

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

Let M represent the total adult female mosquito population size and H the total host population size. For now, in order to focus on mosquito population dynamics, 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”) for the host population. Notably, the familiar logistic population model satisfies these assumptions: $g(H) = rH(K - H)$.

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

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

where λ_M is the recruitment rate of eggs, K_L is the carrying capacity for aquatic stage mosquitoes, ρ_L is the development rate, μ_L is the density-independent aquatic stage mortality rate, and μ_M is the density-independent adult mortality rate. The rate λ_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 σ_M represent the oviposition rate for mosquitoes.

$$\lambda_M(M) = \sigma_M f M$$

where f is the fecundity of a female mosquito (eggs per female per oviposition cycle).

Case Studies: Multiple blood feeding

We develop two simple models of multiple blood feeding. These models differ in the presumed processes driving heterogeneity in the number of blood meals per gonotrophic cycle. In the first model, the number of blood meals per gonotrophic cycle is determined upon emergence from the aquatic stage, representing a developmental determination for multiple blood feeding behavior. Let B represent the population of female mosquitoes in the blood feeding phase and V the population of female mosquitoes in the oviposition phase.

Suppose now that the compartment B is sub-divided into multiple compartments. For now, to keep things general, assume that $\vec{B} = [B_1, B_2, \dots, B_p]$ though we will change the indexing later. We make the assumptions that i) all newly recruited mosquitoes enter the blood feeding phase, ii) the only way to enter V is to exit B , and iii) the waiting time distribution to leave V is exponential with mean γ . Then we obtain the general model

$$\begin{aligned}\frac{d}{dt}L &= \phi V \left(1 - \frac{L}{K_L}\right) - (\rho_L + \mu_L)L \\ \frac{d}{dt}\vec{B} &= (\rho_L L + \gamma V) \vec{\alpha} + A^T \vec{B} - \mu \vec{B} \\ \frac{d}{dt}V &= (-\mathbf{1}^T A^T \vec{B}) - \gamma V - \mu V\end{aligned}\tag{0.1}$$

where the matrix A describes the transient state rate matrix associated with the phase-type distribution describing the waiting times in the state vector \vec{B} . The vector $\vec{\alpha}$ determines how mosquitoes are distributed as they enter the blood feeding compartments \vec{B} . We will explore two models of multiple blood feeding which are expressed in terms of the matrix A . The table below provides definitions for the parameters common to both models

Parameter symbol	Description	Units	Notes
ϕ	Fecundity	eggs per ovipositing female per unit time	
K_L	Larval carrying capacity	number of individuals	
ρ_L	Larval maturation rate	per time	
μ_L	Larval mortality rate	per time	
γ	Rate leaving oviposition stage	per time	
μ	Adult mortality rate	per time	

TABLE 1. Parameters of the base model

THE “DISRUPT” MODEL

This model envisions multiple blood feeding as being driven by interruptions in feeding, perhaps due to host defensive behaviors, as opposed to inherent biological traits of the individual mosquito (i.e. conditions experienced as a larva). In this case, the waiting time distribution is described by a Coxian distribution. We first have to define an integer describing the upper limit to the number of mosquito blood meals in a single gonotrophic cycle, which we denote k . Then the transient state rate matrix A is a $k \times k$ matrix that is upper-triangular because an individual mosquito can only increase in the number of blood meals it has taken. For the same reason, $\vec{\alpha}$ is a $k \times 1$ vector with a 1 in its first entry and 0 in all others.

$$(0.2) \quad \vec{\alpha} = \begin{bmatrix} 1 \\ 0 \\ \vdots \\ 0 \\ 0 \end{bmatrix}, A = \begin{bmatrix} -\lambda_1 & (1 - \sigma_1) \lambda_1 & \cdots & 0 & 0 \\ 0 & -\lambda_2 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & -\lambda_{k-1} & (1 - \sigma_{k-1}) \lambda_{k-1} \\ 0 & 0 & \cdots & 0 & -\lambda_k \end{bmatrix}$$

Here, the quantities λ_i are the total rates out of compartment B_i and the σ_i are the probabilities of transitioning from B_i directly to V (instead of B_i to B_{i+1}).

Existence of equilibria. We first determine the equilibria of this model. These are solutions to the (system of) equations defined by:

$$(\mu I - A^T) \mathbf{B} = \left(\rho_L \frac{\left(\frac{\phi}{\rho_L + \mu_L} \right) \frac{1}{\gamma + \mu} (-\mathbf{1}^T A^T \mathbf{B})}{K_L + \left(\frac{\phi}{\rho_L + \mu_L} \right) \frac{1}{\gamma + \mu} (-\mathbf{1}^T A^T \mathbf{B})} K_L + \frac{\gamma}{\gamma + \mu} (-\mathbf{1}^T A^T \mathbf{B}) \right) \vec{\alpha}.$$

This system is equivalent to

$$B_1 = \left(\frac{1}{\mu + \lambda_1} \right) \rho_L \frac{\left(\frac{\phi}{\rho_L + \mu_L} \right) \frac{1}{\gamma + \mu} (-\mathbf{1}^T A^T \mathbf{B})}{K_L + \left(\frac{\phi}{\rho_L + \mu_L} \right) \frac{1}{\gamma + \mu} (-\mathbf{1}^T A^T \mathbf{B})} K_L + \left(\frac{1}{\mu + \lambda_1} \right) \frac{\gamma}{\gamma + \mu} (-\mathbf{1}^T A^T \mathbf{B})$$

$$B_i = B_1 \left(\frac{\mu + \lambda_1}{\mu + \lambda_i} \right) \prod_{j=1}^{i-1} \frac{\lambda_j}{\mu + \lambda_j} (1 - \sigma_j), 1 < i \leq k$$

Now, since $-\mathbf{1}^T A^T = [\sigma_i \lambda_i]_{i=1}^k$ (where here $\rho_k = 0$), we obtain $-\mathbf{1}^T A^T \mathbf{B} = \varrho (\mu + \lambda_1) B_1$ where we have defined $\tau = \sum_{i=1}^k \left(\frac{\lambda_i}{\mu + \lambda_i} \right) \sigma_i \prod_{j=1}^{i-1} \left(\frac{\lambda_j}{\mu + \lambda_j} \right) (1 - \sigma_j)$, which represents the total probability of a newly-emerged mosquito surviving to reach the oviposition stage.

Let $e = \left(\frac{\rho_L}{\rho_L + \mu_L} \right) \phi \frac{1}{\gamma + \mu}$. Then e represents the average number of new mosquitoes produced in a single oviposition event since $\phi \frac{1}{\gamma + \mu}$ is the number of eggs a single mosquito lays within an oviposition event, and $\frac{\rho_L}{\rho_L + \mu_L}$ is the probability of the eggs surviving to adulthood. Further, note that $\nu_G = \left[1 - \left(\frac{\gamma}{\gamma + \mu} \right) \tau \right]^{-1} = \sum_{j=1}^{\infty} \left(\frac{\gamma}{\gamma + \mu} \right)^j \tau^j$ represents the average number of gonotrophic cycles survived by

a mosquito. Finally, we can solve for B_1 :

$$B_1 = \left(\frac{1}{\mu + \lambda_1} \right) \left(\frac{\tau e \nu_G - 1}{e \tau} \right) \rho_L K_L$$

We need the equilibrium to be positive which occurs when $e \tau \nu_G > 1$, i.e. when on average a mosquito produces more than one offspring over its lifespan. We define $R = \tau e \nu_G$ to be the reproductive number for the population. As we will see, the sign of $R - 1$ controls the stability of the extinction equilibrium. First, we try to identify any additional equilibria.

The equilibrium values of the remaining compartments can then be calculated from B_1 . Thus there are two equilibria, the extinction equilibrium $E_0 = [0, \mathbf{0}, 0]$ and the persistence equilibrium $E_1 = [L^*, \mathbf{B}^*, V^*]$ where

$$\begin{aligned} L^* &= \left(\frac{e \tau \nu_G - 1}{e \tau \nu_G} \right) K_L \\ B_1^* &= \left(\frac{1}{\mu + \lambda_1} \right) \rho_L \left(\frac{e \tau \nu_G - 1}{e \tau} \right) K_L \\ B_i^* &= \left[\left(\frac{1}{\mu + \lambda_i} \right) \prod_{j=1}^{i-1} \left(\frac{\lambda_j}{\mu + \lambda_j} \right) (1 - \sigma_j) \right] \rho_L \left(\frac{e \tau \nu_G - 1}{e \tau} \right) K_L, 1 < i \leq k \\ V^* &= \left(\frac{1}{\gamma + \mu} \right) \rho_L \left(\frac{e \tau \nu_G - 1}{e} \right) K_L \end{aligned}$$

Stability of equilibria. We employ the next generation operator approach developed in van den Driessche and Watmough (2002) to determine the stability of the extinction equilibrium. We need to specify which compartment we deem to represent “new” individuals: in this case, we define these to be compartment B_1 , the new reproductively mature mosquitoes (compartment B_1). We will use matrix vector notation throughout where a **bolded** variable represents a quantity of the appropriate size for the displayed operation.

We begin by re-writing our model as

$$\begin{aligned} \frac{d}{dt} \begin{bmatrix} L \\ \mathbf{B} \\ V \end{bmatrix} &= \begin{bmatrix} 0 \\ \rho_L L \vec{\alpha} \\ 0 \end{bmatrix} - \left\{ \begin{bmatrix} (\rho_L + \mu_L) L \\ -D_{\text{diag } A}^T \mathbf{B} + \mu \mathbf{B} \\ (\gamma + \mu) V \end{bmatrix} - \begin{bmatrix} -\phi V \left(1 - \frac{L}{K_L} \right) \\ \gamma V \vec{\alpha} + (A - D_{\text{diag } A})^T \mathbf{B} \\ (-\mathbf{1}^T A^T \mathbf{B}) \end{bmatrix} \right\} \\ &= \mathcal{F} - \mathcal{V} \end{aligned}$$

where D_v denotes a diagonal matrix with diagonal elements defined by the vector v . We now calculate the determinants of \mathcal{F} and \mathcal{V} and evaluate them at the extinction equilibrium, E_0 . The Jacobians of the operators \mathcal{F} and \mathcal{V} are given by

$$\begin{aligned} \mathcal{F}_x &= \begin{bmatrix} 0 & \mathbf{0}_{1 \times k+1} \\ \rho_L \vec{\alpha} & \mathbf{0}_{k+1 \times k+1} \\ 0 & 0 \end{bmatrix}, \\ \mathcal{V}_x &= \begin{bmatrix} (\rho_L + \mu_L) + \phi V \left(\frac{1}{K_L} \right) & \mathbf{0}_{1 \times k} & -\sigma_M f \left(1 - \frac{L}{K_L} \right) \\ \mathbf{0}_{k \times 1} & \mu I - A^T & -\gamma \vec{\alpha} \\ 0 & \mathbf{1}^T A^T & (\gamma + \mu) \end{bmatrix} \end{aligned}$$

and, evaluated these at the extinction equilibrium, we obtain

$$\begin{aligned} F &= \begin{bmatrix} 0 & \mathbf{0}_{1 \times k+1} \\ \rho_L & 0 \\ \mathbf{0}_{k \times 1} & \mathbf{0}_{k \times k+1} \end{bmatrix}, \\ V &= \begin{bmatrix} (\rho_L + \mu_L) & \mathbf{0}_{1 \times k} & -\phi \\ \mathbf{0}_{k \times 1} & \mu I - A^T & -\gamma \vec{\alpha} \\ 0 & \mathbf{1}^T A^T & (\gamma + \mu) \end{bmatrix}. \end{aligned}$$

We now need to determine the eigenvalues of $K = FV^{-1}$.

We first need to find the inverse of the matrix V . Let $W = \begin{bmatrix} (\rho_L + \mu_L) & \mathbf{0}_{1 \times k} \\ \mathbf{0}_{k \times 1} & \mu I - A^T \end{bmatrix}_{k+1 \times k+1}$, $X = \begin{bmatrix} -\phi \\ -\gamma \vec{\alpha} \end{bmatrix}_{k+1 \times 1}$, $Y = [0 \quad \mathbf{1}^T A^T]_{1 \times k+1}$, $Z = [(\gamma + \mu)]_{1 \times 1}$ so that V can be written in block matrix form as $V = \begin{bmatrix} W & X \\ Y & Z \end{bmatrix}$. Clearly Z is invertible but it will be more helpful to find the inverse of W to obtain the inverse of V :

$$W^{-1} = \begin{bmatrix} \frac{1}{\rho_L + \mu_L} & \mathbf{0}_{1 \times k} \\ \mathbf{0}_{k \times 1} & (\mu I - A^T)^{-1} \end{bmatrix}$$

where

$$\begin{aligned} (\mu I - A^T)^{-1} &= \begin{bmatrix} \mu + \lambda_1 & 0 & \cdots & 0 & 0 \\ -(1 - \sigma_1) \lambda_1 & \mu + \lambda_2 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & \mu + \lambda_{k-1} & 0 \\ 0 & 0 & \cdots & -(1 - \sigma_{k-1}) \lambda_{k-1} & \mu + \lambda_k \end{bmatrix}^{-1} \\ &= \begin{bmatrix} \frac{1}{\mu + \lambda_1} & 0 & \cdots & 0 & 0 \\ (1 - \sigma_1) \frac{\lambda_1}{\mu + \lambda_1} \frac{1}{\mu + \lambda_2} & \frac{1}{\mu + \lambda_2} & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ \frac{1}{\mu + \lambda_{k-1}} \prod_{i=1}^{k-2} \frac{\lambda_i}{\mu + \lambda_i} (1 - \sigma_i) & \frac{1}{\mu + \lambda_k} \prod_{i=2}^{k-2} \frac{\lambda_i}{\mu + \lambda_i} (1 - \sigma_i) & \cdots & \mu + \lambda_{k-1} & 0 \\ \frac{1}{\mu + \lambda_k} \prod_{i=1}^{k-1} \frac{\lambda_i}{\mu + \lambda_i} (1 - \sigma_i) & \frac{1}{\mu + \lambda_k} \prod_{i=2}^{k-1} \frac{\lambda_i}{\mu + \lambda_i} (1 - \sigma_i) & \cdots & \frac{1}{\mu + \lambda_k} \frac{\lambda_{k-1}}{\mu + \lambda_{k-1}} (1 - \sigma_{k-1}) & \frac{1}{\mu + \lambda_k} \end{bmatrix} \end{aligned}$$

Now since $V = \begin{bmatrix} W & X \\ Y & Z \end{bmatrix}$ and W is invertible, we can form

$$V^{-1} = \begin{bmatrix} W^{-1} + W^{-1}X(Z - YW^{-1}X)^{-1}YW^{-1} & -W^{-1}X(Z - YW^{-1}X)^{-1} \\ -(Z - YW^{-1}X)^{-1}YW^{-1} & (Z - YW^{-1}X)^{-1} \end{bmatrix}$$

It is useful to note that $Z - YW^{-1}X = (\gamma + \mu) \frac{1}{\nu_G}$ is a scalar, where here we used the definition of $\nu_G = \left[1 - \left(\frac{\gamma}{\gamma + \mu}\right)\tau\right]^{-1}$. Hence we obtain

$$V^{-1} = \begin{bmatrix} W^{-1} + \frac{\nu_G}{\gamma + \mu} W^{-1}XYW^{-1} & -\frac{\nu_G}{\gamma + \mu} W^{-1}X \\ -\frac{\nu_G}{\gamma + \mu} YW^{-1} & \frac{\nu_G}{\gamma + \mu} \end{bmatrix}$$

Note that, because of the form of the matrix F , we need not determine all entries of the matrix $K = FV^{-1}$ to find its eigenvalues. In fact, we will only need to know the entries of the first row of the matrices $W^{-1} + \frac{\nu_G}{\gamma + \mu} W^{-1}XYW^{-1}$ and $-\frac{\nu_G}{\gamma + \mu} W^{-1}X$ since

$$\begin{aligned} K = FV^{-1} &= \begin{bmatrix} 0 & 0 & \cdots & 0 & 0 \\ \rho_L & 0 & \cdots & 0 & 0 \\ 0 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \cdots & 0 & 0 \\ 0 & 0 & \cdots & 0 & 0 \end{bmatrix} \begin{bmatrix} W^{-1} + W^{-1}X(Z - YW^{-1}X)^{-1}YW^{-1} & -W^{-1}X(Z - YW^{-1}X)^{-1} \\ -(Z - YW^{-1}X)^{-1}YW^{-1} & (Z - YW^{-1}X)^{-1} \end{bmatrix} \\ &= \begin{bmatrix} 0 & 0 \\ \left[\rho_L W^{-1} + \rho_L \frac{\nu_G}{\gamma + \mu} W^{-1}XYW^{-1}\right]_{1,\cdot} & \left[-\rho_L \frac{\nu_G}{\gamma + \mu} W^{-1}X\right]_{1,\cdot} \\ 0 & 0 \\ \vdots & \vdots \\ 0 & 0 \end{bmatrix} \end{aligned}$$

where $[M]_{1,\cdot}$ denotes the first row of the matrix M . Since the second row of K is its only non-zero row, the sole non-zero eigenvalue of K must be given by the entry in its second row, second column. This value is the entry in the first row, second column of the matrix $\rho_L W^{-1} + \rho_L \frac{\nu_G}{\gamma+\mu} W^{-1} X Y W^{-1}$. Since $[W^{-1}]_{1,2} = 0$, it just remains to compute $\left[\rho_L \frac{\nu_G}{\gamma+\mu} W^{-1} X Y W^{-1} \right]_{1,2}$. After some tedious calculations, we arrive at $\left[\rho_L \frac{\nu_G}{\gamma+\mu} W^{-1} X Y W^{-1} \right]_{1,2} = \rho_L \frac{\nu_G}{\gamma+\mu} \left(\phi \frac{1}{\rho_L + \mu_L} \tau \right)$.

Hence K has a single non-zero eigenvalue which is given by

$$R = \rho_L \frac{\nu_G}{\gamma + \mu} \left(\phi \frac{1}{\rho_L + \mu_L} \tau \right) = \tau e \nu_G$$

as expected.

THE “FATE” MODEL

In this model, the number of blood meals necessary to attain repletion is determined by the conditions in which the mosquito larvae is reared. Generally, worse larval rearing conditions are associated with a greater number of blood meals necessary for repletion. We assign a “type” to newly-emerged mosquitoes which describes how many blood meals it must take to reach the oviposition stage. Newly-emerged mosquitoes enter compartment $B_{i,1}$ with probability ρ_i . A mosquito in blood feeding compartment $B_{i,j}$ has taken $j-1$ blood meals and needs i blood meals to reach the oviposition stage V_i , where $j \leq i$. After oviposition, mosquitoes in compartment V_i return to compartment $B_{i,1}$. This reflects the assumption that the necessary number of blood meals is determined solely by larval conditions, and hence the “fate” of the mosquito was determined at emergence and never changes.

While we would like to determine a single transient state rate matrix A and vector α to put this model in the general form 0.1, in practice this seems to be more trouble than its worth. Instead, we consider the following system of equations.

$$\begin{aligned} \frac{d}{dt} L &= \phi \left(1 - \frac{L}{K_L} \right) \sum_{i=1}^k V_i - (\rho_L + \mu_L) L \\ \frac{d}{dt} B_{i,1} &= \kappa_i (\rho_L L) + \gamma V_i - \lambda_{i,1} B_{i,1} - \mu B_{i,1} \\ \frac{d}{dt} B_{i,j} &= \lambda_{i,j-1} B_{i,j-1} - \lambda_{i,j} B_{i,j} - \mu B_{i,j} \\ \frac{d}{dt} V_i &= \lambda_{i,i} B_{i,i} - \gamma V_i - \mu V_i \end{aligned} \quad (0.3)$$

We can somewhat condense the system of equations for each mosquito type as follows. Let $\mathbf{B}_i = [B_{i,1}, B_{i,2}, \dots, B_{i,i-1}, B_{i,i}]^T$ be the vector of blood feeding stages for mosquitoes of type i and $\alpha_i = [1, 0, \dots, 0]^T$ a vector of length i . Then

$$\frac{d}{dt} \mathbf{B}_i = (\kappa_i \rho_L L + \gamma V_i) \alpha_i + A_i^T \mathbf{B}_i - \mu \mathbf{B}_i$$

where

$$A_i = \begin{bmatrix} -\lambda_{i,1} & \lambda_{i,1} & 0 & \cdots & 0 \\ 0 & -\lambda_{i,2} & \lambda_{i,2} & \cdots & 0 \\ \vdots & \vdots & \ddots & \ddots & \vdots \\ 0 & 0 & \cdots & -\lambda_{i,i-1} & \lambda_{i,i-1} \\ 0 & 0 & \cdots & 0 & -\lambda_{i,i} \end{bmatrix}$$

is size $i \times i$. It is helpful to note that $\mathbf{1}_i^T A_i^T = [0, 0, \dots, 0, -\lambda_{i,i}]$.

Existence of equilibria. We proceed by solving the system of equations. This process will proceed in two steps. We will first determine the value of a derived quantity β , that is a weighted sum of the equilibrium value of the initial compartments $B_{i,1}^*$. We then compute $B_{i,1}^*$ for each i and use these to find $B_{i,j}^*$, V_i^* , and L .

After some calculation, we obtain a system of equations for each \mathbf{B}_i which depends only on the final blood feeding stages $B_{l,l}$ for $1 \leq l \leq k$.

$$(\mu I - A_i^T) \mathbf{B}_i = \left(\kappa_i K_L \frac{e \sum_{l=1}^k \lambda_{l,l} B_{l,l}}{K_L + \frac{1}{\rho_L} e \sum_{l=1}^k \lambda_{l,l} B_{l,l}} + \frac{\gamma}{\gamma + \mu} \lambda_{i,i} B_{i,i} \right) \boldsymbol{\alpha}_i.$$

This system of equations reduces to

$$\begin{aligned} B_{i,j} &= \left(\frac{\mu + \lambda_{i,1}}{\lambda_{i,j}} \right) \left(\prod_{r=1}^j \frac{\lambda_{i,r}}{\mu + \lambda_{i,r}} \right) B_{i,1}, 1 < j \leq i \\ B_{i,1} &= \left(\frac{1}{\mu + \lambda_{i,1}} \right) \kappa_i K_L \frac{e \sum_{l=1}^k \lambda_{l,l} B_{l,l}}{K_L + \frac{1}{\rho_L} e \sum_{l=1}^k \lambda_{l,l} B_{l,l}} + \left(\frac{1}{\mu + \lambda_{i,1}} \right) \frac{\gamma}{\gamma + \mu} \lambda_{i,i} B_{i,i} \end{aligned}$$

Now let $\tau_l = \prod_{j=1}^l \frac{\lambda_{i,j}}{\mu + \lambda_{i,j}}$, which represents the probability of a newly-emerged mosquito of type l surviving to oviposition. Then $B_{i,i} = \left(\frac{\mu + \lambda_{i,1}}{\lambda_{i,i}} \right) \tau_i B_{i,1}$.

Now define $\beta = \sum_{l=1}^k \lambda_{l,l} B_{l,l}$. We can now write the equation for $B_{i,1}$ totally in terms of β :

$$\begin{aligned} B_{i,1} &= \left(\frac{1}{\mu + \lambda_{i,1}} \right) \kappa_i K_L \frac{e \sum_{l=1}^k \lambda_{l,l} B_{l,l}}{K_L + \frac{1}{\rho_L} e \sum_{l=1}^k \lambda_{l,l} B_{l,l}} + \frac{\gamma}{\gamma + \mu} \tau_i B_{i,1} \\ B_{i,1} &= \frac{1}{\mu + \lambda_{i,1}} \kappa_i K_L \frac{e \beta}{K_L + \frac{1}{\rho_L} e \beta} + \frac{\gamma}{\gamma + \mu} \tau_i B_{i,1} \\ \left(1 - \frac{\gamma}{\gamma + \mu} \tau_i \right) B_{i,1} &= \frac{1}{\mu + \lambda_{i,1}} \kappa_i K_L \frac{e \beta}{K_L + \frac{1}{\rho_L} e \beta} \\ B_{i,1} &= \frac{\rho_L K_L e \beta}{\rho_L K_L + e \beta} \left(\frac{1}{\mu + \lambda_{i,1}} \kappa_i \nu_i \right) \end{aligned}$$

where we defined $\nu_i = \left[1 - \frac{\gamma}{\gamma + \mu} \tau_i \right]^{-1}$, representing the average number of gonotrophic cycles per lifespan for a mosquito of type i . Notice that the prefactor in the equation for $B_{i,1}$ is independent of the index i .

We now use the equation for $B_{i,1}$ above, the definition of $\beta = \sum_{l=1}^k \lambda_{l,l} B_{l,l}$, and the equation $B_{l,l} = \left(\frac{\mu + \lambda_{l,1}}{\lambda_{l,l}} \right) \tau_l B_{l,1}$ to arrive at an expression that allows us to solve for β .

$$\begin{aligned} \beta &= \sum_{l=1}^k (\mu + \lambda_{l,1}) \tau_l B_{l,1} \\ \beta &= \left(\frac{\rho_L K_L e \beta}{\rho_L K_L + e \beta} \right) \left(\sum_{l=1}^k \kappa_l \tau_l \nu_l \right) \end{aligned}$$

Let $\nu_G = \sum_{l=1}^k \kappa_l \tau_l \nu_l$, which may be interpreted to represent the average number of additional gonotrophic cycles undergone by a newly-emerged mosquito, weighted to account for the distribution of the number of bites it needs to attain repletion. The factor τ_l appears because a newly-emerged mosquito must survive to oviposit at least once to be counted. We are now situated to solve for β :

$$\begin{aligned} \beta &= \left(\frac{\rho_L K_L e \beta}{\rho_L K_L + e \beta} \right) \nu_G \\ \beta &= \rho_L K_L \frac{1}{e} (e \nu_G - 1) \end{aligned}$$

Now that we know β , we can find $B_{i,1}$ and the remaining equilibrium values

$$\begin{aligned} L &= K_L \frac{1}{e\nu_G} (e\nu_G - 1), \\ B_{i,1} &= \rho_L K_L \frac{1}{e\nu_G} (e\nu_G - 1) \left(\frac{1}{\mu + \lambda_{i,1}} \kappa_i \nu_i \right), \\ B_{i,j} &= \rho_L K_L \frac{1}{e\nu_G} (e\nu_G - 1) (\kappa_i \nu_i) \left(\frac{1}{\lambda_{i,j}} \right) \left(\prod_{r=1}^j \frac{\lambda_{i,r}}{\mu + \lambda_{i,r}} \right), \\ V_i &= \frac{1}{\gamma + \mu} \rho_L K_L \frac{1}{e\nu_G} (e\nu_G - 1) (\kappa_i \nu_i \tau_i). \end{aligned}$$

Letting $R = e\nu_G$, we will show later that R is the reproductive number determining the existence and stability of a positive (non-extinction) equilibrium.

Stability of equilibria. We again employ the next generation operator approach developed in van den Driessche and Watmough (2002). We now have multiple compartments that may be interpreted as representing “new” mosquitoes. We thus define recruitment as individuals entering any of the compartments $B_{i,1}$.

We begin by re-writing our model as

$$\begin{aligned} \frac{d}{dt} \begin{bmatrix} L \\ \mathbf{B}_1 \\ \mathbf{B}_2 \\ \vdots \\ \mathbf{B}_{k-1} \\ \mathbf{B}_k \\ V_1 \\ V_2 \\ \vdots \\ V_{k-1} \\ V_k \end{bmatrix} &= \begin{bmatrix} 0 \\ \rho_L L \kappa_1 \boldsymbol{\alpha}_1 \\ \rho_L L \kappa_2 \boldsymbol{\alpha}_2 \\ \vdots \\ \rho_L L \kappa_{k-1} \boldsymbol{\alpha}_{k-1} \\ \rho_L L \kappa_k \boldsymbol{\alpha}_k \\ 0 \\ 0 \\ \vdots \\ 0 \\ 0 \end{bmatrix} - \left\{ \begin{bmatrix} (\rho_L + \mu_L) L \\ -D_{\text{diag } A_1}^T \mathbf{B}_1 + \mu \mathbf{B}_1 \\ -D_{\text{diag } A_2}^T \mathbf{B}_2 + \mu \mathbf{B}_2 \\ \vdots \\ -D_{\text{diag } A_{k-1}}^T \mathbf{B}_{k-1} + \mu \mathbf{B}_{k-1} \\ -D_{\text{diag } A_k}^T \mathbf{B}_k + \mu \mathbf{B}_k \\ (\gamma + \mu) V_1 \\ (\gamma + \mu) V_2 \\ \vdots \\ (\gamma + \mu) V_{k-1} \\ (\gamma + \mu) V_k \end{bmatrix} - \begin{bmatrix} \phi \mathbf{1}^T \mathbf{V} \left(1 - \frac{L}{K_L} \right) \\ \gamma V \boldsymbol{\alpha}_1 + (A_i - D_{\text{diag } A_1})^T \mathbf{B}_1 \\ \gamma V \boldsymbol{\alpha}_2 + (A_i - D_{\text{diag } A_2})^T \mathbf{B}_2 \\ \vdots \\ \gamma V \boldsymbol{\alpha}_{k-1} + (A_i - D_{\text{diag } A_{k-1}})^T \mathbf{B}_{k-1} \\ \gamma V \boldsymbol{\alpha}_k + (A_i - D_{\text{diag } A_k})^T \mathbf{B}_k \\ \lambda_{1,1} B_{1,1} \\ \lambda_{2,2} B_{2,2} \\ \vdots \\ \lambda_{k-1,k-1} B_{k-1,k-1} \\ \lambda_{k,k} B_{k,k} \end{bmatrix} \right\} \\ &= \mathcal{F} - \mathcal{V} \end{aligned}$$

where D_v denotes a diagonal matrix with diagonal elements defined by the vector v . We now calculate the Jacobians of \mathcal{F} and \mathcal{V} and evaluate them at the extinction equilibrium, E_0 . We can write the

Jacobian of \mathcal{V} as $\mathcal{V}_x = \begin{bmatrix} \mathcal{V}_1 & \mathcal{V}_2 \\ \mathcal{V}_3 & \mathcal{V}_4 \end{bmatrix}$ where

$$\begin{aligned} \mathcal{V}_1 &= \begin{bmatrix} (\rho_L + \mu_L) + \phi \mathbf{1}^T \mathbf{V} \left(-\frac{1}{K_L}\right) & 0 & 0 & \cdots & 0 & 0 \\ 0 & [(\mu I - A_1^T)] & 0 & \cdots & 0 & 0 \\ \mathbf{0} & \mathbf{0} & [(\mu I - A_2^T)] & \cdots & \mathbf{0} & \mathbf{0} \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \cdots & (\mu I - A_{k-1}^T) & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} & (\mu I - A_k^T) \end{bmatrix} \\ \mathcal{V}_2 &= \begin{bmatrix} -\phi \left(1 - \frac{L}{K_L}\right) & -\phi \left(1 - \frac{L}{K_L}\right) & \cdots & -\phi \left(1 - \frac{L}{K_L}\right) & -\phi \left(1 - \frac{L}{K_L}\right) \\ -\gamma \boldsymbol{\alpha}_1 & 0 & \cdots & 0 & 0 \\ \mathbf{0} & -\gamma \boldsymbol{\alpha}_2 & \cdots & \mathbf{0} & \mathbf{0} \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ \mathbf{0} & \mathbf{0} & \cdots & -\gamma \boldsymbol{\alpha}_{k-1} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} & -\gamma \boldsymbol{\alpha}_k \end{bmatrix} \\ \mathcal{V}_3 &= \begin{bmatrix} 0 & -\lambda_{1,1} \boldsymbol{\omega}_1 & \mathbf{0} & \cdots & 0 & 0 \\ 0 & \mathbf{0} & -\lambda_{2,2} \boldsymbol{\omega}_2 & \cdots & \mathbf{0} & \mathbf{0} \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & \mathbf{0} & \mathbf{0} & \cdots & -\lambda_{k-1,k-1} \boldsymbol{\omega}_{k-1} & \mathbf{0} \\ 0 & \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} & -\lambda_{k,k} \boldsymbol{\omega}_k \end{bmatrix} \\ \mathcal{V}_4 &= (\gamma + \mu) I_k \end{aligned}$$

where $\boldsymbol{\omega}_i = [0, 0, \dots, 0, 1]$ is a row vector of length i . The Jacobian of \mathcal{F} can be written as

$$\mathcal{F}_x = \begin{bmatrix} 0 & \mathbf{0}_{1 \times n+k} \\ \rho_L \boldsymbol{\kappa} \boldsymbol{\alpha} & \mathbf{0}_{n \times n+k} \\ \mathbf{0}_{k \times 1} & \mathbf{0}_{k \times n+k} \end{bmatrix}$$

where $\boldsymbol{\kappa} = [\kappa_1, \kappa_2, \dots, \kappa_k]^T$.

Now, evaluating these at the extinction equilibrium, we obtain $V = \begin{bmatrix} V_1 & V_2 \\ V_3 & V_4 \end{bmatrix}$ where

$$\begin{aligned} V_1 &= \begin{bmatrix} (\rho_L + \mu_L) & 0 & 0 & \cdots & 0 & 0 \\ 0 & [(\mu I - A_1^T)] & 0 & \cdots & 0 & 0 \\ \mathbf{0} & \mathbf{0} & [(\mu I - A_2^T)] & \cdots & \mathbf{0} & \mathbf{0} \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \cdots & (\mu I - A_{k-1}^T) & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} & (\mu I - A_k^T) \end{bmatrix} \\ V_2 &= \begin{bmatrix} -\phi & -\phi & \cdots & -\phi & -\phi \\ -\gamma \boldsymbol{\alpha}_1 & 0 & \cdots & 0 & 0 \\ \mathbf{0} & -\gamma \boldsymbol{\alpha}_2 & \cdots & \mathbf{0} & \mathbf{0} \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ \mathbf{0} & \mathbf{0} & \cdots & -\gamma \boldsymbol{\alpha}_{k-1} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} & -\gamma \boldsymbol{\alpha}_k \end{bmatrix} \\ V_3 &= \begin{bmatrix} 0 & -\lambda_{1,1} \boldsymbol{\omega}_1 & \mathbf{0} & \cdots & 0 & 0 \\ 0 & \mathbf{0} & -\lambda_{2,2} \boldsymbol{\omega}_2 & \cdots & \mathbf{0} & \mathbf{0} \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & \mathbf{0} & \mathbf{0} & \cdots & -\lambda_{k-1,k-1} \boldsymbol{\omega}_{k-1} & \mathbf{0} \\ 0 & \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} & -\lambda_{k,k} \boldsymbol{\omega}_k \end{bmatrix} \\ V_4 &= (\gamma + \mu) I_k \end{aligned}$$

The inverse of V is then given by

$$V^{-1} = \begin{bmatrix} W_1 & W_2 \\ W_3 & W_4 \end{bmatrix}$$

where $W_1 = (V_1 - V_2 V_4^{-1} V_3)^{-1}$, $W_2 = -W_1 V_2 V_4^{-1}$, $W_3 = -V_4^{-1} V_3 W_1$, and $W_4 = V_4^{-1} + V_4^{-1} V_3 W_1 V_2 V_4^{-1}$. V^{-1} exists since the inverse of V_4 exists: $V_4^{-1} = \frac{1}{\gamma+\mu} I_k$.

As before, the form of F simplifies the calculation of $K = FV^{-1}$ substantially. We can write

$$F = \begin{bmatrix} \bar{F}_{n+1 \times n+1} & \mathbf{0}_{n+1 \times k} \\ \mathbf{0}_{k \times n+1} & \mathbf{0}_{k \times k} \end{bmatrix}$$

where the matrix \bar{F} is given by

$$\bar{F} = \begin{bmatrix} 0 & 0 & 0 & \cdots & 0 & 0 \\ \rho_L \kappa_1 \boldsymbol{\alpha}_1 & 0 & 0 & \cdots & 0 & 0 \\ \rho_L \kappa_2 \boldsymbol{\alpha}_2 & 0 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ \rho_L \kappa_{k-1} \boldsymbol{\alpha}_{k-1} & 0 & 0 & \cdots & 0 & 0 \\ \rho_L \kappa_k \boldsymbol{\alpha}_k & 0 & 0 & \cdots & 0 & 0 \end{bmatrix}$$

We can thus write the matrix K in block-matrix form as follows

$$K = FV^{-1} = \begin{bmatrix} [\bar{F}W_1]_{n+1 \times n+1} & [\bar{F}W_2]_{k \times k} \\ \mathbf{0}_{k \times n+1} & \mathbf{0}_{k \times k} \end{bmatrix}$$

Thus K is block upper triangular and its eigenvalues must be the same as those of $\bar{F}W_1$.

We now proceed to compute $W_1 = (V_1 - V_2 V_4^{-1} V_3)^{-1}$. We first calculate $V_1 - V_2 V_4^{-1} V_3$ then determine its inverse.

$$V_1 - V_2 V_4^{-1} V_3 = \begin{bmatrix} (\rho_L + \mu_L) & -\left(\frac{\phi}{\gamma+\mu}\right) \lambda_{1,1} \boldsymbol{\omega}_1 & -\left(\frac{\phi}{\gamma+\mu}\right) \lambda_{2,2} \boldsymbol{\omega}_2 & \cdots & -\left(\frac{\phi}{\gamma+\mu}\right) \lambda_{k-1,k-1} \boldsymbol{\omega}_{k-1} & -\left(\frac{\phi}{\gamma+\mu}\right) \lambda_{k,k} \boldsymbol{\omega}_k \\ 0 & L_1 & 0 & \cdots & 0 & 0 \\ 0 & 0 & L_2 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & L_{k-1} & 0 \\ 0 & 0 & 0 & \cdots & 0 & L_k \end{bmatrix}$$

where $L_i = (\mu I - A_i^T) - \left(\frac{\gamma}{\gamma+\mu}\right) \lambda_{i,i} \boldsymbol{\alpha}_i \boldsymbol{\omega}_i$. The matrix $V_1 - V_2 V_4^{-1} V_3$ is block upper triangular with non-zero diagonal matrix entries each of which are invertible. Hence $V_1 - V_2 V_4^{-1} V_3$ is itself invertible. We next calculate W_1 as:

$$W_1 = \begin{bmatrix} X_1^{-1} + X_1^{-1} X_2 (X_4 - X_3 X_1^{-1} X_2)^{-1} X_3 X_1^{-1} & -X_1^{-1} X_2 (X_4 - X_3 X_1^{-1} X_2)^{-1} \\ -(X_4 - X_3 X_1^{-1} X_2)^{-1} X_3 X_1^{-1} & (X_4 - X_3 X_1^{-1} X_2)^{-1} \end{bmatrix}$$

where $X_1 = [(\rho_L + \mu_L)]$, $X_2 = \left[-\left(\frac{\phi}{\gamma+\mu}\right) \lambda_{1,1} \boldsymbol{\omega}_1, -\left(\frac{\phi}{\gamma+\mu}\right) \lambda_{2,2} \boldsymbol{\omega}_2, \cdots -\left(\frac{\phi}{\gamma+\mu}\right) \lambda_{k-1,k-1} \boldsymbol{\omega}_{k-1}, -\left(\frac{\phi}{\gamma+\mu}\right) \lambda_{k,k} \boldsymbol{\omega}_k\right]$, $X_3 = \mathbf{0}_{k \times 1}$, and $X_4 = \text{diag}([L_1, L_2, \dots, L_{k-1}, L_k])$. Since $X_3 = \mathbf{0}_{k \times 1}$, we can simplify the expression of W_1 a bit:

$$W_1 = \begin{bmatrix} X_1^{-1} & -X_1^{-1} X_2 X_4^{-1} \\ \mathbf{0}_{k \times 1} & X_4^{-1} \end{bmatrix}$$

Now

$$\begin{aligned} \bar{F}W_1 &= \begin{bmatrix} 0 & 0 & \cdots & 0 \\ \rho_L \kappa_1 \alpha_1 & 0 & \cdots & 0 \\ \rho_L \kappa_2 \alpha_2 & 0 & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ \rho_L \kappa_{k-1} \alpha_{k-1} & 0 & \cdots & 0 \\ \rho_L \kappa_k \alpha_k & 0 & \cdots & 0 \end{bmatrix} \begin{bmatrix} \frac{1}{\rho_L + \mu_L} & \frac{1}{\rho_L} e \lambda_{1,1} \omega_1 L_1 & \frac{1}{\rho_L} e \lambda_{2,2} \omega_2 L_2 & \cdots & \frac{1}{\rho_L} e \lambda_{k,k} \omega_k L_k \\ 0 & L_1^{-1} & 0 & \cdots & 0 \\ 0 & 0 & L_2^{-1} & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & \cdots & L_k^{-1} \end{bmatrix} \\ \bar{F}W_1 &= e \begin{bmatrix} 0 & 0 & 0 & \cdots & 0 \\ \left(\frac{\gamma+\mu}{\phi}\right) \kappa_1 \alpha_1 & \lambda_{1,1} \kappa_1 \alpha_1 \omega_1 L_1 & \lambda_{2,2} \kappa_1 \alpha_1 \omega_2 L_2 & \cdots & \lambda_{k,k} \kappa_1 \alpha_1 \omega_k L_k \\ \left(\frac{\gamma+\mu}{\phi}\right) \kappa_2 \alpha_2 & \lambda_{1,1} \kappa_2 \alpha_2 \omega_1 L_1 & \lambda_{2,2} \kappa_2 \alpha_2 \omega_2 L_2 & \cdots & \lambda_{k,k} \kappa_2 \alpha_2 \omega_k L_k \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ \left(\frac{\gamma+\mu}{\phi}\right) \kappa_k \alpha_k & \lambda_{1,1} \kappa_k \alpha_k \omega_1 L_1 & \lambda_{2,2} \kappa_k \alpha_k \omega_2 L_2 & \cdots & \lambda_{k,k} \kappa_k \alpha_k \omega_k L_k \end{bmatrix} \\ \bar{F}W_1 &= e (\text{diag}(\kappa) \alpha) (\text{diag}(\lambda) \omega L) \end{aligned}$$

where $\kappa = [\kappa_1, \dots, \kappa_k]^T$, $\lambda = [\lambda_1, \dots, \lambda_k]^T$, $\omega = [\omega_1, \dots, \omega_k]^T$, and $L = \text{diag}([L_1^{-1}, \dots, L_k^{-1}])$ all have the appropriate sizes to make this product work.

Finally the non-zero eigenvalues of K must be the same as the non-zero eigenvalues of $\bar{F}W_1$. These are the roots of the polynomial in φ of $|\varphi - \bar{F}W_1| = \lambda |\lambda I_n - e (\text{diag}(\kappa) \alpha) (\text{diag}(\lambda) \omega L)|$. By Sylvester's determinant theorem, this is equivalent to finding the roots of

$$\begin{aligned} 0 &= \lambda^{n+1} \left| 1 - \frac{1}{\lambda} e (\text{diag}(\lambda) \omega L) (\text{diag}(\kappa) \alpha) \right| \\ &= \lambda^n |\lambda - e (\text{diag}(\lambda) \omega L) (\text{diag}(\kappa) \alpha)| \\ &= \lambda^n \left| \lambda - e \begin{bmatrix} \lambda_{1,1} \omega_1 L_1 & \lambda_{2,2} \omega_2 L_2 & \cdots & \lambda_{k-1,k-1} \omega_{k-1} L_{k-1} & \lambda_{k,k} \omega_k L_k \end{bmatrix} \begin{bmatrix} \kappa_1 \alpha_1 \\ \kappa_2 \alpha_2 \\ \vdots \\ \kappa_{k-1} \alpha_{k-1} \\ \kappa_k \alpha_k \end{bmatrix} \right| \\ &= \lambda^n \left| \lambda - e \sum_{i=1}^k \kappa_i \lambda_{i,i} \omega_i L_i \alpha_i \right| \\ &= \lambda^n \left| \lambda - e \sum_{i=1}^k \kappa_i \frac{\nu_i}{\lambda_{i,i}} \lambda_{i,i} \tau_i \right| \\ &= \lambda^n |\lambda - e \nu_G| \end{aligned}$$

where $\nu_G = \sum_{i=1}^k \kappa_i \tau_i \nu_i$ and we used the fact that the vector $\omega_i L_i$ is the i -th row of L_i and $\omega_i L_i \alpha_i$ is the first entry of that row:

$$\omega_i L_i \alpha_i = \frac{\nu_i}{\lambda_{i,i}} T_i$$

Hence $R = e \nu_G$ is a reproductive number: a positive equilibrium exists and is locally asymptotically stable if and only if $R > 1$.

COMPARING EQUILIBRIA AND REPRODUCTIVE NUMBERS

We will use the superscript F for the “fate” model and D for the “disruption” model, respectively. For now, we assume the two models have the same parameters except for the “ λ ” rates and “ σ ” and “ κ ” probabilities. Note that for the two models, the quantity $e = \left(\frac{\rho_L}{\rho_L + \mu_L}\right) \sigma_M f \frac{1}{\gamma + \mu}$, the (viable) eggs per female per oviposition cycle, is equivalent.

Reproductive numbers. The comparisons here are fairly straightforward.

The reproductive numbers of each model are given by:

$$R^D = e\tau^D\nu_G^D$$

$$R^D = e\frac{\tau^D}{1 - \frac{\gamma}{\gamma+\mu}\tau^D}$$

where $\tau^D = \sum_{i=1}^k \left(\frac{\lambda_i^D}{\mu + \lambda_i^D} \right) \sigma_i \prod_{j=1}^{i-1} \left(\frac{\lambda_j^D}{\mu + \lambda_j^D} \right) (1 - \sigma_j)$.

$$R^F = e \sum_{i=1}^k \kappa_i \nu_i^F \tau_i^F$$

$$R^F = e \sum_{i=1}^k \kappa_i \frac{\tau_i^F}{1 - \frac{\gamma}{\gamma+\mu}\tau_i^F}$$

where $\tau_i^F = \prod_{j=1}^i \frac{\lambda_{i,j}^F}{\mu + \lambda_{i,j}^F}$, $\nu_i^F = \frac{1}{1 - \frac{\gamma}{\gamma+\mu}\tau_i^F}$, and $\nu_G^F = \sum_{i=1}^k \kappa_i \tau_i \nu_i$.

Equilibrium proportions. We also wish to make two other comparisons. First, we want to determine the equilibrium proportion of mosquitoes that have taken exactly $i-1$ blood meals in a given gonotrophic cycle, which we denote M_i . We'll start with the disruption model.

Disruption model. In this case, it is easy to determine

$$M_i^D = (B_i^D)^*$$

$$= \rho_L K_L \frac{1}{e\tau^D} (e\tau^D \nu_G^D - 1) \left[\left(\frac{1}{\mu + \lambda_i^D} \right) \prod_{j=1}^{i-1} \left(\frac{\lambda_j^D}{\mu + \lambda_j^D} \right) (1 - \sigma_j) \right]$$

Fate model. This is less straightforward, but not so bad. We add up all the mosquitoes which have fed i times. This can only occur for mosquitoes of type s where $i \leq s \leq k$.

$$M_i^F = \sum_{s=i}^k (B_{s,i})^*$$

$$= \rho_L K_L \frac{1}{e\nu_G} (e\nu_G - 1) \left[\sum_{s=i}^k (\kappa_s \nu_s) \left(\frac{1}{\lambda_{s,i}^F} \right) \left(\prod_{r=1}^i \frac{\lambda_{s,r}^F}{\mu + \lambda_{s,r}^F} \right) \right]$$

Special case: All λ 's equal. Now suppose that $\lambda_i^D = \lambda_{i,j}^F = \lambda$ for all $1 \leq j \leq i \leq k$. Let $\xi = \frac{\lambda}{\mu + \lambda}$ and $\bar{\nu}_i = \frac{1}{1 - (\frac{\gamma}{\gamma+\mu})\xi^i}$. $\varsigma_i = \sigma_i \prod_{j=1}^{i-1} (1 - \sigma_j)$. We'll write $q = \frac{\gamma}{\gamma+\mu}$ to save some space.