

## MODELING THE DYNAMICS OF *WOLBACHIA*-INFECTED AND UNINFECTED *Aedes aegypti* POPULATIONS BY DELAY DIFFERENTIAL EQUATIONS

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**Abstract.** Starting from an age structured partial differential model, constructed taking into account the mosquito life cycle and the main features of the *Wolbachia*-infection, we derived a delay differential model using the method of characteristics, to study the colonization and persistence of the *Wolbachia*-transinfected *Aedes aegypti* mosquito in an environment where the uninfected wild mosquito population is already established. Under some conditions, the model can be reduced to a Nicholson-type delay differential system; here, the delay represents the duration of mosquito immature phase that comprises egg, larva and pupa. In addition to mortality and oviposition rates characteristic of the life cycle of the mosquito, other biological features such as cytoplasmic incompatibility, bacterial inheritance, and deviation on sex ratio are considered in the model. The model presents three equilibriums: the extinction of both populations, the extinction of *Wolbachia*-infected population and persistence of uninfected one, and the coexistence. The conditions of existence for each equilibrium are obtained analytically and have been interpreted biologically. It is shown that the increase of the delay can promote, through Hopf bifurcation, stability switch towards instability for the nonzero equilibriums. Overall, when the delay increases and crosses predetermined thresholds, the populations go to extinction.

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### 1. INTRODUCTION

*Aedes aegypti* is a widespread human blood-feeding mosquito responsible for the transmission of several arboviruses including Dengue, Yellow fever, Zika, Murray Valley, La Crosse, Chikungunya and Rift Valley fever. For most of these diseases an efficient vaccine is not available and the reduction of mosquito population still be the only way to prevent epidemics [17]. The traditional approach to diminishing the mosquito population includes the reduction of breeding sites and the use of larvicides and pesticides for adults. In general, mechanical control and the application of larvicides are carried out before the period favorable to the proliferation of mosquitoes, while pesticides for adults are applied during epidemics when the number of infected humans is high [41]. Environmentally-friendly techniques include the use of sterile males (SIT) [8, 16] and *Wolbachia*-infected mosquitoes [7, 15]. While the first one focus on the reduction of mosquito population to halt disease

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transmission, the second one aims to replace the wild population for an infected one that is not able to transmit the virus. Both require the release of a large number of mosquitoes, hence a combination between traditional and new technologies are encouraged [33].

The intracellular bacteria of the genus *Wolbachia* manipulates host reproductive systems to increase its transmission by inducing parthenogenesis, feminization, male-killing or cytoplasmic incompatibility (CI) [2, 37]. Additionally, the bacteria is transmitted vertically from mother to its offspring. Put together, these characteristics confer a fitness advantage over uninfected population that can drive the *Wolbachia*-infected population to fixation [20, 24]. The same is not true for the SIT, since the mating with sterile mosquitoes does not produce viable offspring; they must therefore be introduced periodically.

In field, the *Wolbachia* strains that have been used in releases come from *Drosophila melanogaster*, wMel and wMelPop, and from *Aedes albipicus*, wAlbB. Artificial infections with new strains of bacteria still be done in laboratory in order to increase technique factibility. This is because recent research has shown that biotics and abiotics factors can influence *Wolbachia* densities and its distribution in mosquito tissue, and if the thresholds related to heritability and cytoplasmic incompatibility cannot be achieved the technique efficacy is lost [9, 35, 37]. The thermal sensitivity of *Wolbachia*-infection is variable and can differ considerably between host species and strains. High temperatures might reduce its density in hosts, weaken the reproductive effects induced by *Wolbachia*-infection and even eradicate *Wolbachia* completely. In *Ae. aegypti*, the wAlbB infection type is more stable than wMel and wMelPop at high temperatures [35].

Moreover, for poikilothermic species such as the *Aedes aegypti* mosquito, the body temperature depends on external factors and has strong effects over its entomological parameters and behavior. The lower and upper developmental threshold are 16 °C and 34 °C, being the development time shorter at higher temperatures [34]. Also, the survival of immatures and adults may be negatively influenced by large diurnal temperature range since their mortality rates present U-shaped forms [42]. The oviposition rate in turn increases quasi-linearly with temperature increasing [42]. Both flight activity and mating rate were detected to increase with temperature ranging from 18 °C to 31 °C [11]. Moreover, it was found that the length of the gonotrophic cycle was reduced with increasing mean temperatures. Besides, wing beat frequency, blood-feeding, biting activity, host seek among other behavior characters are significantly affected by temperature variation [34].

A lot of mathematical models have been addressing the use of *Wolbachia*-infected mosquitoes to control Dengue (and other viruses) transmission, because the presence of the bacteria reduces vector competence [28, 31, 32]. In [14], a sex-structured model taking into account cytoplasmic incompatibility, male killing, incomplete maternal transmission, and different mortality rates for uninfected/infected population was developed. The boundedness of population was provided by considering competition among females for nesting places which give an upper limit for egg-laying rate. The ordinary differential model was studied analytically, and it was shown that the steady state where the *Wolbachia*-infected individuals dominate the population is possible when the maternal transmission is complete and cytoplasmic incompatibility is high. Coexistence of *Wolbachia*-infected and uninfected mosquito and *Wolbachia*-free equilibrium are found for a large set of relevant biological parameters. By considering that density-dependent death rate controls the exponential growth of populations [27], showed that only when the initial level of infection (given by the percentage of *Wolbachia*-infected population), breaks some critical thresholds that the infection takes off from the population (*i.e.* the threshold for invasion is achieved). In [31], the aquatic stage was also included and population boundedness was guaranteed by considering a logistic carrying capacity on this phase. It was shown that *Wolbachia*-infected mosquitoes always dominate the population provided they persist. The same approach was done in [29] and the existence of a minimum infection frequency above which *Wolbachia* could spread into the whole population of mosquitoes was explored. All of these mathematical models used ordinary differential equations to model the temporal dynamics of the mosquito population.

In turn, partial differential equations (PDE) are much less explored. Some studies such as [19, 21] present reaction-diffusion models for the *Wolbachia*-infected and uninfected populations. They concluded that there is no spatial influence on the stability criteria for the steady states. Moreover [21], focused on determining the threshold for invasion of the wild population by the *Wolbachia*-infected one. Further [13], compares the stability

results of the equilibriums obtained for an age-structured (PDE) with the one of an unstructured (ODE) model. For simplicity, two asexual population were considered, uninfected and *Wolbachia*-infected one.

Finally, rarer is the use of delay differential equations (DDE) for such problem. In [22], a DDE phase-structured model (larva and adult populations) evaluated the suppression of the wild population of *Aedes* mosquitoes by releasing a continuous constant number of *Wolbachia*-infected male. This is modeled by changing the growing rate of the population. The model considered two delays, one representing the average time from adult emergence to the hatching of the first larval stage (which determines larva population growth), and the other the average time from the first larval stage to adult emergence (which models adult population growth). Also, a strong density-dependent death rate was considered in the larval stage. They concluded that the delays do not impact population suppression. A modification of this model was proposed in [23] to compare two opposite phenomena which are the decrease on mating competitiveness of the released males relative to the wild males and the fitness advantage given by the cytoplasmic incompatibility probability to the *Wolbachia*-infected population over the wild one. The model considers only adult population and the delay gives the contribution of the last generation to the growth of the new population. They showed that CI plays a more important role in the suppression of *Aedes* population.

Here, starting from an age structured PDE model that considers the mosquito entomological parameters and also biological features associated to *Wolbachia* infection, a new two-population DDE model is obtained and carefully assessed. Analytical results such as positiveness, boundedness, and uniqueness of solutions are provided. Thresholds for existence and stability of the steady states were obtained and interpreted in the context of population fitness. The role played by the delay on the insect temporal dynamics can help to understanding the effect of changing on abiotic factors such as the temperature on the long-run behavior of this population. The model appears for the first time in [15] where numerical results concerning population dynamics were obtained.

## 2. AGE STRUCTURED PARTIAL DIFFERENTIAL MODEL

Let  $w$  and  $u$  be *Wolbachia*-infected and uninfected mosquito status. We denote  $f_j := f_j(t, a)$ , with  $j \in \{w, u\}$  the female population density of mosquito,  $a \in [0, \tau)$  the physiological age of the immature phase including egg, larva and pupa,  $a \geq \tau$  the physiological age of the mature phase (fertile adults),  $t$  the calendar time,  $\mu_w$  and  $\mu_u$  the adult mortality rates, and  $\mu$  the immature mortality rate. We assume that the parameters  $\tau$  and  $\mu$  are the same for infected and uninfected mosquitoes [31]. The temporal evolution of mosquito population satisfies the following age-structured Lotka-McKendrick system

$$\frac{\partial f_j}{\partial t} + \frac{\partial f_j}{\partial a} = -\kappa_j(a)f_j, \quad j \in \{w, u\}, \quad (2.1)$$

where

$$\kappa_j(a) = \begin{cases} \mu, & a \in [0, \tau), \\ \mu_j, & a \geq \tau. \end{cases}$$

The *Wolbachia* bacteria is transmitted from mother to its offspring with probability  $\xi_w \in (0, 1)$ . Thus, with probability

$$\xi_u := 1 - \xi_w \quad (2.2)$$

an infected female can produce uninfected offspring. The mating probability between an uninfected female and an infected male is denoted by  $\nu \in (0, 1)$  and the probability of cytoplasmic incompatibility occurrence is  $q \in (0, 1)$ . This means that the fraction of matings between uninfected females and infected males that produce viable eggs is given by  $1 - q\nu$ . The average birth rates are  $\phi_w > 0$ ,  $\phi_u > 0$  with the average percentage of female

births  $r_w, r_u \in (0, 1)$ . We denote by

$$F_j(t) = \int_{\tau}^{+\infty} f_j(t, a) da, \quad j \in \{w, u\}, \quad (2.3)$$

the total population of infected and uninfected adult females, respectively. Therefore, the newborn individuals introduced into the population are given at  $a = 0$  by

$$\begin{aligned} f_w(t, 0) &= \xi_w r_w \phi_w F_w(t) G(F_w(t), F_u(t)), \\ f_u(t, 0) &= [(1 - q\nu)r_u \phi_u F_u(t) + \xi_u r_w \phi_w F_w(t)] G(F_w(t), F_u(t)), \end{aligned} \quad (2.4)$$

where  $G(X, Y) = e^{-\alpha(E_w X + E_u Y)^\eta}$  measures competition among individuals. More precisely, to take into account the competition between mosquitoes for oviposition sites, the number of eggs per female is multiplied by the density-dependent factor  $G(F_w(t), F_u(t))$ . The parameters  $\alpha > 0$  and  $\eta > 0$  are, respectively, the environmental carrying capacity and the measurement of how rapidly it is achieved [12]. The parameters  $E_w$  and  $E_u$  take into account the different behaviors between infected and uninfected females. In addition, the populations are assumed to satisfy

$$\lim_{a \rightarrow +\infty} f_j(t, a) = 0, \quad j \in \{w, u\}, \quad t > 0. \quad (2.5)$$

The initial age-distribution  $f_j(0, a)$ ,  $j \in \{w, u\}$ , is assumed to be known. Finally, as we are assuming that the mating between male and female is given by a constant parameter  $\nu$ , we do not need to explicitly model the male population, and we will omit it from the analysis.

### 3. REDUCTION TO A DELAY DIFFERENTIAL SYSTEM

Henceforth, we reduce the system (2.1)–(2.5) to delay differential equations. We denote by

$$F_j^i(t) = \int_0^{\tau} f_j(t, a) da, \quad j \in \{w, u\}, \quad (3.1)$$

the total population of immature females, *Wolbachia*-infected and uninfected, respectively. By integrating the system (2.1) over the age variable from 0 to  $\tau$  and from  $\tau$  to  $+\infty$ , respectively, we get for  $j \in \{w, u\}$ ,

$$\begin{cases} \frac{d}{dt} F_j^i(t) = -\mu F_j^i(t) + f_j(t, 0) - f_j(t, \tau), \\ \frac{d}{dt} F_j(t) = -\mu_j F_j(t) + f_j(t, \tau), \end{cases}$$

where  $F_j$  is given by (2.3) and  $F_j^i$  by (3.1). On the other hand, the method of characteristics (see [36]) implies that

$$f_j(t, \tau) = \begin{cases} f_j(0, \tau - t)e^{-\mu t}, & 0 \leq t \leq \tau, \\ f_j(t - \tau, 0)e^{-\mu\tau}, & t > \tau. \end{cases}$$

As we are interested on the asymptotic behavior of the population, we can assume that  $t$  is large enough such that  $t > \tau$ . Then,

$$f_j(t, \tau) = f_j(t - \tau, 0)e^{-\mu\tau}, \quad j \in \{w, u\}.$$

By adding the boundary conditions (2.4), we get the following delay differential system

$$\left\{ \begin{array}{l} \frac{d}{dt} F_w^i(t) = -\mu F_w^i(t) + \xi_w r_w \phi_w F_w(t) G(F_w(t), F_u(t)) \\ \quad - e^{-\mu\tau} \xi_w r_w \phi_w F_w(t-\tau) G(F_w(t-\tau), F_u(t-\tau)), \\ \frac{d}{dt} F_w(t) = -\mu_w F_w(t) + e^{-\mu\tau} \xi_w r_w \phi_w G(F_w(t-\tau), F_u(t-\tau)) F_w(t-\tau), \\ \frac{d}{dt} F_u^i(t) = -\mu F_u^i(t) + [(1-q\nu)r_u \phi_u F_u(t) + (1-\xi)r_w \phi_w F_w(t)] \\ \quad \times G(F_w(t), F_u(t)) \\ \quad - e^{-\mu\tau} [(1-q\nu)r_u \phi_u F_u(t-\tau) + \xi_u r_w \phi_w F_w(t-\tau)] \\ \quad \times G(F_w(t-\tau), F_u(t-\tau)), \\ \frac{d}{dt} F_u(t) = -\mu_u F_u(t) + e^{-\mu\tau} [(1-q\nu)r_u \phi_u F_u(t-\tau) + \xi_u r_w \phi_w F_w(t-\tau)] \\ \quad \times G(F_w(t-\tau), F_u(t-\tau)), \end{array} \right.$$

where  $F_j^i$ ,  $F_j$ ,  $j \in \{w, u\}$ , are the total population of immature and adult females, *Wolbachia*-infected and uninfected, respectively. We can see that the equations of mature population  $F_j$  are independent on the equations of immature one  $F_j^i$ . Then, we will omit the system of  $F_j^i$  and concentrate only on  $F_j$ . Remembering that the nonlinear function  $G$  is given by

$$G(X, Y) = e^{-\alpha(E_w X + E_u Y)^\eta},$$

we carry out the transformations

$$w(t) := \alpha^{\frac{1}{\eta}} E_w F_w(t), \quad u(t) := \alpha^{\frac{1}{\eta}} E_u F_u(t),$$

and we define the new parameters

$$P_w := \xi_w r_w \phi_w, \quad P_u := (1-q\nu)r_u \phi_u \quad \text{and} \quad P_{wu} := \xi_u r_w \phi_w; \quad (3.2)$$

respectively, the number of infected eggs per time per infected individual that will hatch, the number of uninfected eggs per time per uninfected individual that will hatch, and the number of uninfected eggs per time per infected individual that will hatch.

Then, the model can be reduced, for  $t > \tau$ , to

$$\left\{ \begin{array}{l} \frac{d}{dt} w(t) = -\mu_w w(t) + e^{-\mu\tau} P_w w(t-\tau) e^{-(w(t-\tau)+u(t-\tau))^\eta}, \\ \frac{d}{dt} u(t) = -\mu_u u(t) + e^{-\mu\tau} [P_u u(t-\tau) + P_{wu} w(t-\tau)] e^{-(w(t-\tau)+u(t-\tau))^\eta}, \end{array} \right. \quad (3.3)$$

with initial conditions given by

$$(w(t), u(t)) = (\bar{\Psi}_w(t), \bar{\Psi}_u(t)), \quad t \in [0, \tau]. \quad (3.4)$$

We make a translation in time so as to define the system (3.3) on the interval  $[0, +\infty)$  and the initial conditions (3.4) on the interval  $[-\tau, 0]$ .

**Remark 3.1.** If we consider the case

$$\mu_w = \mu_u := \delta, \quad P_w + P_{wu} = P_u \quad \text{and} \quad \eta = 1,$$

then, we obtain the famous Nicholson's blowflies equation

$$N'(t) = -\delta N(t) + pN(t - \tau)e^{-N(t-\tau)}, \quad (3.5)$$

where  $N = w + u$  and  $p = P_u e^{-\mu\tau}$ . The equation (3.5) has been extensively studied in the literature [5, 6, 10]. The main results on equation (3.5) deal with the global attractivity of the positive steady state and the existence of oscillatory solutions (see [6]).

#### 4. POSITIVITY AND BOUNDEDNESS OF SOLUTIONS

The positivity and boundedness of solutions are important in biological models. We first establish an existence and uniqueness theorem about the positive solution for the nonlinear delay differential system (3.3)–(3.4).

**Theorem 4.1.** *For any nonnegative continuous initial function  $(\bar{\Psi}_w, \bar{\Psi}_u)$  on  $[-\tau, 0]$ , there is a unique nonnegative global solution  $(w, u)$  of the problem (3.3)–(3.4). Furthermore,  $t \mapsto (w(t), u(t))$  is such that  $w(t) > 0$ ,  $u(t) > 0$ , for  $t \geq 0$  provided that  $\bar{\Psi}_w(t) \geq 0$ ,  $\bar{\Psi}_u(t) \geq 0$ , for all  $t \in [-\tau, 0)$  and  $\bar{\Psi}_w(0) > 0$ ,  $\bar{\Psi}_u(0) > 0$ .*

*Proof.* It follows from the standard existence theorem [26], that there exists a unique local solution  $(w, u)$  of the problem (3.3)–(3.4), defined on an interval  $[-\tau, t_0)$ ,  $t_0 > 0$ . By steps, suppose that  $t \in [0, \tau]$ . Then,  $t - \tau \in [-\tau, 0]$ , and using the variation of constants formula for the system (3.3)–(3.4), we obtain for  $t \in [0, \tau]$ ,

$$w(t) = \bar{\Psi}_w(0)e^{-\mu_w t} + P_w e^{-\mu\tau} e^{-\mu_w t} \int_0^t \bar{\Psi}_w(s - \tau) e^{-(\bar{\Psi}_w(s-\tau) + \bar{\Psi}_u(s-\tau))^\eta} e^{\mu_w s} ds \quad (4.1)$$

and

$$u(t) = \bar{\Psi}_u(0)e^{-\mu_u t} + e^{-\mu\tau} e^{-\mu_u t} \int_0^t [P_u \bar{\Psi}_u(s - \tau) + P_{wu} \bar{\Psi}_w(s - \tau)] \times e^{-(\bar{\Psi}_w(s-\tau) + \bar{\Psi}_u(s-\tau))^\eta} e^{\mu_u s} ds. \quad (4.2)$$

Then, for a nonnegative initial condition  $(\bar{\Psi}_w, \bar{\Psi}_u)$  on  $[-\tau, 0]$ , we have a nonnegative solution  $(w, u)$  on  $[0, \tau]$ . Through the method of steps, we have  $w(t) \geq 0$ ,  $u(t) \geq 0$  on  $[\tau, 2\tau]$ ,  $[2\tau, 3\tau]$ , and so on. Thus,  $w(t) \geq 0$ ,  $u(t) \geq 0$  for all  $t \in [0, t_0)$ . We suppose by contradiction that  $(w, u)$  exists only on an interval  $[-\tau, t_0)$  with  $0 < t_0 < \infty$ . Let

$$y(t) = w(t) + u(t), \quad t \in [-\tau, t_0).$$

Then,  $\lim_{t \rightarrow t_0^-} y(t) = +\infty$ . We define the constant  $M = e^{-\mu\tau} \max\{P_u, P_w + P_{wu}\}$  and the function  $g(x) = xe^{-x^\eta}$ . We have

$$\max_{x \geq 0} g(x) = g\left(\left(\frac{1}{\eta}\right)^{\frac{1}{\eta}}\right) = \left(\frac{1}{\eta e}\right)^{\frac{1}{\eta}}.$$

Then, from the system (3.3), we can write the following estimation

$$\begin{aligned} \frac{d}{dt}y(t) &= -\mu_w w(t) - \mu_u u(t) \\ &\quad + e^{-\mu\tau} [P_u u(t-\tau) + (P_w + P_{wu})w(t-\tau)] e^{-(w(t-\tau)+u(t-\tau))^\eta}, \\ &\leq -\min\{\mu_w, \mu_u\}y(t) + M \left( \frac{1}{\eta e} \right)^{\frac{1}{\eta}}. \end{aligned}$$

Hence,  $y$  is bounded on the interval  $[-\tau, t_0)$ . This gives a contradiction and proves that the problem (3.3)–(3.4) has a global solution on the interval  $[-\tau, +\infty)$ . Now, we assume that  $\bar{\Psi}_w, \bar{\Psi}_u \geq 0$  on  $[-\tau, 0)$  and  $\bar{\Psi}_w(0), \bar{\Psi}_u(0) > 0$ . Using the variation of constants formulas (4.1)–(4.2), we get  $w(t), u(t) > 0$ , for all  $t \in [0, \tau]$ . By steps, we prove that  $w(t), u(t) > 0$ , for all  $t \geq 0$ .  $\square$

**Proposition 4.2.** *The solution  $(w, u)$  of the system (3.3)–(3.4) is bounded on the interval  $[0, +\infty)$ , with*

$$\limsup_{t \rightarrow +\infty} w(t) \leq \frac{P_w e^{-\mu\tau}}{\mu_w} \left( \frac{1}{\eta e} \right)^{\frac{1}{\eta}}, \quad \limsup_{t \rightarrow +\infty} u(t) \leq \frac{(P_u + P_{wu}) e^{-\mu\tau}}{\mu_u} \left( \frac{1}{\eta e} \right)^{\frac{1}{\eta}}.$$

*Proof.* Let  $f(x) = P_w e^{-\mu\tau} g(x)$ , for  $x \geq 0$ . We have

$$\max_{x \geq 0} f(x) = P_w e^{-\mu\tau} g \left( \left( \frac{1}{\eta} \right)^{\frac{1}{\eta}} \right) = P_w e^{-\mu\tau} \left( \frac{1}{\eta e} \right)^{\frac{1}{\eta}}.$$

Then, from (3.3) we obtain

$$\frac{d}{dt}w(t) \leq -\mu_w w(t) + P_w e^{-\mu\tau} w(t-\tau) e^{-w(t-\tau)^\eta} \leq -\mu_w w(t) + P_w e^{-\mu\tau} \left( \frac{1}{\eta e} \right)^{\frac{1}{\eta}}.$$

The last inequality implies that

$$w(t) \leq \frac{P_w e^{-\mu\tau}}{\mu_w} \left( \frac{1}{\eta e} \right)^{\frac{1}{\eta}} [1 - e^{-\mu_w t}] + e^{-\mu_w t} w(0).$$

Then,

$$\limsup_{t \rightarrow +\infty} w(t) \leq \frac{P_w e^{-\mu\tau}}{\mu_w} \left( \frac{1}{\eta e} \right)^{\frac{1}{\eta}}.$$

This completes the proof of the boundedness of  $w(t)$ .

By using the same argument, we can write

$$\frac{d}{dt}u(t) \leq -\mu_u u(t) + (P_u + P_{wu}) e^{-\mu\tau} \left( \frac{1}{\eta e} \right)^{\frac{1}{\eta}}.$$

This implies that

$$u(t) \leq \frac{(P_u + P_{wu})e^{-\mu\tau}}{\mu_u} \left( \frac{1}{\eta e} \right)^{\frac{1}{\eta}} [1 - e^{-\mu_u t}] + e^{-\mu_u t} u(0).$$

Then, we conclude that

$$\limsup_{t \rightarrow +\infty} u(t) \leq \frac{(P_u + P_{wu})e^{-\mu\tau}}{\mu_u} \left( \frac{1}{\eta e} \right)^{\frac{1}{\eta}}.$$

□

## 5. EXISTENCE OF STEADY STATES

Let  $(w^*, u^*)$  be a steady state of the system (3.3). Then,

$$\begin{cases} P_w e^{-\mu\tau} w^* e^{-(w^*+u^*)^\eta} - \mu_w w^* & = 0, \\ (P_u u^* + P_{wu} w^*) e^{-\mu\tau} e^{-(w^*+u^*)^\eta} - \mu_u u^* & = 0. \end{cases} \quad (5.1)$$

Defining

$$\delta_w := \frac{P_w}{\mu_w} = \frac{\xi_w r_w \phi_w}{\mu_w}, \quad \delta_u := \frac{P_u}{\mu_u} = \frac{(1 - q\nu) r_u \phi_u}{\mu_u} \quad (5.2)$$

and

$$\delta_{wu} := \frac{P_{wu}}{\mu_u} = \frac{\xi_u r_w \phi_w}{\mu_u}, \quad (5.3)$$

the system (5.1) can be rewritten as

$$\begin{cases} \delta_w e^{-\mu\tau} w^* e^{-(w^*+u^*)^\eta} - w^* & = 0, \\ (\delta_u u^* + \delta_{wu} w^*) e^{-\mu\tau} e^{-(w^*+u^*)^\eta} - u^* & = 0, \end{cases}$$

and we obtain three solutions  $\mathbf{S}_0$ ,  $\mathbf{S}_u$  and  $\mathbf{S}_{wu}$  of this system:

- (i) Extinction of both populations (trivial equilibrium)

$$\mathbf{S}_0 = (0, 0); \quad (5.4)$$

- (ii) Extinction of infected population and persistence of uninfected one

$$\mathbf{S}_u = \left( 0, (\ln R_u)^{\frac{1}{\eta}} \right), \quad \text{with } R_u = \delta_u e^{-\mu\tau}; \quad (5.5)$$

- (iii) Persistence of both populations (coexistence of infected and uninfected mosquitoes)

$$\begin{aligned} \mathbf{S}_{wu} &= \left( (\ln R_w)^{\frac{1}{\eta}} (1 - \beta_{wu}), (\ln R_w)^{\frac{1}{\eta}} \beta_{wu} \right), \\ \text{with } R_w &= \delta_w e^{-\mu\tau} \quad \text{and} \quad \beta_{wu} = \frac{\delta_{wu}}{\delta_w - \delta_u + \delta_{wu}}. \end{aligned} \quad (5.6)$$



By examining the components of the steady states, we can deduce the following existence conditions.

- Proposition 5.1.** (a)  $\mathbf{S}_0$  always exists;  
 (b)  $\mathbf{S}_u$  exists if and only if  $R_u > 1$ ;  
 (c)  $\mathbf{S}_{wu}$  exists if and only if  $R_w > \max\{1, R_u\}$ .

In terms of the original parameters, we have

$$R_w = \frac{\xi_w r_w \phi_w}{\mu_w} e^{-\mu\tau} \quad \text{and} \quad R_u = \frac{(1 - q\nu) r_u \phi_u}{\mu_u} e^{-\mu\tau}.$$

The two dimensionless parameters  $R_w$  and  $R_u$  are, respectively, the mean number of female infected offspring produced by a *Wolbachia*-infected female mosquito during her whole life, and the mean number of female uninfected offspring produced by an uninfected female mosquito during her whole life.

As we are interested on the relationship between temperature variation (that affects strongly the maturation time  $\tau$ ) and population dynamics of both *Wolbachia*-infected and uninfected mosquitoes, we have to study the existence of the steady states in terms of the delay  $\tau$ . We consider the following thresholds of the maturation time

$$\tau_j = \frac{1}{\mu} \ln(\delta_j), \quad j \in \{w, u\}. \quad (5.7)$$

In fact,  $\tau_j \in \mathbb{R}$  and we have:

1.  $\tau_j \geq 0$  if and only if  $\delta_j \geq 1$ , and
2.  $\tau_j < 0$  if and only if  $0 < \delta_j < 1$ .

In terms of the delay, we obtain the following result.

- Proposition 5.2.** 1.  $\mathbf{S}_u$  exists if and only if

$$0 \leq \tau < \tau_u.$$

2.  $\mathbf{S}_{wu}$  exists if and only if

$$0 \leq \tau < \tau_w \quad \text{and} \quad \tau_u < \tau_w.$$

We remark that the steady states  $\mathbf{S}_u$  and  $\mathbf{S}_{wu}$  exist in the same time if and only if

$$0 \leq \tau < \tau_u \quad \text{and} \quad \tau_u < \tau_w.$$

In summary, we can distinguish four situations.

- Proposition 5.3.** (i) Assume that  $0 < \delta_u \leq 1$  and  $0 < \delta_w \leq 1$  (which is equivalent to  $\tau_u \leq 0$  and  $\tau_w \leq 0$ ). Then, for all  $\tau \geq 0$ ,  $\mathbf{S}_0$  is the only steady state.

- (ii) Assume that  $\tau_u > 0$  and  $\tau_w \leq \tau_u$ . Then,

- (a) if  $0 \leq \tau < \tau_u$ , there are two steady states  $\mathbf{S}_0$  and  $\mathbf{S}_u$ , with

$$\lim_{\tau \rightarrow \tau_u} \mathbf{S}_u = \mathbf{S}_0;$$

- (b) if  $\tau \geq \tau_u$ ,  $\mathbf{S}_0$  is the only steady state.

- (iii) Assume that  $\tau_u \leq 0 < \tau_w$ ,  $\tau_u \leq 0$  means  $0 < \delta_u \leq 1$ . Then,

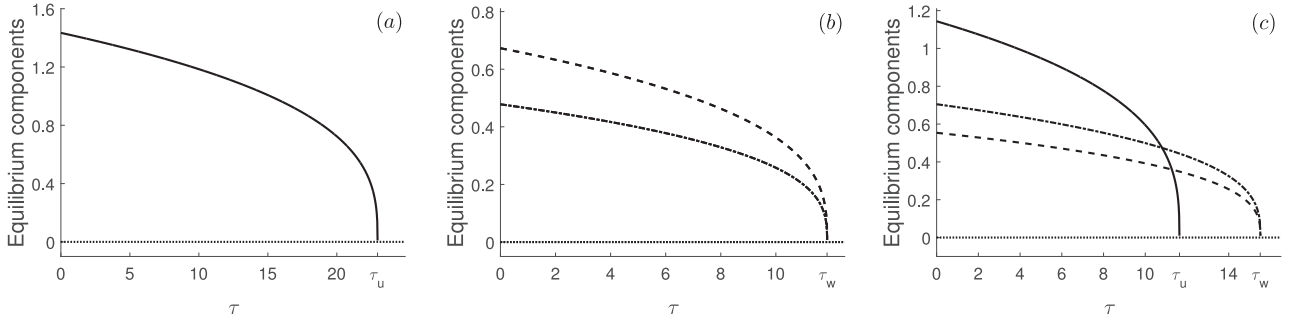


FIGURE 1. Components  $X$  and  $Y$  of the steady states  $\mathbf{S}_j = (X, Y)$ , with  $\mathbf{j} = \{\mathbf{0}, \mathbf{u}, \mathbf{wu}\}$  versus the delay  $\tau$ . The parameter sets used in the simulations are given in Table 1, and in all cases  $\eta = 3.0$ . In (a), we plotted case (ii) in which  $\tau_u > 0$  and  $\tau_w \leq \tau_u$ . Then, if  $0 \leq \tau < \tau_u$ , there are two steady states  $\mathbf{S}_0$  and  $\mathbf{S}_u$ , and if  $\tau \geq \tau_u$ ,  $\mathbf{S}_0$  is the only steady state. In (b), we plotted case (iii) in which  $\tau_u \leq 0 < \tau_w$ . Then, if  $0 \leq \tau < \tau_w$  there are two steady states  $\mathbf{S}_0$  and  $\mathbf{S}_{\mathbf{wu}}$ , and if  $\tau \geq \tau_w$ ,  $\mathbf{S}_0$  is the only steady state. In (c), we plotted case (iv) in which  $0 < \tau_u < \tau_w$ . Then, if  $0 \leq \tau < \tau_u$ , there are three steady states  $\mathbf{S}_0$ ,  $\mathbf{S}_u$  and  $\mathbf{S}_{\mathbf{wu}}$ , if  $\tau_u \leq \tau < \tau_w$ , there are two steady states  $\mathbf{S}_0$  and  $\mathbf{S}_{\mathbf{wu}}$ , and if  $\tau \geq \tau_w$ ,  $\mathbf{S}_0$  is the only steady state. In all panels  $\mathbf{S}_0$  component  $Y$  appears as a dotted line,  $\mathbf{S}_u$  component  $Y$  appears as a solid, and  $\mathbf{S}_{\mathbf{wu}}$  component  $X$  and  $Y$  appear, respectively, as a dot-dashed and dashed line.

(a) if  $0 \leq \tau < \tau_w$ , there are two steady states  $\mathbf{S}_0$  and  $\mathbf{S}_{\mathbf{wu}}$ , with

$$\lim_{\tau \rightarrow \tau_w} \mathbf{S}_{\mathbf{wu}} = \mathbf{S}_0;$$

(b) if  $\tau \geq \tau_w$ ,  $\mathbf{S}_0$  is the only steady state.

(iv) Assume that  $0 < \tau_u < \tau_w$ . Then,

(a) if  $0 \leq \tau < \tau_u$ , there are three steady states  $\mathbf{S}_0$ ,  $\mathbf{S}_u$  and  $\mathbf{S}_{\mathbf{wu}}$ , with

$$\lim_{\tau \rightarrow \tau_u} \mathbf{S}_u = \mathbf{S}_0;$$

(b) if  $\tau_u \leq \tau < \tau_w$ , there are two steady states  $\mathbf{S}_0$  and  $\mathbf{S}_{\mathbf{wu}}$ , with

$$\lim_{\tau \rightarrow \tau_w} \mathbf{S}_{\mathbf{wu}} = \mathbf{S}_0;$$

(c) if  $\tau \geq \tau_w$ ,  $\mathbf{S}_0$  is the only steady state.

Figure 1 summarizes the results obtained in Proposition 5.3. The different scenarios correspond to the three parameter sets shown in Table 1. For each  $\tau$  the corresponding steady state was obtained from (5.5) or (5.6). The panel (a) corresponds to case (ii), the panel (b) to case (iii), and the panel (c) to case (iv).

## 6. STABILITY ANALYSIS OF THE STEADY STATES

### 6.1. Local asymptotic stability of the trivial steady state $\mathbf{S}_0$

We conclude from the four scenarios of Proposition 5.3, that the trivial steady state is the only equilibrium if and only if

$$\tau > \max\{0, \tau_u, \tau_w\}. \quad (6.1)$$

TABLE 1. Parameters sets used in all Figures [1, 3, 30, 31, 38–40, 43].

Parameter	Value			Range [units]
	case (ii)	case (iii)	case (iv)	
$q$	0.3	0.8	0.7	(0,1)
$\nu$	0.3	0.8	0.7	[0,1]
$\phi_u$	3.0	1.25	1.25	(0.35,11.2) [per day per female]
$\phi_w$	$2.1\phi_u$	$2.1\phi_u$	$2.1\phi_u$	(0.10,11.0) [per day per female]
$r_u$	0.5	0.5	0.5	(0,1)
$r_w$	0.5	0.5	0.5	(0,1)
$\mu_u$	1/14	1/4	1/14	(1/4,1/37) [per day]
$\mu_w$	1/7	1/7	1/7	(1/4,1/32) [per day]
$\mu$	1/7.78	1/7.78	1/7.78	(1/7.5,1/30) [per day]
$\xi_w$	0.8	0.5	0.8	(0,1]
$\xi_u$	0.2	0.5	0.2	calculated by (2.2)
$P_u$	1.37	0.22	0.32	calculated by (3.2) [number of eggs per day per female]
$P_w$	2.52	0.65	1.05	calculated by (3.2) [number of eggs per day per female]
$P_{wu}$	0.63	0.65	0.26	calculated by (3.2) [number of eggs per day per female]
$\delta_u$	19.11	0.9	4.46	calculated by (5.2) [number of eggs per female]
$\delta_w$	17.64	4.59	7.35	calculated by (5.2) [number of eggs per female]
$\delta_{wu}$	8.82	2.63	3.67	calculated by (5.2) [number of eggs per female]
$\beta_{wu}$	1.2	0.41	0.56	calculated by (5.6)
$\tau_u$	22.95	-0.81	11.64	calculated by (5.7) [days]
$\tau_w$	22.33	11.86	15.52	calculated by (5.7)[days]

We prove in Theorem 6.2 that the local asymptotic stability of the trivial steady state  $\mathbf{S}_0$  is given by the condition (6.1). We will need the following useful lemma.

**Lemma 6.1.** [Theorem A.5 in [26], p. 416, see also [18]] All roots of the algebraic equation

$$\lambda + a + be^{-\lambda\tau} = 0,$$

have negative real parts if and only if

- (i)  $a\tau > -1$ ,
- (ii)  $a + b > 0$ ,
- (iii)  $b < \zeta \sin \zeta - a\tau \cos \zeta$ , where  $\zeta$  is the root of

$$\zeta = \begin{cases} -a\tau \tan \zeta, & 0 < \zeta < \pi, \quad a \neq 0, \\ \pi/2, & a = 0. \end{cases}$$

**Theorem 6.2.** 1. If (6.1) is satisfied, then the trivial steady state  $\mathbf{S}_0$  is locally asymptotically stable.  
 2. If (6.1) is not satisfied, then the trivial steady state  $\mathbf{S}_0$  is unstable.

*Proof.* We linearize the system (3.3) around  $\mathbf{S}_0$ . Then, we obtain

$$\begin{cases} \frac{d}{dt}x(t) = -\mu_w x(t) + e^{-\mu\tau} P_w x(t - \tau), \\ \frac{d}{dt}y(t) = -\mu_u y(t) + e^{-\mu\tau} P_{wu} x(t - \tau) + e^{-\mu\tau} P_u y(t - \tau). \end{cases}$$

The corresponding characteristic equation is given by

$$\det(\lambda I - A - Be^{-\lambda\tau}) = 0,$$

with

$$A = \begin{pmatrix} -\mu_w & 0 \\ 0 & -\mu_u \end{pmatrix} \quad \text{and} \quad B = e^{-\mu\tau} \begin{pmatrix} P_w & 0 \\ P_{wu} & P_u \end{pmatrix}$$

and  $I$  the  $2 \times 2$  identity matrix. Therefore,

$$(\lambda + \mu_w - P_w e^{-\mu\tau} e^{-\lambda\tau})(\lambda + \mu_u - P_u e^{-\mu\tau} e^{-\lambda\tau}) = 0. \quad (6.2)$$

The objective is to find conditions such that the solutions of (6.2) have negative real parts. We have to analyze separately the solutions of each factor of the product given by (6.2). For the equation

$$\lambda + \mu_j - P_j e^{-\mu\tau} e^{-\lambda\tau} = 0, \quad j \in \{u, w\},$$

the statement (i)  $a\tau = \mu_j\tau > -1$  of Lemma 6.1, is always satisfied. On the other hand, the condition (ii)  $a + b = \mu_j - P_j e^{-\mu\tau} > 0$  of Lemma 6.1, is equivalent to

$$\tau > \tau_j := \frac{1}{\mu} \ln(\delta_j), \quad j \in \{u, w\}.$$

For the statement (iii) of Lemma 6.1, as  $a \neq 0$ , we remark that the condition  $0 < \zeta < \pi$ , implies that  $\sin \zeta > 0$ . Then, the relation  $\zeta = -\mu_j\tau \tan \zeta$  means that  $\cos \zeta < 0$ . Thus,  $\pi/2 < \zeta < \pi$ . Consequently, the statement (iii) is always satisfied for  $\tau > 0$ . We conclude that the conditions (i)-(iii) of Lemma 6.1, can be summed up in

$$\tau > \max\{0, \tau_u, \tau_w\}.$$

This concludes the proof of Theorem 6.2. □

## 6.2. Global asymptotic stability of the trivial steady state $S_0$

Let's write the nonlinear system (3.3) in the following general form

$$\begin{cases} \frac{dx}{dt} = Ax(t) + F(x(t-\tau)), & t > 0, \\ x(t) = \phi(t), & t \in [-\tau, 0], \end{cases} \quad (6.3)$$

where

$$A = \begin{bmatrix} -\mu_w & 0 \\ 0 & -\mu_u \end{bmatrix}, \quad x(t) = \begin{bmatrix} w(t) \\ u(t) \end{bmatrix}, \quad F(y) = \begin{bmatrix} f_1(y_1, y_2) \\ f_2(y_1, y_2) \end{bmatrix},$$

with

$$\begin{cases} f_1(y_1, y_2) = P_w e^{-\mu\tau} y_1 e^{-(y_1+y_2)^\eta}, \\ f_2(y_1, y_2) = (P_u y_2 + P_{wu} y_1) e^{-\mu\tau} e^{-(y_1+y_2)^\eta}. \end{cases}$$

To prove our result (Thm. 6.4) on the global asymptotic stability of the trivial steady state, we use the following lemma.

**Lemma 6.3.** ([6, 25]). *Suppose that there exists  $\gamma > 0$  such that, for all  $y \in \mathbb{R}_+^2$ ,*

$$\|F(y)\| \leq \gamma \|y\| \quad \text{and} \quad \gamma < -\theta(A),$$

where  $\|\cdot\|$  is a norm in  $\mathbb{R}^2$  and  $\theta(A)$  is the matrix measure of  $A$ ,

$$\theta(A) = \lim_{\epsilon \rightarrow 0^+} \frac{\|I + \epsilon A\| - 1}{\epsilon}.$$

Then, the trivial equilibrium of (6.3) is globally asymptotically stable.

**Theorem 6.4.** *Suppose that*

$$\tau > \frac{1}{\mu} \ln \left( \frac{\max\{P_w, P_u + P_{wu}\}}{\min\{\mu_w, \mu_u\}} \right).$$

Then, the trivial steady state  $\mathbf{S}_0$  of the system (3.3) is globally asymptotically stable.

*Proof.* We have to find  $0 < \gamma < -\theta(A)$ , such that  $\|F(y)\| \leq \gamma \|y\|$ , for all  $y \in \mathbb{R}_+^2$ . We choose the norm  $\|x\| = \max\{|w|, |u|\}$  in  $\mathbb{R}^2$ . Then,

$$\|F(y)\| \leq e^{-\mu\tau} \max\{P_w, P_u + P_{wu}\} \|y\| := \gamma \|y\|.$$

We also have

$$\begin{aligned} \theta(A) &= \lim_{\epsilon \rightarrow 0^+} \frac{\|I + \epsilon A\| - 1}{\epsilon}, \\ &= \lim_{\epsilon \rightarrow 0^+} \frac{\max\{1 - \epsilon\mu_w, 1 - \epsilon\mu_u\} - 1}{\epsilon}, \\ &= \lim_{\epsilon \rightarrow 0^+} \frac{1 - \epsilon \min\{\mu_u, \mu_w\} - 1}{\epsilon}, \\ &= -\min\{\mu_w, \mu_u\}. \end{aligned}$$

Finally, provided that

$$0 < e^{-\mu\tau} \max\{P_w, P_u + P_{wu}\} < \min\{\mu_w, \mu_u\}, \quad (6.4)$$

Lemma 6.3 guarantees the global asymptotic stability of the trivial steady state  $\mathbf{S}_0$ . In fact, the condition (6.4) is equivalent to

$$\tau > \frac{1}{\mu} \ln \left( \frac{\max\{P_w, P_u + P_{wu}\}}{\min\{\mu_w, \mu_u\}} \right).$$

This finishes the proof of the theorem. □

**Remark 6.5.** It is not difficult to see that the condition

$$\tau > \frac{1}{\mu} \ln \left( \frac{\max\{P_w, P_u + P_{wu}\}}{\min\{\mu_w, \mu_u\}} \right)$$

implies in particular that

$$\tau > \max\{0, \tau_u, \tau_w\}.$$

The local asymptotic stability of the other steady states will be analyzed by increasing the delay  $\tau$  from zero with the possibility of eigenvalues to cross on the imaginary axis and the appearance of Hopf bifurcation.

### 6.3. Local asymptotic stability and Hopf bifurcation of *Wolbachia*-free steady state $\mathbf{S}_u$

The *Wolbachia*-free steady state  $\mathbf{S}_u := \left(0, (\ln R_u)^{\frac{1}{\eta}}\right)$ ,  $R_u = \delta_u e^{-\mu\tau}$ , exists only in the scenarios (ii)-(a) and (iv)-(a) of Proposition 5.3. That is under the condition

$$0 \leq \tau < \tau_u.$$

The linearization of the system (3.3) around the steady state  $\mathbf{S}_u$  is given by

$$\begin{cases} \frac{d}{dt}x(t) &= -\mu_w x(t) + \frac{P_w}{\delta_u} x(t-\tau), \\ \frac{d}{dt}y(t) &= -\mu_u y(t) + \frac{P_{wu}}{\delta_u} x(t-\tau) + \frac{P_u}{\delta_u} (1 - \eta \ln(R_u)) y(t-\tau). \end{cases} \quad (6.5)$$

Note that  $P_u = \mu_u \delta_u$ ,  $P_w = \mu_w \delta_w$  and  $P_{wu} = \mu_u \delta_{wu}$ . Then, the characteristic equation associate to (6.5) is given by

$$\left(\lambda + \mu_w - \mu_w \frac{\delta_w}{\delta_u} e^{-\lambda\tau}\right) (\lambda + \mu_u - \mu_u (1 - \eta \ln(R_u)) e^{-\lambda\tau}) = 0. \quad (6.6)$$

The roots of the first term of the characteristic equation (see Lem. 6.1),

$$\lambda + \mu_w - \mu_w \frac{\delta_w}{\delta_u} e^{-\lambda\tau} = 0,$$

have negative real parts if and only if

- (i)  $\mu_w \tau > -1$ ,
- (ii)  $\delta_u > \delta_w$ ,
- (iii)  $-\tau \mu_w \frac{\delta_w}{\delta_u} < \zeta \sin \zeta - \mu_w \tau \cos \zeta$ , where  $\zeta$  is the root of

$$\zeta = -\mu_w \tau \tan \zeta, \quad 0 < \zeta < \pi.$$

The statements (i) and (iii) are always satisfied and the statement (ii) is equivalent to

$$\tau_u > \tau_w.$$

Then, we can immediately conclude the following result.

**Proposition 6.6.** *Suppose that*

$$\tau_u \leq \tau_w \quad \text{and} \quad 0 \leq \tau < \tau_u.$$

Then, the steady state  $\mathbf{S}_u$  is unstable.

Now suppose that

$$\tau_u > \tau_w.$$

Then, the local asymptotic stability of the steady state  $\mathbf{S}_u$  is given by the roots of the second term of the characteristic equation (6.6):

$$\lambda + \mu_u - \mu_u (1 - \eta \ln(R_u)) e^{-\lambda\tau} = 0. \quad (6.7)$$

Thanks to Lemma 6.1, the roots of (6.7) have negative real parts if and only if

- (i)  $\mu_u \tau > -1$ ,
- (ii)  $R_u > 1$ ,
- (iii)  $-\tau \mu_u (1 - \eta \ln(R_u)) < \zeta \sin \zeta - \tau \mu_u \cos \zeta$ , where  $\zeta$  is the root of

$$\zeta = -\tau \mu_u \tan \zeta, \quad 0 < \zeta < \pi.$$

The statement (i) is always satisfied and the statement (ii) is equivalent to the condition that gives the existence of the steady state  $\mathbf{S}_u$ . Suppose that

$$\eta > \frac{1}{\ln(R_u)}. \quad (6.8)$$

Then, the statement (iii) is satisfied and we have the local asymptotic stability of the steady state  $\mathbf{S}_u$ . In fact, the condition (6.8) is equivalent to

$$\max \left\{ 0, \tau_u - \frac{1}{\eta \mu} \right\} < \tau < \tau_u. \quad (6.9)$$

We directly conclude the following result.

**Proposition 6.7.** *If the condition (6.9) is satisfied then, the steady state  $\mathbf{S}_u$  is locally asymptotically stable. In particular, if*

$$\eta < \frac{1}{\ln(\delta_u)},$$

then, for all  $0 \leq \tau < \tau_u$ ,  $\mathbf{S}_u$  is locally asymptotically stable.

Now suppose that

$$\eta > \frac{1}{\ln(\delta_u)}.$$

This inequality is equivalent to

$$\bar{\tau}_u := \tau_u - \frac{1}{\eta \mu} > 0.$$

We proved that  $\mathbf{S}_u$  is locally asymptotically stable for  $\bar{\tau}_u < \tau < \tau_u$ . Suppose that

$$0 \leq \tau < \bar{\tau}_u.$$

When  $\tau = 0$ , the characteristic equation (6.7) reads

$$\Delta(0, \lambda) = \lambda + \mu_u - \mu_u (1 - \eta \ln(\delta_u)) = 0.$$

It has only one root

$$\lambda_0 = -\mu_u \eta \ln(\delta_u) \in \mathbb{R}.$$

As  $\delta_u > 1$ , then  $\lambda_0 < 0$ . We conclude that the steady state  $\mathbf{S}_u$  is locally asymptotically stable for  $\tau = 0$ . By using a continuity argument, it is straightforward that there exists  $\varrho \in (0, \bar{\tau}_u)$ , such that  $\mathbf{S}_u$  is locally asymptotically stable for  $\tau \in [0, \varrho)$ . Consequently, when  $\tau \in [0, \bar{\tau}_u)$  increases, the stability of  $\mathbf{S}_u$  can only be lost if characteristic roots cross on the imaginary axis. We look for purely imaginary roots  $\pm i\omega$ ,  $\omega \in \mathbb{R}$ . Remark that if  $\lambda$  is a characteristic root then its conjugate  $\bar{\lambda}$  is also a characteristic root. Then, we look for purely imaginary roots  $i\omega$  with  $\omega > 0$ . By separating real and imaginary parts in the characteristic equation (6.7), we get

$$\begin{cases} \mu_u (1 - \eta \ln(R_u)) \cos(\tau\omega) &= \mu_u, \\ \mu_u (1 - \eta \ln(R_u)) \sin(\tau\omega) &= -\omega. \end{cases} \quad (6.10)$$

Adding the squares of both hand sides of the last system and using the fact that  $\cos^2(\tau\omega) + \sin^2(\tau\omega) = 1$ , it follows that

$$\frac{\omega^2}{\mu_u^2} = \eta \ln(R_u) (\eta \ln(R_u) - 2).$$

For the existence of  $\omega > 0$ , it is necessary to have

$$0 < \tau < \tilde{\tau}_u := \tau_u - \frac{2}{\eta\mu}.$$

Then, it is immediate to conclude the following result.

**Proposition 6.8.** *If*

$$\eta < \frac{2}{\ln(\delta_u)}$$

*then, for all  $0 \leq \tau < \tau_u$ ,  $\mathbf{S}_u$  is locally asymptotically stable.*

Now suppose that

$$\eta > \frac{2}{\ln(\delta_u)}$$

and consider the function  $\varpi: [0, \tilde{\tau}_u) \rightarrow (0, +\infty)$  defined by

$$\varpi(\tau) = \mu_u \sqrt{\eta \ln(R_u) (\eta \ln(R_u) - 2)}, \quad \text{for all } \tau \in [0, \tilde{\tau}_u).$$



In fact, we have

$$\varpi(\tau) = \eta\mu\mu_u \sqrt{(\tau_u - \tau)(\tilde{\tau}_u - \tau)}, \quad \text{for all } \tau \in [0, \tilde{\tau}_u). \quad (6.11)$$

Then, for each  $\tau \in [0, \tilde{\tau}_u)$ , there is a unique solution  $\Theta(\tau) \in [0, 2\pi)$  of the system

$$\begin{cases} \cos(\Theta(\tau)) &= -\frac{1}{\eta\mu(\tilde{\tau}_u - \tau) + 1} < 0, \\ \sin(\Theta(\tau)) &= \frac{\eta\mu\sqrt{(\tau_u - \tau)(\tilde{\tau}_u - \tau)}}{\eta\mu(\tilde{\tau}_u - \tau) + 1} > 0. \end{cases}$$

Then,  $\Theta(\tau) \in (\pi/2, \pi)$  and it is given by

$$\Theta(\tau) = \arccos\left(-\frac{1}{\eta\mu(\tilde{\tau}_u - \tau) + 1}\right). \quad (6.12)$$

We conclude that the system (6.10) is equivalent to find  $\tau \in [0, \tilde{\tau}_u)$  solution of

$$\tau\varpi(\tau) = \Theta(\tau) + 2k\pi, \quad k \in \mathbb{N},$$

with  $\varpi(\tau)$  given by (6.11) and  $\Theta(\tau)$  by (6.12). We remark here that in all this study, the set  $\mathbb{N}$  includes 0. This is equivalent to solve

$$Z_k(\tau) := \tau - \frac{1}{\varpi(\tau)} [\Theta(\tau) + 2k\pi] = 0, \quad k \in \mathbb{N}, \quad \tau \in [0, \tilde{\tau}_u).$$

More precisely, we have to solve for  $k \in \mathbb{N}$  and  $\tau \in [0, \tilde{\tau}_u)$ ,

$$Z_k(\tau) := \tau - \frac{1}{\eta\mu\mu_u \sqrt{(\tau_u - \tau)(\tilde{\tau}_u - \tau)}} \left[ \arccos\left(-\frac{1}{\eta\mu(\tilde{\tau}_u - \tau) + 1}\right) + 2k\pi \right] = 0. \quad (6.13)$$

The functions  $Z_k(\tau)$  are given explicitly. However, we cannot determine explicitly their roots. The roots can be found numerically. The following lemma states some properties of the functions  $Z_k$ ,  $k \in \mathbb{N}$ .

**Lemma 6.9.** *For all  $k \in \mathbb{N}$  and  $\tau \in [0, \tilde{\tau}_u)$ ,*

$$Z_k(0) < 0, \quad Z_{k+1}(\tau) < Z_k(\tau) \quad \text{and} \quad \lim_{\tau \rightarrow \tilde{\tau}_u} Z_k(\tau) = -\infty.$$

*Therefore, provided that no root of  $Z_k$  is a local extremum, the number of positive roots of  $Z_k$ ,  $k \in \mathbb{N}$ , on the interval  $[0, \tilde{\tau}_u)$  is even.*

This lemma implies, in particular, that, if  $Z_k$  has no root on  $[0, \tilde{\tau}_u)$ , then no function  $Z_j$ , with  $j > k$ , has roots on  $[0, \tilde{\tau}_u)$ . The next proposition is a direct consequence of Lemma 6.9.

**Proposition 6.10.** *If the function  $Z_0$  defined on the interval  $[0, \tilde{\tau}_u)$ , by*

$$Z_0(\tau) := \tau - \frac{\arccos\left(-\frac{1}{\eta\mu(\tilde{\tau}_u - \tau) + 1}\right)}{\eta\mu\mu_u \sqrt{(\tau_u - \tau)(\tilde{\tau}_u - \tau)}} \quad (6.14)$$

has no root, then the steady state  $\mathbf{S}_u$  is locally asymptotically stable for all  $\tau \in [0, \tilde{\tau}_u)$ .

We now suppose that  $Z_0$ , under the condition

$$\eta > \frac{2}{\ln(\delta_u)},$$

has at least one positive root on the interval  $[0, \tilde{\tau}_u)$ . Let  $\tau_u^* \in (0, \tilde{\tau}_u)$  be the smallest root of  $Z_0$ . Then,  $\mathbf{S}_u$  is locally asymptotically stable for  $\tau \in [0, \tau_u^*)$ , and loses its stability when  $\tau = \tau_u^*$ . A finite number of stability switch may occurs as  $\tau$  increases and passes through roots of the  $Z_k$  functions.

Our next objective is to prove that  $\mathbf{S}_u$  can be destabilized through a Hopf bifurcation as  $\tau \in [0, \tilde{\tau}_u)$  increases. We start by proving that if an imaginary characteristic root  $i\omega$  exists then, it is simple. Suppose, by contradiction, that  $\lambda = i\omega$  is not a simple characteristic root. Then,  $\lambda$  is a solution of

$$\Delta(\tau, \lambda) = 0 \quad \text{and} \quad \frac{\partial}{\partial \lambda} \Delta(\tau, \lambda) = 0,$$

where

$$\Delta(\tau, \lambda) = \lambda + \mu_u - \mu_u (1 - \eta \ln(R_u)) e^{-\lambda\tau}. \quad (6.15)$$

This is equivalent to

$$\begin{cases} e^{\lambda\tau} [\lambda + \mu_u] &= \mu_u [1 - \eta \ln(R_u)], \\ e^{\lambda\tau} &= -\tau \mu_u [1 - \eta \ln(R_u)]. \end{cases} \quad (6.16)$$

The two equations of the system (6.16) lead to

$$(\lambda + \mu_u)\tau + 1 = 0.$$

This a contradiction with the fact that  $\lambda = i\omega$ .

As  $\tau_u^*$  is the smallest root of  $Z_0$  then, from the definition of  $Z_0$ , the characteristic equation (6.15) has purely imaginary roots  $\pm i\varpi(\tau_u^*)$ , where  $\varpi$  is defined by (6.11). The stability of the positive steady state switches from stable to unstable as  $\tau$  passes through  $\tau_u^*$ . Other stability switch occur when  $\tau$  passes through roots of the  $Z_k$  functions (see [4]).

Now, we rewrite the characteristic equation (6.15) in the following form

$$\Delta(\tau, \lambda) := A(\tau, \lambda) + B(\tau)e^{-\lambda\tau} = 0.$$

We define, for  $\lambda = i\omega$ , the polynomial function

$$H(\tau, \omega) := |A(\tau, i\omega)|^2 - |B(\tau)|^2.$$

Then,

$$H(\tau, \omega) = \omega^2 - \eta^2 \mu^2 \mu_u^2 (\tau_u - \tau) (\tilde{\tau}_u - \tau).$$

Let  $\lambda(\tau)$  be a branch of roots of (6.15) such that  $\lambda(\tau_u^*) = i\varpi(\tau_u^*)$ . The Hopf bifurcation theorem says that a Hopf bifurcation occurs at  $\mathbf{S}_u$  when  $\tau = \tau_u^*$  if

$$\text{sign} \left[ \left( \frac{d\Re(\lambda(\tau))}{d\tau} \right)_{\tau=\tau_u^*} \right] > 0.$$

We know from [4] that

$$\text{sign} \left[ \left( \frac{d\Re(\lambda(\tau))}{d\tau} \right)_{\tau=\tau_u^*} \right] = \text{sign} \left( \frac{\partial h}{\partial z}(\tau_u^*, \varpi^2(\tau_u^*)) \right) \text{sign} \left( \frac{dZ_0(\tau_u^*)}{d\tau} \right),$$

with

$$h(\tau, \omega^2) := H(\tau, \omega).$$

That is to say

$$h(\tau, z) = z - \eta^2 \mu^2 \mu_u^2 (\tau_u - \tau) (\tilde{\tau}_u - \tau).$$

It is clear that

$$\frac{\partial h}{\partial z}(\tau_u^*, \varpi^2(\tau_u^*)) = 1.$$

It follows

$$\text{sign} \left[ \left( \frac{d\Re(\lambda(\tau))}{d\tau} \right)_{\tau=\tau_u^*} \right] = \text{sign} \left( \frac{dZ_0(\tau_u^*)}{d\tau} \right).$$

The following proposition states the existence of a Hopf bifurcation at  $\tau = \tau_u^*$  that destabilizes the positive steady state  $\mathbf{S}_u$ .

**Proposition 6.11.** *If  $Z_0(\tau)$  has at least one positive root on the interval  $(0, \tilde{\tau}_u)$ , then the positive steady state  $\mathbf{S}_u$  is locally asymptotically stable for  $\tau \in [0, \tau_u^*)$ , where  $\tau_u^*$  is the smallest root of  $Z_0(\tau)$  on  $(0, \tilde{\tau}_u)$ , and  $\mathbf{S}_u$  loses its stability when  $\tau = \tau_u^*$ . A finite number of stability switch may occur as  $\tau$  passes through roots of the  $Z_k$  functions. Moreover, if*

$$\frac{dZ_0(\tau_u^*)}{d\tau} > 0,$$

*then a Hopf bifurcation occurs at  $\mathbf{S}_u$  for  $\tau = \tau_u^*$ .*

Figure 2 shows, for two set of parameters, the existence or non-existence of roots for the functions  $Z_0$  and  $Z_1$ , given by the equation (6.13). In each case,  $\tau \in (0, \tilde{\tau}_u)$ . On the left, we have  $\eta = 2.0$  and no root for  $Z_k$ . Then, the equilibrium  $\mathbf{S}_u$  stays locally asymptotically stable on the interval  $(0, \tilde{\tau}_u)$ . On the right, we have  $\eta = 3.0$  and two roots for  $Z_0$  (no root for  $Z_1$ ). A Hopf bifurcation occurs at  $\tau = \tau_u^*$  and periodic oscillations around the equilibrium  $\mathbf{S}_u$  are observed until the threshold  $\tau = \tau_u^+$ . The equilibrium  $\mathbf{S}_u$  corresponds to the extinction of *Wolbachia*-infected mosquito and the persistence of uninfected one.

For the set of parameters given in the case (ii), Table 1, where the equilibrium  $\mathbf{S}_u$  exists for  $\tau \in [0, \tau_u)$ , we can see in Figure 3, for each value of  $\eta$ , the roots of  $Z_0$ . For  $\eta$  less than a threshold,  $\eta_{\min}$  ( $\eta_{\min} \approx 2$ ),  $Z_0$  has no

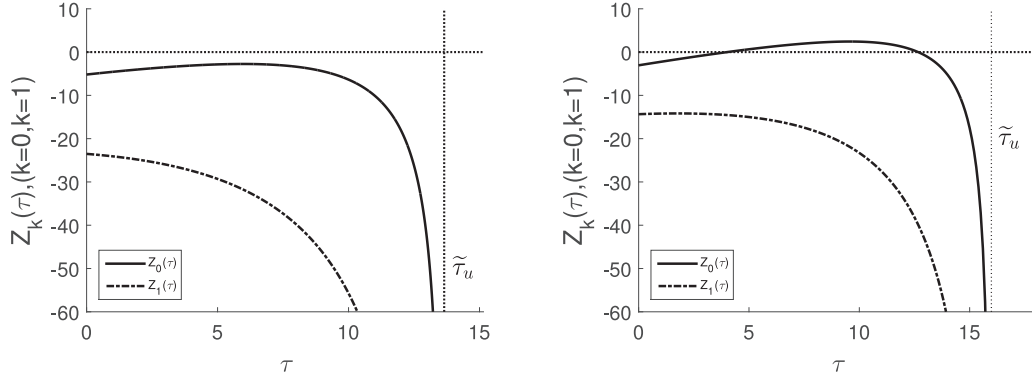


FIGURE 2. The functions  $Z_k$ ,  $k = 0, 1$ , given by the equation (6.13), versus  $\tau$ . On the left, we can see that  $Z_0$  and  $Z_1$  have no roots. The vertical line shows the right end of  $Z_k$  domain,  $\tilde{\tau}_u = 13.65$ . On the right, we can see that  $Z_0$  has two roots  $\tau_u^* = 4.01$  and  $\tau_u^+ = 12.67$ , and  $Z_1$  has no root. The vertical line shows the right end of  $Z_k$  domain  $\tilde{\tau}_u = 15.98$ . At  $\tau = \tau_u^*$  a Hopf bifurcation occurs and periodic oscillations around the equilibrium are observed until  $\tau = \tau_u^+$ ; outside the interval  $(\tau_u^*, \tau_u^+)$ , the equilibrium  $\mathbf{S}_u$  is locally asymptotically stable. In both panels, we use the parameter set from case (ii) (Tab. 1). On the left, we set  $\eta = 2.0$ , and on the right, we set  $\eta = 3.0$ .

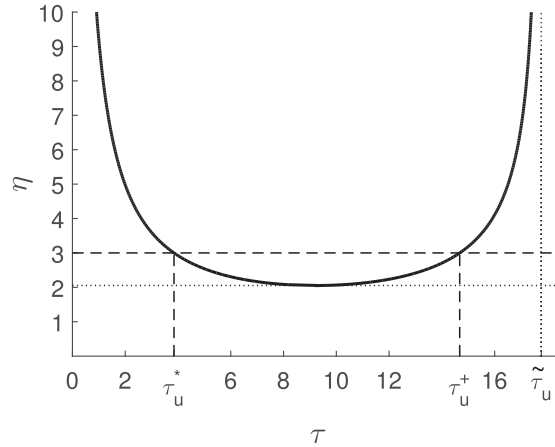


FIGURE 3.  $\eta$  versus  $\tau$ . The continuous curve provides the roots of  $Z_0(\tau)$  given  $\eta$  (see 6.14). For the set of parameters chosen, case (ii) (Tab. 1), the horizontal dotted line highlights the lower threshold to have Hopf bifurcation. The domain of  $Z_0$  is given by  $(0, \tilde{\tau}_u)$  with  $\tilde{\tau}_u = 17.76$ . As an example, the dashed line is set for  $\eta = 3.0$ . For this value of  $\eta$ , the corresponding roots of  $Z_0$  are  $\tau_u^* = 3.85$  and  $\tau_u^+ = 14.67$ . As  $dZ_0(\tau_u^*)/d\tau > 0$  a Hopf bifurcation occurs at  $\tau = \tau_u^*$  by Proposition 6.11. At this point, the equilibrium  $\mathbf{S}_u$  loses his stability and periodic oscillations can be seen until  $\tau_u^+$ . At  $\tau = \tau_u^+$  the stability of  $\mathbf{S}_u$  is recovered. This corresponds to the extinction of *Wolbachia*-infected mosquito and persistence of uninfected one.

root which implies that the steady state  $\mathbf{S}_u$  is stable. For  $\eta$  greater than  $\eta_{\min}$ ,  $Z_0$  has two roots  $\tau_u^*$  and  $\tau_u^+$ . In this case,  $\mathbf{S}_u$  loses stability at  $\tau = \tau_u^*$  and periodic oscillations can be seen. For  $\tau = \tau_u^+$  the stability of  $\mathbf{S}_u$  is recovered. The equilibrium  $\mathbf{S}_u$  corresponds to the extinction of *Wolbachia*-infected mosquito and persistence of uninfected one.

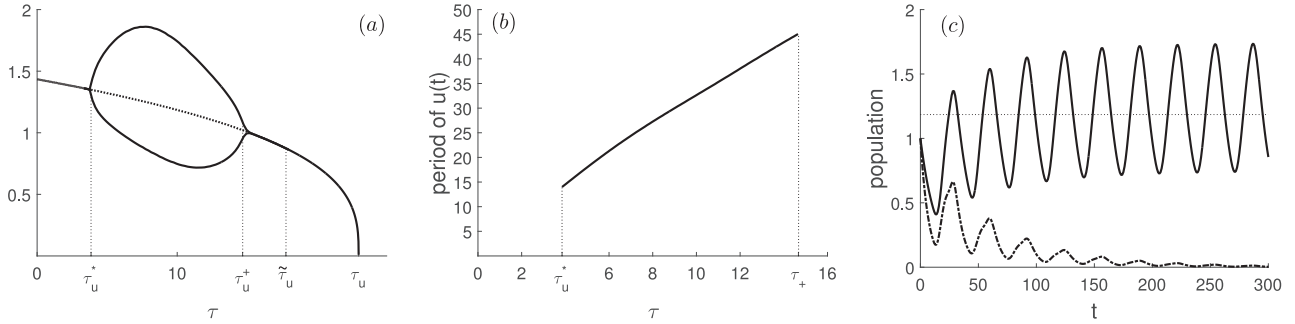


FIGURE 4. From the left to the right we have: (a) the minimum and the maximum values of the component  $u(t)$  of the system (3.3) plotted against  $\tau \in (\tau_u^*, \tau_u^+)$ ; (b) the period of the oscillations of  $u(t)$  versus  $\tau \in (\tau_u^*, \tau_u^+)$ ; and (c) the temporal evolution of  $u(t)$  (solid line) and  $w(t)$  (dot-dash line) given by the system (3.3) with  $\tau = 10$ . In all panels, the parameters were taken from Table 1 case (iv) and  $\eta = 3$ . The thresholds given by  $\tau_u^* = 3.85$ ,  $\tau_u^+ = 14.67$ ,  $\tilde{\tau}_u = 17.76$  and  $\tau_u = 22.95$  are, respectively, the first and second roots of  $Z_0$ , the right end of the domain of the function  $Z_0$ , and the right end of  $\tau$  that allows the existence of  $\mathbf{S}_u$ .

Using the set of parameters from case (ii), Table 1, and  $\eta = 3.0$ , in Figure 4, we can see in the panel (a) the minimum and the maximum values of the periodic solutions  $u(t)$  of the system (3.3) plotted for  $\tau_u^* \leq \tau < \tau_u^+$  (where  $\mathbf{S}_u$  is unstable). This corresponds to the amplitude of  $u(t)$  for  $\tau_u^* \leq \tau < \tau_u^+$ . In the panel (b), we plotted the period of these periodic oscillations which is an increasing function of  $\tau \in (\tau_u^*, \tau_u^+)$ . Finally in the panel (c), we can see an example of temporal evolution of the system (3.3) for  $\eta = 3.0$  and  $\tau = 10$ . The component  $u(t)$  oscillates around the steady state and the component  $w(t)$  tends to zero with positive damped oscillations.

#### 6.4. Local asymptotic stability of the coexistence steady state $\mathbf{S}_{wu}$

The coexistence steady state

$$\mathbf{S}_{wu} = (w^*, u^*) := \left( (\ln R_w)^{\frac{1}{\eta}} (1 - \beta_{wu}), (\ln R_w)^{\frac{1}{\eta}} \beta_{wu} \right),$$

with  $R_w = \delta_w e^{-\mu\tau}$  and  $\beta_{wu} = \frac{\delta_{wu}}{\delta_w - \delta_u + \delta_{wu}}$ , exists only under the condition

$$\tau_u < \tau_w \quad \text{and} \quad 0 \leq \tau < \tau_w.$$

The linearization of the system (3.3) around the steady state  $\mathbf{S}_{wu}$  is given by

$$\begin{cases} \frac{d}{dt}x(t) &= -\mu_w x(t) + b_{11}x(t - \tau) + b_{12}y(t - \tau), \\ \frac{d}{dt}y(t) &= -\mu_u y(t) + b_{21}x(t - \tau) + b_{22}y(t - \tau), \end{cases}$$

with

$$\begin{cases} b_{11} &= P_w e^{-\mu\tau} e^{-(w^*+u^*)^\eta} (1 - \eta w^* (w^* + u^*)^{\eta-1}), \\ b_{12} &= -\eta P_w e^{-\mu\tau} e^{-(w^*+u^*)^\eta} w^* (w^* + u^*)^{\eta-1}, \\ b_{21} &= e^{-\mu\tau} e^{-(w^*+u^*)^\eta} (P_{wu} - \eta(P_u u^* + P_{wu} w^*) (w^* + u^*)^{\eta-1}), \\ b_{22} &= e^{-\mu\tau} e^{-(w^*+u^*)^\eta} (P_u - \eta(P_u u^* + P_{wu} w^*) (w^* + u^*)^{\eta-1}). \end{cases}$$

When  $\tau = 0$ , the Jacobian matrix evaluated at  $\mathbf{S}_{\mathbf{w}\mathbf{u}}$  is given by

$$\mathbf{J}(\mathbf{S}_{\mathbf{w}\mathbf{u}}) = \begin{bmatrix} -\eta\mu_w(1 - \beta_{wu}) \ln(\delta_w) & -\eta\mu_w(1 - \beta_{wu}) \ln(\delta_w) \\ \frac{P_{wu}}{\delta_w} - \eta\mu_u\beta_{wu} \ln(\delta_w) & \frac{P_u}{\delta_w} - \eta\mu_u\beta_{wu} \ln(\delta_w) - \mu_u \end{bmatrix}.$$

Hence, the eigenvalues  $\lambda$  of  $J(\mathbf{S}_{\mathbf{w}\mathbf{u}})$  satisfy the characteristic equation

$$\begin{aligned} \lambda^2 + \lambda \left( -\frac{P_u}{\delta_w} + \eta\mu_w(1 - \beta_{wu}) \ln(\delta_w) + \eta\mu_u\beta_{wu} \ln(\delta_w) + \mu_u \right) \\ + \left( \frac{P_{wu} - P_u}{\delta_w} + \mu_u \right) \eta\mu_w(1 - \beta_{wu}) \ln(\delta_w) = 0. \end{aligned}$$

Thus, by the Routh-Hurwitz criterion, the steady state  $\mathbf{S}_{\mathbf{w}\mathbf{u}}$  is stable when the following conditions are satisfied.

$$\begin{cases} \mu_u \left( 1 - \frac{\delta_u}{\delta_w} \right) + \eta\mu_w(1 - \beta_{wu}) \ln(\delta_w) + \eta\mu_u\beta_{wu} \ln(\delta_w) &> 0, \\ \eta\mu_u\mu_w \left( \frac{\delta_{wu} + \delta_w - \delta_u}{\delta_w} \right) (1 - \beta_{wu}) \ln(\delta_w) &> 0. \end{cases}$$

Remember that the condition for the existence of  $\mathbf{S}_{\mathbf{w}\mathbf{u}}$  for  $\tau = 0$ , is given by

$$\delta_u < \delta_w \quad \text{and} \quad \delta_w > 1.$$

This means in particular, that  $0 < \beta_{wu} < 1$ . We conclude that the steady state  $\mathbf{S}_{\mathbf{w}\mathbf{u}}$  is always locally asymptotically stable for  $\tau = 0$ . Thus, it is straightforward that there exists  $\varrho \in (0, \tau_w)$ , such that  $\mathbf{S}_{\mathbf{w}\mathbf{u}}$  is locally asymptotically stable for  $\tau \in [0, \varrho)$ . Consequently, when  $\tau \in [0, \tau_w)$  increases, the stability of  $\mathbf{S}_{\mathbf{w}\mathbf{u}}$  can only be lost if characteristic roots cross on the imaginary axis. Indeed, we showed numerically that this really happens and, similarly to  $\mathbf{S}_{\mathbf{u}}$ , there exists Hopf bifurcation for  $\mathbf{S}_{\mathbf{w}\mathbf{u}}$ . As an example, we plotted Figure 5. In (a), we can see for each value of  $\eta > 0$  the corresponding values of  $\tau$  that limit the region where the equilibrium  $\mathbf{S}_{\mathbf{w}\mathbf{u}}$  is stable and unstable (with periodic oscillations). For  $\eta = 4$ , a Hopf bifurcation occurs at  $\tau \approx 3.5$  and the stability of  $\mathbf{S}_{\mathbf{w}\mathbf{u}}$  is restored at  $\tau \approx 8.2$ . For values of  $\tau \in [3.5, 8.2[$  the temporal behaviour of the system (3.3) shows periodic oscillations around  $\mathbf{S}_{\mathbf{w}\mathbf{u}}$ .

## 7. DISCUSSION

Starting from an age structured partial differential model (4-equations), constructed taking into account the mosquito life cycle and the main features of the *Wolbachia*-infection, we derived a delay differential model (2-equations) using the method of characteristics, to study the colonization and persistence of the *Wolbachia*-transinfected *Aedes aegypti* mosquito in an environment where the uninfected wild mosquito population is already established. The reduction of the model to a delay differential system permits that several important

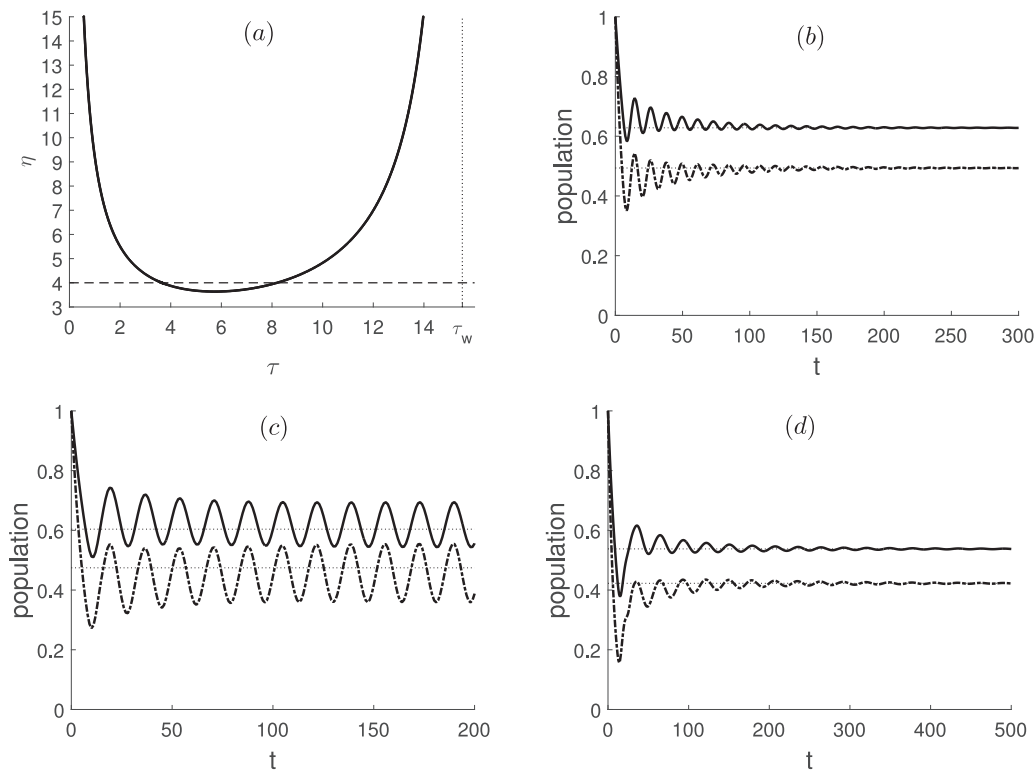


FIGURE 5. In (a),  $\eta$  versus  $\tau$  (it was obtained using the package DDE-BIFTOOL v. 3.1.1 and MATLAB R2019). For  $\eta = 4$  the panels (b), (c) and (d) show the temporal evolution of  $u(t)$  (solid line) and  $w(t)$  (dot-dash line) given by (3.3) with  $\tau = 3.2$ ,  $\tau = 5$  and  $\tau = 8.9$ , respectively. The other parameters were taken from the case (iv) of Table 1. A Hopf bifurcation occurs at  $\tau \approx 3.5$  and the stability of  $\mathbf{S}_{\mathbf{w}\mathbf{u}}$  is restored at  $\tau \approx 8.2$ ;  $\tau \in (0, 22.33)$ .

and interesting questions, such as the equilibriums and their local and global stability, can be analytically addressed while keeping all the biological assumptions behind the model.

Thus, the positivity, boundedness and uniqueness of solutions were proved. The model admits three steady states: extinction of both populations ( $\mathbf{S}_0$ ), extinction of infected population and persistence of uninfected population ( $\mathbf{S}_u$ ), and persistence of both populations ( $\mathbf{S}_{\mathbf{w}\mathbf{u}}$ ). The conditions of existence of each equilibrium were established as a combination of the entomological parameters that describe mosquito life's cycle (such as mortality, oviposition and development rates) and the effects of the *Wolbachia* presence in the host (vertical transmission of the bacteria, cytoplasmic incompatibility, and sex-ratio-distorting). The two thresholds  $R_w$  and  $R_u$  can be interpreted as the net reproductive rates which are defined as the average numbers of female offspring that a female produces during her lifetime. Therefore,  $R_w$  measured the number of infected offspring produced by an infected female and  $R_u$  measured the number of uninfected offspring produced by an uninfected female. Moreover, we could prove that  $\mathbf{S}_0$  always exists,  $\mathbf{S}_u$  exists if and only if  $R_u > 1$  and  $\mathbf{S}_{\mathbf{w}\mathbf{u}}$  exists if and only if  $R_w > \max\{1, R_u\}$ .

As we were interested in analyzing the effect of variation on developmental time in population dynamics, we rewrote the condition of existence of each equilibrium in terms of the delay  $\tau$  which measures the time spent from egg to adult. Four scenarios can be drawn (Fig. 1): (i) assume that  $\tau_u, \tau_w \leq 0$  (these thresholds are equivalent to the ones on  $R_u$  and  $R_w$ , respectively). Then, for all  $\tau \geq 0$ ,  $\mathbf{S}_0$  is the only steady state; (ii) assume that  $\tau_u > 0$  and  $\tau_w \leq \tau_u$ . Then, if  $0 \leq \tau < \tau_u$ , there are two steady states  $\mathbf{S}_0$  and  $\mathbf{S}_u$ , and if  $\tau \geq \tau_u$ ,  $\mathbf{S}_0$  is the only steady state; assume that  $\tau_u \leq 0 < \tau_w$ . Then, if  $0 \leq \tau < \tau_w$ , there are two steady states  $\mathbf{S}_0$  and  $\mathbf{S}_{\mathbf{w}\mathbf{u}}$ , if

$\tau \geq \tau_w$ ,  $\mathbf{S}_0$  is the only steady state; (iv) assume that  $0 < \tau_u < \tau_w$ . Then, if  $0 \leq \tau < \tau_u$ , there are three steady states  $\mathbf{S}_0$ ,  $\mathbf{S}_u$  and  $\mathbf{S}_{wu}$ , if  $\tau_u \leq \tau < \tau_w$ , there are two steady states  $\mathbf{S}_0$  and  $\mathbf{S}_{wu}$ , and if  $\tau \geq \tau_w$ ,  $\mathbf{S}_0$  is the only steady state.

The global stability of  $\mathbf{S}_0$  was obtained under the condition  $\tau > \frac{1}{\mu} \ln(\max\{P_w, P_u + P_{wu}\} / \min\{\mu_w, \mu_u\})$ . Therefore, the increase of the immature development time  $\tau$  (which could occur under decreasing temperature for example) leads both populations to extinction. Interestingly, the increase of the delay can also destabilize, by a Hopf bifurcation, the equilibria  $\mathbf{S}_u$  and  $\mathbf{S}_{wu}$ . For the equilibrium  $\mathbf{S}_u$ , we could determine analytically a threshold  $\tau_u^*$  for the appearance of Hopf bifurcation (Fig. 2). It depends on  $\tau_u$ ,  $\mu$ ,  $\mu_u$  and  $\eta$ , which are respectively the threshold for the existence of  $\mathbf{S}_u$ , the mortality rates of immature and mature uninfected individuals and the velocity at which the carrying capacity is achieved. In turn, the bigger  $\eta$  the wider the range of  $\tau$  wherein oscillations around  $\mathbf{S}_u$  are observed (Figs 3 and 4) as well as stability switch occurs earlier (*i.e.* for smaller  $\tau$  values). Observe that during the transient time, damped oscillations are seen in one of the components of  $\mathbf{S}_u$ . Although, we could not prove analytically the occurrence of Hopf bifurcation for the equilibrium  $\mathbf{S}_{wu}$ , we could get oscillations around this equilibrium numerically (Fig. 5).

For many arthropod-borne diseases such as Dengue, Zika, and others, vector control is the only available way to control the transmission of the disease to the human population. In this context, the threshold for the persistence of the disease depends on the ratio between the vector and the human population. As the mosquito infected with *Wolbachia* transmits the virus less than the wild mosquito, the increase in the population of infected mosquitoes with a good choice of bacterial strains (that promotes an increase of  $R_w$ ), can make interesting the technique proposed in this paper for mosquito control.

Several studies have addressed the importance of temperature on the dynamics of infected mosquitoes, since the spread and quantity of bacteria on mosquito tissues are modulated by this abiotic factor [34, 35]. Reproduction, dispersal, mating behavior, bacterial inheritance and cytoplasmic incompatibility can be strongly affected by temperature variations in the field. In our model, we varied the parameters  $R_u$  and  $R_w$  to take into account the change in these factors which could lead to the extinction of one or both populations, or their coexistence.

Based on observations both in laboratories and in nature, [34, 35], there is evidence of oscillations in mosquito populations due to the variation in temperature. We showed in this paper that an increase in the duration of the aquatic phase (the delay), due to a decrease in temperature, for instance, gives one of the following two scenarios. In the first scenario, an increase in the delay leads to the extinction of the infected mosquito and the persistence of the uninfected one (with oscillations that are first damped and then become periodic for the uninfected mosquito). In the second scenario, an increase in the delay maintains the persistence of the two populations with, first the appearance of damped oscillations and then the oscillations become periodic. The existence of periodic solutions can be rather simply understood from the mathematical point of view as produced by a Hopf bifurcation.

Finally, variation in temperature may make ineffective the use of *Wolbachia*-infected mosquito as a biological technique to reduce the population of wild mosquito. In addition, several types of infection adapted to different field conditions are necessary; besides, the right time for the release of infected mosquito to optimize the invasion and colonization of this population in an environment already occupied by the wild population is an important problem to be addressed. The present work may contribute to the study of the influence of abiotic factors on the temporal dynamics of mosquito population.

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## REFERENCES

- [1] T.H. Ant, C.S. Herd, V. Geoghegan, A.A. Hoffmann and S.P. Sinkins, The *wolbachia* strain wau provides highly efficient virus transmission blocking in *aedes aegypti*. *PLoS Pathogens* **14** (2018) e1006815.



- [2] Z.A. Awrahan, F. Champion de Crespigny and N. Wedell, The impact of *wolbachia*, male age and mating history on cytoplasmic incompatibility and sperm transfer in *drosophila simulans*. *J. Evolut. Biol.* **27** (2014) 1–10.
- [3] J.K. Axford, P.A. Ross, H.L. Yeap, A.G. Callahan and A.A. Hoffmann, Fitness of walbb *wolbachia* infection in *aedes aegypti*: parameter estimates in an outcrossed background and potential for population invasion. *Am. J. Trop. Med. Hygiene* **94** (2016) 507–516.
- [4] E. Beretta and Y. Kuang, Geometric stability switch criteria in delay differential systems with delay dependent parameters. *SIAM J. Math. Anal.* **33** (2002) 1144–1165.
- [5] L. Berezhansky, E. Braverman and L. Idels, Nicholson’s blowflies differential equations revisited: Main results and open problems. *Appl. Math. Model.* **34** (2010) 1405–1417.
- [6] L. Berezhansky, L. Idels and L. Troib, Global dynamics of nicholson-type delay systems with applications. *Nonlinear Anal.: Real World Appl.* **12** (2011) 436–445.
- [7] P.-A. Bliman, M.S. Aronna, F.C. Coelho and M.A. H.B. da Silva, Ensuring successful introduction of *wolbachia* in natural populations of *aedes aegypti* by means of feedback control. *J. Math. Biol.* **76** (2018) 1269–1300.
- [8] P.-A. Bliman, D. Cardona-Salgado, Y. Dumont and O. Vasilieva, Implementation of control strategies for sterile insect techniques. *Math. Biosci.* **314** (2019) 43–60.
- [9] S.R. Bordenstein and S.R. Bordenstein, Temperature affects the tripartite interactions between bacteriophage wo, *wolbachia*, and cytoplasmic incompatibility. *PLoS ONE* **6** (2011) e29106.
- [10] E. Braverman and D. Kinzebulatov, Nicholson’s blowflies equation with a distributed delay. *Can. Appl. Math. Quart.* **14** (2006) 107–128.
- [11] R.A. Costello, *Effects of environmental and physiological factors on the acoustic behavior of Aedes aegypti (L.) (Diptera: Culicidae)*. PhD thesis, University of Manitoba, Canada (1974).
- [12] C. Dye, Models for the population dynamics of the yellow fever mosquito, *Aedes aegypti*. *J. Animal Ecol.* **53** (1984) 247–268.
- [13] J.Z. Farkas and P. Hinow, Structured and unstructured continuous models for *wolbachia* infections. *Bull. Math. Biol.* **72** (2010) 2067–2088.
- [14] J.Z. Farkas, S.A. Gourley, R. Liu and A.A. Yakubu, Modelling *wolbachia* infection in a sex-structured mosquito population carrying west nile virus. *J. Math. Biol.* **75** (2017).
- [15] C.P. Ferreira, *Aedes aegypti* and *wolbachia* interaction: population persistence in a changing environment. *Theor. Ecol.* (2019).
- [16] C.P. Ferreira, H.M. Yang and L. Esteva, Assessing the suitability of sterile insect technique applied to *Aedes aegypti*. *J. Biol. Syst.* **16** (2008) 565–577.
- [17] D.J. Gubler, The global emergence/resurgence of arboviral diseases as public health problems. *Arch. Med. Res.* **33** (2002) 330–342.
- [18] N.D. Hayes, Roots of the transcendental equation associated with a certain difference-differential equation. *J. London Math. Soc.* (1950) 226–232.
- [19] S.P. Hernandez, A.M. Loaiza and C.A.A. Minoli, A reaction-diffusion model for controlling the *Aedes aegypti* with *wolbachia*. *Int. J. Contemp. Math. Sci.* **11** (2016) 385–394.
- [20] A.A. Hoffmann, B.L. Montgomery, J. Popovici, I. Iturbe-Ormaetxe, P.H. Johnson, F. Muzzi, M. Greenfield, M. Durkan, Y.S. Leonga, Y. Dong, H. Cook, J. Axford, A.G. Callahan, N. Kenny, C. Omodei, E.A. McGraw, P.A. Ryan, S.A. Ritchie, M. Turelli and S.L. O’Neill, Successful establishment of *wolbachia* in *aedes* populations to suppress dengue transmission. *Nature* **476** (2011) 454–457.
- [21] M. Huang, M.X. Tang and J.S. Yu, *Wolbachia* infection dynamics by reaction-diffusion equations. *Sci. China Math.* **58** (2015) 77–96.
- [22] M. Huang, J. Luo, L. Hu, B. Zheng and J. Yu, Assessing the efficiency of *wolbachia* driven *aedes* mosquito suppression by delay differential equations. *J. Theor. Biol.* **440** (2018).
- [23] M.G. Huang, M.X. Tang, J.S. Yu and B. Zheng, The impact of mating competitiveness and incomplete cytoplasmic incompatibility on *wolbachia*-driven mosquito population suppression. *Math. Biosci. Eng.* **16** (2019) 4741–4757.
- [24] H. Hughes and N. Britton, Modelling the use of *wolbachia* to control dengue fever transmission. *Bull. Math. Biol.* **75** (2013).
- [25] L. Idels and M Kipnis, Stability criteria for a nonlinear nonautonomous system with delays. *Appl. Math. Model.* **33** (2009) 2293–2297.
- [26] S. Lunel and J. Hale, Introduction to functional differential equations. In Vol. 99 of *Applied Mathematical Sciences*. Springer-Verlag (1993).
- [27] M. Keeling, F.M. Jiggins and J.M. Read, The invasion and coexistence of competing *wolbachia* strains. *Heredity* **91** (2003) 382–388.
- [28] J.G. King, C. Souto-Maior, L.M. Sartori, R.M. de Freitas and M. Gomes, Variation in *wolbachia* effects on *aedes* mosquitoes as a determinant of invasiveness and vectorial capacity. *Nat. Commun.* **9** (2018).
- [29] X. Ling, A.M. Carrie, T. Panpim and M.H. James, Two-sex mosquito model for the persistence of *wolbachia*. *J. Biol. Dyn.* **11** (2017) 216–237.
- [30] C.J. McMeniman, R.V. Lane, B.N. Cass, A.W.C. Fong, M. Sidhu, Y.-F. Wang and S.L. O’Neill, Stable introduction of a life-shortening *wolbachia* infection into the mosquito *Aedes aegypti*. *Science* **323** (2009) 141–144.
- [31] M. Ndiï, R. Hickson and G. Mercer, Modelling the introduction of *wolbachia* into *Aedes aegypti* mosquitoes to reduce dengue transmission. *ANZIAM J.* **53** (2012) 213–227.
- [32] Z. Qu, L. Xue and J. Hyman, Modeling the transmission of *wolbachia* in mosquitoes for controlling mosquito-borne diseases. *SIAM J. Appl. Math.* **78** (2018) 826–852.

- [33] M. Rafikov, E. Rafikova and H.M. Yang, Optimization of the *Aedes aegypti* control strategies for integrated vector management. *J. Appl. Math.* **2015** (2015) 918194.
- [34] J.M. Reinhold, C.R. Lazzari and C. Lahondère, Effects of the environmental temperature on *Aedes aegypti* and *Aedes albopictus* mosquitoes: a review. *Insects* **9** (2018) 158.
- [35] P.A. Ross, I. Wiwatanaratnabutr, J.K. Axford, V.L. White, N.M. Endersby-Harshman and A.A. Hoffmann, *Wolbachia* infections in *aedes aegypti* differ markedly in their response to cyclical heat stress (2017).
- [36] I.E. Leonard T. Hillen and H. Van Roessel, *Partial Differential Equations: Theory and Completely Solved Problems*. Wiley (2012).
- [37] Z. Veneti, M.E. Clark, T.L. Karr, C. Savakis and K. Bourtzis, Heads or tails: Host-parasite interactions in the *drosophila-wolbachia* system. *Appl. Environ. Microbiol.* **70** (2004) 5366–5372.
- [38] P.F. Viana-Medeiros, D.F. Bellinato, A.J. Martins and D. Valle, Insecticide resistance, associated mechanisms and fitness aspects in two Brazilian *Stegomyia aegypti* (= *Aedes aegypti*) populations. *Med. Veterin. Entomol.* **31** (2017) 340–350.
- [39] T. Walker, P.H. Johnson, L.A. Moreira, I. Iturbe-Ormaetxe, F.D. Frentiu, C.J. McMeniman, Y.S. Leong, Y. Dong, J. Axford, P. Kriesner, A.L. Lloyd, S.A. Ritchie, S.L. O’Neill and A.A. Hoffmann, The WMEL *wolbachia* strain blocks dengue and invades caged *Aedes aegypti* populations. *Nature* **475** (2011) 450–453.
- [40] Z. Xi, C.C. Khoo and S.L. Dobson, *Wolbachia* establishment and invasion in an *Aedes aegypti* laboratory population. *Science* **310** (2005) 326–328.
- [41] H.M. Yang and C.P. Ferreira, Assessing the effects of vector control on dengue transmission. *Appl. Math. Comput.* **198** (2008) 401–413.
- [42] H.M. Yang, M.L. Macoris, K.C. Galvani, M.T. Andrighetti and D.M. Wanderley, Assessing the effects of temperature on the population of *Aedes aegypti*, the vector of dengue. *Epidemiol. Infection* **137** (2009) 1188–1202.
- [43] H.L. Yeap, P. Mee, T. Walker, A.R. Weeks, S.L. O’Neill, P. Johnson, S.A. Ritchie, K.M. Richardson, C. Noteg, N.M. Endersby and A.A. Hoffmann, Dynamics of the ‘popcorn’ *wolbachia* infection in outbred *Aedes aegypti* informs prospects for mosquito vector control. *Genetics* **187** (2011) 583–595.