

# NOTES ON MULTIPLE BLOOD FEEDING IN MOSQUITO-BORNE DISEASE TRANSMISSION MODELS

Throughout, I will use the terms abundance and density interchangeably. These are of course two different quantities but the distinction is not meaningful until we use actual parameter estimates.

Let  $M$  represent the total adult female mosquito population size and  $H$  the total host population size. For now, we assume a simple general model for the demographic dynamics of the host, namely  $\frac{d}{dt}H = g(H)$  where  $g(0) = 0$ ,  $g'(0) > 0$ ,  $g''(H) < 0$  and there exists  $K > 0$  such that  $g(K) = 0$ . This ensures the existence of an unstable extinction equilibrium and a stable positive equilibrium (“carrying capacity”). Notably, the familiar logistic population model satisfies these assumptions.

The mosquito population is separated into aquatic stages (eggs, larvae and pupae) and adults. Let  $L$  represent the total female aquatic stage population. We use the following system of equations as the overall model of mosquito demography

$$\begin{aligned}\frac{d}{dt}L &= \lambda_M \left(1 - \frac{L}{K_L}\right) - (\rho_L + \mu_L)L \\ \frac{d}{dt}M &= \rho_L L - \mu_M M\end{aligned}$$

where  $\lambda_M$  is the recruitment rate of eggs,  $K_L$  is the carrying capacity for aquatic stage mosquitoes,  $\rho_L$  is the development rate,  $\mu_L$  is the density-independent aquatic stage mortality rate, and  $\mu_M$  is the density-independent adult mortality rate. The rate  $\lambda_M$  should depend on the reproductive capacity of the adult population, namely the total abundance and biting rate of adults. We will come back to the biting rate later, but for now let  $b_M$  represent the biting rate for mosquitoes.

$$\lambda_M(M) = bfM$$

where  $f$  is the fecundity of a female mosquito (eggs per female per day).

## Part 1. Generalizing mosquito biting rates

Henceforth, I will refer to the total adult female mosquito population as just the mosquito population,  $M$ . We divide  $M$  into several compartments representing the varying (generalized) stages of the mosquito gonotrophic (reproductive) cycle. The first stage,  $S$ , includes mosquitoes seeking a blood meal. After feeding to repletion, mosquitoes proceed to the oviposition stage,  $V$ . After egg-laying, these individuals begin seeking another blood meal and return to  $S$ .

Following Hurtado and Kirosingh (2019), let  $\mathcal{S}_X$  be the survival function for the dwell time distribution for an individual entering compartment  $X$  at time  $\tau$ ,  $h(t, \tau)$  the density function for that distribution, and  $\mathcal{I}_X$  the inflow rate to compartment  $X$ . Then a general model for the dynamics of oviposition and blood meal seeking can be given by the integral equations:

$$\begin{aligned}S(t) &= s_0 \mathcal{S}_S(t, 0) + \int_0^t \left[ \mathcal{I}_S(\tau) + v_0 h_V(\tau, 0) + \int_0^\tau \mathcal{I}_V(s) h_V(\tau, s) ds \right] \mathcal{S}_S(t, \tau) d\tau \\ V(t) &= v_0 \mathcal{S}_V(t, 0) + \int_0^t \left[ \mathcal{I}_V(\tau) + s_0 h_S(\tau, 0) + \int_0^\tau \mathcal{I}_S(s) h_S(\tau, s) ds \right] \mathcal{S}_V(t, \tau) d\tau\end{aligned}$$

where  $\mathcal{I}_S(t)$  and  $\mathcal{I}_V(t)$  are the additional inflow rates into states  $S$  and  $V$ , respectively. We make the further assumptions that i) all newly recruited adults start in stage  $S$  and ii) the only way to enter  $V$  is after exiting stage  $S$ , and iii) the waiting period in compartment  $V$  is exponentially distributed with mean  $\gamma$ . This translates to the equations

$$\begin{aligned}v_0 &= 0, \\ \mathcal{I}_S(t) &= \rho_L L(t) + \gamma V(t), \\ \mathcal{I}_V(t) &= 0.\end{aligned}$$

Hence we arrive at the following system of equations

$$\begin{aligned} S(t) &= s_0 \mathcal{S}_S(t, 0) + \int_0^t [\rho_L L(\tau) + \gamma V(\tau)] \mathcal{S}_S(t, \tau) d\tau \\ V(t) &= \int_0^t \left[ s_0 h_S(\tau, 0) + \int_0^\tau [\rho_L L(s) + \gamma V(s)] h_S(\tau, s) ds \right] e^{-(t-\tau)/\gamma} d\tau \end{aligned}$$

It remains to describe the distribution of the waiting time to leave the host seeking class,  $S$ , which is in fact the main point of this project.

**Problem 1.** (Erlang distributed biting rate) Suppose that individuals bite on average at a rate of  $b$  and must make, on average,  $k$  bites to reach repletion and reproduce. Then the dwell time distribution out of  $S$  has an Erlang( $r, k$ ) distribution with shape parameter  $k$  and rate  $r = \frac{k}{b}$ . Then

$$\begin{aligned} \mathcal{S}_S(t, \tau) &= \frac{1}{r} \sum_{j=1}^k g^j(t - \tau), \\ g^j(t) &= r \frac{(rt)^{j-1}}{(j-1)!} e^{-rt} \end{aligned}$$

Note that this distribution has mean  $\mu = \frac{k}{r}$ . Using the Linear Chain Trick, we can convert the system of integral equations above to a system of ODEs. Let

$$S_j(t) = s_0 \frac{1}{r} g^j(t) + \int_0^t \mathcal{I}_S(\tau) \frac{1}{r} g^j(t - \tau) d\tau$$

with  $S_1(0) = x_0$  and  $S_j(0) = 0$  for  $j \geq 2$ . Then

$$\begin{aligned} \frac{d}{dt} S_1(t) &= \frac{d}{dt} \left[ s_0 \frac{1}{r} r e^{-rt} + \int_0^t \mathcal{I}_S(\tau) \frac{1}{r} r e^{-r(t-\tau)} d\tau \right] \\ &= \frac{d}{dt} \left[ s_0 e^{-rt} + \int_0^t \mathcal{I}_S(\tau) e^{-r(t-\tau)} d\tau \right] \\ &= s_0 \frac{d}{dt} e^{-rt} + \mathcal{I}_S(t) e^{-r(t-t)} + \int_0^t \frac{d}{dt} \mathcal{I}_S(\tau) e^{-r(t-\tau)} d\tau \\ &= -s_0 r e^{-rt} + \mathcal{I}_S(t) - r \int_0^t \mathcal{I}_S(\tau) e^{-r(t-\tau)} d\tau \\ &= \mathcal{I}_S(t) - r \left[ s_0 e^{-rt} - \int_0^t \mathcal{I}_S(\tau) e^{-r(t-\tau)} d\tau \right] \\ &= \mathcal{I}_S(t) - r S_1(t) \end{aligned}$$

$$\begin{aligned} \frac{d}{dt} S_j(t) &= s_0 \frac{1}{r} \frac{d}{dt} g^j(t) + \frac{d}{dt} \int_0^t \mathcal{I}_S(\tau) \frac{1}{r} g^j(t - \tau) d\tau \\ &= s_0 [g^{j-1}(t) - g^j(t)] + \mathcal{I}_S(t) \frac{1}{r} g^j(0) + \int_0^t \mathcal{I}_S(\tau) [g^{j-1}(t - \tau) - g^j(t - \tau)] d\tau \\ &= s_0 [g^{j-1}(t) - g^j(t)] + \int_0^t \mathcal{I}_S(\tau) [g^{j-1}(t - \tau) - g^j(t - \tau)] d\tau \\ &= r \left[ s_0 \frac{1}{r} g^{j-1}(t) + \int_0^t \mathcal{I}_S(\tau) \frac{1}{r} g^{j-1}(t - \tau) d\tau \right] - r \left[ s_0 \frac{1}{r} g^j(t) + \int_0^t \mathcal{I}_S(\tau) \frac{1}{r} g^j(t - \tau) d\tau \right] \\ &= r S_{j-1}(t) - r S_j(t) \end{aligned}$$

Note additionally that

$$\begin{aligned}\frac{d}{dt}S(t) &= \sum_{j=1}^k \frac{d}{dt}S_j(t) \\ &= \mathcal{I}_S(t) - rS_1(t) + \sum_{j=2}^k [rS_{j-1}(t) - rS_j(t)] \\ &= \mathcal{I}_S(t) - rS_k(t)\end{aligned}$$

where we liberally used the fact that

$$\begin{aligned}\frac{d}{dt}g^1(t) &= -rg^1(t), \\ \frac{d}{dt}g^j(t) &= r[g^{j-1}(t) - g^j(t)]\end{aligned}$$

**Problem 2.** Suppose, similar to above, that individual mosquitoes, on average, bite at a rate  $b$  and must take  $k$  bites to repletion. Additionally, assume that if an individual does not reach repletion, on average, within  $1/\rho$  days, then they experience mortality. In this case, the dwell time distribution for  $S$  is given by the minimum of an Erlang  $(\frac{k}{b}, k)$  distribution and an Exponential  $(\rho)$  distribution. The generalized linear chain trick will give us a way to deal with this scenario. The assumption of mortality can be relaxed so that individuals which do not blood feed to repletion go to feed on sugar sources to prevent mortality and then return back to blood feed (by then requiring a full set of blood-meals). Both of these cases can be dealt with rather easily using the GLCT. See sections 3.5.1 and 3.5.4 from Hurtado and Kirosingh 2019.

**Problem 3.** So far we have assumed that the time between biting events (equivalently, the biting rate) is constant. However, it is realistic to assume that the animals upon which mosquitoes feed i) are able to engage in behaviors to limit how often they are bitten and ii) may be difficult to find. A simple model which takes these two assumptions into account is due to Chitnis et al. (Chitnis et al., 2006). This model assumes that there is a theoretical maximum mosquito biting rate,  $\sigma_M$ , and a theoretical maximum rate at which an animal can be bitten,  $\sigma_H$ . Then, the actual biting rate for mosquitoes,  $b$ , is a function of these theoretical maxima and the abundances of mosquitoes and hosts:

$$b(t) = \sigma_M \left( \frac{\sigma_H H}{\sigma_M M + \sigma_H H} \right)$$

Notice this is now dependent on time through the state variables  $H$  and  $M$ . We can return to the set up of Problem 2, this time using  $b$  as above. This can also be converted to a system of ODEs using the GLCT since it is still a Poisson process (although in this case it is inhomogeneous). In fact, since  $b(t)$  is only dependent on time through the state parameters, the system of ODEs will remain autonomous, so equilibrium analyses will be straightforward.

## Part 2. Defensive behaviors and mosquito biting

While the Chitnis dynamic contact rate model fairly represents some important aspects of defensive behaviors and host-seeking behaviors, we can do a little better.

### Simple model with transmission

#### 1. MODEL SET-UP

The basic demographic model is given by:

$$\begin{aligned}\frac{d}{dt}H &= (\lambda_H - \mu_H) H \left( 1 - \frac{H}{K_H} \right) \\ \frac{d}{dt}M &= \Lambda_M - \mu_M M\end{aligned}$$

Assume that the time-between-egg-laying distribution is Erlang  $(b, k)$ . Let  $B$  be the compartment of biting mosquitoes and  $W$  the compartment of egg-laying mosquitoes. Then we can decompose  $B$  as  $B = \sum_{i=1}^k B_i$  where

$$\begin{aligned}\frac{d}{dt}B_1 &= \Lambda_M + \gamma_W W - bB_1 - \mu_M B_1 \\ \frac{d}{dt}B_j &= b(B_{j-1} - B_j) - \mu_M B_j \\ \frac{d}{dt}W &= bB_k - \gamma_W W - \mu_M W\end{aligned}$$

Finally, putting this together into a simple transmission model.

$$\begin{aligned}\frac{d}{dt}S_H &= \left[ \lambda_H H - \left( \frac{\lambda_H - \mu_H}{K_H} \right) H^2 \right] - \beta_{MH} \frac{S_H}{N_H} \left( b \sum_{j=1}^k I_{B,j} \right) - \mu_H S_H \\ \frac{d}{dt}I_H &= \beta_{MH} \frac{S_H}{N_H} \left( b \sum_{j=1}^k I_{B,j} \right) - \mu_H I_H - \gamma_H I_H \\ \frac{d}{dt}R_H &= \gamma_H I_H - \mu_H R_H\end{aligned}$$

$$\begin{aligned}\frac{d}{dt}S_{B,1} &= \Lambda_M + \gamma_W S_W - bS_{B,1} - \mu_M S_{B,1} \\ \frac{d}{dt}S_{B,j} &= bS_{B,j-1} \left( 1 - \frac{I_H}{N_h} \right) - bS_{B,j} - \mu_M S_{B,j} \\ \frac{d}{dt}S_B &= \Lambda_M + \gamma_W S_W - bS_{B,k} \left( 1 - \frac{I_H}{N_h} \right) - \frac{I_H}{N_h} bS_B - \mu_M S_B \\ \frac{d}{dt}I_{B,1} &= \gamma_W I_W - bI_{B,1} - \mu_M I_{B,1} \\ \frac{d}{dt}I_{B,j} &= bS_{B,j-1} \left( \frac{I_H}{N_h} \right) + bI_{B,j-1} - bI_{B,j} - \mu_M I_{B,j} \\ \frac{d}{dt}I_B &= \gamma_W I_W - bI_{B,k} - \mu_M I_B\end{aligned}$$

$$\begin{aligned}\frac{d}{dt}S_W &= bS_{B,k} \left( 1 - \frac{I_H}{N_h} \right) - \gamma_W S_W - \mu_M S_W \\ \frac{d}{dt}I_W &= bS_{B,k} \left( \frac{I_H}{N_h} \right) + bI_{B,k} - \gamma_W I_W - \mu_M I_W\end{aligned}$$

where  $S_B = \sum_{j=1}^k S_{B,j}$  and  $I_B = \sum_{j=1}^k I_{B,j}$ .

For simplicity, we assume that i) there is no disease-induced mortality in either the host of vector and ii) the host is at carrying capacity:  $H = K_H$ . Then the equations simplify to

$$\begin{aligned}
\frac{d}{dt}S_H &= \mu_H K_H - \beta_{MH} b I_B \frac{S_H}{K_H} - \mu_H S_H \\
\frac{d}{dt}I_H &= \beta_{MH} b I_B \frac{S_H}{K_H} - \mu_H I_H - \gamma_H I_H \\
\frac{d}{dt}R_H &= \gamma_H I_H - \mu_H R_H \\
\frac{d}{dt}S_{B,1} &= \Lambda_M + \gamma_W S_W - b S_{B,1} - \mu_M S_{B,1} \\
\frac{d}{dt}S_{B,j} &= \left(1 - \beta_{HM} \frac{I_H}{K_H}\right) b S_{B,j-1} - (b + \mu_M) S_{B,j} \\
\frac{d}{dt}I_{B,1} &= \gamma_W I_W - (b + \mu_M) I_{B,1} \\
\frac{d}{dt}I_{B,j} &= \left(\beta_{HM} \frac{I_H}{K_H}\right) b S_{B,j-1} + b I_{B,j-1} - (b + \mu_M) I_{B,j} \\
\frac{d}{dt}S_W &= \left(1 - \beta_{HM} \frac{I_H}{K_H}\right) b S_{B,k} - \gamma_W S_W - \mu_M S_W \\
\frac{d}{dt}I_W &= \beta_{HM} b S_{B,k} \left(\frac{I_H}{K_H}\right) + b I_{B,k} - \gamma_W I_W - \mu_M I_W
\end{aligned}$$

Note that

$$\left(1 - \beta_{HM} \frac{I_H}{K_H}\right) b S_{B,j-1} = b S_{B,j-1} \left[ \left(1 - \frac{I_H}{K_H}\right) + (1 - \beta_{HM}) \left(\frac{I_H}{K_H}\right) \right]$$

## 2. EQUILIBRIA

**2.1. Disease-free equilibria.** Suppose that  $I_H = I_{B,j} = I_W = 0$ . Then we solve for any equilibria:

$$\begin{aligned}
S_H &= K_H \\
R_H &= 0 \\
(b + \mu_M) S_{B,1} &= \Lambda_M + \gamma_W S_W \\
S_{B,j} &= \left(\frac{b}{b + \mu_M}\right) S_{B,j-1} \\
(\gamma_W + \mu_M) S_W &= b S_{B,k}
\end{aligned}$$

The last three equations require a little work. Note that  $S_{B,j} = \left(\frac{b}{b + \mu_M}\right)^{j-1} S_{B,1}$ .

$$\begin{aligned}
S_W &= \left(\frac{1}{\gamma_W + \mu_M}\right) b \left(\frac{b}{b + \mu_M}\right)^{k-1} S_{B,1} \\
(b + \mu_M) S_{B,1} &= \Lambda_M + b \left(\frac{b}{b + \mu_M}\right)^{k-1} S_{B,1} - \left(\frac{\mu_M}{\gamma_W + \mu_M}\right) b \left(\frac{b}{b + \mu_M}\right)^{k-1} S_{B,1} \\
S_{B,1} &= \left(\frac{1}{b + \mu_M}\right) \Lambda_M + \left(\frac{\gamma_W}{\gamma_W + \mu_M}\right) \left(\frac{b}{b + \mu_M}\right)^k S_{B,1} \\
\left[1 - \left(\frac{\gamma_W}{\gamma_W + \mu_M}\right) \left(\frac{b}{b + \mu_M}\right)^k\right] S_{B,1} &= \left(\frac{1}{b + \mu_M}\right) \Lambda_M \\
S_{B,1} &= \left(\frac{1}{b + \mu_M}\right) \left[1 - \left(\frac{\gamma_W}{\gamma_W + \mu_M}\right) \left(\frac{b}{b + \mu_M}\right)^k\right]^{-1} \Lambda_M
\end{aligned}$$

$$\begin{aligned}
S_{B,1} &= \left( \frac{1}{b + \mu_M} \right) \left[ 1 - \left( \frac{\gamma_W}{\gamma_W + \mu_M} \right) \left( \frac{b}{b + \mu_M} \right)^k \right]^{-1} \Lambda_M \\
S_{B,j} &= \frac{1}{b} \left( \frac{b}{b + \mu_M} \right)^j \left[ 1 - \left( \frac{\gamma_W}{\gamma_W + \mu_M} \right) \left( \frac{b}{b + \mu_M} \right)^k \right]^{-1} \Lambda_M \\
S_W &= \left( \frac{1}{\gamma_W + \mu_M} \right) \left( \frac{b}{b + \mu_M} \right)^k \left[ 1 - \left( \frac{\gamma_W}{\gamma_W + \mu_M} \right) \left( \frac{b}{b + \mu_M} \right)^k \right]^{-1} \Lambda_M
\end{aligned}$$

Note that the total equilibrium mosquito population size should be independent of  $k$ .

$$\begin{aligned}
M &= S_W + S_{B,1} + \sum_{j=2}^k S_{B,j} \\
&= n_G \Lambda_M \left\{ \left( \frac{1}{\gamma_W + \mu_M} \right) \left( \frac{b}{b + \mu_M} \right)^k + \frac{1}{b} \sum_{j=1}^k \left( \frac{b}{b + \mu_M} \right)^j \right\} \\
&= n_G \Lambda_M \left\{ \left( \frac{1}{\gamma_W + \mu_M} \right) \left( \frac{b}{b + \mu_M} \right)^k + \frac{1}{b} \left[ \frac{\left( \frac{b}{b + \mu_M} \right)^k - 1}{\left( \frac{b}{b + \mu_M} \right) - 1} \right] \right\} \\
&= n_G \Lambda_M \left\{ -\frac{1}{n_G} + 1 + \frac{b + \mu_M}{b} \frac{1}{\mu_M} \left[ 1 - \left( \frac{b}{b + \mu_M} \right)^k \right] \right\}
\end{aligned}$$

where  $n_G = \left[ 1 - \left( \frac{\gamma_W}{\gamma_W + \mu_M} \right) \left( \frac{b}{b + \mu_M} \right)^k \right]^{-1}$  !!! This isn't working any more?h

**2.2. Endemic equilibria.** Now assume that at least one of  $I_H, I_{B,j}, I_W \neq 0$ .

**2.3. Basic reproduction number.** The infected compartments are  $I_H, I_W$ , and  $I_{B,j}, j = 1, \dots, k$ . Let  $x = (I_H, I_W, I_{B,1}, \dots, I_{B,k})$ . Let  $J$  be the Jacobian of the system above written with the state

variables in the order:  $I_H, I_{B,1}, \dots, I_{B,k}, I_W, S_H, S_{B,1}, \dots, S_{B,k}, S_W$

$$J = \begin{pmatrix} S_{B,k} & S_H & I_H & R_H & S_{B,1} \\ \mu_H K_H - \beta_{MH} b I_B \frac{S_H}{K_H} - \mu_H S_H & I_{B,1} & \dots & I_{B,j-1} & I_{B,j} \\ 0 & -\beta_{MH} b I_B \frac{1}{K_H} - \mu_H & 0 & 0 & 0 \\ \beta_{MH} b I_B \frac{S_H}{K_H} - \mu_H I_H - \gamma_H I_H & -\beta_{MH} b \frac{S_H}{K_H} & \dots & -\beta_{MH} b \frac{S_H}{K_H} & -\beta_{MH} b \frac{S_H}{K_H} \\ 0 & \beta_{MH} b I_B \frac{1}{K_H} & -\mu_H - \gamma_H & 0 & 0 \\ \gamma_H I_H - \mu_H R_H & \beta_{MH} b \frac{S_H}{K_H} & \dots & \beta_{MH} b \frac{S_H}{K_H} & \beta_{MH} b \frac{S_H}{K_H} \\ 0 & 0 & \gamma_H & -\mu_H & 0 \\ \Lambda_M + \gamma_W S_W - b S_{B,1} - \mu_M S_{B,1} & 0 & \dots & 0 & 0 \\ 0 & 0 & 0 & 0 & -b - \mu_M \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ b S_{B,j-1} \left(1 - \beta_{HM} \frac{I_H}{K_H}\right) - b S_{B,j} - \mu_M S_{B,j} & 0 & b S_{B,j-1} \left(-\frac{1}{K_h}\right) & 0 & 0 \\ 0 & 0 & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ b S_{B,k-1} \left(1 - \beta_{HM} \frac{I_H}{K_H}\right) - b S_{B,k} - \mu_M S_{B,k} & 0 & b S_{B,k-1} \left(-\frac{1}{K_h}\right) & 0 & 0 \\ -b - \mu_M & 0 & \dots & 0 & 0 \\ \gamma_W I_W - b I_{B,1} - \mu_M I_{B,1} & 0 & 0 & 0 & 0 \\ 0 & -b - \mu_M & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ \beta_{HM} b S_{B,j-1} \left(\frac{I_H}{K_H}\right) + b I_{B,j-1} - b I_{B,j} - \mu_M I_{B,j} & 0 & b S_{B,j-1} \left(\frac{1}{K_H}\right) & 0 & 0 \\ 0 & 0 & \dots & b & -b - \mu_M \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ \beta_{HM} b S_{B,k-1} \left(\frac{I_H}{K_H}\right) + b I_{B,k-1} - b I_{B,k} - \mu_M I_{B,k} & 0 & b S_{B,k-1} \left(\frac{1}{K_H}\right) & 0 & 0 \\ 0 & 0 & \dots & 0 & 0 \\ b S_{B,k} \left(1 - \frac{I_H}{K_h}\right) - \gamma_W S_W - \mu_M S_W & 0 & b S_{B,k} \left(-\frac{1}{K_h}\right) & 0 & 0 \\ b \left(1 - \frac{I_H}{K_h}\right) & 0 & \dots & 0 & 0 \\ b S_{B,k} \left(\frac{I_H}{K_H}\right) + b I_{B,k} - \gamma_W I_W - \mu_M I_W & 0 & b S_{B,k} \left(\frac{1}{K_H}\right) & 0 & 0 \\ 0 & 0 & \dots & 0 & 0 \end{pmatrix}$$

Re-ordering this and only including the infected state variables, gives us

$$\hat{J}(x) = \begin{pmatrix} -\mu_H - \gamma_H & \beta_{MH} b \frac{S_H}{K_H} & \dots & \beta_{MH} b \frac{S_H}{K_H} & \beta_{MH} b \frac{S_H}{K_H} & \dots & \beta_{MH} b \frac{S_H}{K_H} & \beta_{MH} b \frac{S_H}{K_H} & 0 \\ 0 & -b - \mu_M & \dots & 0 & 0 & \dots & 0 & 0 & \gamma_W I_W \\ \vdots & \vdots & \ddots & \vdots & \vdots & \ddots & \vdots & \vdots & \vdots \\ b S_{B,j-1} \left(\frac{1}{K_H}\right) & 0 & \dots & b & -b - \mu_M & \dots & 0 & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots & \ddots & \vdots & \vdots & \vdots \\ b S_{B,k-1} \left(\frac{1}{K_H}\right) & 0 & \dots & 0 & 0 & \dots & b & -b - \mu_M & 0 \\ b S_{B,k} \left(\frac{1}{K_H}\right) & 0 & \dots & 0 & 0 & \dots & 0 & b & -\gamma_W - \mu_M \end{pmatrix}$$

Finally, evaluating at the disease-free equilibrium defined above, we obtain

$$\hat{J}(\mathbf{0}) = \begin{pmatrix} -\mu_H - \gamma_H & \beta_{MH}b & \cdots & \beta_{MH}b & \beta_{MH}b & \cdots & \beta_{MH}b & \beta_{MH}b & 0 \\ 0 & -b - \mu_M & \cdots & 0 & 0 & \cdots & 0 & 0 & \gamma_W I_W \\ \vdots & \vdots & \ddots & \vdots & \vdots & \ddots & \vdots & \vdots & \vdots \\ bS_{B,j-1} \left( \frac{1}{K_H} \right) & 0 & \cdots & b & -b - \mu_M & \cdots & 0 & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots & \ddots & \vdots & \vdots & \vdots \\ bS_{B,k-1} \left( \frac{1}{K_H} \right) & 0 & \cdots & 0 & 0 & \cdots & b & -b - \mu_M & 0 \\ bS_{B,k} \left( \frac{1}{K_H} \right) & 0 & \cdots & 0 & 0 & \cdots & 0 & b & -\gamma_W - \mu_M \end{pmatrix}$$

The new infections operator  $\mathcal{F}(x)$  is given by

$$\begin{aligned} \frac{d}{dt} I_H &= \beta_{MH} b I_B \frac{S_H}{K_H} - \mu_H I_H - \gamma_H I_H \\ \frac{d}{dt} I_W &= \beta_{HM} b S_{B,k} \left( \frac{I_H}{K_H} \right) + b I_{B,k} - \gamma_W I_W - \mu_M I_W \\ \frac{d}{dt} I_{B,1} &= \gamma_W I_W - (b + \mu_M) I_{B,1} \\ \frac{d}{dt} I_{B,j} &= \left( \beta_{HM} \frac{I_H}{K_H} \right) b S_{B,j-1} + b I_{B,j-1} - (b + \mu_M) I_{B,j} \end{aligned}$$

$$\mathcal{F}(x) = \begin{pmatrix} \beta_{MH} b I_B \frac{S_H}{K_H} \\ \beta_{HM} b S_{B,k} \left( \frac{I_H}{K_H} \right) \\ 0 \\ \beta_{HM} b S_{B,1} \left( \frac{I_H}{K_H} \right) \\ \vdots \\ \beta_{HM} b S_{B,j-2} \left( \frac{I_H}{K_H} \right) \\ \beta_{HM} b S_{B,j-1} \left( \frac{I_H}{K_H} \right) \\ \vdots \\ \beta_{HM} b S_{B,k-2} \left( \frac{I_H}{K_H} \right) \\ \beta_{HM} b S_{B,k-1} \left( \frac{I_H}{K_H} \right) \end{pmatrix}$$

and the net rate out of all other transitions operator,  $\mathcal{V}(x)$  is given by

$$\begin{aligned} \frac{d}{dt} I_H &= \beta_{MH} b I_B \frac{S_H}{K_H} - \mu_H I_H - \gamma_H I_H \\ \frac{d}{dt} I_W &= \beta_{HM} b S_{B,k} \left( \frac{I_H}{K_H} \right) + b I_{B,k} - \gamma_W I_W - \mu_M I_W \\ \frac{d}{dt} I_{B,1} &= \gamma_W I_W - (b + \mu_M) I_{B,1} \\ \frac{d}{dt} I_{B,j} &= \left( \beta_{HM} \frac{I_H}{K_H} \right) b S_{B,j-1} + b I_{B,j-1} - (b + \mu_M) I_{B,j} \end{aligned}$$



$$\mathcal{V}(x) = \begin{pmatrix} (\mu_H + \gamma_H) I_H \\ (\gamma_W + \mu_M) I_W - b I_{B,k} \\ (b + \mu_M) I_{B,1} - \gamma_W I_W \\ (b + \mu_M) I_{B,2} - b I_{B,1} \\ \vdots \\ (b + \mu_M) I_{B,j-1} - b I_{B,j-2} \\ (b + \mu_M) I_{B,j} - b I_{B,j-1} \\ \vdots \\ (b + \mu_M) I_{B,k-1} - b I_{B,k-2} \\ (b + \mu_M I_{B,k}) - b I_{B,k-1} \end{pmatrix}$$

Linearize these operators by computing their Jacobians and then evaluating at the disease-free equilibrium,  $x_0 = (0, 0, \dots, 0, 0)$

$$F(x) = \begin{pmatrix} 0 & 0 & \beta_{MH} b \frac{S_H}{K_H} & \beta_{MH} b \frac{S_H}{K_H} & \cdots & \beta_{MH} b \frac{S_H}{K_H} & \beta_{MH} b \frac{S_H}{K_H} & \cdots & \beta_{MH} b \frac{S_H}{K_H} & \beta_{MH} b \frac{S_H}{K_H} \\ \beta_{HM} b S_{B,k} \left( \frac{1}{K_H} \right) & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ \beta_{HM} b S_{B,1} \left( \frac{1}{K_H} \right) & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \ddots & \vdots & \vdots \\ \beta_{HM} b S_{B,j-2} \left( \frac{1}{K_H} \right) & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ \beta_{HM} b S_{B,j-1} \left( \frac{1}{K_H} \right) & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \ddots & \vdots & \vdots \\ \beta_{HM} b S_{B,k-2} \left( \frac{1}{K_H} \right) & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ \beta_{HM} b S_{B,k-1} \left( \frac{1}{K_H} \right) & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \end{pmatrix}$$

$$F = \begin{bmatrix} 0 & 0 & \beta_{MH} b & \beta_{MH} b & \cdots & \beta_{MH} b & \beta_{MH} b & \cdots & \beta_{MH} b & \beta_{MH} b \\ \beta_{HM} \rho_b^k [1 - \rho_W \rho_b^k]^{-1} \Lambda_M \left( \frac{1}{K_H} \right) & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ \beta_{HM} \rho_b [1 - \rho_W \rho_b^k]^{-1} \Lambda_M \left( \frac{1}{K_H} \right) & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \ddots & \vdots & \vdots \\ \beta_{HM} \rho_b^{j-2} [1 - \rho_W \rho_b^k]^{-1} \Lambda_M \left( \frac{1}{K_H} \right) & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ \beta_{HM} \rho_b^{j-1} [1 - \rho_W \rho_b^k]^{-1} \Lambda_M \left( \frac{1}{K_H} \right) & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \ddots & \vdots & \vdots \\ \beta_{HM} \rho_b^{k-2} [1 - \rho_W \rho_b^k]^{-1} \Lambda_M \left( \frac{1}{K_H} \right) & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ \beta_{HM} \rho_b^{k-1} [1 - \rho_W \rho_b^k]^{-1} \Lambda_M \left( \frac{1}{K_H} \right) & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \end{bmatrix}$$

where  $\rho_W = \frac{\gamma_W}{\gamma_W + \mu_M}$  and  $\rho_b = \frac{b}{b + \mu_M}$ . Similarly for the linearized net-rate-out operator:

$$\mathcal{V}(x) = \begin{pmatrix} (\mu_H + \gamma_H) I_H \\ (\gamma_W + \mu_M) I_W - b I_B \\ (b + \mu_M) I_B - \gamma_W I_W \end{pmatrix}$$

$$\begin{aligned}
 V &= \begin{bmatrix} (\gamma_H + \mu_H) & 0 & 0 \\ 0 & (\gamma_W + \mu_M) & -b \\ 0 & -\gamma_W & (b + \mu_M) \end{bmatrix} \\
 V^{-1} &= \begin{bmatrix} 1/(\gamma_H + \mu_H) & 0 & 0 \\ 0 & \left(\frac{1}{\gamma_W + \mu_M}\right) \left[1 - \left(\frac{\gamma_W}{\gamma_W + \mu_M}\right) \left(\frac{b}{b + \mu_M}\right)\right]^{-1} & \left(\frac{1}{\gamma_W + \mu_M}\right) \left(\frac{b}{b + \mu_M}\right) \left[1 - \left(\frac{\gamma_W}{\gamma_W + \mu_M}\right) \left(\frac{b}{b + \mu_M}\right)\right]^{-1} \\ 0 & \left(\frac{1}{b + \mu_M}\right) \left(\frac{\gamma_W}{\gamma_W + \mu_M}\right) \left[1 - \left(\frac{\gamma_W}{\gamma_W + \mu_M}\right) \left(\frac{b}{b + \mu_M}\right)\right]^{-1} & \left(\frac{1}{b + \mu_M}\right) \left[1 - \left(\frac{\gamma_W}{\gamma_W + \mu_M}\right) \left(\frac{b}{b + \mu_M}\right)\right] \end{bmatrix} \\
 &= \begin{bmatrix} 1/(\gamma_H + \mu_H) & 0 & 0 \\ 0 & \left(\frac{1}{\gamma_W + \mu_M}\right) [1 - \rho_W \rho_B]^{-1} & \left(\frac{1}{\gamma_W + \mu_M}\right) \rho_B [1 - \rho_W \rho_B]^{-1} \\ 0 & \left(\frac{1}{b + \mu_M}\right) \rho_W [1 - \rho_W \rho_B]^{-1} & \left(\frac{1}{b + \mu_M}\right) [1 - \rho_W \rho_B] \end{bmatrix} \\
 F &= \begin{bmatrix} 0 & 0 & \beta_{MH} b \\ \beta_{HM} \rho_b^k [1 - \rho_W \rho_b^k]^{-1} \Lambda_M \left(\frac{1}{K_H}\right) & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix} \\
 K &= FV^{-1} \\
 &= \begin{bmatrix} 0 & 0 & \beta_{MH} b \\ \beta_{HM} \rho_b^k [1 - \rho_W \rho_b^k]^{-1} \Lambda_M \left(\frac{1}{K_H}\right) & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix} \begin{bmatrix} 1/(\gamma_H + \mu_H) & 0 & 0 \\ 0 & \left(\frac{1}{\gamma_W + \mu_M}\right) [1 - \rho_W \rho_B]^{-1} & \left(\frac{1}{\gamma_W + \mu_M}\right) \rho_B [1 - \rho_W \rho_B]^{-1} \\ 0 & \left(\frac{1}{b + \mu_M}\right) \rho_W [1 - \rho_W \rho_B]^{-1} & \left(\frac{1}{b + \mu_M}\right) [1 - \rho_W \rho_B] \end{bmatrix}
 \end{aligned}$$

$$V = \begin{bmatrix} (\gamma_H + \mu_H) & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ 0 & (\gamma_W + \mu_M) & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & -b \\ 0 & -\gamma_W & (b + \mu_M) & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & -b & (b + \mu_M) & \cdots & 0 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & 0 & \cdots & (b + \mu_M) & 0 & \cdots & 0 & 0 \\ 0 & 0 & 0 & 0 & \cdots & -b & (b + \mu_M) & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & (b + \mu_M) & 0 \\ 0 & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & -b & (b + \mu_M) \end{bmatrix}$$

Note that the lower-right  $k + 1$  by  $k + 1$  matrix is near circulant.

If we assume that  $\gamma_W = b$ , then the lower-right  $k + 1$  by  $k + 1$  block matrix of  $V(x_0)$  is circulant and we can invert  $V$ . Let  $G_k$  denote this lower block.

$$\begin{aligned}
 G_k &= \begin{bmatrix} (b + \mu_M) & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & -b \\ -b & (b + \mu_M) & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ 0 & -b & (b + \mu_M) & \cdots & 0 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & (b + \mu_M) & 0 & \cdots & 0 & 0 \\ 0 & 0 & 0 & \cdots & -b & (b + \mu_M) & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & (b + \mu_M) & 0 \\ 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & -b & (b + \mu_M) \end{bmatrix} \\
 G_4 &= \begin{bmatrix} (b + \mu_M) & 0 & 0 & -b \\ -b & (b + \mu_M) & 0 & 0 \\ 0 & -b & (b + \mu_M) & 0 \\ 0 & 0 & -b & (b + \mu_M) \end{bmatrix} \\
 G_5 &= \begin{bmatrix} (b + \mu_M) & 0 & 0 & 0 & -b \\ -b & (b + \mu_M) & 0 & 0 & 0 \\ 0 & -b & (b + \mu_M) & 0 & 0 \\ 0 & 0 & -b & (b + \mu_M) & 0 \\ 0 & 0 & 0 & -b & (b + \mu_M) \end{bmatrix}
 \end{aligned}$$

$$\begin{aligned}
 G_4^{-1} &= \frac{1}{(b + d)^4 - b^4} \begin{bmatrix} (b + d)^{4-1} & b^{4-1} & b^{4-2} (b + d)^{4-3} & b^{4-3} (b + d)^{4-2} \\ b^{4-3} (b + d)^{4-2} & (b + d)^{4-1} & b^{4-1} & b^{4-2} (b + d)^{4-3} \\ b^{4-2} (b + d)^{4-3} & b^{4-3} (b + d)^{4-2} & (b + d)^{4-1} & b^{4-1} \\ b^{4-1} & b^{4-2} (b + d)^{4-3} & b^{4-3} (b + d)^{4-2} & (b + d)^{4-1} \end{bmatrix} \\
 G_k^{-1} &= \frac{1}{(b + d)^k - b^k} \begin{bmatrix} (b + d)^{k-1} & b^{k-1} & b^{k-2} (b + d)^1 & \cdots & b^{k-j+1} (b + d)^{j-2} & b^{k-j} (b + d)^{j-1} \\ b^{k-(k-1)} (b + d)^{(k-1)-1} & (b + d)^{k-1} & b^{k-1} & \cdots & b^{k-j+2} (b + d)^{j-3} & b^{k-j+1} (b + d)^{j-2} \\ b^{k-(k-2)} (b + d)^{(k-2)-1} & b^{k-(k-1)} (b + d)^{(k-1)-1} & (b + d)^{k-1} & \cdots & \vdots & \vdots \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ b^{k-2} (b + d)^1 & \vdots & \vdots & \ddots & \vdots & \vdots \\ b^{k-1} & \vdots & \vdots & \ddots & \vdots & \vdots \end{bmatrix}
 \end{aligned}$$

In any case,  $G_k^{-1}$  is also circulant. For now, just let  $G_k^{-1} = [\varphi_{i,k}]_{i=1,\dots,k+1}$ . Then

$$\begin{aligned}
 FV^{-1} &= \begin{bmatrix} 0 & 0 & \beta_{MH}b & \beta_{MH}b & \cdots & \beta_{MH}b & \beta_{MH}b & \cdots & \beta_{MH}b & \beta_{MH}b \\ \beta_{HM}\rho_b^k [1 - \rho_W\rho_b^k]^{-1} \Lambda_M\left(\frac{1}{K_H}\right) & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ \beta_{HM}\rho_b [1 - \rho_W\rho_b^k]^{-1} \Lambda_M\left(\frac{1}{K_H}\right) & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \ddots & \vdots & \vdots \\ \beta_{HM}\rho_b^{j-2} [1 - \rho_W\rho_b^k]^{-1} \Lambda_M\left(\frac{1}{K_H}\right) & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ \beta_{HM}\rho_b^{j-1} [1 - \rho_W\rho_b^k]^{-1} \Lambda_M\left(\frac{1}{K_H}\right) & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \ddots & \vdots & \vdots \\ \beta_{HM}\rho_b^{k-2} [1 - \rho_W\rho_b^k]^{-1} \Lambda_M\left(\frac{1}{K_H}\right) & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ \beta_{HM}\rho_b^{k-1} [1 - \rho_W\rho_b^k]^{-1} \Lambda_M\left(\frac{1}{K_H}\right) & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \end{bmatrix} \begin{bmatrix} 1/(\gamma_H + \mu_H) \\ 0 \\ 0 \\ 0 \\ \vdots \\ 0 \\ 0 \\ \vdots \\ 0 \\ 0 \end{bmatrix} \\
 &= \begin{bmatrix} 0 & \beta_{MH}b \sum_{i \neq 1} \varphi_{i,k} & \beta_{MH}b \sum_{i \neq 2} \varphi_{i,k} & \beta_{MH}b \sum_{i \neq 3} \varphi_{i,k} & \beta_{MH}b \sum_{i \neq 4} \varphi_{i,k} \\ \beta_{HM}\rho_b^k [1 - \rho_W\rho_b^k]^{-1} \Lambda_M\left(\frac{1}{K_H}\right) / (\gamma_H + \mu_H) & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ \beta_{HM}\rho_b [1 - \rho_W\rho_b^k]^{-1} \Lambda_M\left(\frac{1}{K_H}\right) / (\gamma_H + \mu_H) & 0 & 0 & 0 & 0 \\ 0 & \vdots & \vdots & \vdots & \vdots \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ \beta_{HM}\rho_b^{j-2} [1 - \rho_W\rho_b^k]^{-1} \Lambda_M\left(\frac{1}{K_H}\right) / (\gamma_H + \mu_H) & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ \beta_{HM}\rho_b^{j-1} [1 - \rho_W\rho_b^k]^{-1} \Lambda_M\left(\frac{1}{K_H}\right) / (\gamma_H + \mu_H) & 0 & 0 & 0 & 0 \\ 0 & \vdots & \vdots & \vdots & \vdots \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ \beta_{HM}\rho_b^{k-2} [1 - \rho_W\rho_b^k]^{-1} \Lambda_M\left(\frac{1}{K_H}\right) / (\gamma_H + \mu_H) & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ \beta_{HM}\rho_b^{k-1} [1 - \rho_W\rho_b^k]^{-1} \Lambda_M\left(\frac{1}{K_H}\right) / (\gamma_H + \mu_H) & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \end{bmatrix}
 \end{aligned}$$

The eigenvalues of this simplified version are given by zero (multiplicity  $k$ ) and

$$\begin{aligned}
 \lambda_{\pm} &= \pm \sqrt{\beta_{HM}\beta_{MH}b [1 - \rho_W\rho_b^k]^{-1} \left(\frac{\Lambda_M}{K_H}\right) \left(\frac{1}{\gamma_H + \mu_H}\right)} \sqrt{\rho_b^k \sum_{i \neq 1} \varphi_{i,k} + 0 + \rho_b \sum_{i \neq 3} \varphi_{i,k} + \cdots + \rho_b^{j-2} \sum_{i \neq j-1} \varphi_{i,k} + \rho_b^{j-1} \sum_{i \neq j} \varphi_{i,k}} \\
 \frac{\lambda_{\pm}}{\sqrt{\beta_{HM}\beta_{MH}b [1 - \rho_W\rho_b^k]^{-1} \left(\frac{\Lambda_M}{K_H}\right) \left(\frac{1}{\gamma_H + \mu_H}\right)}} &= \pm \sqrt{\rho_b^k \sum_{i \neq 1} \varphi_{i,k} + 0 + \rho_b \sum_{i \neq 3} \varphi_{i,k} + \rho_b^2 \sum_{i \neq 4} \varphi_{i,k} + \cdots + \rho_b^{j-3} \sum_{i \neq j-1} \varphi_{i,k} + \rho_b^{j-2} \sum_{i \neq j} \varphi_{i,k}} \\
 &= \pm \sqrt{\rho_b^k \sum_{i \neq 1} \varphi_{i,k} + \sum_{j=3}^k \rho_b^{j-2} \sum_{i \neq j} \varphi_{i,k}}
 \end{aligned}$$

Thus, since there is exactly one positive eigenvalue, it must be the basic reproduction number:

$$\mathcal{R}_0 = \sqrt{\beta_{HM}\beta_{MH}b(1-\rho_W\rho_b^k)^{-1}\left(\frac{\Lambda_M}{K_H}\right)\left(\frac{1}{\gamma_H+\mu_H}\right)} \sqrt{\rho_b^k \sum_{i \neq 1} \varphi_{i,k} + \sum_{j=3}^{k+1} \rho_b^{j-2} \sum_{i \neq j} \varphi_{i,k}}$$

There's probably some little trick I can do using the fact that

$$\begin{aligned} \rho_b^k \sum_{i \neq 1} \varphi_{i,k} + \sum_{j=3}^{k+1} \rho_b^{j-2} \sum_{i \neq j} \varphi_{i,k} &= \left( \rho_b^k \sum_{i \neq 1} \varphi_{i,k} + \sum_{i \neq 2} \varphi_{i,k} + \sum_{j=3}^{k+1} \rho_b^{j-2} \sum_{i \neq j} \varphi_{i,k} \right) - \sum_{i \neq 2} \varphi_{i,k} \\ &= \left( \sum_{j=1}^k \rho_b^{j-1} \sum_{i \neq j+1} \varphi_{i,k} + \rho_b^k \sum_{i \neq 1} \varphi_{i,k} \right) - \sum_{i \neq 2} \varphi_{i,k} \end{aligned}$$

Note that

$$\sum_{i=1}^k \varphi_{i,k} = \frac{1}{\mu_M}$$

hence

$$\sum_{i \neq j} \varphi_{i,k} = \frac{1}{\mu_M} - \varphi_{j,k}$$

So

$$\begin{aligned} \rho_b^k \sum_{i \neq 1} \varphi_{i,k} + \sum_{j=3}^{k+1} \rho_b^{j-2} \sum_{i \neq j} \varphi_{i,k} &= \left( \sum_{j=1}^k \rho_b^{j-1} \sum_{i \neq j+1} \varphi_{i,k} + \rho_b^k \sum_{i \neq 1} \varphi_{i,k} \right) - \sum_{i \neq 2} \varphi_{i,k} \\ &= \left( \sum_{j=1}^k \rho_b^{j-1} \left( \frac{1}{\mu_M} - \varphi_{j+1,k} \right) + \rho_b^k \left( \frac{1}{\mu_M} - \varphi_{1,k} \right) \right) - \left( \frac{1}{\mu_M} - \varphi_{2,k} \right) \\ &= \frac{1}{\mu_M} \left( \sum_{j=0}^k \rho_b^j - 1 \right) - \left( \rho_b^k \varphi_{1,k} + \sum_{j=1}^k \rho_b^{j-1} \varphi_{j+1,k} \right) \\ &= \frac{1}{\mu_M} \left( \frac{\rho_b(\rho_b^k - 1)}{\rho_b - 1} - 1 \right) - \left( \rho_b^k \varphi_{1,k} + \sum_{j=1}^k \rho_b^{j-1} \varphi_{j+1,k} \right) \\ &= \frac{1}{\mu_M} \left( \frac{\rho_b^{k+1} + 1}{\rho_b - 1} \right) - \left( \rho_b^k \varphi_{1,k} + \sum_{j=1}^{k-1} \rho_b^{j-1} \varphi_{j+1,k} \right) \end{aligned}$$

!!! Move on to simulations for now

## Model with biting number dependent variables

### 3. MODEL SET-UP

The basic demographic model is given by:

$$\begin{aligned} \frac{d}{dt}H &= (\lambda_H - \mu_H)H \left( 1 - \frac{H}{K_H} \right) \\ \frac{d}{dt}M &= \Lambda_M - \mu_M M \end{aligned}$$

Assume that the time-between-egg-laying distribution is Erlang  $(\frac{b}{k}, k)$ . Let  $B$  be the compartment of biting mosquitoes and  $W$  the compartment of egg-laying mosquitoes. Then we can decompose  $B$  as

$B = \sum_{i=1}^k B_k$  where

$$\begin{aligned}
 \frac{d}{dt} B_1 &= \Lambda_{M,k} + \gamma_W W - bkB_1 - (\mu + \mu_k) B_1 \\
 \frac{d}{dt} B_j &= bk(B_{j-1} - B_j) - (\mu + \mu_k) B_j \\
 \frac{d}{dt} B &= \Lambda_{M,k} + \gamma_W W - bkB_k - (\mu + \mu_k) B \\
 \frac{d}{dt} W &= bkB_k - \gamma_W W - \mu W \\
 \frac{d}{dt} M &= \frac{d}{dt} B + \frac{d}{dt} W \\
 &= \Lambda_{M,k} - (\mu + \mu_k) M
 \end{aligned}$$

Let  $\Lambda_{M,k} = \left( \frac{\mu + \mu_k}{\mu + \mu_1} \right) \Lambda_{M,1}$

$$\begin{aligned}
 \frac{\Lambda_{M,k}}{(\mu + \mu_k)} &= \frac{\Lambda_{M,1}}{(\mu + \mu_1)} \\
 \Lambda_{M,k} &= \left( \frac{\mu + \mu_k}{\mu + \mu_1} \right) \Lambda_{M,1}
 \end{aligned}$$

Finally, putting this together into a simple transmission model.

$$\begin{aligned}
 \frac{d}{dt} S_H &= \left[ \lambda_H H - \left( \frac{\lambda_H - \mu_H}{K_H} \right) H^2 \right] - bk \left( \sum_{j=1}^k \beta_{MH,j} I_{B,j} \right) \frac{S_H}{N_H} - \mu_H S_H \\
 \frac{d}{dt} I_H &= bk \left( \sum_{j=1}^k \beta_{MH,j} I_{B,j} \right) \frac{S_H}{N_H} - \mu_H I_H - \gamma_H I_H \\
 \frac{d}{dt} R_H &= \gamma_H I_H - \mu_H R_H
 \end{aligned}$$

$$\begin{aligned}
 \frac{d}{dt}S_{B,1} &= \Lambda_M + \gamma_W S_W - bkS_{B,1} - (\mu + \mu_k) S_{B,1} \\
 \frac{d}{dt}S_{B,j} &= \left(1 - \beta_{HM,j-1} \frac{I_H}{N_H}\right) bkS_{B,j-1} - bkS_{B,j} - (\mu + \mu_k) S_{B,j} \\
 \frac{d}{dt}S_B &= \frac{d}{dt} \sum_{j=1}^k S_{B,j} \\
 &= \Lambda_M + \gamma_W S_W - bkS_{B,1} - (\mu + \mu_k) S_{B,1} + \sum_{j=2}^k \left[ \left(1 - \beta_{HM,j-1} \frac{I_H}{N_H}\right) bkS_{B,j-1} - bkS_{B,j} - (\mu + \mu_k) S_{B,j} \right] \\
 &= \Lambda_M + \gamma_W S_W - bkS_{B,k} - (\mu + \mu_k) S_B - bk \sum_{j=1}^{k-1} (\beta_{HM,j} S_{B,j}) \frac{I_H}{N_H}
 \end{aligned}$$

$$\begin{aligned}
 \frac{d}{dt}I_{B,1} &= \gamma_W I_W - bkI_{B,1} - (\mu + \mu_k) I_{B,1} \\
 \frac{d}{dt}I_{B,j} &= \left(\beta_{HM,j-1} \frac{I_H}{N_H}\right) bkS_{B,j-1} + bkI_{B,j-1} - bkI_{B,j} - (\mu + \mu_k) I_{B,j} \\
 \frac{d}{dt}I_B &= \frac{d}{dt} \sum_{j=1}^k I_{B,j} \\
 &= \gamma_W I_W - \frac{b}{k} I_{B,1} - (\mu + \mu_k) I_{B,1} + \sum_{j=2}^k \left[ \left(\beta_{HM,j-1} \frac{I_H}{N_H}\right) \frac{b}{k} S_{B,j-1} + \frac{b}{k} I_{B,j-1} - \frac{b}{k} I_{B,j} - (\mu + \mu_k) I_{B,j} \right] \\
 &= \gamma_W I_W - \frac{b}{k} I_{B,k} + \frac{b}{k} \sum_{j=1}^{k-1} (\beta_{HM,j} S_{B,j}) \frac{I_H}{N_H} - (\mu + \mu_k) I_B
 \end{aligned}$$

!!! FIX  $\frac{b}{k} \rightarrow bk$

$$\begin{aligned}
 \frac{d}{dt}S_W &= \left(1 - \beta_{HM,k} \frac{I_H}{N_H}\right) \frac{b}{k} S_{B,k} - \gamma_W S_W - \mu S_W \\
 \frac{d}{dt}I_W &= \beta_{HM,k} \frac{I_H}{N_H} \frac{b}{k} S_{B,k} + \frac{b}{k} I_{B,k} - \gamma_W I_W - \mu I_W
 \end{aligned}$$

where  $S_B = \sum_{j=1}^k S_{B,j}$  and  $I_B = \sum_{j=1}^k I_{B,j}$ .

For simplicity, we assume that i) there is no disease-induced mortality in either the host of vector and ii) the host is at carrying capacity:  $H = K_H$ . Then the equations simplify to

$$\begin{aligned}
 \frac{d}{dt} S_H &= \mu_H K_H - \left( \sum_{j=1}^k \beta_{MH,j} I_{B,j} \right) bk \frac{S_H}{K_H} - \mu_H S_H \\
 \frac{d}{dt} I_H &= \left( \sum_{j=1}^k \beta_{MH,j} I_{B,j} \right) bk \frac{S_H}{K_H} - \mu_H I_H - \gamma_H I_H \\
 \frac{d}{dt} R_H &= \gamma_H I_H - \mu_H R_H \\
 \frac{d}{dt} S_{B,1} &= \Lambda_M + \gamma_W S_W - bk S_{B,1} - (\mu + \mu_k) S_{B,1} \\
 \frac{d}{dt} S_{B,j} &= \left( 1 - \beta_{HM,j-1} \frac{I_H}{K_H} \right) bk S_{B,j-1} - (bk + \mu + \mu_k) S_{B,j} \\
 \frac{d}{dt} S_B &= \frac{d}{dt} \sum_{j=1}^k S_{B,j} \\
 &= \Lambda_M + \gamma_W S_W - bk S_{B,k} - (\mu + \mu_k) S_B - bk \sum_{j=1}^{k-1} (\beta_{HM,j} S_{B,j}) \frac{I_H}{K_H} \\
 \frac{d}{dt} I_{B,1} &= \gamma_W I_W - (bk + \mu + \mu_k) I_{B,1} \\
 \frac{d}{dt} I_{B,j} &= \left( \beta_{HM,j-1} \frac{I_H}{K_H} \right) bk S_{B,j-1} + bk I_{B,j-1} - (bk + \mu + \mu_k) I_{B,j} \\
 \frac{d}{dt} I_B &= \frac{d}{dt} \sum_{j=1}^k I_{B,j} \\
 &= \gamma_W I_W - bk I_{B,k} - \mu I_B + bk \sum_{j=1}^{k-1} (\beta_{HM,j} S_{B,j}) \frac{I_H}{K_H} - \sum_{j=1}^k \mu_{M,j} I_{B,j} \\
 \frac{d}{dt} S_W &= \left( 1 - \beta_{HM,k} \frac{I_H}{K_H} \right) bk S_{B,k} - \gamma_W S_W - \mu S_W \\
 \frac{d}{dt} I_W &= \beta_{HM,k} bk S_{B,k} \left( \frac{I_H}{K_H} \right) + bk I_{B,k} - \gamma_W I_W - \mu I_W
 \end{aligned}$$

Note that

$$\left( 1 - \beta_{HM,j-1} \frac{I_H}{K_H} \right) bk S_{B,j-1} = bk S_{B,j-1} \left[ \left( 1 - \frac{I_H}{K_H} \right) + (1 - \beta_{HM,j-1}) \left( \frac{I_H}{K_H} \right) \right]$$

#### 4. EQUILIBRIA

4.1. **Disease-free equilibria.** Suppose that  $I_H = I_{B,j} = I_W = 0$ . Then we solve for any equilibria:

$$\begin{aligned}
 S_H &= K_H \\
 R_H &= 0 \\
 S_{B,1} &= \left( \frac{1}{bk + \mu + \mu_k} \right) (\Lambda_M + \gamma_W S_W) \\
 S_{B,j} &= \left( \frac{bk}{bk + \mu + \mu_k} \right) S_{B,j-1} \\
 bk S_{B,k} + (\mu + \mu_k) S_B &= \Lambda_M + \gamma_W S_W \\
 S_W &= \left( \frac{1}{\mu + \gamma_W} \right) bk S_{B,k}
 \end{aligned}$$



Let  $\rho_{B,k} = \frac{bk}{bk+\mu+\mu_k}$  and  $\rho_W = \frac{\gamma_W}{\gamma_W+\mu}$ . Then  $S_{B,j} = S_{B,1} \left( \frac{bk+\mu+\mu_k}{bk} \right) \rho_{B,j}$  for  $j > 1$ .

$$\begin{aligned} S_{B,j} &= \rho_{B,k}^{j-1} S_{B,1} \\ S_W &= \left( \frac{1}{\mu + \gamma_W} \right) bk \rho_{B,k}^{k-1} S_{B,1} \\ S_{B,1} &= \left( \frac{1}{bk + \mu + \mu_k} \right) (\Lambda_M + \gamma_W S_W) \\ S_{B,1} &= \left( \frac{1}{bk + \mu + \mu_k} \right) (\Lambda_M + \rho_W bk \rho_{B,k}^{k-1} S_{B,1}) \\ S_{B,1} &= \left( \frac{1}{bk + \mu + \mu_k} \right) \Lambda_M + \rho_W \rho_{B,k}^k S_{B,1} \\ (1 - \rho_W \rho_{B,k}^k) S_{B,1} &= \left( \frac{1}{bk + \mu + \mu_k} \right) \Lambda_M \\ S_{B,1} &= \Lambda_{M,k} n_G \left( \frac{1}{bk + \mu + \mu_k} \right) \end{aligned}$$

Note that  $(1 - \rho_W \rho_{B,k})^{-1}$  represents the average number of gonotrophic cycles a mosquito will complete before succumbing to mortality since

$$\sum_{i=1}^{\infty} (\rho_W \rho_{B,k})^i = \frac{1}{1 - \rho_W \rho_{B,k}}.$$

Setting  $n_G = (1 - \rho_W \rho_{B,k})^{-1}$ , this will be used as an independent parameter used to help decide the dependence of  $\mu_{M,k}$  on  $k$ .

$$\begin{aligned} S_W &= \Lambda_{M,k} n_G \left( \frac{1}{\mu + \gamma_W} \right) \rho_{B,k}^k \\ S_{B,1} &= \Lambda_{M,k} n_G \left( \frac{1}{bk + \mu + \mu_k} \right) \\ S_{B,j} &= \Lambda_{M,k} n_G \rho_{B,k}^{j-1} \left( \frac{1}{bk + \mu + \mu_k} \right) \\ K_M &= S_W + \sum_{j=1}^k S_{B,j} \\ &= \Lambda_{M,k} n_G \left( \frac{1}{\mu + \gamma_W} \right) \rho_{B,k}^k + \sum_{j=1}^k \Lambda_{M,k} n_G \rho_{B,k}^{j-1} \left( \frac{1}{bk + \mu + \mu_k} \right) \\ &= \Lambda_{M,k} n_G \left[ \left( \frac{1}{\mu + \gamma_W} \right) \rho_{B,k}^k + \left( \frac{1}{bk + \mu + \mu_k} \right) \frac{1}{\rho_{B,k}} \sum_{j=1}^k \rho_{B,k}^j \right] \\ &= \Lambda_{M,k} n_G \left[ \left( \frac{1}{\mu + \gamma_W} \right) \rho_{B,k}^k + \left( \frac{1}{bk + \mu + \mu_k} \right) \frac{1}{\rho_{B,k}} \left( \frac{\rho_{B,k}^k - 1}{\rho_{B,k} - 1} \right) \right] \\ &= \Lambda_{M,k} n_G \left[ \frac{1}{\gamma_W} \rho_W \rho_{B,k}^k + \left( \frac{1}{bk} \right) \left( \frac{\rho_{B,k}^k - 1}{\rho_{B,k} - 1} \right) \right] \\ K_M &= \Lambda_{M,k} n_G \left[ \frac{1}{\gamma_W} \left( 1 - \frac{1}{n_G} \right) + \left( \frac{1}{bk} \right) \left( \frac{\rho_{B,k}^k - 1}{\rho_{B,k} - 1} \right) \right] \end{aligned}$$

Assume that  $M^* = M_1^* = M_k^*$  so that

$$\begin{aligned} \Lambda_{M,k} &= K_M \frac{1}{n_G} \left[ \frac{1}{\gamma_W} \left( 1 - \frac{1}{n_G} \right) + \left( \frac{1}{bk} \right) \left( \frac{\rho_{B,k}^k - 1}{\rho_{B,k} - 1} \right) \right]^{-1} \\ M_k^* &= M_1^* \\ \Lambda_{M,k} n_G \left[ \frac{1}{\gamma_W} \left( 1 - \frac{1}{n_G} \right) + \left( \frac{b}{k} \right)^{-1} \left( \frac{\rho_{B,k}^k - 1}{\rho_{B,k} - 1} \right) \right] &= \Lambda_{M,1} n_G \left[ \frac{1}{\gamma_W} \left( 1 - \frac{1}{n_G} \right) + \frac{1}{b} \right] \\ \Lambda_{M,k} &= \Lambda_{M,1} \left[ \frac{1}{\gamma_W} \left( 1 - \frac{1}{n_G} \right) + \frac{1}{b} \right] \left[ \frac{1}{\gamma_W} \left( 1 - \frac{1}{n_G} \right) + \left( \frac{b}{k} \right)^{-1} \left( \frac{\rho_{B,k}^k - 1}{\rho_{B,k} - 1} \right) \right]^{-1} \end{aligned}$$

Note that the total equilibrium mosquito population size should be independent of  $k$ , but ensuring this is the case may be very difficult.

Suppose that  $\mu_k = \alpha^{k-1} (b + \mu + \mu_1) - bk - \mu$  where  $\alpha > 1$  is given and  $\mu_1$  is determined as described below. Note that, by this definition,  $bk + \mu_k + \mu > 0$  as long as  $\alpha > 0$ .  $\alpha$  is defined below.

$$\begin{aligned} n_G &= (1 - \rho_W \rho_{B,k})^{-1} \\ \rho_{B,k} &= \frac{1}{\rho_W} \left( 1 - \frac{1}{n_G} \right) \\ \prod_{i=1}^k \left( \frac{bk}{bk + \mu + \mu_k} \right) &= \frac{1}{\rho_W} \left( 1 - \frac{1}{n_G} \right) \\ (bk)^k \prod_{i=1}^k \left( \frac{1}{bk + \mu + \mu_k} \right) &= \frac{1}{\rho_W} \left( 1 - \frac{1}{n_G} \right) \\ \prod_{i=1}^k (bk + \mu + \mu_k) &= (bk)^k \rho_W \left( 1 - \frac{1}{n_G} \right)^{-1} \\ \prod_{i=1}^k (bk + \mu + \alpha^{k-1} (b + \mu + \mu_1) - bk - \mu) &= (bk)^k \rho_W \left( 1 - \frac{1}{n_G} \right)^{-1} \\ \prod_{i=1}^k (\alpha^{k-1} (b + \mu + \mu_1)) &= (bk)^k \rho_W \left( 1 - \frac{1}{n_G} \right)^{-1} \\ \alpha^{k(k-1)} &= \left( \frac{b}{b + \mu + \mu_1} \right)^k k^k \rho_W \left( 1 - \frac{1}{n_G} \right)^{-1} \\ \alpha &= \left[ \rho_B^k \rho_W k^k \left( 1 - \frac{1}{n_G} \right)^{-1} \right]^{\frac{1}{k(k-1)}} \end{aligned}$$

where  $\rho_B = \frac{b}{b + \mu + \mu_1}$ . Note that  $\alpha_1 = 1$  since in this case  $\rho_W \rho_B = \frac{1}{1 - n_G}$ .

To ensure that  $\mu_k > 0$ , we require that

$$\begin{aligned}
 & \alpha^{k-1} (b + \mu + \mu_1) - bk - \mu > 0 \\
 & \left[ \rho_B^k \rho_W k^k \left( 1 - \frac{1}{n_G} \right)^{-1} \right]^{\frac{k-1}{k(k-1)}} (b + \mu + \mu_1) > bk + \mu \\
 & \left[ \rho_B \rho_W^{\frac{1}{k}} k \left( 1 - \frac{1}{n_G} \right)^{-\frac{1}{k}} \right] (b + \mu + \mu_1) > bk + \mu \\
 & \left[ \frac{b}{b + \mu + \mu_1} \rho_W^{\frac{1}{k}} k \left( 1 - \frac{1}{n_G} \right)^{-\frac{1}{k}} \right] (b + \mu + \mu_1) > bk + \mu \\
 & \left( \frac{bk}{bk + \mu} \right) \rho_W^{\frac{1}{k}} \left( 1 - \frac{1}{n_G} \right)^{-\frac{1}{k}} > 1 \\
 & \left( \frac{bk}{bk + \mu} \right)^k \rho_W > 1 - \frac{1}{n_G}
 \end{aligned}$$

For  $k = 1$ ,  $n_G = 1 - \frac{1}{\rho_B \rho_W}$ . If we specify  $n_G$ , we can then solve for  $\mu_1$  as follows:

$$\begin{aligned}
 n_G &= 1 - \frac{1}{\rho_B \rho_W} \\
 \rho_B &= \frac{1}{\rho_W} \left( 1 - \frac{1}{n_G} \right) \\
 \frac{b}{b + \mu + \mu_1} &= \frac{1}{\rho_W} \left( 1 - \frac{1}{n_G} \right) \\
 b \rho_W \left( 1 - \frac{1}{n_G} \right)^{-1} - b - \mu &= \mu_1 \\
 \mu_1 &= b \rho_W \left( 1 - \frac{1}{n_G} \right)^{-1} - b - \mu
 \end{aligned}$$

Assuming that, all things being equal, the fitness effect of additional bites per gonotrophic cycle is neutral means that the reproductive ratio for the mosquito population should be fixed. That is, for any  $k \geq 1$

$$0 = \frac{d}{dt} M = \frac{d}{dt} M_k$$

**4.2. Endemic equilibria.** Now assume that at least one of  $I_H, I_{B,j}, I_W \neq 0$ .

**4.3. Basic reproduction number.** The infected compartments are  $I_H, I_W$ , and  $I_{B,j}$ ,  $j = 1, \dots, k$ . Let  $x = (I_H, I_W, I_{B,1}, \dots, I_{B,k})$ . Let  $J$  be the Jacobian of the system above written with the state

variables in the order:  $I_H, I_{B,1}, \dots, I_{B,k}, I_W, S_H, S_{B,1}, \dots, S_{B,k}, S_W$

$$J = \begin{pmatrix} S_{B,k} & S_H & I_H & R_H & S_{B,1} \\ \mu_H K_H - \beta_{MH} b I_B \frac{S_H}{K_H} - \mu_H S_H & I_{B,1} & \dots & I_{B,j-1} & I_{B,j} \\ 0 & -\beta_{MH} b I_B \frac{1}{K_H} - \mu_H & 0 & 0 & 0 \\ \beta_{MH} b I_B \frac{S_H}{K_H} - \mu_H I_H - \gamma_H I_H & -\beta_{MH} b \frac{S_H}{K_H} & \dots & -\beta_{MH} b \frac{S_H}{K_H} & -\beta_{MH} b \frac{S_H}{K_H} \\ 0 & \beta_{MH} b I_B \frac{1}{K_H} & -\mu_H - \gamma_H & 0 & 0 \\ \gamma_H I_H - \mu_H R_H & \beta_{MH} b \frac{S_H}{K_H} & \dots & \beta_{MH} b \frac{S_H}{K_H} & \beta_{MH} b \frac{S_H}{K_H} \\ 0 & 0 & \gamma_H & -\mu_H & 0 \\ \Lambda_M + \gamma_W S_W - b S_{B,1} - \mu_M S_{B,1} & 0 & \dots & 0 & 0 \\ 0 & 0 & 0 & 0 & -b - \mu_M \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ b S_{B,j-1} \left(1 - \beta_{HM} \frac{I_H}{K_H}\right) - b S_{B,j} - \mu_M S_{B,j} & 0 & b S_{B,j-1} \left(-\frac{1}{K_h}\right) & 0 & 0 \\ 0 & 0 & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ b S_{B,k-1} \left(1 - \beta_{HM} \frac{I_H}{K_H}\right) - b S_{B,k} - \mu_M S_{B,k} & 0 & b S_{B,k-1} \left(-\frac{1}{K_h}\right) & 0 & 0 \\ -b - \mu_M & 0 & \dots & 0 & 0 \\ \gamma_W I_W - b I_{B,1} - \mu_M I_{B,1} & 0 & 0 & 0 & 0 \\ 0 & -b - \mu_M & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ \beta_{HM} b S_{B,j-1} \left(\frac{I_H}{K_H}\right) + b I_{B,j-1} - b I_{B,j} - \mu_M I_{B,j} & 0 & b S_{B,j-1} \left(\frac{1}{K_H}\right) & 0 & 0 \\ 0 & 0 & \dots & b & -b - \mu_M \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ \beta_{HM} b S_{B,k-1} \left(\frac{I_H}{K_H}\right) + b I_{B,k-1} - b I_{B,k} - \mu_M I_{B,k} & 0 & b S_{B,k-1} \left(\frac{1}{K_H}\right) & 0 & 0 \\ 0 & 0 & \dots & 0 & 0 \\ b S_{B,k} \left(1 - \frac{I_H}{K_h}\right) - \gamma_W S_W - \mu_M S_W & 0 & b S_{B,k} \left(-\frac{1}{K_h}\right) & 0 & 0 \\ b \left(1 - \frac{I_H}{K_h}\right) & 0 & \dots & 0 & 0 \\ b S_{B,k} \left(\frac{I_H}{K_H}\right) + b I_{B,k} - \gamma_W I_W - \mu_M I_W & 0 & b S_{B,k} \left(\frac{1}{K_H}\right) & 0 & 0 \\ 0 & 0 & \dots & 0 & 0 \end{pmatrix}$$

Re-ordering this and only including the infected state variables, gives us

$$\hat{J}(x) = \begin{pmatrix} -\mu_H - \gamma_H & \beta_{MH} b \frac{S_H}{K_H} & \dots & \beta_{MH} b \frac{S_H}{K_H} & \beta_{MH} b \frac{S_H}{K_H} & \dots & \beta_{MH} b \frac{S_H}{K_H} & \beta_{MH} b \frac{S_H}{K_H} & 0 \\ 0 & -b - \mu_M & \dots & 0 & 0 & \dots & 0 & 0 & \gamma_W I_W \\ \vdots & \vdots & \ddots & \vdots & \vdots & \ddots & \vdots & \vdots & \vdots \\ b S_{B,j-1} \left(\frac{1}{K_H}\right) & 0 & \dots & b & -b - \mu_M & \dots & 0 & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots & \ddots & \vdots & \vdots & \vdots \\ b S_{B,k-1} \left(\frac{1}{K_H}\right) & 0 & \dots & 0 & 0 & \dots & b & -b - \mu_M & 0 \\ b S_{B,k} \left(\frac{1}{K_H}\right) & 0 & \dots & 0 & 0 & \dots & 0 & b & -\gamma_W - \mu_M \end{pmatrix}$$

Finally, evaluating at the disease-free equilibrium defined above, we obtain

$$\hat{J}(\mathbf{0}) = \begin{pmatrix} -\mu_H - \gamma_H & \beta_{MH}b & \cdots & \beta_{MH}b & \beta_{MH}b & \cdots & \beta_{MH}b & \beta_{MH}b & 0 \\ 0 & -b - \mu_M & \cdots & 0 & 0 & \cdots & 0 & 0 & \gamma_W I_W \\ \vdots & \vdots & \ddots & \vdots & \vdots & \ddots & \vdots & \vdots & \vdots \\ bS_{B,j-1}\left(\frac{1}{K_H}\right) & 0 & \cdots & b & -b - \mu_M & \cdots & 0 & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots & \ddots & \vdots & \vdots & \vdots \\ bS_{B,k-1}\left(\frac{1}{K_H}\right) & 0 & \cdots & 0 & 0 & \cdots & b & -b - \mu_M & 0 \\ bS_{B,k}\left(\frac{1}{K_H}\right) & 0 & \cdots & 0 & 0 & \cdots & 0 & b & -\gamma_W - \mu_M \end{pmatrix}$$

The new infections operator  $\mathcal{F}(x)$  is given by

$$\begin{aligned} \frac{d}{dt}I_H &= \left( \sum_{j=1}^k \beta_{MH,j} I_{B,j} \right) \frac{b}{k} \frac{S_H}{K_H} - \mu_H I_H - \gamma_H I_H \\ \frac{d}{dt}I_W &= \beta_{HM,k} \frac{b}{k} S_{B,k} \left( \frac{I_H}{K_H} \right) + \frac{b}{k} I_{B,k} - \gamma_W I_W - \mu I_W \\ \frac{d}{dt}I_{B,1} &= \gamma_W I_W - \left( \frac{b}{k} + \mu + \mu_k \right) I_{B,1} \\ \frac{d}{dt}I_{B,j} &= \beta_{HM,j-1} \frac{b}{k} S_{B,j-1} \left( \frac{I_H}{K_H} \right) + \frac{b}{k} I_{B,j-1} - \left( \frac{b}{k} + \mu + \mu_k \right) I_{B,j} \end{aligned}$$

$$\mathcal{F}(x) = \begin{pmatrix} \left( \sum_{j=1}^k \beta_{MH,j} I_{B,j} \right) \frac{b}{k} \frac{S_H}{K_H} \\ \beta_{HM,k} \frac{b}{k} S_{B,k} \left( \frac{I_H}{K_H} \right) \\ 0 \\ \beta_{HM,1} \frac{b}{k} S_{B,1} \left( \frac{I_H}{K_H} \right) \\ \vdots \\ \beta_{HM,j-2} \frac{b}{k} S_{B,j-2} \left( \frac{I_H}{K_H} \right) \\ \beta_{HM,j-1} \frac{b}{k} S_{B,j-1} \left( \frac{I_H}{K_H} \right) \\ \vdots \\ \beta_{HM,k-2} \frac{b}{k} S_{B,k-2} \left( \frac{I_H}{K_H} \right) \\ \beta_{HM,k-1} \frac{b}{k} S_{B,k-1} \left( \frac{I_H}{K_H} \right) \end{pmatrix}$$

and the net rate out of all other transitions operator,  $\mathcal{V}(x)$  is given by

$$\begin{aligned} \frac{d}{dt}I_H &= \left( \sum_{j=1}^k \beta_{MH,j} I_{B,j} \right) \frac{b}{k} \frac{S_H}{K_H} - \mu_H I_H - \gamma_H I_H \\ \frac{d}{dt}I_W &= \beta_{HM,k} \frac{b}{k} S_{B,k} \left( \frac{I_H}{K_H} \right) + \frac{b}{k} I_{B,k} - \gamma_W I_W - \mu I_W \\ \frac{d}{dt}I_{B,1} &= \gamma_W I_W - \left( \frac{b}{k} + \mu + \mu_k \right) I_{B,1} \\ \frac{d}{dt}I_{B,j} &= \beta_{HM,j-1} \frac{b}{k} S_{B,j-1} \left( \frac{I_H}{K_H} \right) + \frac{b}{k} I_{B,j-1} - \left( \frac{b}{k} + \mu + \mu_k \right) I_{B,j} \end{aligned}$$

$$\mathcal{V}(x) = \begin{pmatrix} (\mu_H + \gamma_H) I_H \\ (\gamma_W + \mu) I_W - \frac{b}{k} I_{B,k} \\ \left(\frac{b}{k} + \mu + \mu_k\right) I_{B,1} - \gamma_W I_W \\ \left(\frac{b}{k} + \mu + \mu_k\right) I_{B,2} - \frac{b}{k} I_{B,1} \\ \vdots \\ \left(\frac{b}{k} + \mu + \mu_k\right) I_{B,j-1} - \frac{b}{k} I_{B,j-2} \\ \left(\frac{b}{k} + \mu + \mu_k\right) I_{B,j} - \frac{b}{k} I_{B,j-1} \\ \vdots \\ \left(\frac{b}{k} + \mu + \mu_k\right) I_{B,k-1} - \frac{b}{k} I_{B,k-2} \\ \left(\frac{b}{k} + \mu + \mu_k\right) I_{B,k} - \frac{b}{k} I_{B,k-1} \end{pmatrix}$$

Linearize these operators by computing their Jacobians and then evaluating at the disease-free equilibrium,  $x_0 = (0, 0, \dots, 0, 0)$

$$\mathcal{F}(x) = \begin{pmatrix} \left(\sum_{j=1}^k \beta_{MH,j} I_{B,j}\right) \frac{b}{k} \frac{S_H}{K_H} \\ \beta_{HM,k} \frac{b}{k} S_{B,k} \left(\frac{I_H}{K_H}\right) \\ 0 \\ \beta_{HM,1} \frac{b}{k} S_{B,1} \left(\frac{I_H}{K_H}\right) \\ \vdots \\ \beta_{HM,j-2} \frac{b}{k} S_{B,j-2} \left(\frac{I_H}{K_H}\right) \\ \beta_{HM,j-1} \frac{b}{k} S_{B,j-1} \left(\frac{I_H}{K_H}\right) \\ \vdots \\ \beta_{HM,k-2} \frac{b}{k} S_{B,k-2} \left(\frac{I_H}{K_H}\right) \\ \beta_{HM,k-1} \frac{b}{k} S_{B,k-1} \left(\frac{I_H}{K_H}\right) \end{pmatrix}$$

$$F(x) = \begin{pmatrix} 0 & 0 & \beta_{MH,1} \frac{b}{k} \frac{S_H}{K_H} & \beta_{MH,2} \frac{b}{k} \frac{S_H}{K_H} & \cdots & \beta_{MH,j-2} \frac{b}{k} \frac{S_H}{K_H} & \beta_{MH,j-1} \frac{b}{k} \frac{S_H}{K_H} & \cdots & \beta_{MH,k-1} \frac{b}{k} \frac{S_H}{K_H} \\ \beta_{HM,k} \frac{b}{k} S_{B,k} \left(\frac{1}{K_H}\right) & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 \\ 0 & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 \\ \beta_{HM,1} \frac{b}{k} S_{B,1} \left(\frac{1}{K_H}\right) & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \ddots & \vdots \\ \beta_{HM,j-2} \frac{b}{k} S_{B,j-2} \left(\frac{1}{K_H}\right) & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 \\ \beta_{HM,j-1} \frac{b}{k} S_{B,j-1} \left(\frac{1}{K_H}\right) & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \ddots & \vdots \\ \beta_{HM,k-2} \frac{b}{k} S_{B,k-2} \left(\frac{1}{K_H}\right) & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 \\ \beta_{HM,k-1} \frac{b}{k} S_{B,k-1} \left(\frac{1}{K_H}\right) & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 \end{pmatrix}$$

$$F = \begin{bmatrix} 0 & 0 & \beta_{MH,1} \frac{b}{k} & \beta_{MH,2} \frac{b}{k} & \cdots & \beta_{MH,j-2} \frac{b}{k} & \beta_{MH,j-1} \frac{b}{k} & \cdots & \beta_{MH,k-1} \frac{b}{k} & \beta_{MH,k} \frac{b}{k} \\ \beta_{HM,k} \frac{b}{k} S_{B,k} \left( \frac{1}{K_H} \right) & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ \beta_{HM,1} \frac{b}{k} S_{B,1} \left( \frac{1}{K_H} \right) & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \ddots & \vdots & \vdots \\ \beta_{HM,j-2} \frac{b}{k} S_{B,j-2} \left( \frac{1}{K_H} \right) & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ \beta_{HM,j-1} \frac{b}{k} S_{B,j-1} \left( \frac{1}{K_H} \right) & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \ddots & \vdots & \vdots \\ \beta_{HM,k-2} \frac{b}{k} S_{B,k-2} \left( \frac{1}{K_H} \right) & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ \beta_{HM,k-1} \frac{b}{k} S_{B,k-1} \left( \frac{1}{K_H} \right) & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \end{bmatrix}$$

where  $\rho_W = \frac{\gamma_W}{\gamma_W + \mu_M}$  and  $\rho_b = \frac{b}{b + \mu_M}$ . Similarly for the linearized net-rate-out operator:

$$\mathcal{V}(x) = \begin{pmatrix} (\mu_H + \gamma_H) I_H \\ (\gamma_W + \mu) I_W - \frac{b}{k} I_{B,k} \\ \left( \frac{b}{k} + \mu + \mu_k \right) I_{B,1} - \gamma_W I_W \\ \left( \frac{b}{k} + \mu + \mu_k \right) I_{B,2} - \frac{b}{k} I_{B,1} \\ \vdots \\ \left( \frac{b}{k} + \mu + \mu_k \right) I_{B,j-1} - \frac{b}{k} I_{B,j-2} \\ \left( \frac{b}{k} + \mu + \mu_k \right) I_{B,j} - \frac{b}{k} I_{B,j-1} \\ \vdots \\ \left( \frac{b}{k} + \mu + \mu_k \right) I_{B,k-1} - \frac{b}{k} I_{B,k-2} \\ \left( \frac{b}{k} + \mu + \mu_k \right) I_{B,k} - \frac{b}{k} I_{B,k-1} \end{pmatrix}$$

$$V = \begin{bmatrix} (\gamma_H + \mu_H) & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 \\ 0 & (\gamma_W + \mu) & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 \\ 0 & -\gamma_W & \left( \frac{b}{k} + \mu + \mu_k \right) & 0 & \cdots & 0 & 0 & \cdots & 0 \\ 0 & 0 & -\frac{b}{k} & \left( \frac{b}{k} + \mu + \mu_k \right) & \cdots & 0 & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & 0 & \cdots & \left( \frac{b}{k} + \mu + \mu_k \right) & 0 & \cdots & 0 \\ 0 & 0 & 0 & 0 & \cdots & -\frac{b}{k} & \left( \frac{b}{k} + \mu + \mu_k \right) & \cdots & 0 \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & \left( \frac{b}{k} + \mu + \mu_k \right) \\ 0 & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & -\frac{b}{k} \end{bmatrix} \quad \left( \frac{b}{k} + \mu + \mu_k \right)$$

Note that the lower-right  $k+1$  by  $k+1$  matrix is near circulant.

If we assume that  $\gamma_W = b$ , then the lower-right  $k+1$  by  $k+1$  block matrix of  $V(x_0)$  is circulant and we can invert  $V$ . Let  $G_k$  denote this lower block.

$$G_4^{-1} = \frac{1}{(b+d)^4 - b^4} \begin{bmatrix} (b+d)^{4-1} & b^{4-1} & b^{4-2}(b+d)^{4-3} & b^{4-3}(b+d)^{4-2} & \\ b^{4-3}(b+d)^{4-2} & (b+d)^{4-1} & b^{4-1} & b^{4-2}(b+d)^{4-3} & \\ b^{4-2}(b+d)^{4-3} & b^{4-3}(b+d)^{4-2} & (b+d)^{4-1} & b^{4-1} & \\ b^{4-1} & b^{4-2}(b+d)^{4-3} & b^{4-3}(b+d)^{4-2} & (b+d)^{4-1} & \end{bmatrix}$$

$$G_k^{-1} = \frac{1}{(b+d)^k - b^k} \begin{bmatrix} (b+d)^{k-1} & b^{k-1} & b^{k-2}(b+d)^1 & \dots & b^{k-j+1}(b+d)^{j-2} & b^{k-j}(b+d)^{j-1} \\ b^{k-(k-1)}(b+d)^{(k-1)-1} & (b+d)^{k-1} & b^{k-1} & \dots & b^{k-j+2}(b+d)^{j-3} & b^{k-j+1}(b+d)^{j-2} \\ b^{k-(k-2)}(b+d)^{(k-2)-1} & b^{k-(k-1)}(b+d)^{(k-1)-1} & (b+d)^{k-1} & \dots & \vdots & \vdots \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ b^{k-2}(b+d)^1 & & & \dots & & \\ b^{k-1} & & & \dots & & \end{bmatrix}$$



In any case,  $G_k^{-1}$  is also circulant. For now, just let  $G_k^{-1} = [\varphi_{i,k}]_{i=1,\dots,k+1}$ . Then

$$\begin{aligned}
 FV^{-1} &= \begin{bmatrix} 0 & 0 & \beta_{MH}b & \beta_{MH}b & \cdots & \beta_{MH}b & \beta_{MH}b & \cdots & \beta_{MH}b & \beta_{MH}b \\ \beta_{HM}\rho_b^k [1 - \rho_W \rho_b^k]^{-1} \Lambda_M \left( \frac{1}{K_H} \right) & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ \beta_{HM}\rho_b [1 - \rho_W \rho_b^k]^{-1} \Lambda_M \left( \frac{1}{K_H} \right) & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \ddots & \vdots & \vdots \\ \beta_{HM}\rho_b^{j-2} [1 - \rho_W \rho_b^k]^{-1} \Lambda_M \left( \frac{1}{K_H} \right) & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ \beta_{HM}\rho_b^{j-1} [1 - \rho_W \rho_b^k]^{-1} \Lambda_M \left( \frac{1}{K_H} \right) & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \ddots & \vdots & \vdots \\ \beta_{HM}\rho_b^{k-2} [1 - \rho_W \rho_b^k]^{-1} \Lambda_M \left( \frac{1}{K_H} \right) & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ \beta_{HM}\rho_b^{k-1} [1 - \rho_W \rho_b^k]^{-1} \Lambda_M \left( \frac{1}{K_H} \right) & 0 & 0 & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \end{bmatrix} \begin{bmatrix} 1/(\gamma_H + \mu_H) \\ 0 \\ 0 \\ 0 \\ \vdots \\ 0 \\ 0 \\ \vdots \\ 0 \\ 0 \end{bmatrix} \\
 &= \begin{bmatrix} 0 & \beta_{MH}b \sum_{i \neq 1} \varphi_{i,k} & \beta_{MH}b \sum_{i \neq 2} \varphi_{i,k} & \beta_{MH}b \sum_{i \neq 3} \varphi_{i,k} & \beta_{MH}b \sum_{i \neq 4} \varphi_{i,k} \\ \beta_{HM}\rho_b^k [1 - \rho_W \rho_b^k]^{-1} \Lambda_M \left( \frac{1}{K_H} \right) / (\gamma_H + \mu_H) & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ \beta_{HM}\rho_b [1 - \rho_W \rho_b^k]^{-1} \Lambda_M \left( \frac{1}{K_H} \right) / (\gamma_H + \mu_H) & 0 & 0 & 0 & 0 \\ 0 & \vdots & \vdots & \vdots & \vdots \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ \beta_{HM}\rho_b^{j-2} [1 - \rho_W \rho_b^k]^{-1} \Lambda_M \left( \frac{1}{K_H} \right) / (\gamma_H + \mu_H) & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ \beta_{HM}\rho_b^{j-1} [1 - \rho_W \rho_b^k]^{-1} \Lambda_M \left( \frac{1}{K_H} \right) / (\gamma_H + \mu_H) & 0 & 0 & 0 & 0 \\ 0 & \vdots & \vdots & \vdots & \vdots \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ \beta_{HM}\rho_b^{k-2} [1 - \rho_W \rho_b^k]^{-1} \Lambda_M \left( \frac{1}{K_H} \right) / (\gamma_H + \mu_H) & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ \beta_{HM}\rho_b^{k-1} [1 - \rho_W \rho_b^k]^{-1} \Lambda_M \left( \frac{1}{K_H} \right) / (\gamma_H + \mu_H) & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \end{bmatrix}
 \end{aligned}$$

The eigenvalues of this simplified version are given by zero (multiplicity  $k$ ) and

$$\begin{aligned}
 \lambda_{\pm} &= \pm \sqrt{\beta_{HM}\beta_{MH}b [1 - \rho_W \rho_b^k]^{-1} \left( \frac{\Lambda_M}{K_H} \right) \left( \frac{1}{\gamma_H + \mu_H} \right)} \sqrt{\rho_b^k \sum_{i \neq 1} \varphi_{i,k} + 0 + \rho_b \sum_{i \neq 3} \varphi_{i,k} + \cdots + \rho_b^{j-3} \sum_{i \neq j-1} \varphi_{i,k} + \rho_b^{j-2} \sum_{i \neq j} \varphi_{i,k}} \\
 \frac{\lambda_{\pm}}{\sqrt{\beta_{HM}\beta_{MH}b [1 - \rho_W \rho_b^k]^{-1} \left( \frac{\Lambda_M}{K_H} \right) \left( \frac{1}{\gamma_H + \mu_H} \right)}} &= \pm \sqrt{\rho_b^k \sum_{i \neq 1} \varphi_{i,k} + 0 + \rho_b \sum_{i \neq 3} \varphi_{i,k} + \rho_b^2 \sum_{i \neq 4} \varphi_{i,k} + \cdots + \rho_b^{j-3} \sum_{i \neq j-1} \varphi_{i,k} + \rho_b^{j-2} \sum_{i \neq j} \varphi_{i,k}} \\
 &= \pm \sqrt{\rho_b^k \sum_{i \neq 1} \varphi_{i,k} + \sum_{j=3}^k \rho_b^{j-2} \sum_{i \neq j} \varphi_{i,k}}
 \end{aligned}$$

Thus, since there is exactly one positive eigenvalue, it must be the basic reproduction number:

$$\mathcal{R}_0 = \sqrt{\beta_{HM}\beta_{MH}b(1-\rho_W\rho_b^k)^{-1}\left(\frac{\Lambda_M}{K_H}\right)\left(\frac{1}{\gamma_H+\mu_H}\right)} \sqrt{\rho_b^k \sum_{i \neq 1} \varphi_{i,k} + \sum_{j=3}^{k+1} \rho_b^{j-2} \sum_{i \neq j} \varphi_{i,k}}$$

There's probably some little trick I can do using the fact that

$$\begin{aligned} \rho_b^k \sum_{i \neq 1} \varphi_{i,k} + \sum_{j=3}^{k+1} \rho_b^{j-2} \sum_{i \neq j} \varphi_{i,k} &= \left( \rho_b^k \sum_{i \neq 1} \varphi_{i,k} + \sum_{i \neq 2} \varphi_{i,k} + \sum_{j=3}^{k+1} \rho_b^{j-2} \sum_{i \neq j} \varphi_{i,k} \right) - \sum_{i \neq 2} \varphi_{i,k} \\ &= \left( \sum_{j=1}^k \rho_b^{j-1} \sum_{i \neq j+1} \varphi_{i,k} + \rho_b^k \sum_{i \neq 1} \varphi_{i,k} \right) - \sum_{i \neq 2} \varphi_{i,k} \end{aligned}$$

Note that

$$\sum_{i=1}^k \varphi_{i,k} = \frac{1}{\mu_M}$$

hence

$$\sum_{i \neq j} \varphi_{i,k} = \frac{1}{\mu_M} - \varphi_{j,k}$$

So

$$\begin{aligned} \rho_b^k \sum_{i \neq 1} \varphi_{i,k} + \sum_{j=3}^{k+1} \rho_b^{j-2} \sum_{i \neq j} \varphi_{i,k} &= \left( \sum_{j=1}^k \rho_b^{j-1} \sum_{i \neq j+1} \varphi_{i,k} + \rho_b^k \sum_{i \neq 1} \varphi_{i,k} \right) - \sum_{i \neq 2} \varphi_{i,k} \\ &= \left( \sum_{j=1}^k \rho_b^{j-1} \left( \frac{1}{\mu_M} - \varphi_{j+1,k} \right) + \rho_b^k \left( \frac{1}{\mu_M} - \varphi_{1,k} \right) \right) - \left( \frac{1}{\mu_M} - \varphi_{2,k} \right) \\ &= \frac{1}{\mu_M} \left( \sum_{j=0}^k \rho_b^j - 1 \right) - \left( \rho_b^k \varphi_{1,k} + \sum_{j=1}^k \rho_b^{j-1} \varphi_{j+1,k} \right) \\ &= \frac{1}{\mu_M} \left( \frac{\rho_b(\rho_b^k - 1)}{\rho_b - 1} - 1 \right) - \left( \rho_b^k \varphi_{1,k} + \sum_{j=1}^k \rho_b^{j-1} \varphi_{j+1,k} \right) \\ &= \frac{1}{\mu_M} \left( \frac{\rho_b^{k+1} + 1}{\rho_b - 1} \right) - \left( \rho_b^k \varphi_{1,k} + \sum_{j=1}^{k-1} \rho_b^{j-1} \varphi_{j+1,k} \right) \end{aligned}$$

!!! Move on to simulations for now