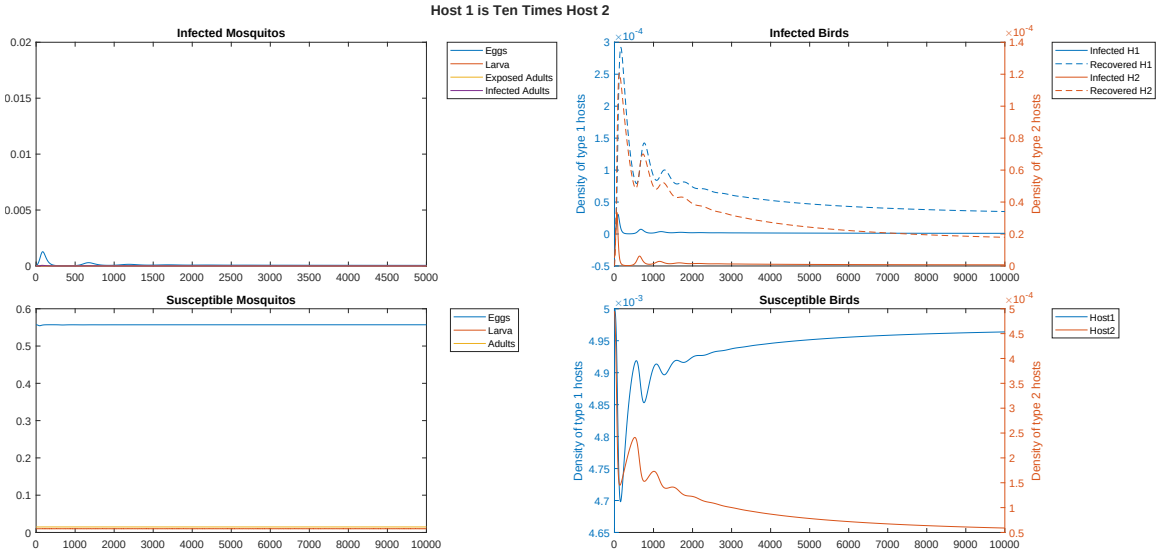

Figure 4: Simulation of the two-host model with infection originating within a small initial density of type 2 hosts (i.e. hosts with high WNV mortality). Specifically, the initial density of $H_{I_2} = 0.01 \times C_{H_2}$. All other initial values are taken from the disease-free steady-state. The carrying capacity of host 1 ($C_{H_1} = 0.005$ birds per m^2) is ten times that of host 2 ($C_{H_2} = 0.0005$ birds per m^2) so that the sum of the two carrying capacities (N_H) is 0.0055 birds per m^2. Other parameters are as in Tables 3 and 4. This yields a reproduction number of $\mathcal{R}_0 = 1.2881$.

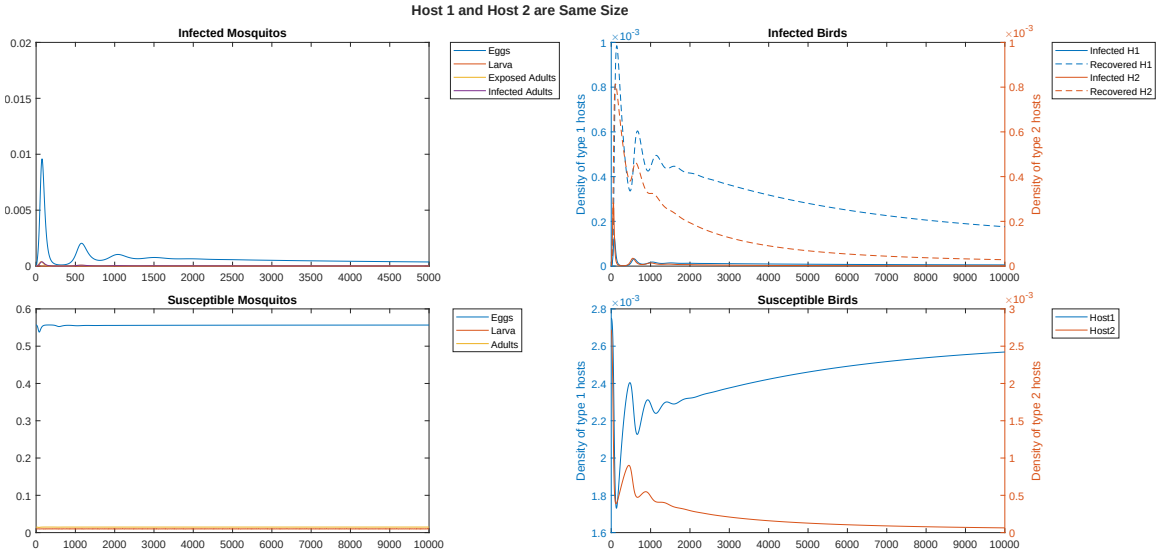

Figure 5: Simulation of the two-host model with infection originating within a small initial density of type 2 hosts (i.e. hosts with high WNV mortality). Specifically, the initial density of $H_{I_2} = 0.01 \times C_{H_2}$. All other initial values are taken from the disease-free steady-state. The carrying capacity of host 1 ($C_{H_1} = 0.0025$ birds per m^2) is equal to that of host 2 ($C_{H_2} = 0.0025$ birds per m^2) so that the sum of the two carrying capacities (N_H) is 0.0055 birds per m^2. Other parameters are as in Tables 3 and 4. This yields a reproduction number of $\mathcal{R}_0 = 1.2893$.

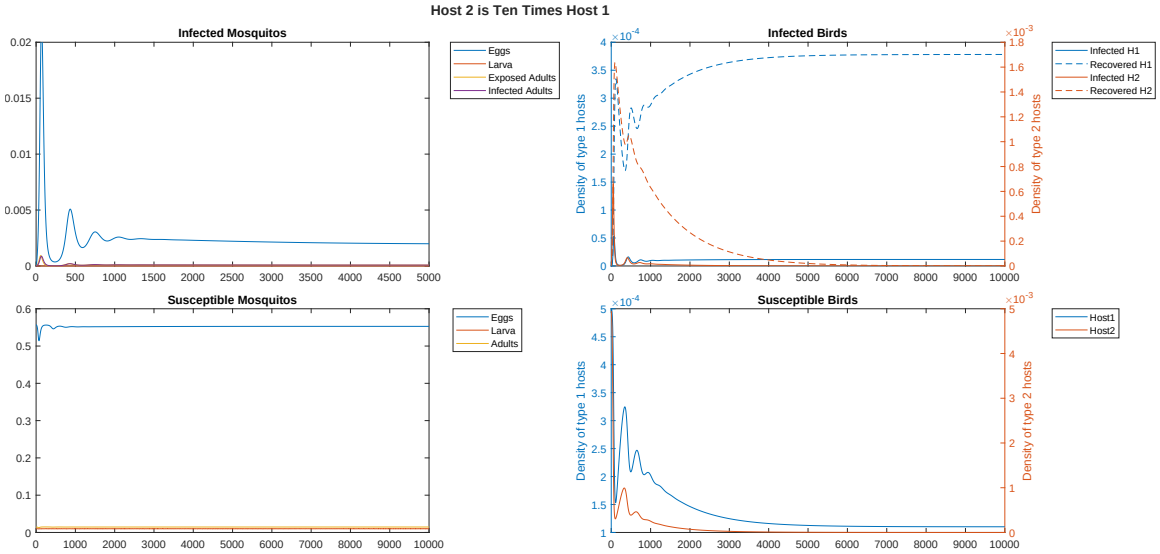

Figure 6: Simulation of the two-host model with infection originating within a small initial density of type 2 hosts (i.e. hosts with high WNV mortality). Specifically, the initial density of $H_{I_2} = 0.01 \times C_{H_2}$. All other initial values are taken from the disease-free steady-state. The carrying capacity of host 1 ($C_{H_1} = 0.0005$ birds per m^2) is one tenth that of host 2 ($C_{H_2} = 0.005$ birds per m^2) so that the sum of the two carrying capacities (N_H) is 0.0055 birds per m^2. Other parameters are as in Tables 3 and 4. This yields a reproduction number of $\mathcal{R}_0 = 1.2906$.

4.5 Small Initial Density of Infected Eggs

In Figures 7, 8, and 9 we observe that if the the infection originates with the mosquito eggs, then the outbreak for all populations takes longer to occur compared with either of the the scenarios in which the infection originates within one of the bird populations. As before, an endemic equilibrium does exist mathematically, but is unlikely to actually occur due to seasonal effects not included in this model. The dilution effect from previous scenarios is also present here as well. Also as before, a dominant Host 2 causes higher rates of infection within the mosquito population. It does not appear to matter much for the Host 1 population if the disease originates with Host 2 or with mosquito eggs.

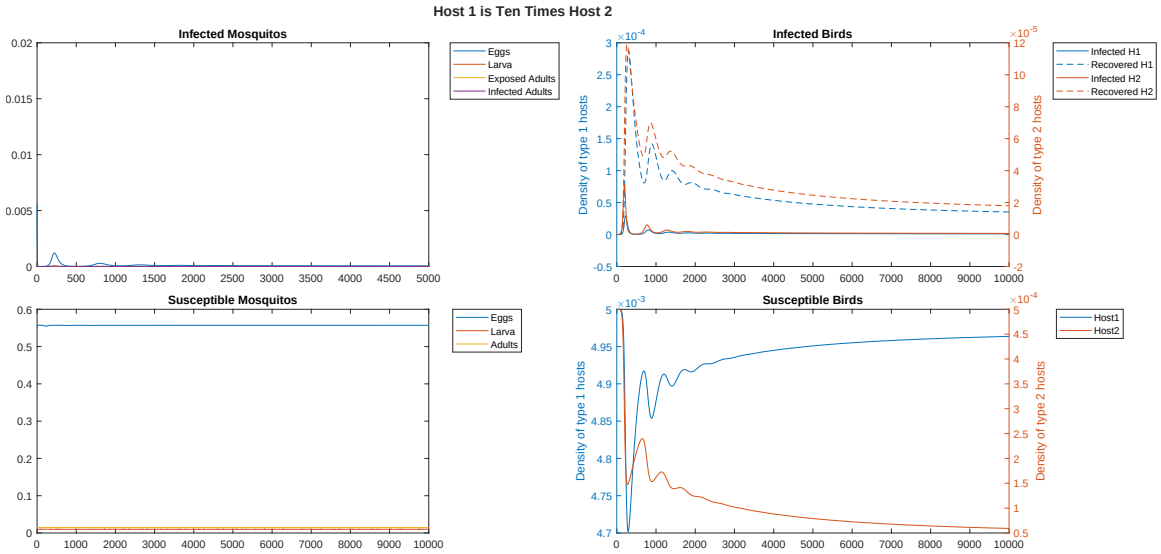

Figure 7: Simulation of the two-host model with infection originating within a small initial density of mosquitoes eggs. Specifically, the initial density of $E_I = 0.01 \times E_S^*$. All other initial values are taken from the disease-free steady-state. The carrying capacity of host 1 ($C_{H_1} = 0.005$ birds per m^2) is ten times that of host 2 ($C_{H_2} = 0.0005$ birds per m^2) so that the sum of the two carrying capacities (N_H) is 0.0055 birds per m^2. Other parameters are as in Tables 3 and 4. This yields a reproduction number of $\mathcal{R}_0 = 1.2881$.

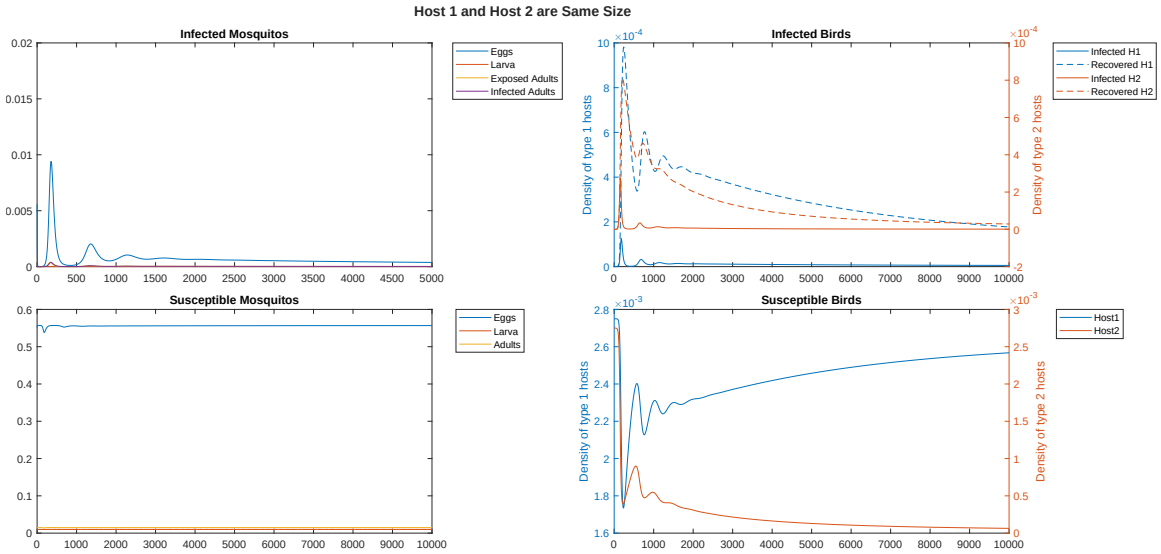

Figure 8: Simulation of the two-host model with infection originating within a small initial density of mosquitoes eggs. Specifically, the initial density of $E_I = 0.01 \times E_S^*$. All other initial values are taken from the disease-free steady-state. The carrying capacity of host 1 ($C_{H_1} = 0.0025$ birds per m^2) is equal to that of host 2 ($C_{H_2} = 0.0025$ birds per m^2) so that the sum of the two carrying capacities (N_H) is 0.0055 birds per m^2. Other parameters are as in Tables 3 and 4. This yields a reproduction number of $\mathcal{R}_0 = 1.2893$.

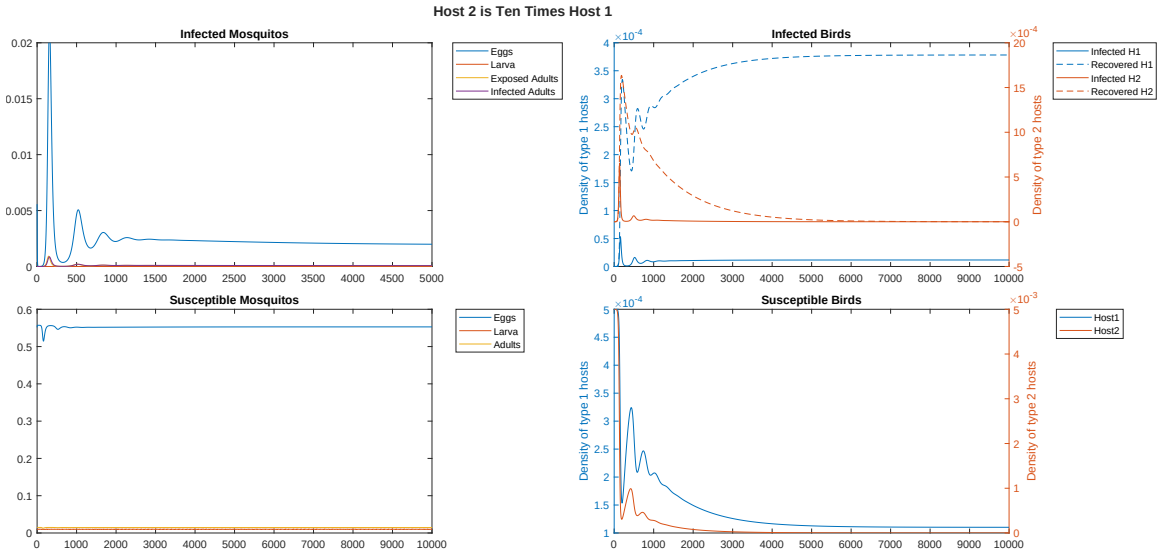

Figure 9: Simulation of the two-host model with infection originating within a small initial density of mosquitoes eggs. Specifically, the initial density of $E_I = 0.01 \times E_S^*$. All other initial values are taken from the disease-free steady-state. The carrying capacity of host 1 ($C_{H_1} = 0.0005$ birds per m^2) is one tenth that of host 2 ($C_{H_2} = 0.005$ birds per m^2) so that the sum of the two carrying capacities (N_H) is 0.0055 birds per m^2. Other parameters are as in Tables 3 and 4. This yields a reproduction number of $\mathcal{R}_0 = 1.2906$.

4.6 Small Initial Density of Infected Adult Mosquitoes

In Figures 10, 11, and 12 we observe that if the the infection originates with the adult mosquitoes, then the outbreak for all populations occurs much earlier then any of the previous scenarios. Otherwise, the dynamics are very similar to the scenarios in which the disease originates within mosquito eggs.

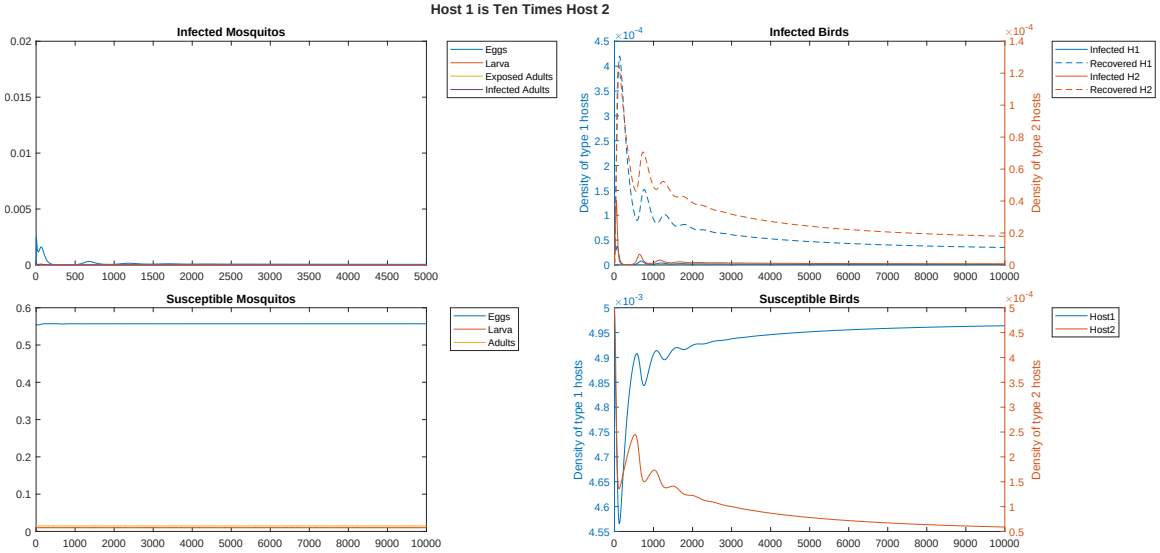

Figure 10: Simulation of the two-host model with infection originating within a small initial density of adult mosquitoes. Specifically, the initial density of $M_I = 0.01 \times M_S^*$. All other initial values are taken from the disease-free steady-state. The carrying capacity of host 1 ($C_{H_1} = 0.005$ birds per m^2) is ten times that of host 2 ($C_{H_2} = 0.0005$ birds per m^2) so that the sum of the two carrying capacities (N_H) is 0.0055 birds per m^2. Other parameters are as in Tables 3 and 4. This yields a reproduction number of $\mathcal{R}_0 = 1.2881$.

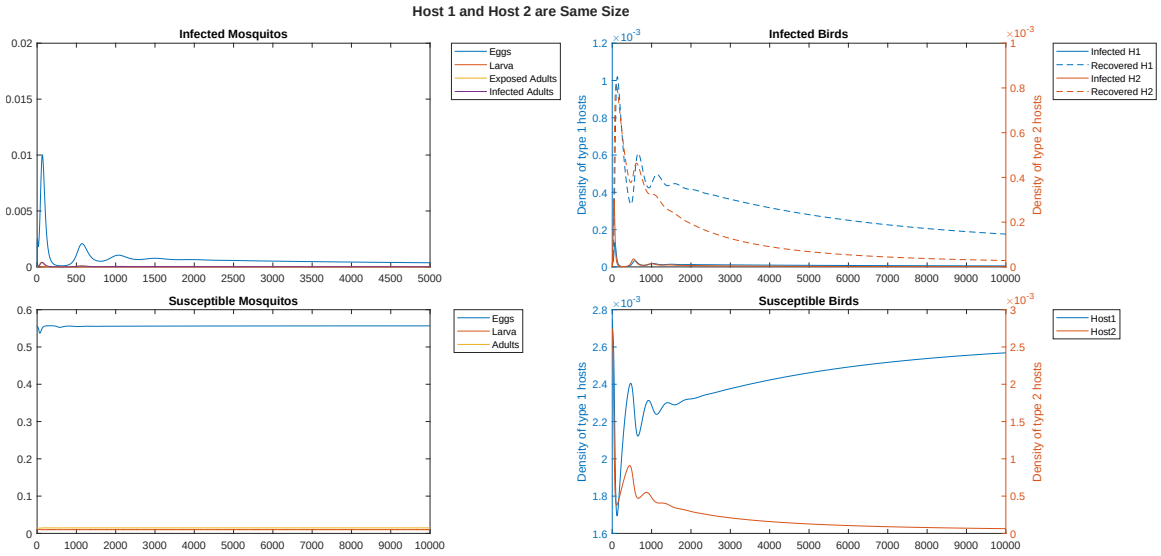

Figure 11: Simulation of the two-host model with infection originating within a small initial density of adult mosquitoes. Simulation of the two-host model with infection originating within a small initial density of adult mosquitoes. Specifically, the initial density of $M_I = 0.01 \times M_S^*$. All other initial values are taken from the disease-free steady-state. The carrying capacity of host 1 ($C_{H_1} = 0.0025$ birds per m^2) is equal to that of host 2 ($C_{H_2} = 0.0025$ birds per m^2) so that the sum of the two carrying capacities (N_H) is 0.0055 birds per m^2. Other parameters are as in Tables 3 and 4. This yields a reproduction number of $\mathcal{R}_0 = 1.2893$.

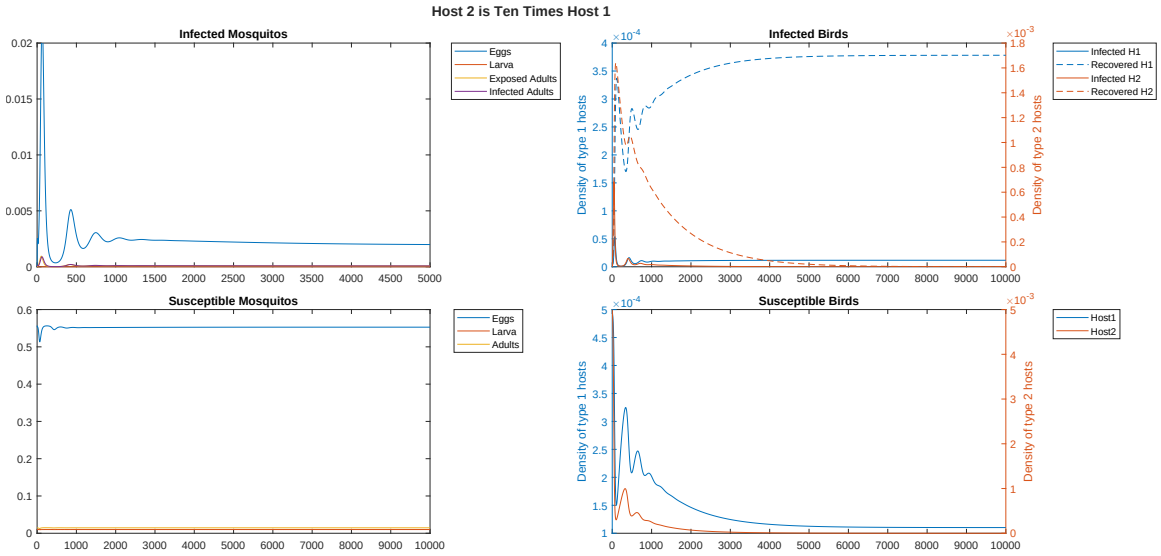

Figure 12: Simulation of the two-host model with infection originating within a small initial density of adult mosquitoes. Simulation of the two-host model with infection originating within a small initial density of adult mosquitoes. Specifically, the initial density of $M_I = 0.01 \times M_S^*$. All other initial values are taken from the disease-free steady-state. The carrying capacity of host 1 ($C_{H_1} = 0.0005$ birds per m^2) is one tenth that of host 2 ($C_{H_2} = 0.005$ birds per m^2) so that the sum of the two carrying capacities (N_H) is 0.0055 birds per m^2. Other parameters are as in Tables 3 and 4. This yields a reproduction number of $\mathcal{R}_0 = 1.2906$.

CHAPTER 5

CONCLUSION

The reproduction number results here are consistent with the litany of work demonstrating that the mosquito to host ratio ($M_S^* : N_H$) greatly effects the reproduction number. It is interesting to note that, in the two-host model case, the ratios of specific host populations to the total host population ($N_{H_j} : N_H$) also play a role in computing the reproduction number. This can also be seen in the numerical simulations, where changing the Host1 to Host2 ratios has little impact on the reproduction number, but can significantly alter the course of an epidemic. Specifically, if the said ratio favors the less competent host population then the more vulnerable host population is protected from extinction.

The simulations demonstrate that this model does have endemic steady-states that arise mathematically if not necessarily biologically. Future work might incorporate seasonal effects into this model to see if periodic endemic solutions exist. The previous simplified model in [2] did not have any endemic steady-states due to epidemic burnout in the absence of host recruitment. It would be interesting to explore the relative impacts of host demographics, horizontal, vertical, and host-vector transmission on the endemic equilibrium and WNV maintenance over the winter. Futurely, we will also consider optimal control of this model. Further questions of interest are: Does the inclusion of more detailed bird dynamics impact the timing or magnitude of the optimal control? How are model dynamics and optimal control features impacted by the density of birds in each category?

Table 2: **Variables in Model**

Variable	Description
$N_H(t)$	Total Population of All Hosts
$H_j(t)$	Total Population of Host Group j
$H_{S_j}(t)$	Susceptible Population of Host Group j
$H_{I_j}(t)$	Infected Population of Host Group j
$H_{R_j}(t)$	Recovered Population of Host Group j
$E_S(t)$	Eggs Laid by Susceptible or Exposed Mosquitoes
$E_I(t)$	Eggs Laid by Infected Mosquitoes
$L_S(t)$	Susceptible Larvae
$L_I(t)$	Infected Larvae
$M_S(t)$	Susceptible Mosquitoes
$M_E(t)$	Exposed Mosquitoes
$M_I(t)$	Infected Mosquitoes

Table 3: **Mosquito Parameters in Model**

Parameter	Description	Value	Range	Citation
b	Mosquito Biting Rate	$\frac{1}{5}$ day^{-1}	$(0, 0.4)$	[15]
C_L	Carrying Capacity, Larval Mosquitoes	$0.01 \frac{\text{indv}}{m^2}$	$(0.001, 0.01)$	[19]
μ_L	Death Rate, Larval Mosquitoes	0.16 day^{-1}	$(0.0014, 0.24)$	[15]
μ_M	Death Rate, Adult Mosquitoes	$\frac{1}{10.4}$ day^{-1}	$(\frac{1}{10.4}, \frac{1}{6.25})$	[10]
m_E	Hatch Rate, Mosquito Eggs	$\frac{1}{2}$ day^{-1}	$(0.1, 1)$	[6, 9]
m_L	Maturation Rate, Larval Mosquitoes	$\frac{1}{7}$ day^{-1}	$(\frac{1}{24}, \frac{1}{6})$	[6, 9]
r_S	Egg Laying Rate, Susceptible & Exposed Mosquitoes	$\frac{150}{8} \cdot \frac{\text{eggs}}{\text{mosquito} \cdot \text{day}}$		[16]
r_I	Egg Laying Rate, Infected Mosquitoes	$\frac{100}{8} \cdot \frac{\text{eggs}}{\text{mosquito} \cdot \text{day}}$		[16]
q_S	Fraction of Eggs Hatched from Uninfected Mosquitoes	0.56		[16]
q_I	Fraction of Eggs Hatched from Infected Mosquitoes	0.43		[16]
ϕ	Fraction of Eggs Born Infected from Infected Mosquitoes	0.003		[3]
k_L	Disease Progression Rate in Mosquitoes	$\frac{1}{10}$ day^{-1}		[16]

Table 4: **Bird Parameters in Model**

Parameter	Description	Value: $j = 1$	Value: $j = 2$	Citation
Λ_j	Recruitment Rate, Host Group j	0.0044	0.0033	[1]
P_{MH_j}	Mosquito-to-Host Transmission, Host Group j	0.5	0.5	[1]
P_{HH_j}	Contract Rate, Host Group j	0	9.2029	[1]
P_{H_jM}	Host-to-Mosquito Transmission, Host Group j	0.2146	0.4067	[1]
ω_j	Direct Transmission Rate, Host Group j	0	0.1590	[1]
C_{H_j}	Carrying Capacity, Host Group j	0.0005	0.0005	[1]
γ_{H_j}	WNV Death Rate, Host Group j	0	0.0988	[1]
g_{I_j}	WNV Recovery Rate, Host Group j	0.1429	0.0603	[1]
μ_{H_j}	Natural Death Rate, Host Group j	0.0020	0.0023	[1]

Composite Parameters:

$$\begin{aligned} d_L &= \frac{m_L r_S q_S}{\mu_M} - \mu_L - m_L & \tau &= m_L + \mu_L + \frac{d_L L_S^*}{C_L} \\ d_{H_j} &= \Lambda_j - \mu_{H_j} & s_j &= \gamma_{H_j} + g_{I_j} + \mu_{H_j} + d_{H_j} \end{aligned}$$

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