

1 The Model

1.1 Model Development

We begin by borrowing a slightly modified equation for humans in [3]. The model is based on the Ross-Macdonald model [5]:

$$(1.1) \quad \dot{I}_h(t) = -r_h I_h(t) + \left(\frac{k}{N_h} \right) b S_h(t - \tau_h) I_v(t - \tau_h) \theta.$$

We assume that human population remains a constant denoted by N_h . In (1.1), I_h , I_v denote the number of humans and mosquitoes infected with dengue, respectively, r_h is the recovery rate (1/day) of human from dengue so that $1/r_h$ is the duration of the disease for humans, and k is the biting-rate per mosquito (number of bites/day) so that the number of bites per mosquito per human per day is k/N_h . Let b (unitless) be the probability a mosquito bite produces an infection. Then the rate of number of exposed humans produced is $(k/N_h)bS_hI_v$. Suppose the incubation period of dengue in humans is τ_h (days), then an infected human must be exposed τ_h days ago multiplied by the probability (θ) that the individual remains exposed for τ_h days (not recovered or died). Finally, we ignore immigration and emigration since the rates are much smaller than the rest of the parameters. We ignore movement of individuals and assume homogeneous mixing meaning that each individual comes in contact with all the mosquitoes. There is no evidence that humans can transmit *Wolbachia*. These assumptions explain the right-hand side of (1.1).

Equation (1.1) is a delay equation and delay equations are harder to study (book by Hal Smith). Some researchers introduce an exposed class to avoid studying delay equations but we do not do so here. Now $N_h = S_h + I_h + R_h$ but since we assume permanent immunity, $R_h = N_h - S_h - I_h$. Actually, there are 4 serotypes of dengue and permanent immunity is only for the same serotype. It offers cross-immunity to other serotypes but the immunity decreases over time. We also assume that $\theta = e^{-r_h \tau_h}$ (exponential). Our model for humans is therefore

$$(1.2) \quad \begin{aligned} \dot{S}_h(t) &= \mu_h N_h - \left(\frac{kb}{N_h} \right) S_h(t - \tau_h) I_v(t - \tau_h) e^{-r_h \tau_h} - \mu_h S_h \\ \dot{I}_h(t) &= -r_h I_h(t) + \left(\frac{kb}{N_h} \right) S_h(t - \tau_h) I_v(t - \tau_h) e^{-r_h \tau_h} - \mu_h I_h \end{aligned}$$

We also only model one serotype of dengue. For delay equations, it is customary to include time in delay equations; hence, $S_h(t)$ instead of S_h etc. in the above equations.

We now turn to model mosquitoes. First we ignore *Wolbachia*. Incubation period for dengue is τ_v , death-rate is μ_v . Since life-span of mosquitoes is a few weeks, say $\mu_v = 1/(7 \times 4)$, so incubation time cannot be ignored in the model. We assume that dengue does not affect birth-rate or death-rate of mosquitoes (reference needed) and there is no recovery for mosquitoes from dengue (this is true). c is the probability of transmission from infected human to susceptible

mosquito during a bite. We also assume that dengue cannot be transmitted to offsprings by an infected mosquito (possible but rare). For now, we don't take aquatic stage (egg, larva, pupa) into account. Then our model for mosquitoes is

$$\begin{aligned}\dot{S}_v(t) &= \text{birth-rate } A - \left(\frac{kc}{N_h}\right) S_v(t - \tau_v) I_h(t - \tau_v) e^{-\mu_v \tau_v} - \mu_v S_v(t) \\ \dot{I}_v(t) &= \left(\frac{kc}{N_h}\right) S_v(t - \tau_v) I_h(t - \tau_v) e^{-\mu_v \tau_v} - \mu_v I_v(t)\end{aligned}$$

Now let us see how (1.3) has to be changed to include *Wolbachia* in our model. Each one of our assumptions below need to be checked in the literature.

1. Let us consider co-infection. It is clear that co-infection can only happen through birth since *Wolbachia* can be transmitted only through birth, and not between adult mosquitoes or by biting an *Wolbachia*-infected human. A female mosquito lay eggs which are fertilized by *Wolbachia*-infected male, then a large percentage of the eggs do not hatch (this is called cytoplasmic incompatibility, CI). We assume 100% do not hatch in our model. A *Wolbachia*-infected female mosquito lay eggs fertilized by a dengue-infected male mosquito, then eggs may be co-infected. We assume that this does not happen. So no co-infection. This simplifies the model by Hughes and Britton.
2. *Wolbachia* can only be transmitted through birth maternally and unlike dengue there is no incubation period.
3. We study only one strain of *Wolbachia* even though there are 4 strains. Parameters are strain-dependent. There is one vaccine for dengue but it is not commonly given to adults. The chance of developing dengue hemorrhagic fever is small for adults. Most of the time, adults just develop some flu-like symptoms and recover.
4. We only model female mosquitoes because only female mosquitoes bite. We also assume that male and female mosquitoes are equal in number.
5. Cytoplasmic Incompatibility (CI) means that an infected male and an uninfected female give rise to eggs that only certain percentage, $1 - s_h$, of the eggs hatches. s_h is *Wolbachia* strain dependent. We shall later assume $s_h = 1$.
6. *Wolbachia* infected mosquitoes also have lower birth-rate and higher death-rate.
7. Equation for *Wolbachia*-infected mosquitoes, I_w , is

$$(1.3) \quad \dot{I}(t) = \text{birth-rate } B - \mu_w I_w .$$

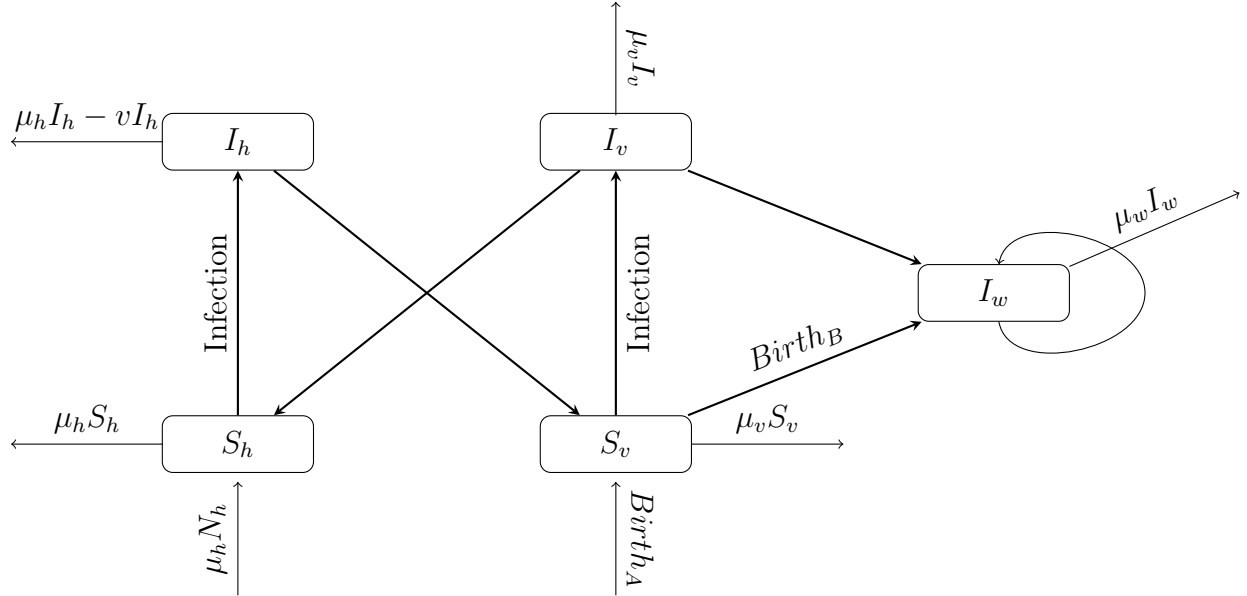
8. We *Wolbachia*-infected mosquitoes have shorter life-span: $\mu_w > \mu_v$. We also assume density dependent per-capita growth rate f (all mosquitoes). When temperature is warm and that are plenty of rainfall, then eggs hatches in one or two days. The time from eggs to emerge as an adult mosquito is about 10-14 days (ideal case). So birth-rate B should just be $f(S_v + I_v + I_w)(1 - s_f)b_z v I_w$, where b_z is the birth-rate of wild-type mosquitoes. We assume success of maternal transmission of *Wolbachia* is the fraction v .

Let us model birth-rate A. I borrow this idea from [4], the paragraph right under Table 1 p. 801. Ignore the life-cycle of mosquitoes for the moment. Let $N_z = S_v + I_v + I_w$, total number of mosquitoes. The number of offsprings is $b_z(S_v + I_v) + (1 - v)b_z(1 - s_f)I_w$, where v is fraction of offsprings from *Wolbachia*-infected female that are also *Wolbachia*-infected. But not all eggs are going to hatch because of CI. Assume random mating, the probability of inviability is $s_h I_w / (S_v + I_v + I_w)$, where s_h is the probability of *Wolbachia*-infected male, *Wolbachia*-uninfected female produce inviable eggs. Therefore,

$$\text{birth-rate } A = f(N_z)(1 - s_h I_w / N_z)b_z(S_v + I_v + (1 - v)(1 - s_f)I_w).$$

We assume that male and female mosquitoes are equal in number. See p. 799 of [4] second assumption. For simplicity, we assume that $v = 1$ and $s_h = 1$. So maternal transmission of *Wolbachia* is 100% successful and CI is also 100%.

To incorporate life-cycle into our model, let τ_d be the number of days from laying eggs to emerge as adult mosquitoes. This number is around 10 days under ideal situations but varies widely depending on abundance supply of water and food. So birth-rate terms have to be delayed by τ_d days.



The full model is

$$\begin{aligned}
\dot{S}_h(t) &= \mu_h N_h - \left(\frac{kb}{N_h} \right) S_h(t - \tau_h) I_v(t - \tau_h) e^{-\gamma \tau_h} - \mu_h S_h \\
\dot{I}_h(t) &= -\gamma I_h(t) + \left(\frac{kb}{N_h} \right) S_h(t - \tau_h) I_v(t - \tau_h) e^{-\gamma \tau_h} - \mu_h I_h \\
\dot{S}_v(t) &= \left[f(N_z) \left(1 - \frac{I_w}{N_z} \right) (S_v + I_v) \right] (t - \tau_d) \\
&\quad - \left(\frac{kc}{N_h} \right) S_v(t - \tau_v) I_h(t - \tau_v) e^{-\mu_v \tau_v} - \mu_v S_v(t) \\
\dot{I}_v(t) &= \left(\frac{kc}{N_h} \right) S_v(t - \tau_v) I_h(t - \tau_v) e^{-\mu_v \tau_v} - \mu_v I_v(t) \\
\dot{I}_w(t) &= [f(N_z)(1 - s_f) I_w] (t - \tau_d) - \mu_w I_w.
\end{aligned}
\tag{1.4}$$

Here, $N_z = S_v + I_v + I_w$ and we assume that $f(N) = \max \left\{ b_0 \left(1 - \frac{N}{K} \right) + \frac{\mu_v N}{K}, 0 \right\}$. In [4], $f(N) = b_0 e^{-hN^\alpha}$. The model has 12 positive parameters. Their estimated values found in the literature are given in Table 1.

Parameter (unit)	Range	Meaning
b	(0.10, 0.75)	Probability of infection from infected mosquito to susceptible human
c	(0.10, 0.75)	Probability of infection from infected human to susceptible mosquito
k	(0.33, 1)	Biting rate
K/N_h	{1,2,...,n}	Ratio of mosquito to human population size
μ_h (1/years)	(1/76, 1/60)	Human death-rate
μ_v (1/days)	(1/42, 1/8)	Mosquito death-rate
μ_w (1/days)	check	Death-rate of <i>Wolbachia</i> -infected mosquitoes
γ (1/days)	(1/12, 1/4)	Human recovery rate
τ_h (days)	(4, 10)	IIP for humans
τ_v (days)	(4, 10)	EIP for mosquitoes at 30°C
τ_d (days)	(10, 14)	Development from eggs to eclosion under ideal situation.
b_0 (1/days)	$(\mu_v, \mu_w / (1 - s_f))$	Birth-rate of wildtype mosquitoes

Table 1: **Parameter Values.** Values taken from Table 3 of [1]. We chose the values for *Ae. aegypti* in [1] although *Ae. albopictus* is also a possible carrier. Values of IIP and EIP are taken from the Internet. Also available in [2] but they don't seem to have an agreed number. **This table needs to be updated**

To analyze the limiting (as time goes to infinity) behavior of the solutions of the above model, we first find its steady-states, which are constant solutions of (2.1). There are five

steady-states: E_1, E_2, E_3, E_4, E_5 . To define them, we introduce some notations. Let

$$\begin{aligned}
\beta_1 &= \frac{kb}{N_h} e^{-\gamma\tau_h}, \quad \beta_2 = \frac{kc}{N_h} e^{-\mu_v\tau_v} \\
J &:= b_0(1 - s_f) - \mu_w \\
A_1 &:= \mu_h\beta_2N_h + (\gamma + \mu_h)\mu_v \\
A_2 &:= \mu_h(\beta_1\beta_2KN_h - (\gamma + \mu_h)\mu_v) \\
A_3 &:= \beta_1\mu_vKJ + (b_0 - \mu_v)\mu_h\mu_w \\
A_4 &:= \beta_1\beta_2KN_hJ - (b_0 - \mu_v)(\gamma + \mu_h)\mu_w
\end{aligned}$$

Then, the steady states are:

$$\begin{aligned}
E_1 &:= (N_h, 0, K, 0, 0) \\
E_2 &:= \left(N_h, 0, 0, 0, \frac{KJ}{(1 - s_f)(b_0 - \mu_v)} \right) \\
E_3 &:= \left(N_h, 0, \frac{\mu_vKJ}{(b_0 - \mu_v)\mu_w}, 0, \frac{(\mu_w - \mu_v(1 - s_f))KJ}{(1 - s_f)(b_0 - \mu_v)\mu_w} \right) \\
E_4 &:= \left(\frac{A_1}{\beta_2(\beta_1K + \mu_h)}, \frac{A_2}{\beta_2(\beta_1K + \mu_h)(\gamma + \mu_h)}, \frac{\mu_v(\beta_1K + \mu_h)(\gamma + \mu_h)}{A_1\beta_1}, \frac{A_2}{A_1\beta_1}, 0 \right) \\
E_5 &:= \left(\frac{\mu_w(b_0 - \mu_v)A_1}{A_3\beta_2}, \frac{\mu_h\mu_vA_4}{\beta_2(\gamma + \mu_h)A_3}, \frac{\mu_v(\gamma + \mu_h)A_3}{\beta_1\mu_w(b_0 - \mu_v)A_1}, \frac{\mu_h\mu_vA_4}{\beta_1\mu_w(b_0 - \mu_v)A_1}, \right. \\
&\quad \left. \frac{(\mu_w - \mu_v(1 - s_f))KJ}{(1 - s_f)(b_0 - \mu_v)\mu_w} \right)
\end{aligned}$$

The traditional ways to control mosquitoes are to remove standing water and spray insecticides. These methods reduce b_0 in the model. However, we always assume that

$$(H1) \quad b_0 > \mu_v.$$

Since mosquitoes infected with *Wolbachia* have higher death rates than those uninfected, we also assume throughout the paper that

$$(H2) \quad \mu_w > \mu_v.$$

Note that if $J > 0$, then (H2) implies (H1). According to [3, display (2)], the Basic Reproduction number for the above model is

$$\mathcal{R}_0 := \frac{\beta_1\beta_2KN_h}{(\gamma + \mu_h)\mu_v} = \left(\frac{k^2bcK}{N_h(\gamma + \mu_h)\mu_v} \right) e^{-\gamma\tau_h} e^{-\mu_v\tau_v}.$$

Proposition 1.1. (i) *The total number of mosquitoes for E_1 and E_4 are both equals to K . The total number of mosquitoes for E_2, E_3 and E_5 are the same and equals to $KJ/((1 - s_f)(b_0 - \mu_v))$;*

(ii) E_1 always exists and E_4 exists if and only if $\mathcal{R}_0 > 1$; (iii) If $J < 0$, then E_2, E_3 and E_5 do not exist; (iv) If $J > 0$, then E_2, E_3 exist and E_5 exists if and only if

$$(1.5) \quad \mathcal{R}_0 > r^* := \frac{(b_0 - \mu_v)\mu_w}{\mu_v J} > 1.$$

We now investigate the long term behavior of solutions to (1.4). There are two types of behavior. First is convergence to a steady-state and second is sustained oscillation. They have implications to the actual behavior of the dengue virus and whether our strategy of releasing *Wolbachia* into the mosquito population is effective or not. For example, we shall show later that E_2 and E_4 if exist are both locally asymptotically stable but E_2 is desirable and E_4 is not. If solutions converge to E_2 , then eventually all mosquitoes carry *Wolbachia* so the strategy succeeded but if solutions converge to E_4 , then the opposite occurs; no mosquito is infected with *Wolbachia* and the strategy failed.

A steady-state solution E is said to be locally asymptotically stable (l.a.s.) if there exists a neighborhood in the state space containing E in its interior such that if S_h, I_h, S_v, I_v, I_w start from this neighborhood at time zero, then $S_h(t), I_h(t), S_v(t), I_v(t), I_w(t)$ converge to E as time goes to infinity. If solutions to (1.4) exhibit sustained oscillations, that means there are periodic outbreak of the disease that won't go away with time. These sustained oscillations (stable periodic solution) often bifurcate from a steady-state, which becomes unstable as certain parameter crosses a critical value. The proofs of the following propositions may be found in the Appendix.

For stability analysis, in addition to (H1) and (H2), we will also assume that

$$(H3) \quad b_0 < 3\mu_v.$$

$$(H4) \quad \mu_v \tau_h < 1. \text{ This is biologically reasonable.}$$

Proposition 1.2. *Let $\mathcal{R}_0 < 1$. Then E_1 is stable and E_4 does not exist. If $\mathcal{R}_0 > 1$, then E_1 becomes unstable, E_4 exists and is l.a.s. for sufficiently small $\mu_h > 0$.*

Proposition 1.3. *Let $J > 0$. Then E_2 exists and is l.a.s.*

The analysis of E_3 and E_5 are more complicated. Their characteristic equations share a common factor of the form $H(\lambda) = a_2(e^{-\lambda\tau_d})^2 + a_1(\lambda)e^{-\lambda\tau_d} + a_0(\lambda)$. Here, a_2 is a constant independent of the delays, a_1 is linear in λ with coefficients independent of the delays, and $a_0(\lambda) = \mu_w^2(\lambda + \mu_v)(\lambda + \mu_w)$. The equation $H(\lambda) = 0$ in general has positive root, which renders both E_3 and E_5 unstable.

Proposition 1.4. *Let $J > 0$. Then aside from the instability resulting from the positive roots of $H(\lambda) = 0$, E_3 is stable if $\mathcal{R}_0 < r^*$ and unstable if $\mathcal{R}_0 > r^*$. E_5 does not exist if $\mathcal{R}_0 < r^*$ and aside from the instability resulting from the positive roots of $H(\lambda) = 0$, it is l.a.s. for sufficiently small $\mu_h > 0$.*

We need to consider the case when b_0 is very large.

2 Appendix

In this Appendix, we use the same notations as in the main body of the text but their meanings are slightly different.

We non-dimensionalize (1.4) by dividing the first two equations of (1.4) by N_h and the last three equations by K . Let $\beta_1 = (kbK/N_h)e^{-\gamma\tau_h}$ and let $\beta_2 = kce^{-\mu_v\tau_v}$. Then (1.4) becomes

$$\begin{aligned}
\dot{S}_h(t) &= \mu_h - \beta_1 S_h(t - \tau_h) I_v(t - \tau_h) - \mu_h S_h \\
\dot{I}_h(t) &= -\gamma I_h(t) + \beta_1 S_h(t - \tau_h) I_v(t - \tau_h) - \mu_h I_h \\
\dot{S}_v(t) &= \left[f(N_z) \left(1 - \frac{I_w}{N_z} \right) (S_v + I_v) \right] (t - \tau_d) \\
&\quad - \beta_2 S_v(t - \tau_v) I_h(t - \tau_v) - \mu_v S_v(t) \\
\dot{I}_v(t) &= \beta_2 S_v(t - \tau_v) I_h(t - \tau_v) - \mu_v I_v(t) \\
\dot{I}_w(t) &= [f(N_z)(1 - s_f) I_w] (t - \tau_d) - \mu_w I_w \\
N_z &:= S_v + I_v + I_w \\
f_1(N_z) &:= b_0 e^{-hx^\alpha} \\
f_2(N_z) &:= \max\{b_0(1 - N_v) + \mu_v N_v, 0\}.
\end{aligned}$$

Let

$$\begin{aligned}
J &:= b_0(1 - s_f) - \mu_w \\
A_1 &:= \mu_h \beta_2 + (\gamma + \mu_h) \mu_v \\
A_2 &:= \mu_h (\beta_1 \beta_2 - (\gamma + \mu_h) \mu_v) \\
A_3 &:= \beta_1 \mu_v J + (b_0 - \mu_v) \mu_h \mu_w \\
A_4 &:= \beta_1 \beta_2 J - (b_0 - \mu_v) (\gamma + \mu_h) \mu_w \\
W_0 &:= \frac{(\mu_w - \mu_v(1 - s_f)) J}{(1 - s_f)(b_0 - \mu_v) \mu_w}
\end{aligned}$$

Then, the steady states are:

$$\begin{aligned}
E_1 &:= (1, 0, 1, 0, 0) \\
E_2 &:= \left(1, 0, 0, 0, \frac{J}{(1 - s_f)(b_0 - \mu_v)} \right) \\
E_3 &:= \left(1, 0, \frac{\mu_v J}{\mu_w(b_0 - \mu_v)}, 0, W_0 \right) \\
E_4 &:= \left(\frac{A_1}{\beta_2(\beta_1 + \mu_h)}, \frac{A_2}{\beta_2(\beta_1 + \mu_h)(\gamma + \mu_h)}, \frac{\mu_v(\beta_1 + \mu_h)(\gamma + \mu_h)}{A_1 \beta_1}, \frac{A_2}{A_1 \beta_1}, 0 \right) \\
E_5 &:= \left(\frac{\mu_w(b_0 - \mu_v) A_1}{A_3 \beta_2}, \frac{\mu_h \mu_v A_4}{\beta_2(\gamma + \mu_h) A_3}, \frac{\mu_v(\gamma + \mu_h) A_3}{\beta_1 \mu_w(b_0 - \mu_v) A_1}, \frac{\mu_h \mu_v A_4}{\beta_1 \mu_w(b_0 - \mu_v) A_1}, W_0 \right)
\end{aligned}$$

2.1 Characteristic Equations

If we let $\mathbf{y}(t) = [S_1(t), I_1(t), S_2(t), I_2(t), I_w(t)]^t$, then system (2.1) may be written as

$$\begin{aligned}\dot{\mathbf{y}}(t) &= \mathbf{f}(\mathbf{y}(t), \mathbf{y}(t - \tau_h), \mathbf{y}(t - \tau_v), \mathbf{y}(t - \tau_d)) \\ &= \mathbf{f}(\mathbf{y}, \mathbf{w}, \mathbf{x}, \mathbf{z}).\end{aligned}$$

Linearizing the right-hand side of \mathbf{f} and evaluating at a steady-state, we have

$$\dot{\mathbf{y}}(t) = M\mathbf{y}(t) := B_0\mathbf{y}(t) + B_1\mathbf{y}(t - \tau_h) + B_2\mathbf{y}(t - \tau_v) + B_3\mathbf{y}(t - \tau_d),$$

where $B_0 = D\mathbf{f}/D\mathbf{y}$, $B_1 = D\mathbf{f}/D\mathbf{w}$, $B_2 = D\mathbf{f}/D\mathbf{x}$, $B_3 = D\mathbf{f}/D\mathbf{z}$ are Jacobian matrices evaluated at the steady-state. Let $\mathbf{y} = \mathbf{y}_0 e^{\lambda t}$. We have,

$$\begin{aligned}\lambda \mathbf{y}_0 e^{\lambda t} &= B_0 e^{\lambda t} \mathbf{y}_0 + B_1 e^{\lambda(t - \tau_h)} \mathbf{y}_0 + B_2 e^{\lambda(t - \tau_v)} \mathbf{y}_0 + B_3 e^{\lambda(t - \tau_d)} \mathbf{y}_0 \\ \lambda \mathbf{y}_0 &= (B_0 + B_1 e^{-\lambda \tau_h} + B_2 e^{-\lambda \tau_v} + B_3 e^{-\lambda \tau_d}) \mathbf{y}_0.\end{aligned}$$

Therefore, the (transcendental) characteristic equation is

$$(2.1) \quad \det(\lambda I - B_0 - B_1 e^{-\lambda \tau_h} - B_2 e^{-\lambda \tau_v} - B_3 e^{-\lambda \tau_d}) = 0.$$

Using Maple, we found the characteristic equations of the five steady-states as follows.

E_1 Characteristic equation is

$$\begin{aligned}p_1(\lambda) &= (\lambda + \mu_h)[e^{-\lambda \tau_d}(b_0 - 2\mu_v) + \lambda + \mu_v][e^{-\lambda \tau_d}\mu_v(s_f - 1) + \lambda + \mu_w] \\ &\quad [e^{-\lambda(\tau_h + \tau_v)}\beta_1\beta_2 - (\lambda + \mu_v)(\lambda + \gamma + \mu_h)]\end{aligned}$$

E_2 Characteristic equation is

$$p_2(\lambda) = (\lambda + \mu_h)(\lambda + \gamma + \mu_h)(\lambda + \mu_v)^2 [e^{-\lambda \tau_d}(b_0(1 - s_f) - 2\mu_w) + \lambda + \mu_w]$$

E_3 Characteristic equation is

$$\begin{aligned}p_3(\lambda) &= \frac{1}{(b_0 - \mu_v)\mu_w^3} (\lambda + \mu_h)h_1(\lambda)h_2(\lambda) \\ h_1(\lambda) &= \mu_w(b_0 - \mu_v)(\lambda + \mu_v)(\lambda + \gamma + \mu_h) - \beta_1\beta_2\mu_v(b_0(1 - s_f) - \mu_w)e^{-\lambda(\tau_h + \tau_v)} \\ h_2(\lambda) &= a_2(e^{-\lambda \tau_d})^2 + a_1(e^{-\lambda \tau_d}) + a_0 \\ a_2 &= -\mu_v\mu_w(2\mu_w - \mu_v(1 - s_f))(b_0(1 - s_f) - 2\mu_w) \\ a_1 &= \{[\mu_v^2(1 - s_f)^2 - \mu_v\mu_w(1 - s_f)^2 + \mu_w^2(1 - s_f)]b_0 - \mu_w^2(\mu_v + \mu_v s_f + 2\mu_w)\}\lambda \\ &\quad + \mu_v\mu_w^2((b_0 + \mu_v)(1 - s_f) - 4\mu_w) \\ a_0 &= \mu_w^2(\lambda + \mu_v)(\lambda + \mu_w)\end{aligned}$$

E_4 Characteristic equation is

$$\begin{aligned}
p_4(\lambda) &= \frac{[e^{-\lambda\tau_d}(b_0 - 2\mu_v) + \lambda + \mu_v][e^{-\lambda\tau_d}\mu_v(s_f - 1) + \lambda + \mu_w]}{(\mu_h\beta_2 + \gamma\mu_v + \mu_h\mu_v)(\gamma + \mu_h)(\beta_1 + \mu_h)} h(\lambda) \\
h(\lambda) &= a + be^{-\lambda\tau_v} + ce^{-\lambda\tau_h} + de^{-\lambda(\tau_h + \tau_v)} \\
c_1 &= \mu_h\beta_2 + \gamma\mu_v + \mu_h\mu_v \\
c_2 &= -\beta_1\beta_2 + \gamma\mu_v + \mu_h\mu_v \\
a &= (\gamma + \mu_h)(\beta_1 + \mu_h)c_1(\lambda + \mu_h)(\lambda + \gamma + \mu_h)(\lambda + \mu_v) \\
b &= -\mu_hc_1c_2(\lambda + \mu_h)(\lambda + \gamma + \mu_h) \\
c &= -\mu_h(\gamma + \mu_h)(\beta_1 + \mu_h)c_2(\lambda + \mu_v)(\lambda + \gamma + \mu_h) \\
d &= -\mu_h(\gamma + \mu_h)[\beta_1\gamma^2\mu_v^2 + O(\mu_h)] - [\beta_1\gamma^3\mu_v^2 + \gamma^2\mu_v(\beta_1\beta_2 + 3\beta_1\mu_v + \gamma\mu_v)\mu_h + O(\mu_h^2)]\lambda
\end{aligned}$$

If $\mu_h = 0$, then the denominator of $p_4(\lambda)$ becomes $\beta_1\gamma^2\mu_v$ and $h(\lambda)$ becomes

$$(2.2) \quad h_s(\lambda) = -\gamma^2\beta_1\mu_v\lambda[e^{-\lambda(\tau_h + \tau_v)}\gamma\mu_v - (\lambda + \mu_v)(\lambda + \gamma)]$$

E_5 Characteristic equation is

$$\begin{aligned}
p_5(\lambda) &= \frac{k_1(\lambda)k_2(\lambda)}{-A_3\mu_w^3(b_0 - \mu_v)(\mu_h\beta_2 + \gamma\mu_v + \mu_h\mu_v)(\gamma + \mu_h)} \\
k_1(\lambda) &= a + be^{-\lambda\tau_v} + ce^{-\lambda\tau_h} + de^{-\lambda(\tau_h + \tau_v)} \\
&\quad \text{where } a, b, c, d \text{ are complicated expressions independent of } \tau_h, \tau_v, \tau_d \text{ but depend on } \lambda \\
k_2(\lambda) &= \text{same as } h_2(\lambda) \text{ in } E_3
\end{aligned}$$

2.2 Local Stability

The following is taken from Proposition 4.9 of [6]:

Theorem 2.1. *Consider the equation $p(\lambda) + q(\lambda)e^{-\lambda r} = 0$, where p, q are polynomials in λ and typically $\deg(p) > \deg(q)$. Suppose (a) $p(\lambda) \neq 0$ for $\operatorname{Re}(\lambda) \geq 0$; (ii) $|q(iy)| < |p(iy)|$, $0 \leq y < \infty$; (iii) $\lim_{|\lambda| \rightarrow \infty, \operatorname{Re}(\lambda) \geq 0} |q(\lambda)/p(\lambda)| = 0$. Then $\operatorname{Re}(\lambda) < 0$ for every root λ of the above equation and all $r > 0$.*

Corollary 2.2. *Let $q(\lambda) = c_1, p(\lambda) = \lambda + c_2$, where $c_2 > |c_1| > 0$. Then the conclusion of Theorem 2.1 is valid.*

Proof. $|p(iy)| = |iy + c_2| = \sqrt{y^2 + c_2^2} \geq c_2 > |c_1| = |q(iy)|$. The rest are clear. \square

We continue to assume hypotheses (H1) to (H4). The following is a consequence of (H4). Actually, it is not (H4) but the following inequality that is needed in the proofs.

$$(2.3) \quad \mathcal{E} := \gamma^2\mu_v^2\tau_h^2 - \gamma^2\mu_v^2\tau_v^2 - 2\gamma^2\mu_v\tau_v - 2\gamma\mu_v^2\tau_v - 2\gamma^2 - 2\gamma\mu_v - 2\mu_v^2 < 0.$$

The following expression occurs frequently in our proofs

$$(2.4) \quad \mathcal{F} := \gamma\mu_v\tau_h + \gamma\mu_v\tau_v + \gamma + \mu_v.$$

Proof of Proposition 1.3

Hypothesis (H3) implies that $b_0(1 - s_f) < 3\mu_w$. The proposition follows from Corollary 2.2.

Proof of Proposition 1.2

The eigenvalues of the characteristic equation $p_1(\lambda) = 0$ are $-\mu_h$ and the roots of the other three equations. For the equation $e^{-\lambda\tau_d}(b_0 - 2\mu_v) + \lambda + \mu_v = 0$. The above corollary implies that the roots of this equation have negative real parts if $|b_0 - 2\mu_v| < \mu_v$ or $\mu_v < b_0 < 3\mu_v$. This follows from (H1) and (H2). Similarly, for the second equation, the condition $-\mu_w < \mu_v(1 - s_f) < \mu_w$ is satisfied. For the last equation, condition (i) of Theorem 2.1 is

$$\begin{aligned} p(\lambda) &= (\lambda_1 + i\lambda_2)^2 + (\gamma + \mu_h + \mu_v)(\lambda_1 + i\lambda_2) + \mu_v(\gamma + \mu_h) \\ \operatorname{Re}(p) &= \lambda_1^2 - \lambda_2^2 + (\gamma + \mu_h + \mu_v)\lambda_1 + \mu_v(\gamma + \mu_h) \\ \operatorname{Im}(p) &= [(\gamma + \mu_h + \mu_v) + 2\lambda_1]\lambda_2 \end{aligned}$$

If $p(\lambda) = 0$ and $\lambda_1 \geq 0$, then from $\operatorname{Im}(p) = 0$, we have $\lambda_2 = 0$. Then from $\operatorname{Re}(p) = 0$, λ_1 cannot have nonnegative roots. By letting $\lambda_1 = 0, \lambda_2 = iy$, the condition $|q(iy)| < |p(iy)|$ translates into $(\beta_1\beta_2)^2 < |p(iy)|^2 = \mu_v^2(\gamma + \mu_h)^2 + ((\gamma + \mu_h)^2 + \mu_v^2)y^2 + y^4$. This is valid as long as

$$\beta_1\beta_2 < \mu_v(\gamma + \mu_h).$$

But this is the condition $\mathcal{R}_0 < 1$. Condition (iii) is clearly satisfied. Thus, E_1 is l.a.s. if $\mathcal{R}_0 < 1$ holds. Now suppose $\mathcal{R}_0 > 1$. Let $z_1(\lambda) = e^{-\lambda(\tau_h + \tau_v)}$ and let $z_2(\lambda) = (\lambda + \mu_v)(\lambda + \gamma + \mu_h)/(\beta_1\beta_2)$. $z_1(\lambda)$ is decreasing for $\lambda > 0$ while $z_2(\lambda)$ is a parabola facing upward. Also, $z_2(0) < z_1(0) = 1$ because $\mathcal{R}_0 > 1$. Thus, the two curves intersect for some $\lambda > 0$ and E_1 is unable.

We now turn to the analysis of the local stability of E_4 . The first two factors of $p_4(\lambda)$ are identical to those in $p_1(\lambda)$ and have been analyzed. From (2.2), $h_s(\lambda) = 0$ has two zero roots, and we need to show that these zero roots move into the negative half complex plane as μ_h turns positive. We substitute $\lambda = \sqrt{\mu_h}\lambda_1 + \mu_h\lambda_2$ into the equation $h(\lambda) = 0$, where λ_1, λ_2 can be any real or complex numbers and expand the results in series of μ_h , we have $h(\lambda) = A_1\mu_h + A_2\mu_h^{3/2} + O(\mu_h^2)$. If we set $A_1 = 0$, then $\lambda_1^2 = A/B := -(\beta_1\beta_2 - \gamma\mu_v)/\mathcal{F} < 0$ so λ_1 is pure imaginary. Setting $A_2 = 0$, we obtain

$$\lambda_2 = \frac{w_0 + w_2\lambda_1^2}{4\gamma\mu_v\beta_h\mathcal{F}}$$

If we substitute A/B for λ_1^2 , the sign of λ_2 is determined by the sign of $N := Bw_0 + Aw_2$. Expanding N in series of β_1 and β_2 , we have $N = C_0 + C_1\beta_1 + C_2\beta_1\beta_2 + \mathcal{E}\beta_1^2\beta_2$. Now $C_0 = 2\mathcal{F}\gamma^2\mu_v^2 > 0$, $C_1 = -\gamma^2\mu_v^2$ (positive quantity) < 0 , $C_2 = -2\mathcal{F}\gamma\mu_v < 0$ and $\mathcal{E} < 0$ because of

condition (2.3). Since $C_0 + C_2\beta_1\beta_2 = -2\gamma\mu_v\mathcal{F}(\beta_1\beta_2 - \gamma\mu_v) < 0$, we have $\lambda_2 < 0$ and E_4 is l.a.s. for sufficiently small μ_h . The proof of Proposition 1.2 is complete.

We now turn to the analysis of E_3 and E_5 . Recall the characteristic equations $p_3(\lambda) = 0$ and $p_5(\lambda) = 0$ defined above.

Lemma 2.3. (i) For E_3 , the roots of the equation $h_1(\lambda) = 0$ have negative real parts if $\mathcal{R}_0 < r^*$ and some roots have positive real parts if $\mathcal{R}_0 > r^*$. Note that r^* is defined in (1.5). (ii) E_5 exists if $\mathcal{R}_0 > r^*$. The roots of the equation $k_1(\lambda) = 0$ have negative real parts for sufficiently small $\mu_h > 0$. (iii) The identical equations $h_2(\lambda) = 0$ and $k_2(\lambda) = 0$ have roots with positive real parts for sufficiently small $\tau_d > 0$.

Proof. The proof of (i) is similar to the proof of the equation $e^{-\lambda(\tau_h+\tau_v)}\beta_1\beta_2 - (\lambda + \mu_v)(\lambda + \gamma + \mu_h) = 0$ given in the analysis of E_1 above and will be omitted here. (ii) We follow the method described in the analysis of $h(\lambda) = 0$ above. Substituting $\lambda = \sqrt{\mu_h}\lambda_1 + \mu_h\lambda_2$ into the equation $k_1(\lambda) = 0$, we have $k_1(\lambda) = A_1\mu_h + A_2\mu_h^{3/2} + O(\mu_h^2)$. Setting $A_1 = 0$, then from (??), we have

$$\lambda_1^2 = -\frac{\mu_v[\beta_1\beta_2(b_0(1-s_f) - \mu_w) - (b_0 - \mu_v)\gamma\mu_w]}{\mu_w(b_0 - \mu_v)\mathcal{F}} < 0$$

Thus, λ_1 is pure imaginary. If we set $A_2 = 0$ and proceed just like in the case of E_4 above, then

$$A_2 = -\frac{L_0 + L_1\beta_1 + L_2\beta_1\beta_2 + L_3\beta^2\beta_2}{4\gamma\beta_1\mu_w(b_0(1-s)f) - \mu_w(b_0 - \mu_v)\mathcal{F}}$$

where

$$\begin{aligned} L_0 &= -2\gamma^2\mu_w^2(b_0 - \mu_v)^2\mathcal{F} \\ L_1 &= \gamma^2\mu_w(b_0(1-s_f) - \mu_w)(b_0 - \mu_v)\mu_v(3\gamma\mu_v\tau_h^2 + 4\gamma\mu_v\tau_h\tau_v + \gamma\mu_v\tau_v^2 + 4\mu_v\tau_h + 2\mu_v\tau_v + \\ &\quad 2 + 4\gamma\tau_h + 2\gamma\tau_v) \\ L_2 &= 2\gamma\mu_w(b_0(1-s_f) - \mu_w)(b_0 - \mu_v)\mathcal{F} \\ L_3 &= -(s_fb_0 - b_0 + \mu_w)^2\mathcal{E} \end{aligned}$$

Condition (??) implies $\beta_1\beta_2 > (\gamma + \mu_h)(b_0 - \mu_v)\mu_w/(b_0(1-s_f) - \mu_w)$, so that $L_0 + L_2\beta_1\beta_2 > 0$. From hypothesis (H3), L_1 and L_3 are positive so the $A_2 < 0$ for sufficiently small $\mu_h > 0$. \square

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