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## Mathematical Models of Mosquito Populations

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MATHEMATICAL MODELS OF MOSQUITO POPULATIONS

by

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A thesis submitted in partial fulfillment of the requirements  
for the Honors in the Major Program in Mathematics  
in the College of Sciences  
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Orlando, Florida

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## ABSTRACT

The intent of this thesis is to develop ordinary differential equation models to better understand the mosquito population. We first develop a framework model, where we determine the condition under which a natural mosquito population can persist in the environment. *Wolbachia* is a bacterium which limits the replication of viruses inside the mosquito which it infects. As a result, infecting a mosquito population with *Wolbachia* can decrease the transmission of viral mosquito-borne diseases, such as dengue. We develop another ODE model to investigate the invasion of *Wolbachia* in a mosquito population. In a biologically feasible situation, we determine three coexisting equilibria: a stable *Wolbachia*-free equilibrium, an unstable coexistence equilibrium, and a complete invasion equilibrium. We establish the conditions under which a population of *Wolbachia* infected mosquitoes may persist in the environment via the next generation number and determine when a natural mosquito population may experience a complete invasion of *Wolbachia*.

## **DEDICATION**

For my fiancé, Christopher,  
who has always believed in me and encouraged me to  
never give up.

For my mentor, Zhisheng,  
who taught me to reach for the stars.

## **ACKNOWLEDGEMENTS**

I would like to thank all the professors who have helped me during my time at the University of Central Florida. Those who encouraged and inspired me to pursue knowledge and who have enabled me to get to this point.

I would like to thank the individuals in my life who have encouraged me to pursue my goals and who have made me smile along the way.

There were many times where I wanted to give up,  
but I didn't because of the support system I had in my  
family and friends.

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## INTRODUCTION

*Wolbachia* is bacteria that is naturally occurring in about 60% of insect species. When a host is infected by *Wolbachia*, a mutually beneficial relationship arises. *Wolbachia* is endosymbiotic bacteria that behaves like an “accessory immune system” to its host – it helps keep viral pathogens at bay [5]. This, of course, is very beneficial to the insect host and allows the bacteria to reside comfortably inside the host. An interesting phenomenon occurs when the *Aedes aegypti* mosquito is infected with *Wolbachia*, which greatly benefits the human population. The transmission of viral mosquito-borne diseases, such as dengue, is inhibited. When a mosquito bites a host infected with DENV, the virus infects and replicates inside the mosquito's midgut before colonizing other parts. If the virus is not able to colonize the mosquito's salivary glands, then the virus will not be spread through mosquito-human contact [2]. Cohorts of *Wolbachia* infected mosquitoes are already being released into the environment, though the exact mechanisms behind the anti-viral effects of *Wolbachia* are still poorly understood [5]. Locations in countries such as Australia, Brazil, Colombia, Indonesia, and Vietnam have participated in these releases to disrupt the transmission of dengue and Zika viruses [5].

*Wolbachia* alters host biology to increase its own transmission and survival. Unlike many other bacterial infections, a *Wolbachia* infection is not spread through contact – *Wolbachia* is transmitted via maternal vertical transmission, i.e. a female infected with *Wolbachia* will transmit the bacteria to her offspring. On the other hand, if a male has *Wolbachia*, his offspring will not necessarily have *Wolbachia*. Since *Wolbachia* is spread by females and males are

essentially a “dead end”, *Wolbachia* may alter the reproductive biology of its hosts through either feminization, parthenogenesis, male killing, or cytoplasmic incompatibility, depending on the insect species that it is residing in [9].

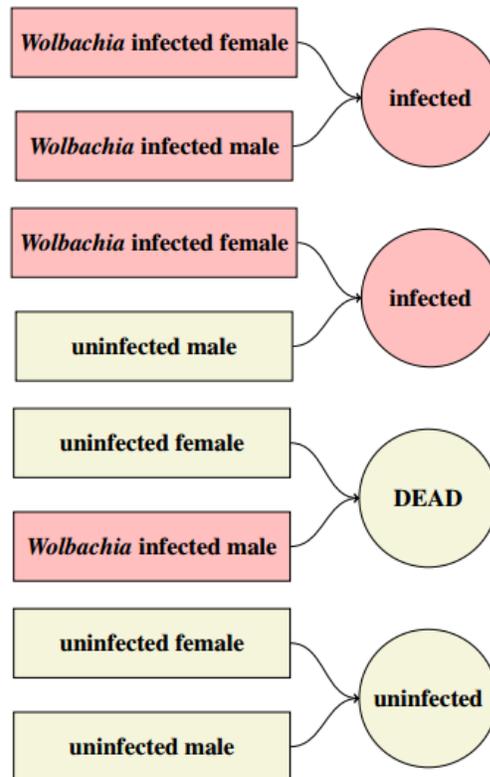


Figure 1: Effects of Cytoplasmic Incompatibility

In *Ae. Aegypti*, cytoplasmic incompatibility (CI) occurs. CI affects the reproductive ability of non-infected females. When an uninfected female mates with an infected male, the sperm is damaged during the process of spermatogenesis and typically results in a dead embryo. All other combinations of mating are compatible as described in Figure 1. The presence of the *Wolbachia* infected population will reduce the population growth of the natural population because of CI. A natural question arises: Will the introduction of an infected population invade and overthrow the existing population, i.e. will all mosquitoes in that environment eventually be

infected? Research shows that this is indeed the case – *Wolbachia* infected mosquitoes can eventually replace the natural population.

## DEVELOPMENT OF A FRAMEWORK MODEL

We would first like to focus on a framework mosquito population model that investigates the dynamics of the mosquito population. We consider two populations –  $P(t)$ : the size of the parous mosquito population at time  $t$ , and  $E(t)$  : the size of the immature population at time  $t$ . We consider the immature population to be male and female mosquito eggs, larvae, pupae, and new adult mosquitoes. The parous population are female mosquitoes that have reached the reproductive stage of their lives – in which case they will be blood feeding and producing offspring.

We will consider  $\gamma$  to be the proportion of female mosquitoes in a typical cohort of eggs laid. This ratio is developed through the development of the aquatic stages through varying survival rates due to biological differences of the sexes [4]. There is generally a 5:3 male: female ratio of adult mosquitoes [4] and hence, we will consider  $\gamma = \frac{3}{8}$  as the proportion of females in the population.

The expected lifespan of an adult mosquito is roughly 14-30 days depending on the environmental conditions [10]. We will assume a constant lifespan of 21 days. Female mosquitoes are in the nulliparous stage for about 3-5 days [1]. Hence, we will assume that the natural death rate for parous mosquitoes is  $\delta_P = \frac{1}{21-4} = \frac{1}{17}$  to be the death rate of the parous population. We will utilize  $\delta_E = 0.02$  for the natural death rate of the immature stages [7].

Parous mosquitoes may have 100-200 eggs ready to deposit during their reproductive cycle [10]. The size of the cohort is dependent on the size of the blood-meal the mosquito took

previously. To simplify this process, we will assume that each mosquito has an average blood-meal and thus the cohort size will be about 150 eggs.

At 86 degrees Fahrenheit (30 degrees Celsius) *Aedes aegypti* mosquitoes take about 5 days to begin to deposit eggs after having a blood-meal \cite{temp}. *Aedes Aegypti* deposit their eggs at multiple sites naturally – this process may take anywhere from a few hours to a few days depending on breeding site availability. We will assume that the process of laying eggs will only take a day.

We assume that a moderate blood-meal will always be found, suitable males will be available for breeding, and suitable breeding sites will be available Hence we will consider  $n = \frac{150}{6} = 25$  eggs per day.

We will define the maturation rate of mosquitos from the immature stage to the parous stage as  $\frac{1}{lifespan} = \frac{1}{\sum t_i} = \frac{1}{12}$  where  $t_i$  is the time spent in the  $i^{th}$  stage of maturation. Here, we assume that an egg develops into a parous mosquito in 12 days.

Recall that  $P(t)$  is the number of parous mosquitoes at time  $t$ . We assume that the death rate of the parous population is  $\delta_p$  and hence we have  $\delta_p P$  parous mosquitoes dying per unit time. We found that, on average, each parous mosquito will lay eggs at a rate of  $n$  and thus there will be  $nP$  newly laid eggs per unit time. These eggs will be new individuals to the immature mosquito population. Death from the immature population can be reasoned in a similar fashion. We assume that the proportion of females in the immature population is  $\gamma$  and that the immature population matures at a rate of  $m$ , and so  $\gamma m E(t)$  eggs mature into parous females at time  $t$ .

Similarly,  $(1 - \gamma)mE(t)$  eggs mature into adult male mosquitoes. Since we are only concerned about the parous mosquito population, we will expel male mosquitoes from the model once they have matured. We may visualize this information in the flow-diagram depicted in Figure 2.

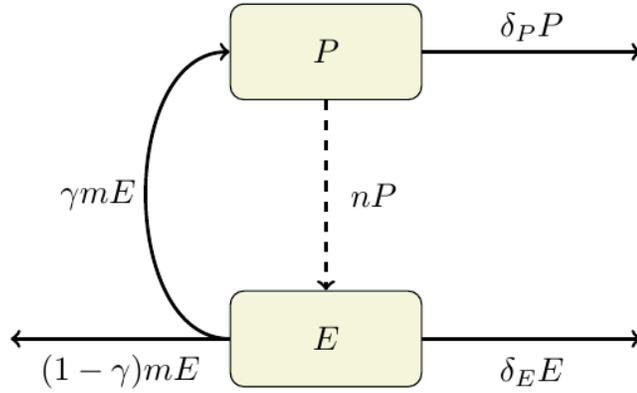


Figure 2: Flow Diagram of Framework Model

We may derive the following model:

$$\dot{P} = \gamma m E - \delta_P P$$

$$\dot{E} = n P - m E - \delta_E E$$

We may solve the system  $\dot{P} = \dot{E} = 0$  and determine that we have one fixed point:  $(0,0)$  which is stable for  $R_0 = \frac{\gamma mn}{\delta_P(m + \delta_E)} < 1$  and otherwise unstable. This means that  $R_0 > 1$  indicates that the population will persist in the environment and if  $R_0 < 1$  indicates that our population will die out; however, we know that a mosquito population can persist in the environment

without growing to infinity. We would like to see our model reflect more realistic population dynamics, so we will consider more limitations on the population.

Let  $k$  be the insecticide threshold, i.e. the size of the parous population that becomes too bothersome for the human population. If  $P > k$ , then the human population will administer insecticides to decrease the population. If  $P < k$ , then the mosquito population will be, for the most part, left alone. Consider the following model with a growth inhibiting term dependent on the current parous mosquito population:

$$\begin{aligned}\dot{P} &= \gamma m E \left(1 - \frac{P}{k}\right) - \delta_p P \\ \dot{E} &= nP - mE - \delta_E E\end{aligned}$$

This new term helps to regulate the parous population: now, the parous population will not grow to infinity and, subsequently, neither will the immature population. Consider the term  $\gamma m E \left(1 - \frac{P}{k}\right) = \gamma m E \left(\frac{k-P}{k}\right)$ . We may think of  $\frac{k-P}{k}$  to be the proportion of the acceptable population size that has not been yet occupied. At time  $t$ , there are  $\gamma m E$  new parous mosquitoes entering the parous population. We may think of  $\frac{\gamma m E P}{k}$  as individuals that will die due to administered insecticide.

## MATHEMATICAL ANALYSIS OF FRAMEWORK MODEL

We may solve the system  $\dot{P} = \dot{E} = 0$  and determine that our fixed points are the trivial equilibrium (TE)  $(0,0)$ , and the persistence equilibrium (PE),  $(P^*, E^*)$ :

$$(P^*, E^*) = \left( \frac{\gamma mnk - \delta_P k(m + \delta_E)}{\gamma mn}, \frac{\gamma mnk - \delta_P k(m + \delta_E)}{\gamma m(m + \delta_E)} \right)$$

**Theorem.** Let  $R_0 = \frac{\gamma mn}{\delta_P(m + \delta_E)}$ . If  $R_0 > 1$  then TE is unstable and there exists a stable positive equilibrium PE, which corresponds to a population that persists in the environment. If  $R_0 < 1$ , then TE is stable and PE does not exist in the feasible region, in which case the population will die out.

**Proof.** We wish to find a feasible, nontrivial equilibrium. We require that  $P^*, E^* > 0$  and clearly this is the case if  $R_0 = \frac{\gamma mn}{\delta_P(m + \delta_E)} > 1$ . Now, we may utilize the Jacobian matrix of our system to determine the stability of our equilibria.

$$J(P, E) = \begin{bmatrix} \frac{-\gamma m E}{k} - \delta_P & \gamma m \left(1 - \frac{P}{k}\right) \\ n & -(m + \delta_E) \end{bmatrix}$$

Now, consider TE:

$$J(0, 0) = \begin{bmatrix} -\delta_P & \gamma m \\ n & -(m + \delta_E) \end{bmatrix}$$

We see that we have a negative trace. We may solve for our determinant,  $\det(J(0,0)) = -\gamma mn + \delta_P(m + \delta_E)$  and find that clearly TE is stable for  $R_0 < 1$  and unstable for  $R_0 > 1$ .

Now we may evaluate the Jacobian matrix at PE:

$$J(P^*, E^*) = \begin{bmatrix} \frac{-\gamma m E^*}{k} - \delta_P & \gamma m \left(1 - \frac{P^*}{k}\right) \\ n & -(m + \delta_E) \end{bmatrix}$$

Clearly the trace of this matrix is negative. We only need to look at  $\det(J(P^*, E^*)) = \gamma mn - \delta_P(m + \delta_E)$  to determine the stability of PE. Clearly the PE is stable for  $R_0 > 1$  and unstable for  $R_0 < 1$ . ■

For the sake mathematical curiosity, we shall investigate the possibilities for the nontrivial equilibrium to exist in the remaining quadrants. Note that  $\dot{P} = \dot{E} = 0$  implies that  $E^* = \frac{nP^*}{m + \delta_E}$ . This implies that the populations are either both positive, both zero, or both negative. This tells us that the nontrivial equilibrium may only lie in quadrants I or III. As we have discussed,  $R_0 > 1$  implies that we have two equilibria: an unstable TE, and a stable PE corresponding to a population that persists in the environment. If it is the case that  $R_0 < 1$ , we would have a stable TE and an unstable PE which resides outside the feasible region (in quadrant III) corresponding to a population that will die out.

## INCORPORATING SEASONALITY TO OUR FRAMEWORK MODEL

Assume that the egg-laying rate of the parous population and the maturation rate of the immature population can be described by continuous, periodic function that have a period of one year. We now have that the egg-laying rate of parous mosquitoes is  $n(t)$  which is bounded by 0 and the optimal egg-laying rate,  $n$ , and the maturation rate of the immature population is  $m(t)$ , which is bounded by 0 and the optimal maturation rate,  $m$ .

We may incorporate both factors by considering the following model:

$$\begin{aligned}\dot{P} &= \gamma m(t) E \left(1 - \frac{P}{k}\right) - \delta_P P \\ \dot{E} &= n(t) P - m(t) E - \delta_E E\end{aligned}$$

By incorporating time dependence, it becomes much more difficult to analytically analyze the model and so we turn to simulations to understand what is going on. For sake of seeing how these time dependence terms affect the model, we will assume a hypothetical situation in which case the following functions can describe the egg-laying rate and maturation rate:

$$\begin{aligned}n(t) &= \frac{n_0}{2} \sin\left(\frac{2\pi t}{365}\right) + \frac{n_0}{2} \\ m(t) &= \frac{m_0}{2} \sin\left(\frac{2\pi t}{365}\right) + \frac{m_0}{2}\end{aligned}$$

Now we may run simulations on our model utilizing the parameter values that we have listed in Figure 3. We ran the simulations in MATLAB with initial populations  $P(0) = 3000$ ,

and  $E(0) = 120000$ . We decided to show the trajectories separately as the magnitude of the populations vary greatly. The population of the parous population over the time span of a year can be seen in Figure 4, and the immature population can be seen in Figure 5.

Parameter	Description	Value	Unit
$\gamma$	proportion of females	3/8	unitless
$m_0$	optimal per capita maturation rate	1/12	day <sup>-1</sup>
$n_0$	optimal per capita egg laying rate	25	day <sup>-1</sup>
$k$	insecticide threshold	30,000	individuals
$\delta_P$	$P$ death rate	1/17	day <sup>-1</sup>
$\delta_E$	$E$ death rate	0.02	day <sup>-1</sup>

Table 1: Seasonality Simulations Parameters

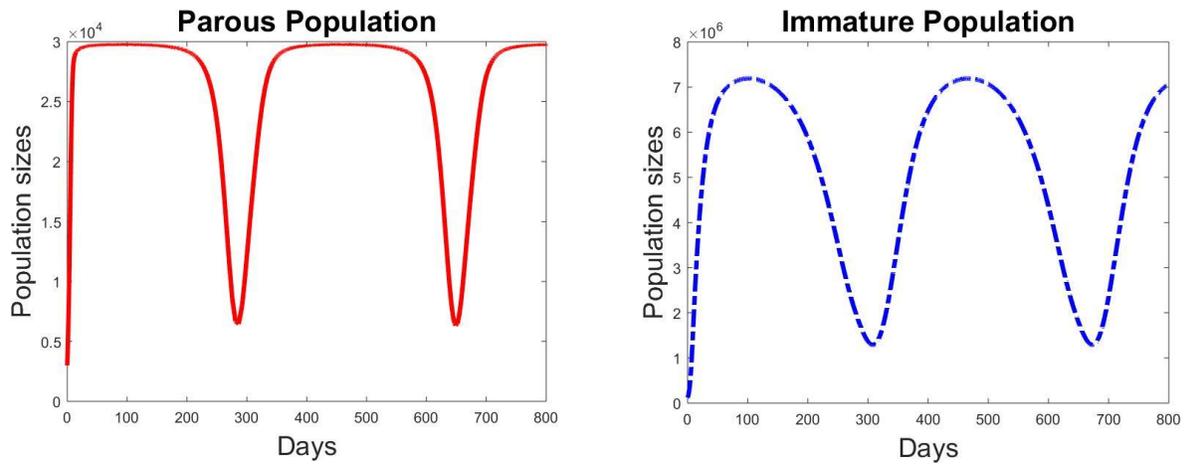


Figure 3: Seasonality Simulations

## INVESTIGATING THE SPREAD OF *WOLBACHIA*

We will modify the previous model by making it multi-group to consider both the infected and uninfected population as well as considering the effects of cytoplasmic incompatibility and some other factors which we will discuss soon. We consider two types of mosquito populations:  $P$  and  $E$ , the uninfected population and  $P_w$  and  $E_w$ , the *Wolbachia* infected population.

In the uninfected population, we want to account for some eggs not developing due to CI. Recall that  $\gamma$  is the proportion of females in the populations and hence  $\frac{1-\gamma}{\gamma}$  is the ratio of males to females and hence there are  $\frac{1-\gamma}{\gamma}P$  uninfected males in the population at a given time. Similarly, there are  $\frac{1-\gamma}{\gamma}P_w$  infected males at a given time. We will assume that males, whether infected or not, are equally successful in mating with a given female [7]. We assume that the proportion of eggs laid by uninfected females that will not hatch due to cytoplasmic incompatibility is equal to the proportion of infected males in the population. That is, only  $\frac{nP^2}{P+P_w}$  eggs will hatch.

We will consider  $k$  to be the insecticide threshold, as before. That is, if there are more than  $k$  parous mosquitoes, then insecticide will be applied to decrease the parous population. If there are less than  $k$  parous mosquitoes, the population won't be considered a bother to the human population and less insecticide will be administered. We will assume that infected and uninfected mosquitoes are indistinguishable to the human population. Hence, the human population desires that  $P + P_w < k$  for  $P_w$ , the infected parous population, and  $P$ , the uninfected

population. Now we have that  $\frac{k-P-P_w}{k}$  is the fraction of space left in the environment for new parous mosquitoes. We construct the following model:

$$\begin{aligned}\dot{P} &= m\gamma E \left(1 - \frac{P_w + P}{K}\right) - \delta_P P \\ \dot{E} &= \frac{nP^2}{P + P_w} - mE - \delta_E E \\ \dot{P}_w &= m\gamma E_w \left(1 - \frac{P_w + P}{K}\right) - \delta_{P_w} P_w \\ \dot{E}_w &= nP_w - mE_w - \delta_{E_w} E_w\end{aligned}$$

which is depicted in the following flow diagram:

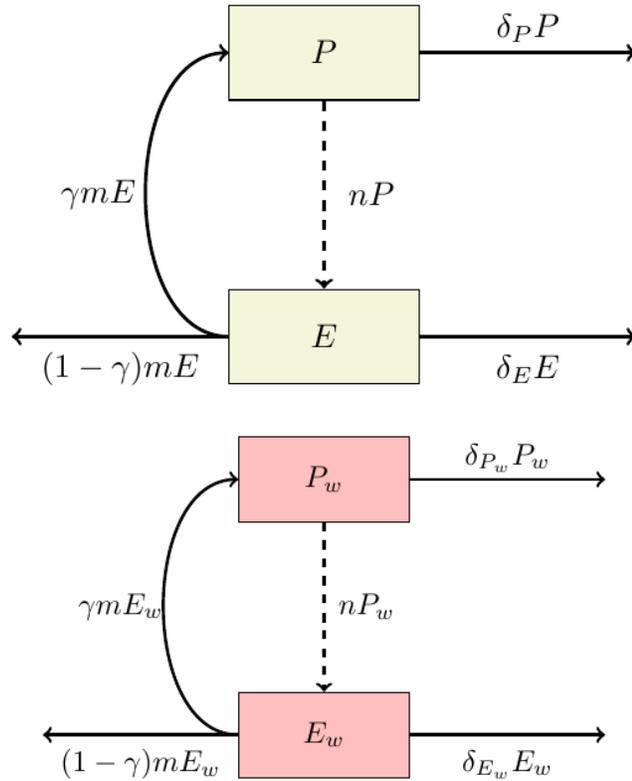


Figure 4: Flow Diagram of Wolbachia Model

We would like to define what a feasible population is and thus define the feasible region,  $\Omega$ , for our model. All populations must be nonnegative. We must have that the parous populations are less than the insecticide threshold  $k$ . Hence, we have that our feasible region is as follows:

$$\Omega = \begin{cases} P(t), E(t), P_w(t), E_w(t) \geq 0 \forall t \geq 0 \\ P(t) + P_w(t) \leq k \end{cases}$$

We will assume that all initial populations are within the feasible region and that this region is invariant; however in the future, we will need to prove this.

## MATHEMATICAL ANALYSIS OF THE *WOLBACHIA* MODEL

We may consider the following system to solve for the equilibria of the system:

$$\begin{aligned}\dot{P} &= m\gamma E \left(1 - \frac{P_w + P}{K}\right) - \delta_P P = 0 \\ \dot{E} &= \frac{nP^2}{P + P_w} - mE - \delta_E E = 0 \\ \dot{P}_w &= m\gamma E_w \left(1 - \frac{P_w + P}{K}\right) - \delta_{P_w} P_w = 0 \\ \dot{E}_w &= nP_w - mE_w - \delta_{E_w} E_w = 0\end{aligned}$$

We find three equilibria: the *Wolbachia*-free equilibrium (WFE), corresponding to an environment that is free of any infected mosquitoes  $(\hat{P}, \hat{E}, 0, 0)$ , the complete invasion equilibrium (CIE), corresponding to an environment that is composed of only infected mosquitoes  $(0, 0, \bar{P}_w, \bar{E}_w)$ , and a coexistence equilibrium, corresponding to an environment where both uninfected and infected populations may persist simultaneously  $(P^*, E^*, P_w^*, E_w^*)$ . Solving for these equilibria explicitly, we have:

$$\begin{aligned}(\hat{P}, \hat{E}, 0, 0) &= \left( \frac{k(\gamma mn - \delta_P(m + \delta_E))}{\gamma mn}, \frac{k(\gamma mn - \delta_P(m + \delta_E))}{\gamma m(m + \delta_E)}, 0, 0 \right) \\ (0, 0, \bar{P}_w, \bar{E}_w) &= \left( 0, 0, \frac{k(\gamma mn - \delta_{P_w}(m + \delta_{E_w}))}{\gamma mn}, \frac{k(\gamma mn - \delta_{P_w}(m + \delta_{E_w}))}{\gamma m(m + \delta_{E_w})} \right)\end{aligned}$$

We find  $(P^*, E^*, P_w^*, E_w^*)$  is such that:

$$\begin{aligned}
P^* &= \frac{2k\delta_P(m + \delta_E)^2 + k[(\delta_{P_w} + k\delta_P(m + \delta_E)) - kmn\gamma] - 2km\gamma n(m + \delta_{E_w})}{2mn\gamma(m + \delta_{E_w})} \\
E^* &= \frac{nP^{*2}}{(P^* + P_w^*)(m + \delta_{E_w})} \\
P_w^* &= \frac{k[\delta_{P_w}(m + \delta_E) + (m + \delta_{E_w})(k\delta_P(m + \delta_E) - kmn\gamma) - mn\gamma]}{2mn\gamma(m + \delta_{E_w})} \\
E_w^* &= \frac{nk[\delta_{P_w}(m + \delta_E) + (m + \delta_{E_w})(k\delta_P(m + \delta_E) - kmn\gamma) - mn\gamma]}{2mn\gamma(m + \delta_{E_w})^2}
\end{aligned}$$

Notice that there is a singularity for  $P = P_w = 0$  in our system as well as in our coexistence equilibria. For now, we will assume that it is never the case that  $P = P_w = 0$ .

We may determine the next generation number for the WFE,  $G_{Ou} = \frac{\gamma mn}{\delta_P(m + \delta_E)}$  by multiplying the average time spent in the immature stage  $\frac{1}{m + \delta_E}$ , the probability of the egg being female  $\gamma$ , the per capita developing rate  $m$ , and the average eggs laid before death  $\frac{n}{\delta_P}$ . This quantity reveals the average number of uninfected eggs produced by one uninfected egg [7]. Similarly, we may find the next generation number for the CIE,  $G_{Ow} = \frac{\gamma mn}{\delta_{P_w}(m + \delta_{E_w})}$ , in a similar fashion.

Necessarily, we require that the next generation number be greater than or equal to one for the population to be able to persist in the environment. We assume that  $G_{Ou} > 1$  [7].

We may use the next generation matrix method to solve for  $R_0$ . First, we let  $X$  be the *Wolbachia* infected subsystem. We let  $F$  be the matrix of new infections and  $V$  to be the matrix of transitions. We may write the following:

$$\begin{aligned}
\dot{X} &= \frac{d}{dt} \begin{bmatrix} P_w \\ E_w \end{bmatrix} = \begin{bmatrix} m\gamma E_w \left(1 - \frac{P_w+P}{K}\right) - \delta_{P_w} P_w \\ nP_w - mE_w - \delta_{E_w} E_w \end{bmatrix} \\
&= \begin{bmatrix} 0 \\ nP_w \end{bmatrix} - \begin{bmatrix} -m\gamma E_w \left(1 - \frac{P_w+P}{K}\right) + \delta_{P_w} P_w \\ (m + \delta_{E_w}) E_w \end{bmatrix} = F - V
\end{aligned}$$

We may determine the Jacobian matrices of  $F$  and  $V$ :

$$\begin{aligned}
J_F &:= \frac{\partial F}{\partial X} = \begin{bmatrix} 0 & 0 \\ n & 0 \end{bmatrix} \\
J_V &:= \frac{\partial V}{\partial X} = \begin{bmatrix} \frac{m\gamma E_w}{k} + \delta_{P_w} & -m\gamma \left(1 - \frac{P+P_w}{k}\right) \\ 0 & (m + \delta_{E_w}) \end{bmatrix}
\end{aligned}$$

We may solve for  $J_V^{-1}$  and then compute  $J_F J_V^{-1}$ :

$$\begin{aligned}
J_V^{-1} &= \begin{bmatrix} \frac{k}{m\gamma E_w + \delta_{P_w} k} & \frac{kmn\gamma}{(m + \delta_{E_w})(m\gamma E_w + \delta_{P_w} k)} \left(1 - \frac{P+P_w}{k}\right) \\ 0 & \frac{1}{m + \delta_{E_w}} \end{bmatrix} \\
J_F J_V^{-1} &= \begin{bmatrix} 0 & 0 \\ \frac{nk}{m\gamma E_w + \delta_{P_w} k} & \frac{kmn\gamma}{(m + \delta_{E_w})(m\gamma E_w + \delta_{P_w} k)} \left(1 - \frac{P+P_w}{k}\right) \end{bmatrix}
\end{aligned}$$

$R_0$  is the spectral radius or largest eigenvalue of  $J_F J_V^{-1}$ . We find that the spectral radius is

$$\rho(J_F J_V^{-1}) = \frac{kmn\gamma}{(m+\delta_{E_w})(m\gamma E_w + \delta_{P_w} k)} \left(1 - \frac{P+P_w}{k}\right) = \frac{\delta_P}{\delta_{P_w}}$$

after evaluating at the WFE and assuming that  $\delta_E = \delta_{E_w}$  [7].

**Theorem.** *There is a stable Wolbachia-free equilibrium,  $WFE \in \Omega$ , and a stable complete*

*invasion equilibrium,  $CIE \in \Omega$ , if  $G_{ou} = \frac{\gamma mn}{\delta_P(m+\delta_E)} > 1$ ,  $G_{ow} = \frac{\gamma mn}{\delta_{P_w}(m+\delta_{E_w})} > 1$ , and  $R_0 =$*

$$\frac{\delta_P}{\delta_{P_w}} < 1.$$

**Proof.** Assume that  $G_{ou} = \frac{\gamma mn}{\delta_P(m+\delta_E)} > 1$  and  $G_{ow} = \frac{\gamma mn}{\delta_{P_w}(m+\delta_{E_w})} > 1$ . Clearly, the WFE and the

CIE are feasible. If  $R_0 < 1$ , it must be the case that the WFE is stable. We may determine the

stability of the CIE by looking at the Jacobian matrix of the system evaluated at the CIE:

$$J(0, 0, P_w, E_w) = \begin{bmatrix} -\delta_P & \gamma m \left(1 - \frac{P_w}{k}\right) & 0 & 0 \\ 0 & -(m + \delta_E) & 0 & 0 \\ -\frac{\gamma m E_w}{k} & 0 & -\frac{\gamma m E_w}{k} - \delta_{P_w} & \gamma m \left(1 - \frac{P_w}{k}\right) \\ 0 & 0 & n & -(m + \delta_E) \end{bmatrix}$$

The eigenvalues of  $J(0, 0, P_w, E_w)$  are equal to the eigenvalues of the following matrices:

$$A = \begin{bmatrix} -\delta_P & \gamma m \left(1 - \frac{\bar{P}_w}{k}\right) \\ 0 & -(m + \delta_E) \end{bmatrix}$$

$$B = \begin{bmatrix} -\frac{\gamma m \bar{E}_w}{k} - \delta_{P_w} & \gamma m \left(1 - \frac{\bar{P}_w}{k}\right) \\ n & -(m + \delta_E) \end{bmatrix} = \begin{bmatrix} \frac{-\gamma mn}{(m + \delta_{E_w})} & \frac{\delta_{P_w}(m + \delta_{E_w})}{n} \\ n & -(m + \delta_E) \end{bmatrix}$$

Clearly, the eigenvalues of  $A$  are negative. We may determine the sign of the eigenvalues of  $B$  by looking at the trace and determinant of  $B$ . If we can find that the trace is negative and the determinant is positive, then we may conclude that  $B$  has both negative eigenvalues. Clearly, the trace is negative. We may look at the determinant and see that  $\text{DET}(B) = \gamma mn -$

$\delta_{P_w}(m + \delta_E) > 0$  given that  $G_{ow} = \frac{\gamma mn}{\delta_{P_w}(m + \delta_{E_w})} > 1$ . We have shown that the CIE is stable. ■

**Conjecture.** *The coexistence equilibria of the system is feasible and unstable if  $G_{ou} =$*

$$\frac{\gamma mn}{\delta_P(m + \delta_E)} > 1, G_{ow} = \frac{\gamma mn}{\delta_{P_w}(m + \delta_{E_w})} > 1, \text{ and } R_0 = \frac{\delta_P}{\delta_{P_w}} < 1$$

We have not yet proven this conjecture.

## SIMULATIONS OF THE *WOLBACHIA* MODEL

We assume that the egg-laying rate and maturation rates of the infected and uninfected populations are identical. We consider an insecticide threshold of  $k = 30,000$  for these simulations. We assume that  $\delta_E = \delta_{E_w}$  and  $\delta_{P_w} = \frac{1}{15.8}$  [7]. We will use the parameter values in the following table. For our simulations, we will consider an established natural mosquito population with  $P(0) = 30,000$  and  $E(0) = 7,000,000$ .

Parameter	Description	Value	Unit
$\gamma$	proportion of females	3/8	unitless
$m$	per capita maturation rate	1/12	day <sup>-1</sup>
$n$	per capita egg laying rate	25	day <sup>-1</sup>
$k$	insecticide threshold	30,000	individuals
$\delta_P$	$P$ death rate	1/17	day <sup>-1</sup>
$\delta_E$	$E$ death rate	0.02	day <sup>-1</sup>
$\delta_{P_w}$	$P_w$ death rate	1/15.8	day <sup>-1</sup>
$\delta_{E_w}$	$E_w$ death rate	0.02	day <sup>-1</sup>

*Table 2: Wolbachia Simulations Parameters*

In the following simulations, it is the case that  $G_{ou} > 1$ ,  $G_{ow} > 1$ , and  $R_0 > 1$ . In this case, we have proven that we have two stable equilibria: a *Wolbachia*-free equilibrium and a complete invasion equilibrium. In the following figures, we only plot the population sizes of the parous populations for the sake of simplicity and clarity. In figure 6, we introduce 1,000 *Wolbachia* infected and see that our trajectories approach the stable WFE. This demonstrates how the *Wolbachia* infected population will die out if too small of a cohort is introduced. In figure 7, we

introduce 5,000 *Wolbachia* infected and see a completely different picture. The introduction of a large enough cohort of infected mosquitoes will result in the complete invasion of the natural population.

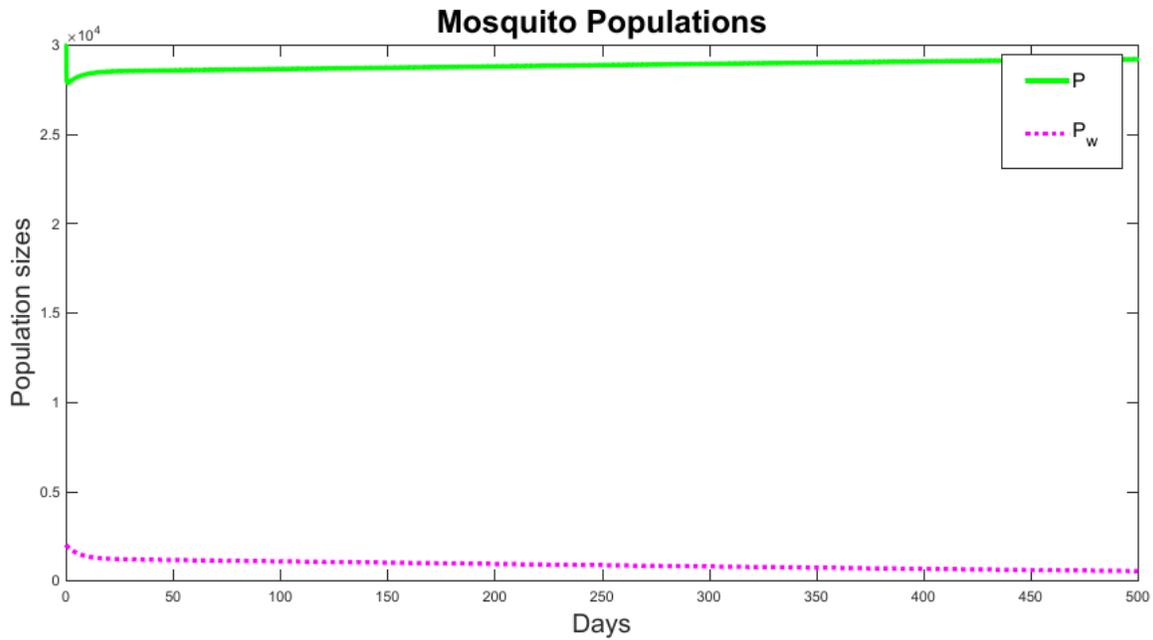


Figure 5: *Wolbachia* Simulations,  $P_w(t) = 1000$  and  $E(t) = 0$

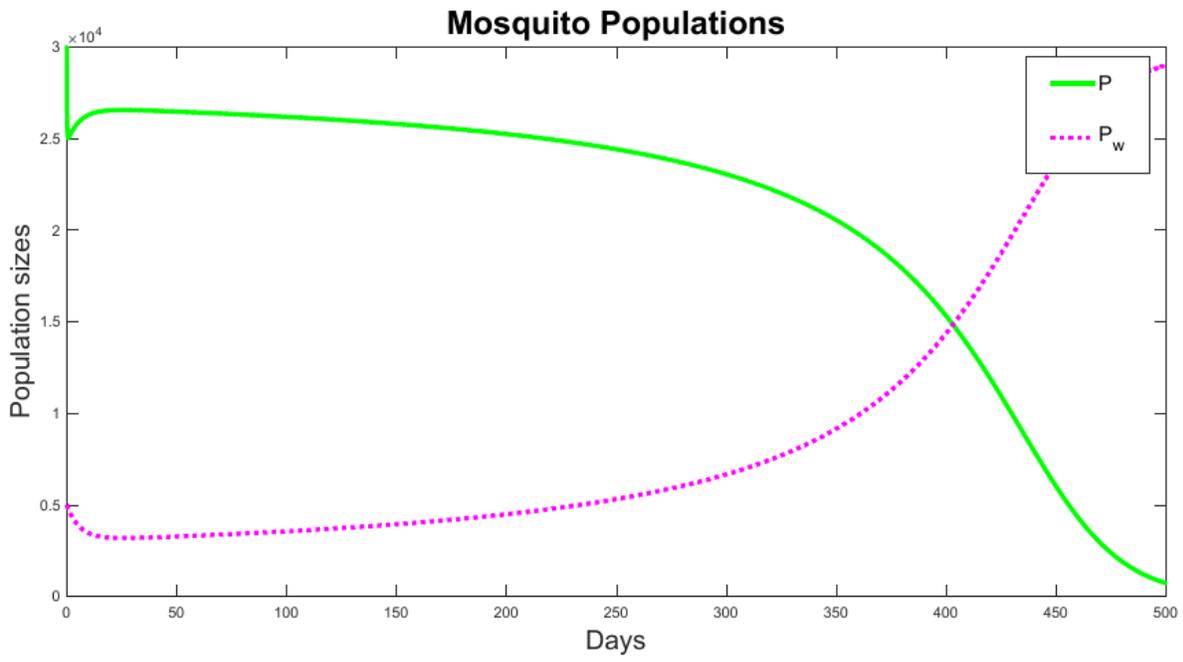


Figure 6: Wolbachia Simulations,  $P_w(t) = 5000$  and  $E_w(t) = 0$

## DISCUSSION AND FUTURE WORK

We have developed a framework mosquito population model that describes the population dynamics of a mosquito population and we have shown how seasonality can be incorporated and analyzed using simulations. For the framework model, we evaluated the dynamics by finding equilibria and determining their local stability. We discovered that a mosquito population will persist in the environment if and only if  $R_0 = \frac{\gamma mn}{\delta_P(m + \delta_E)} > 1$ . Otherwise, the population will die out. In the future, we would like to determine the global stability of this model.

We have created a model to describe the effects of the introduction of a *Wolbachia* infected population and have seen that in a biologically feasible situation, depending on the initial populations, the *Wolbachia* infected population may die out or completely invade the natural population. We have determined critical values, such as  $R_0$  and the next generation numbers which we use to interpret our results. We have shown the existence of the stable WFE and the stable CIE under the conditions that  $G_{ou} > 1$ ,  $G_{ow} > 1$ , and  $R_0 > 1$ . In the future, we wish to prove our conjecture regarding the coexistence equilibria. We have defined a feasible region  $\Omega$  which we would like to prove is invariant. We would also like to investigate the spacial spread of a *Wolbachia* invasion. In our model, we assume a constant sex ratio which greatly limits the variability of the types of releases of *Wolbachia* infected mosquitoes. We also assume that there is perfect maternal vertical transmission of *Wolbachia*. In other research, incorporating imperfect maternal transmission yields more interesting dynamics and we would like to see the results of incorporating imperfect vertical transmission into our model [7].

## APPENDIX

The following MATLAB code was used to run the simulations in Figures # and #.

```
%Defining Parameters:

m = 1/12; %maturation rate (egg -> parous)

n = 25; %egg-laying rate

gamma = 3/8; %ratio of females/population

K = 30000; %insecticide threshold of parous population

d_P = 1/17; %natural death rate of parous

d_E = 0.02; %natural death rate of immature stages

d_P_w = 1/15.8; %natural death rate of infected parous

d_E_w = 0.02; %natural death rate of infected immature stages

%equations:

% P'(t) = x1, E'(t)=x2, P_w'(t) = x3, E_w'(t)=x4

f = @(t,x) [m*gamma*x(2)*(1-(x(3)+x(1))/K) - d_P*x(1);

n*x(1)*x(1)/(x(1)+x(3))-m*x(2)-d_E*x(2);

m*gamma*x(4)*(1-(x(3)+x(1))/K) - d_P_w*x(3);
```

```
n*x(3)-m*x(4)-d_E_w*x(4)];
```

```
%Solving the ODE system
```

```
[t,xa]=ode45(f,[0 1000], [300000 70000000 0 0]);
```

```
%Plotting the trajectories
```

```
plot(t,xa(:,1),'-r', 'linewidth', 2)%plot P(t)
```

```
hold on
```

```
plot(t,xa(:,2),'-b', 'linewidth', 2)%plot E(t)
```

```
plot(t,xa(:,3),'-m', 'linewidth', 2)%plot P_w(t)
```

```
plot(t,xa(:,4),'-y', 'linewidth', 2)%plot E_w(t)
```

```
title('Mosquito Population with Some Insecicide Usage')
```

```
xlabel('Days')
```

```
ylabel('Population sizes')
```

```
legend('P', 'I', 'P_w','I_W')
```

```
hold off
```

The following MATLAB code is used to run the simulations in Figure #:

```
%Defining Parameters:
```

```
m = 1/12; %maturation rate (egg -> parous)
```

```
n = 25; %egg-laying rate
```

```
gamma = 3/8; %ratio of females/population
```

```
K = 30000; %insecticide threshold of parous population
```

```
d_P = 1/17; %natural death rate of parous
```

```
d_E = 0.020; %natural death rate of immature stages
```

```
%equations:
```

```
% P'(t) = x1, E'(t)=x2
```

```
f = @(t,x) [(m/2*sin(2*pi*t/365)+m/2)*gamma*x(2)*(1-x(1)/K)
```

```
- d_P*x(1);
```

```
(n/2*sin(2*pi*t/365)+n/2)*x(1)-(m/2*sin(2*pi*t/365)+m/2)*x(2)
```

```
-d_E*x(2)];
```

```
[t,xa]=ode45(f,[0 800], [3000 120000]);

%use either P(t) or E(t)

%plot(t,xa(:,1),'-r', 'linewidth', 2)%plot P(t)

plot(t,xa(:,2),'-b', 'linewidth', 2)%plot E(t)

title('Seasonal Mosquito Population')

xlabel('Days')

ylabel('Population sizes')

legend('E')

hold on
```

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