



*Research article*

## **Sex-structured wild and sterile mosquito population models with different release strategies**

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**Abstract:** In this paper, we propose sex-structured mathematical models in terms of continuous-time differential equations. We investigate the interactive dynamics of the sex-structured wild and sterile mosquitoes from several aspects including the existence of equilibria and their stability. We consider different strategies of releasing the sterile mosquitoes to control mosquitoes in an effective way. In addition, numerical simulations are provided to illustrate the dynamical features of the models.

**Keywords:** sex structure; mosquito-borne diseases; sterile mosquitoes; release strategies; Allee effects; stability

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### **1. Introduction**

Mosquito-borne diseases, such as malaria [24] and dengue fever [31], have become a considerable public health concern all over the world. These diseases are transmitted between human beings by blood-feeding mosquitoes. According to the latest World Malaria Report [38] released in November 2017, there were 216 million cases of malaria in 2016, up from 211 million cases in 2015, and estimated 445,000 people died in 2016 due to this mosquito-borne disease. An effective way to control the spread of diseases is to control or reduce mosquitoes. Among control measures, the sterile insect technique (SIT) has proven to be an important and environmentally-friendly way to control mosquito-borne diseases. Knipling [20, 21, 22] proposed control measures by subjecting insects to gamma radiation in order to block reproduction and sterilize them, and then releasing them into the wild

population. The released insects are preferably male, because female mosquitoes may damage crops by laying eggs or take blood from humans. A wild female mosquito that mates with a sterile male mosquito will either not reproduce, or produce eggs but the eggs will not hatch, thus reducing the size of the next generation mosquito population. Although SIT has been conducted in the laboratories, questions such as the assessment of the effects of releasing sterile mosquitoes into the field of wild mosquito populations are still keeping challenging [15, 22, 34, 39].

To gain insight into such challenging questions, mathematical models considering the sterile mosquitoes [3, 4, 5, 6, 7, 9, 13, 15, 17, 24, 26, 28, 36] are adopted more and more when it comes to study in population dynamics or epidemiology. In particular, dynamics of the interactive wild and sterile mosquitoes with different strategies of releasing sterile mosquitoes have been explored in several studies such as [9, 26, 27, 28]. Cai et al. [9] formulated continuous-time mathematical models for the interactive dynamics of the wild and sterile mosquitoes with different releasing strategies and the mosquito population had been assumed to be homogeneous without distinguishing their gender. Moreover, all mosquitoes go through four distinct stages (e.g., egg, pupa, larva, and adult) during their whole lifetime. The first three stages occur in water, but the adult are active in the air. Only the female mosquitoes bite and feed on the blood of human beings or other animals. Li et al. [27] divided the mosquito population into only two classes (the larvae and the adult) and formulated stage-structured mosquito population models with different strategies for releasing the sterile mosquitoes. Soon afterwards, Li [26] revised the models studied in [27] and formulated new models which considered the density dependence on the newborns survivals. In recent years, several interesting mathematical models have also been developed to investigate the dynamics of sterile mosquitoes, for instance, the discrete models in [29], the delayed models in [8], and the stage-structured discrete models in [30]. Discrete-time models for releases of sterile mosquitoes with Beverton-Holt-type of survivability were formulated by Y. Li and J. Li in [29]. In these discrete models, complexity in fact may not be created by the interaction of the wild and sterile mosquitoes but is from the Ricker type nonlinearity [28]. A similar technique by utilizing bacterial symbiont *Wolbachia* has also been applied to prevent and control Dengue Fever and Zika transmissions. Mathematical models, including those based on delay differential equations [19, 40], have been formulated recently to study the mosquito suppression dynamics. While these existing studies in the literature focused on applications of SIT to mosquitoes control have made significant progress to help us answer those challenging questions, most of them have assumed homogeneous populations or populations with stage structures without distinguishing the genders of mosquitoes.

Because the next generations of mosquitoes are produced by sexual reproduction and we only release sterile male mosquitoes into the environment, sex structure needs to be considered in mathematical models. Esteva et al. [15] proposed a sex-structured model to assess the effectiveness of SIT applied to the *Aedes aegypti* mosquito population. They divided the life cycle of an insect into two stages: the immature (eggs, larvae and pupae) and the adult (females before mating, mating fertilized females, mating unfertilized females, males). For the disadvantages of that study, theoretical analysis for the global asymptotic stability of the equilibria was not carried out. Recently, a sex-structured model was developed for a mosquito population infected with *Wolbachia* [16]. The model captured the key effects of *Wolbachia* infection including cytoplasmic incompatibility and male killing. The conditions for the existence and local stability of equilibria, including boundary equilibria, were obtained. As the progress on sexual structure mosquitoes populations has been made in those studies, the focus was on

other control measures than SIT, and the transmission mechanism for SIT is different.

In this paper, we include sexual structure in models for interactive wild and sterile mosquitoes following the line in [9, 26], and concentrate on the dynamics of the sex-structured models in the absence or presence of sterile mosquitoes and explore the impact of different strategies of releasing sterile mosquitoes on the model dynamics. We first consider the mosquito population with distinguishing male and female individuals in the absence of sterile mosquitoes, and the cases with or without Allee effects [1, 12] are both considered in the model formulation in Section 2. Complete mathematical analysis is performed. Then, we formulate a two-sex model in the presence of sterile mosquitoes, where the release rate of sterile mosquitoes is constant in Section 3. To have a more optimal and economically effective strategy [2, 32] in an area where the population size of wild mosquitoes is relatively small, we establish a model with the release rate of sterile mosquitoes proportional to the population size of the wild male mosquitoes in Section 4. Since it is possibly difficult for mosquitoes to find mates in an area with small population size, we incorporate the Allee effects in the model formulation. We provide complete mathematical analysis and numerical simulations to show the complexity of the model dynamics as well. We finally give brief discussions in Section 5.

## 2. In the absence of sterile mosquitoes

We first consider, in the absence of sterile mosquitoes, two different situations where the wild mosquito population size is sufficiently large or relatively small so that the Allee effects need to be included or not.

### 2.1. Without Allee effects

Let  $F$  and  $M$  be the wild female and male mosquito populations. If no Allee effect is included, the model equations are given by

$$\begin{aligned} F' &= \alpha CF \left(1 - \frac{F+M}{K}\right) - \mu_F F, \\ M' &= (1-\alpha)CF \left(1 - \frac{F+M}{K}\right) - \mu_M M. \end{aligned} \quad (2.1)$$

where  $\alpha$  is the fraction of female newborns,  $C$  is the number of wild offspring produced per unit time, per female mosquito through all mating [2, 10, 14, 18, 35, 37], and  $\mu_F$  and  $\mu_M$  are the death rates of the wild female and male mosquito respectively. Notice that the  $M$ -axis is an invariant set of system (2.1). Then the set

$$\Omega_1 := \{(F, M) : 0 \leq F + M \leq K\}$$

is a positively invariant and attracting set for the flows of (2.1) in the nonnegative quadrant.

The origin is an equilibrium, and the Jacobian matrix of system (2.1) at the origin is

$$\begin{pmatrix} \alpha C - \mu_F & 0 \\ \cdot & -\mu_M \end{pmatrix} = \begin{pmatrix} \mu_F(r_0 - 1) & 0 \\ \cdot & -\mu_M \end{pmatrix},$$

where

$$r_0 := \frac{\alpha C}{\mu_F} \quad (2.2)$$

is the intrinsic growth rate, which is the difference between an average birth rate and an average death rate. As the mosquito population persistently exists in nature, we assume  $r_0 > 1$ . Under this assumption, it is easy to prove that the origin is unstable.

We next consider positive equilibria of system (2.1) which we denote as  $(F^*, M^*)$ . A positive equilibrium satisfies

$$\begin{aligned}\alpha C \left(1 - \frac{F^* + M^*}{K}\right) &= \mu_F, \\ (1 - \alpha)CF^* \left(1 - \frac{F^* + M^*}{K}\right) &= \mu_M M^*.\end{aligned}\tag{2.3}$$

It follows from (2.3) that

$$F^* = \frac{\alpha\mu_M}{(1 - \alpha)\mu_F} M^* := PM^*.\tag{2.4}$$

Substituting (2.4) into (2.3), we have

$$F^* = PM^*, \quad M^* = \left(\frac{\alpha C}{\mu_F} - 1\right) \frac{K\mu_F}{\alpha C(1 + P)} = (r_0 - 1) \frac{K\mu_F}{\alpha C(1 + P)}.\tag{2.5}$$

Then there exists a unique positive equilibrium  $E_0^* := (F^*, M^*)$  if and only if  $r_0 > 1$ .

The Jacobian matrix at  $E_0^*$  has the form

$$J_0 := \begin{pmatrix} -\frac{\alpha C}{K} F^* & -\frac{\alpha C}{K} F^* \\ (1 - \alpha)C \left(1 - \frac{2F^* + M^*}{K}\right) & -\frac{(1 - \alpha)C}{K} F^* - \mu_M \end{pmatrix}.$$

Then

$$\text{tr} J_0 = -\frac{C}{K} F^* - \mu_M < 0,$$

and

$$\det J_0 = \frac{\alpha C}{K} F^* \left( (1 - \alpha)C \left(1 - \frac{F^* + M^*}{K}\right) + \mu_M \right) > 0,$$

Thus  $E_0^*$  is locally asymptotically stable.

Write the right-hand side of system (2.1) as  $f_1$  and  $f_2$ , respectively. Then it follows from

$$\frac{\partial}{\partial F} \left(\frac{f_1}{F}\right) + \frac{\partial}{\partial M} \left(\frac{f_2}{F}\right) < 0,$$

for  $F > 0$  and  $M > 0$ , that system (2.1) has no closed orbits.

In summary, we have the following results.

**Theorem 2.1.** *For the system (2.1), the origin  $(0, 0)$  is globally asymptotically stable if  $r_0 \leq 1$  and unstable if  $r_0 > 1$ . There exists a unique positive equilibrium  $E_0^*$  given by (2.5) if and only if  $r_0 > 1$  and this unique positive equilibrium is globally asymptotically stable if it exists.*

## 2.2. With Allee effects

We now incorporate the Allee effect [33] to account for the difficulty and stochasticity of finding mates when the population of mosquitoes is small. Then we consider the following model equations

$$\begin{aligned} F' &= \alpha CF \frac{M}{\gamma + M} \left(1 - \frac{F + M}{K}\right) - \mu_F F, \\ M' &= (1 - \alpha)CF \frac{M}{\gamma + M} \left(1 - \frac{F + M}{K}\right) - \mu_M M, \end{aligned} \quad (2.6)$$

where  $\gamma > 0$  is a parameter to characterize the Allee effects.

Clearly, set  $\Omega_1$  is also a positively invariant and attracting set for the flows of (2.6) in the nonnegative quadrant.

The origin  $(0, 0)$  is an equilibrium and the eigenvalues of the Jacobian at it are  $-\mu_F$  and  $-\mu_M$ . Thus it is always locally asymptotically stable.

We then investigate the existence of positive equilibria which satisfy

$$\begin{aligned} \alpha C \frac{M}{\gamma + M} \left(1 - \frac{F + M}{K}\right) &= \mu_F, \\ (1 - \alpha)C \frac{F}{\gamma + M} \left(1 - \frac{F + M}{K}\right) &= \mu_M. \end{aligned} \quad (2.7)$$

Similarly as in (2.4), we have  $F = PM$ . Substituting it into the first equation in (2.7), we have

$$\alpha CM(K - (1 + P)M) = \mu_F K(\gamma + M), \quad (2.8)$$

or, equivalently, the following quadratic equation

$$\alpha C(1 + P)M^2 + K(\mu_F - \alpha C)M + \mu_F K\gamma = 0. \quad (2.9)$$

Then there exists no, one positive equilibrium  $(F, M) = (PM, M)$  with

$$M = \frac{K(\alpha C - \mu_F)}{2\alpha C(1 + P)},$$

or two positive equilibria  $(PM^-, M^-)$  and  $(PM^+, M^+)$  where

$$M^\mp = \frac{K(\alpha C - \mu_F) \mp \sqrt{\Delta}}{2\alpha C(1 + P)} \quad (2.10)$$

with

$$\Delta := K^2(\mu_F - \alpha C)^2 - 4\alpha C\mu_F K\gamma(1 + P), \quad (2.11)$$

if  $\Delta < 0$ ,  $\Delta = 0$ , or  $\Delta > 0$ , respectively.

We next determine the stability of the positive equilibria as follows.

The Jacobian matrix of system (2.6) at an equilibrium has the form

$$J_1 := \begin{pmatrix} \frac{\alpha CFM}{K(\gamma + M)} & \frac{\mu_F \gamma F}{M(\gamma + M)} - \frac{\alpha CFM}{K(\gamma + M)} \\ \frac{\mu_M M}{F} - \frac{(1 - \alpha)CFM}{K(\gamma + M)} & -\frac{\mu_M M}{\gamma + M} - \frac{(1 - \alpha)CFM}{K(\gamma + M)} \end{pmatrix}. \quad (2.12)$$

It is clear that  $\text{tr}J_1 < 0$  and

$$\begin{aligned} \det J_1 &= \frac{\alpha C \mu_M F M^2}{K(\gamma + M)^2} + \frac{\alpha(1 - \alpha)C^2 F^2 M^2}{K^2(\gamma + M)^2} \\ &\quad - \frac{\mu_F \mu_M \gamma}{\gamma + M} + \frac{\alpha C \mu_M M^2}{K(\gamma + M)} + \frac{(1 - \alpha)C \mu_F \gamma F^2}{K(\gamma + M)^2} - \frac{\alpha(1 - \alpha)C^2 F^2 M^2}{K^2(\gamma + M)^2} \\ &= \frac{\alpha C \mu_M F M^2}{K(\gamma + M)^2} - \frac{\mu_F \mu_M \gamma}{\gamma + M} + \frac{\alpha C \mu_M M^2}{K(\gamma + M)} + \frac{(1 - \alpha)C \mu_F \gamma F^2}{K(\gamma + M)^2}, \end{aligned}$$

that is,

$$\begin{aligned} (K(\gamma + M)^2) \det J_1 &= \alpha C \mu_M F M^2 + (1 - \alpha)C \mu_F \gamma F^2 + (\alpha C \mu_M M^2 - K \mu_F \mu_M \gamma)(\gamma + M) \\ &= \alpha C \mu_M P M^3 + (1 - \alpha)C \mu_F \gamma P^2 M^2 + \alpha C \mu_M M^3 \\ &\quad + \alpha C \mu_M \gamma M^2 - \mu_F \gamma K(\gamma + M) \mu_M. \end{aligned}$$

It then follows from (2.8) that

$$\begin{aligned} (K(\gamma + M)^2) \det J_1 &= \alpha C \mu_M (1 + P) M^3 + C \gamma ((1 - \alpha) \mu_F P^2 + \alpha \mu_M) M^2 \\ &\quad - \alpha C \gamma M (K - (1 + P) M) \mu_M, \end{aligned}$$

that is,

$$\begin{aligned} \frac{K(\gamma + M)^2}{CM} \det J_1 &= \alpha \mu_M (1 + P) M^2 + \gamma ((1 - \alpha) \mu_F P^2 + \alpha \mu_M + \alpha \mu_M (1 + P)) M \\ &\quad - \alpha \mu_M \gamma K. \end{aligned} \quad (2.13)$$

Write the right-hand side of (2.13) as quadratic function  $H(M)$ . Then the unique positive root of  $H(M)$  is

$$\begin{aligned} M_c &:= \frac{\sqrt{\gamma^2 ((1 - \alpha) \mu_F P^2 + \alpha \mu_M + \alpha \mu_M (1 + P))^2 + 4 \alpha^2 \mu_M^2 \gamma (1 + P) K}}{2 \alpha \mu_M (1 + P)} \\ &\quad - \frac{\gamma ((1 - \alpha) \mu_F P^2 + \alpha \mu_M + \alpha \mu_M (1 + P))}{2 \alpha \mu_M (1 + P)}. \end{aligned} \quad (2.14)$$

It follows from

$$P = \frac{\alpha \mu_M}{(1 - \alpha) \mu_F}$$

that

$$\begin{aligned} (1 - \alpha) \mu_F P^2 + \alpha \mu_M + \alpha \mu_M (1 + P) &= \alpha \mu_M P + \alpha \mu_M + \alpha \mu_M (1 + P) \\ &= 2 \alpha \mu_M (1 + P). \end{aligned} \quad (2.15)$$

Thus

$$\begin{aligned} &\gamma^2 ((1 - \alpha) \mu_F P^2 + \alpha \mu_M + \mu_M \alpha (1 + P))^2 + 4 \alpha^2 \mu_M^2 \gamma (1 + P) K \\ &= \gamma^2 (2 \alpha \mu_M (1 + P))^2 + 4 \alpha^2 \mu_M^2 \gamma (1 + P) K \\ &= (2 \alpha \mu_M)^2 \gamma (1 + P) (\gamma (1 + P) + K), \end{aligned} \quad (2.16)$$

and hence

$$M_c = \frac{\sqrt{\gamma(1+P)(\gamma(1+P)+K)}}{1+P} - \gamma = \sqrt{\gamma\left(\gamma + \frac{K}{1+P}\right)} - \gamma. \quad (2.17)$$

Suppose  $\Delta > 0$  such that there exist two positive equilibria  $M^\mp$ . Notice that  $H(0) = -\alpha\mu_M K < 0$  and  $H(M_c) = 0$ . If  $M^- < M_c$  and  $M^+ > M_c$ , and thus

$$H(M^-) = \frac{K(\gamma + M^-)^2}{CM^-} \det J_1|_{M^-} < 0, \quad H(M^+) = \frac{K(\gamma + M^+)^2}{CM^+} \det J_1|_{M^+} > 0,$$

then equilibrium  $(PM^-, M^-)$  is unstable and  $(PM^+, M^+)$  is locally asymptotically stable.

To this end, we first consider

$$\alpha C(1+P)(M^- - M_c)(M^+ - M_c) = Q(M_c). \quad (2.18)$$

Then, it is clear that to show  $M^- < M_c$  and  $M^+ > M_c$  is equivalent to show  $Q(M_c) < 0$ .

It follows from (2.9) that

$$\begin{aligned} Q(M_c) &= \alpha C(1+P)M_c^2 + K(\mu_F - \alpha C)M_c + \mu_F K\gamma \\ &= \alpha C(1+P) \left( \sqrt{\gamma\left(\gamma + \frac{K}{1+P}\right)} - \gamma \right)^2 \\ &\quad + K(\mu_F - \alpha C) \left( \sqrt{\gamma\left(\gamma + \frac{K}{1+P}\right)} - \gamma \right) + \mu_F K\gamma \\ &= \alpha C(1+P) \left( \gamma\left(2\gamma + \frac{K}{1+P}\right) - 2\sqrt{\gamma\left(\gamma + \frac{K}{1+P}\right)} \right) \\ &\quad + K(\mu_F - \alpha C) \left( \sqrt{\gamma\left(\gamma + \frac{K}{1+P}\right)} - \gamma \right) + \mu_F K\gamma \\ &= 2\alpha C(1+P)\gamma^2 + 2\alpha CK\gamma - 2\alpha C(1+P)\gamma \sqrt{\gamma\left(\gamma + \frac{K}{1+P}\right)} \\ &\quad + K(\mu_F - \alpha C) \sqrt{\gamma\left(\gamma + \frac{K}{1+P}\right)}. \end{aligned}$$

Thus  $Q(M_c) < 0$  if and only if

$$2\alpha C\gamma((1+P)\gamma + K) < (2\alpha C(1+P)\gamma + K(\alpha C - \mu_F)) \sqrt{\gamma\left(\gamma + \frac{K}{1+P}\right)}. \quad (2.19)$$

By squaring both sides of (2.19), it is equivalent to

$$(1+P)(2\alpha C)^2\gamma^2((1+P)\gamma + K)^2 < (2\alpha C(1+P)\gamma + K(\alpha C - \mu_F))^2\gamma(1+P)\gamma + K),$$

which leads to

$$(1+P)(2\alpha C)^2\gamma((1+P)\gamma + K) < (2\alpha C(1+P)\gamma + K(\alpha C - \mu_F))^2,$$

that is,

$$\begin{aligned} (2\alpha C)^2 (1 + P)^2 \gamma^2 + (2\alpha C)^2 (1 + P) K \gamma < (2\alpha C (1 + P) \gamma + K (\alpha C - \mu_F))^2 \\ = (2\alpha C (1 + P) \gamma)^2 + (2\alpha C)^2 (1 + P) K \gamma - 4\alpha C (1 + P) \gamma K \mu_F + K^2 (\alpha C - \mu_F)^2, \end{aligned}$$

or

$$0 < -4\alpha C (1 + P) \gamma K \mu_F + K^2 (\alpha C - \mu_F)^2 = \Delta.$$

Hence, if  $\Delta > 0$  such that there exist two positive equilibria  $M^\mp$ , equilibrium  $(PM^-, M^-)$  is unstable and  $(PM^+, M^+)$  is locally asymptotically stable.

Moreover, write the right-hand side of system (2.6) as  $g_1$  and  $g_2$ , respectively, and  $D := \frac{\gamma + M}{FM}$  for  $FM > 0$ . Then it follows from

$$\frac{\partial (g_1 D)}{\partial F} + \frac{\partial (g_2 D)}{\partial M} < 0,$$

for  $F > 0$  and  $M > 0$ , that system (2.6) has no closed orbits.

The existence and stability of all equilibria of system (2.6) can be summarized as follows.

**Theorem 2.2.** *For system (2.6) with Allee effects, we have the following results with  $\Delta$  given in (2.11).*

1. *System (2.6) has no closed orbits.*
2. *If  $\Delta < 0$ , there exists no positive equilibrium and the origin  $(0, 0)$  is globally asymptotically stable.*
3. *If  $\Delta = 0$ , there exists one positive equilibrium  $(F, M) = (PM, M)$  which is an unstable saddle-node and the origin  $(0, 0)$  is locally asymptotically stable.*
4. *If  $\Delta > 0$ , there exist two positive equilibria  $(PM^-, M^-)$  and  $(PM^+, M^+)$  where  $M^\mp$  are given in (2.10). The origin  $(0, 0)$  is locally asymptotically stable, equilibrium  $(PM^-, M^-)$  is unstable and equilibrium  $(PM^+, M^+)$  is locally asymptotically stable.*

### 3. Constant releases of sterile mosquitoes

Let  $\tilde{M}$  be the sterile mosquito population and  $\mu_2$  be the death rate of the sterile mosquitoes. We now assume that sterile mosquitoes are released constantly into the wild mosquito field. Since, in this case, mosquitoes should always be able to find mates, Allee effects need not be included. Then the model equations for the wild mosquitoes are based on (2.1) and the interactive dynamics are governed by the system

$$\begin{aligned} F' &= \alpha C F \frac{M}{M + \beta \tilde{M}} \left( 1 - \frac{F + M}{K} \right) - \mu_F F, \\ M' &= (1 - \alpha) C F \frac{M}{M + \beta \tilde{M}} \left( 1 - \frac{F + M}{K} \right) - \mu_M M, \\ \tilde{M}' &= b - \mu_2 \tilde{M}, \end{aligned} \tag{3.1}$$

where  $\beta$  measures the competition between wild and sterile male mosquitoes for female mates.

The equation for  $\tilde{M}'$  is decoupled from the first two equations in (3.1) and it is clear that  $\lim_{t \rightarrow \infty} \tilde{M} = \frac{b}{\mu_2} := \tilde{M}_0$ . Then since the  $F$ - and  $M$ -axes both are an invariant set of system (3.1), the planar set

$$\Omega_2 := \{(F, M, \tilde{M}) : 0 \leq F + M \leq K, \tilde{M} = \tilde{M}_0\}$$



is a positively invariant and attracting set for the flows of (3.1) in the nonnegative octant. Moreover, write the right-hand sides of the first two equations in (3.1) as  $h_1$  and  $h_2$ , respectively. Then it follows from

$$\frac{\partial(h_1L)}{\partial F} + \frac{\partial(h_2L)}{\partial M} = -\frac{\alpha C}{K(M + \beta\tilde{M})} - \frac{(1 - \alpha)C}{(M + \beta\tilde{M})^2} \left(1 - \frac{F + M}{K}\right) - \frac{(1 - \alpha)C}{K(M + \beta\tilde{M})} < 0,$$

where  $L = \frac{1}{FM}$ , that system (3.1) has no closed orbits in the interior of  $\Omega_2$ .

System (2.6) has a boundary equilibrium  $E_0 := (0, 0, \tilde{M}_0)$  with  $\tilde{M}_0 := b/\mu_2$ , and the eigenvalues of the Jacobian at  $E_0$  are  $-\mu_F$ ,  $-\mu_M$ , and  $-\mu_2$ . Thus boundary equilibrium  $E_0$  is always locally asymptotically stable.

We then investigate the existence of positive equilibria which satisfy

$$\begin{aligned} \alpha C \frac{M}{M + \beta\tilde{M}} \left(1 - \frac{F + M}{K}\right) &= \mu_F, \\ (1 - \alpha)C \frac{F}{M + \beta\tilde{M}} \left(1 - \frac{F + M}{K}\right) &= \mu_M, \\ b &= \mu_2\tilde{M}. \end{aligned} \tag{3.2}$$

At a positive equilibrium,  $\tilde{M} = \tilde{M}_0$ . Substituting it into the first two equations in (3.2) and letting  $\gamma = \beta\tilde{M}_0$  in system (2.7), we can immediately obtain, from (2.11), the existence threshold

$$\Delta_c = K^2(\mu_F - \alpha C)^2 - 4\alpha C\mu_F K\beta\tilde{M}_0(1 + P) = K^2(\mu_F - \alpha C)^2 - 4\alpha C\mu_F K\beta(1 + P)\frac{b}{\mu_2},$$

and then define the threshold value for the sterile mosquito release rate as

$$b_c := \frac{K^2(\mu_F - \alpha C)^2\mu_2}{4\alpha C\mu_F K\beta(1 + P)} = \frac{K(\mu_F - \alpha C)^2\mu_2(1 - \alpha)}{4\alpha C\beta(\alpha\mu_M + (1 - \alpha)\mu_F)}. \tag{3.3}$$

Thus there exists no, one positive equilibrium  $(F, M, \tilde{M}_0) = (PM_c, M_c, \tilde{M}_0)$  where

$$M_c = \frac{K(\alpha C - \mu_F)}{2\alpha C(1 + P)},$$

or two positive equilibria  $E_c^- := (PM_c^-, M_c^-, \tilde{M}_0)$  and  $E_c^+ := (PM_c^+, M_c^+, \tilde{M}_0)$  where

$$\begin{aligned} M_c^\mp &= \frac{K(\alpha C - \mu_F) \mp 2\sqrt{\frac{\alpha C\mu_F K\beta(1 + P)}{\mu_2}}\sqrt{b_c - b}}{2\alpha C(1 + P)} \\ &= \frac{K\mu_2(\alpha C - \mu_F) \mp 2\sqrt{\alpha C\mu_F\mu_2 K\beta(1 + P)(b_c - b)}}{2\alpha C\mu_2(1 + P)}, \end{aligned} \tag{3.4}$$

if  $b > b_c$ ,  $b = b_c$ , or  $b < b_c$ , respectively.

In the case of  $b > b_c$ , there is no positive equilibrium and then the only boundary equilibrium  $E_0$  is globally asymptotically stable. If  $b < b_c$ , because of the attractability of region  $\Omega_2$ , it follows again from Section 2.2 that equilibrium  $E_c^-$  is unstable and  $E_c^+$  is locally asymptotically stable. In summary, we have the following results.

**Theorem 3.1.** Define threshold  $b_c$  in (3.3) for the releases of sterile mosquitoes for system (3.1). Then

1. System (3.1) has no closed orbits.
2. If  $b > b_c$ , there is no positive equilibrium and the boundary equilibrium  $E_0$  is globally asymptotically stable.
3. If  $b = b_c$ , there is one positive equilibrium  $(F, M, \tilde{M})$  which is an unstable saddle-node, and the boundary equilibrium  $E_0$  is locally asymptotically stable.
4. If  $b < b_c$ , there are two positive equilibrium  $E_c^-$  and  $E_c^+$ . Equilibrium  $E_c^-$  is unstable and  $E_c^+$  is locally asymptotically stable.

To confirm our theoretical results, a numerical example for the constant release of sterile mosquitoes is given below.

*Example 1.* Parameters are given as

$$\alpha = 0.5, C = 10, \mu_F = 0.5, \mu_M = 0.5, \mu_2 = 0.6, K = 6, \beta = 0.5 \quad (3.5)$$

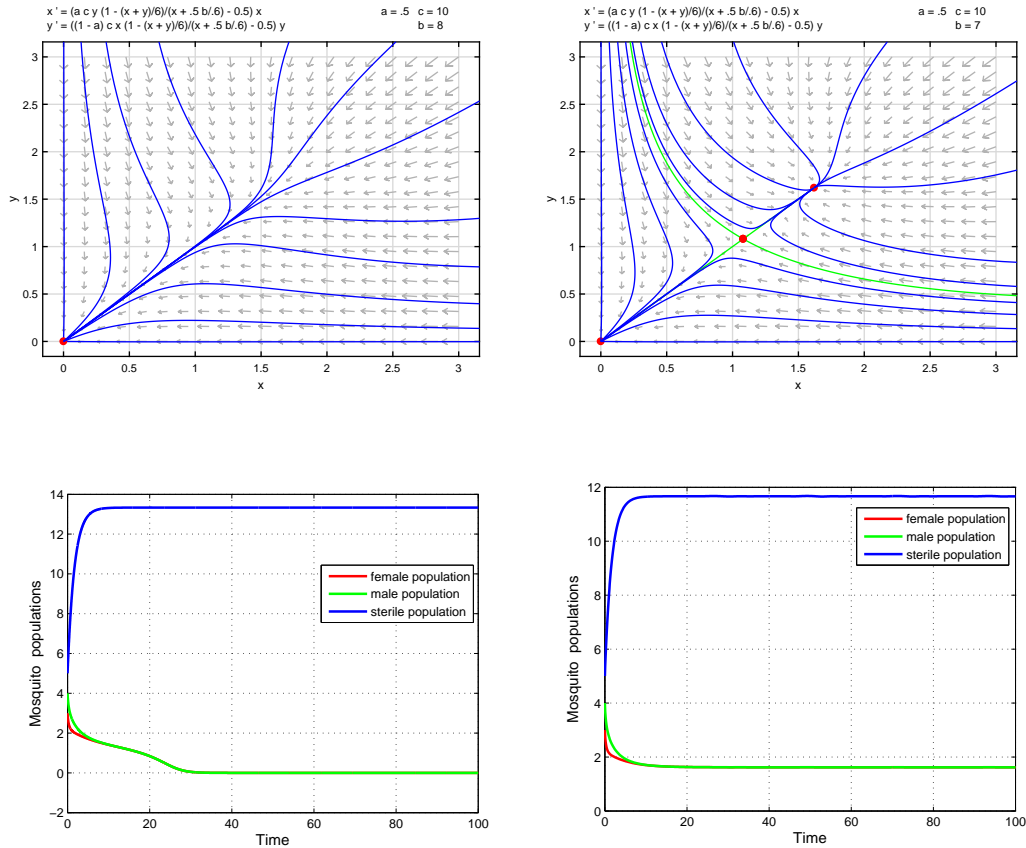
such that the release threshold is  $b_c = 7.29$ . For  $b = 8 > b_c$ , there exists no positive equilibrium. All solutions approach boundary equilibrium  $E_0 = (0, 0, 13.33)$ , as shown in the upper left figure in Figure 1. For  $b = 7 < b_c$ , there exist two positive equilibria  $E_c^- = (1.0902, 1.0902, 11.67)$  and  $E_c^+ = (1.6098, 1.6098, 11.67)$ . Equilibrium  $E_c^-$  is an unstable saddle and  $E_c^+$  is a stable node. Solutions approach either the boundary equilibrium or  $E_c^+$  depending on their initial values, as shown in the upper right figure in Figure 1. (The trajectories versus time  $t$  are also provided in the lower figures in Figure 1.) The wild mosquitoes may be wiped out, or the two types of mosquitoes may coexist, depending on the initial sizes of the wild and sterile mosquitoes in this case.

#### 4. Releases proportional to the wild male mosquito population

In this section, we assume that the release rate of sterile mosquitoes is proportional to the wild male mosquito population size. Considering the sterile mosquitoes compete with the wild male mosquitoes and the sex ratio remains a constant at the positive equilibria, we establish the model with the release rate proportional to only the wild male mosquito population size, which will have little bearing on the result. Moreover, as stated in [2], the effectiveness of SIT is related to the ratio of released sterile males to wild fertile males. In the case where both the wild mosquito population density and the initial sterile mosquito population density are small, mosquitoes may have difficulty finding mates. Then, Allee effects are included in the model, and the model equations for the wild mosquitoes are based on (2.6) and the interactive dynamics are governed by the following system:

$$\begin{aligned} F' &= \alpha CF \frac{M}{1 + M + \beta \tilde{M}} \left( 1 - \frac{F + M}{K} \right) - \mu_F F, \\ M' &= (1 - \alpha) CF \frac{M}{1 + M + \beta \tilde{M}} \left( 1 - \frac{F + M}{K} \right) - \mu_M M, \\ \tilde{M}' &= bM - \mu_2 \tilde{M}, \end{aligned} \quad (4.1)$$

where, similarly,  $\beta$  measures the competition between wild and sterile male mosquitoes for female mates.



**Figure 1.** Parameters are given in (3.5) and the release threshold is  $b_c = 7.29$ . For  $b = 8 > b_c$ , there exists no positive equilibrium. All solutions approach boundary equilibrium  $E_0 = (0, 0, 13.33)$ , as shown in the upper left figure. For  $b = 7 < b_c$ , there exists two positive equilibria  $E_c^- = (1.0902, 1.0902, 11.67)$  and  $E_c^+ = (0.6098, 1.6098, 11.67)$ , as provided in the right-side figure. Equilibrium  $E_c^-$  is an unstable and  $E_c^+$  is a stable node. Solutions approach either boundary equilibrium  $E_0$  or  $E_c^+$  depending on their initial values. The trajectories versus time  $t$  are also provided in the two lower figures, where solutions approach  $E_0$  as on the left figure and approach  $E_c^+$  as on the right figure.

In the nonnegative octant, it is clear that the  $M\tilde{M}$ - and  $F\tilde{M}$ - planes are both an invariant set of system (4.1). On the  $FM$ - plane,  $\tilde{M}' \geq 0$ . Hence the set

$$\Omega_3 := \left\{ (F, M, \tilde{M}) : 0 \leq F + M \leq K, 0 \leq \tilde{M} \leq \frac{bK}{\mu_2} \right\}$$

is a positively invariant and attracting set for the flows of (4.1) in the nonnegative octant.

System (4.1) now has the origin  $(0, 0, 0)$  as a trivial equilibrium and the eigenvalues of the Jacobian at it are  $-\mu_F$ ,  $-\mu_M$ , and  $-\mu_2$ . Thus the origin  $(0, 0, 0)$  is always locally asymptotically stable. It follows from the third equation in system (4.1) that if  $M = 0$ , then  $\tilde{M} = 0$  and  $F = 0$ ; if  $\tilde{M} = 0$ , then  $M = 0$  and  $F = 0$ ; and if  $F = 0$ , then  $M = 0$  and  $\tilde{M} = 0$ . Hence there exists no boundary equilibrium for system (4.1).

We then investigate the existence of positive equilibria which satisfy

$$\begin{aligned} \alpha C \frac{M}{1 + M + \beta \tilde{M}} \left( 1 - \frac{F + M}{K} \right) &= \mu_F, \\ (1 - \alpha) C \frac{F}{1 + M + \beta \tilde{M}} \left( 1 - \frac{F + M}{K} \right) &= \mu_M, \\ \tilde{M} &= \frac{bM}{\mu_2}. \end{aligned} \quad (4.2)$$

Substituting  $\tilde{M}$  into the first two equations in (4.2), we have

$$\begin{aligned} \alpha C \frac{M}{1 + \left( 1 + \frac{b\beta}{\mu_2} \right) M} \left( 1 - \frac{F + M}{K} \right) &= \mu_F, \\ (1 - \alpha) C \frac{F}{1 + \left( 1 + \frac{b\beta}{\mu_2} \right) M} \left( 1 - \frac{F + M}{K} \right) &= \mu_M. \end{aligned} \quad (4.3)$$

Let

$$\bar{\gamma} = \frac{\mu_2}{\mu_2 + b\beta}, \quad \bar{C} := C\bar{\gamma}.$$

Then system (4.3) becomes

$$\begin{aligned} \alpha \bar{C} \frac{M}{\bar{\gamma} + M} \left( 1 - \frac{F + M}{K} \right) &= \mu_F, \\ (1 - \alpha) \bar{C} \frac{F}{\bar{\gamma} + M} \left( 1 - \frac{F + M}{K} \right) &= \mu_M. \end{aligned} \quad (4.4)$$

Based on the results of system (2.7) and equation (2.9), the corresponding quadratic equation is

$$\alpha \bar{C} (1 + P) M^2 + K(\mu_F - \alpha \bar{C}) M + \mu_F K \bar{\gamma} = 0, \quad (4.5)$$

and the threshold value of sterile mosquito releases has the form

$$\begin{aligned} \Delta_p &= K^2 (\alpha \bar{C} - \mu_F)^2 - 4\alpha \bar{C} \mu_F K \bar{\gamma} (1 + P) \\ &= K^2 \left( \frac{\alpha C \mu_2}{\mu_2 + b\beta} - \mu_F \right)^2 - 4\alpha C \mu_F K \left( \frac{\mu_2}{\mu_2 + b\beta} \right)^2 \frac{\alpha \mu_M + (1 - \alpha) \mu_F}{(1 - \alpha) \mu_F}. \end{aligned} \quad (4.6)$$

Solving for  $b > 0$  in (4.6), we then define the threshold value for the sterile mosquito per capita release rate for system (4.1) as

$$b_p := \mu_2 \frac{(\alpha C - \mu_F) \sqrt{K(1 - \alpha)} - 2 \sqrt{\alpha C(\alpha \mu_M + (1 - \alpha)\mu_F)}}{\beta \mu_F \sqrt{K(1 - \alpha)}}, \tag{4.7}$$

such that there exists no, one positive equilibrium  $E^* = \left(F^*, M^*, \frac{b}{\mu_2} M^*\right)$  where

$$M^* = \frac{K(\alpha \bar{C} - \mu_F)}{2\alpha \bar{C}(1 + P)} = \frac{K(\alpha C \bar{\gamma} - \mu_F)}{2\alpha C \bar{\gamma}(1 + P)} = \frac{K(\alpha C - \mu_F(1 + \frac{\beta b}{\mu_2}))}{2\alpha C(1 + P)},$$

or two positive equilibria  $E_p^- := \left(P M_p^-, M_p^-, \frac{b}{\mu_2} M_p^-\right)$  and  $E_p^+ := \left(P M_p^+, M_p^+, \frac{b}{\mu_2} M_p^+\right)$  where

$$\begin{aligned} M_p^\mp &= \frac{K(\alpha \bar{C} - \mu_F) \mp \sqrt{K^2(\alpha \bar{C} - \mu_F)^2 - 4\alpha \bar{C}(1 + P)\mu_F K \bar{\gamma}}}{2\alpha \bar{C}(1 + P)} \\ &= \frac{K(\alpha C - \mu_F(1 + \frac{\beta b}{\mu_2})) \mp \sqrt{K^2(\alpha C - \mu_F(1 + \frac{\beta b}{\mu_2}))^2 - 4\alpha C(1 + P)\mu_F K}}{2\alpha C(1 + P)}, \end{aligned} \tag{4.8}$$

if  $b > b_p$ ,  $b = b_p$ , or  $b < b_p$ , respectively.

We next determine the stability of the positive equilibria as follows.

The Jacobian matrix of system (4.1) at an equilibrium has the form

$$J_2 := \begin{pmatrix} -\frac{\alpha CFM}{K(1 + M + \beta \tilde{M}_0)} & \frac{\mu_F(1 + \beta \tilde{M}_0)F}{M(1 + M + \beta \tilde{M}_0)} & -\frac{\alpha CFM}{K(1 + M + \beta \tilde{M}_0)} & -\frac{\beta \mu_F F}{1 + M + \beta \tilde{M}_0} \\ \frac{\mu_M M}{F} - \frac{(1 - \alpha)CFM}{K(1 + M + \beta \tilde{M}_0)} & -\frac{\mu_M M}{1 + M + \beta \tilde{M}_0} & -\frac{(1 - \alpha)CFM}{K(1 + M + \beta \tilde{M}_0)} & -\frac{\beta \mu_M M}{1 + M + \beta \tilde{M}_0} \\ 0 & b & 0 & -\mu_2 \end{pmatrix}. \tag{4.9}$$

It is clear that  $\text{tr} J_2 < 0$ . We then compute the determinant of  $\det J_2$ .

Simple algebra yields

$$\begin{aligned} \det J_2 &= \begin{vmatrix} -\frac{\alpha}{1 - \alpha} \cdot \frac{\mu_M M}{F} & \frac{\mu_F(1 + \beta \tilde{M}_0)F}{M(1 + M + \beta \tilde{M}_0)} + \frac{\alpha}{1 - \alpha} \cdot \frac{\mu_M M}{1 + M + \beta \tilde{M}_0} & 0 \\ \frac{\mu_M M}{F} - \frac{(1 - \alpha)CFM}{K(1 + M + \beta \tilde{M}_0)} & -\frac{\mu_M M}{1 + M + \beta \tilde{M}_0} - \frac{(1 - \alpha)CFM}{K(1 + M + \beta \tilde{M}_0)} & -\frac{\beta M \mu_M}{1 + M + \beta \tilde{M}_0} \\ 0 & b & -\mu_2 \end{vmatrix} \\ &= \begin{vmatrix} -\mu_F & \frac{\alpha}{1 - \alpha} \mu_M & 0 \\ \frac{\mu_M M}{F} - \frac{(1 - \alpha)CFM}{K(1 + M + \beta \tilde{M}_0)} & -\frac{\mu_M M}{1 + M + \beta \tilde{M}_0} - \frac{(1 - \alpha)CFM}{K(1 + M + \beta \tilde{M}_0)} & -\frac{\beta M \mu_M}{1 + M + \beta \tilde{M}_0} \\ 0 & b & -\mu_2 \end{vmatrix}. \end{aligned} \tag{4.10}$$

Writing

$$\begin{aligned} J_{21} &:= \frac{\mu_M M}{F} - \frac{(1-\alpha)CFM}{K(1+M+\beta\tilde{M}_0)}, \\ J_{22} &:= -\frac{\mu_M M}{1+M+\beta\tilde{M}_0} - \frac{(1-\alpha)CFM}{K(1+M+\beta\tilde{M}_0)}, \\ J_{23} &:= -\frac{\beta M \mu_M}{1+M+\beta\tilde{M}_0}, \end{aligned}$$

we have

$$\begin{aligned} \det J_2 &= \begin{vmatrix} -\mu_F & \mu_F P & 0 \\ J_{21} & J_{22} & J_{23} \\ 0 & b & -\mu_2 \end{vmatrix} \\ &= \begin{vmatrix} -\mu_F & 0 & 0 \\ J_{21} & J_{22} + PJ_{21} & J_{23} \\ 0 & b & -\mu_2 \end{vmatrix} \\ &= \mu_F \mu_2 (J_{22} + PJ_{21} + \frac{b}{\mu_2} J_{23}) \\ &= \mu_F \mu_2 (J_{22} + PJ_{21}) + b \mu_F J_{23}. \end{aligned} \tag{4.11}$$

By further writing  $D := 1 + M + \beta\tilde{M}_0$ , we have

$$\begin{aligned} J_{22} + PJ_{21} &= -\frac{\mu_M M}{D} - \frac{(1-\alpha)CFM}{KD} + \mu_M - P \frac{(1-\alpha)CFM}{KD} \\ &= \mu_M \left(1 - \frac{M}{D}\right) - \frac{(1-\alpha)CFM}{KD} - P \frac{(1-\alpha)CFM}{KD} \\ &= \mu_M \frac{1 + \beta\tilde{M}_0}{D} - (1+P) \frac{(1-\alpha)CPM^2}{KD} \\ &= \mu_M \frac{1 + \beta\tilde{M}_0}{D} - \frac{(1-\alpha)P}{KD} C(1+P)M^2. \end{aligned} \tag{4.12}$$

It follows from (4.5) that

$$\bar{C}(1+P)M^2 = \frac{1}{\alpha} \left( -\mu_F K \bar{\gamma} - K(\mu_F - \alpha \bar{C})M \right),$$

that is,

$$C(1+P)M^2 = -\frac{K}{\alpha} \left( \mu_F + \left( \frac{\mu_F}{\bar{\gamma}} - \alpha C \right) M \right). \tag{4.13}$$

Substituting (4.13) into (4.12) yields

$$\begin{aligned}
 J_{22} + PJ_{21} &= \mu_M \frac{1 + \beta \tilde{M}_0}{D} + \frac{(1 - \alpha)P}{D\alpha} \left( \mu_F + \left( \frac{\mu_F}{\bar{\gamma}} - \alpha C \right) M \right) \\
 &= \mu_M \frac{1 + \beta \tilde{M}_0}{D} + \frac{\mu_M}{D\mu_F} \left( \mu_F + \left( \frac{\mu_F}{\bar{\gamma}} - \alpha C \right) M \right) \\
 &= \frac{\mu_M}{D} \left( 2 + \left( \frac{b\beta}{\mu_2} + \frac{1}{\bar{\gamma}} - \frac{\alpha C}{\mu_F} \right) M \right) \\
 &= \frac{\mu_M}{D} \left( 2 + \left( 1 + \frac{2b\beta}{\mu_2} - \frac{\alpha C}{\mu_F} \right) M \right),
 \end{aligned} \tag{4.14}$$

and then substituting (4.14) into (4.11), we arrive at

$$\begin{aligned}
 \det J_2 &= \frac{\mu_F \mu_M \mu_2}{D} \left( 2 + \left( 1 + \frac{2b\beta}{\mu_2} - \frac{\alpha C}{\mu_F} \right) M \right) - \frac{\beta b \mu_F \mu_M}{D} M \\
 &= \frac{\mu_F \mu_M \mu_2}{D} \left( 2 + \left( 1 + \frac{2b\beta}{\mu_2} - \frac{\alpha C}{\mu_F} \right) M - \frac{\beta b}{\mu_2} M \right) \\
 &= \frac{\mu_F \mu_M \mu_2}{D} \left( 2 - \left( \frac{\alpha C}{\mu_F} - \left( 1 + \frac{b\beta}{\mu_2} \right) \right) M \right) \\
 &= \frac{\mu_F \mu_M \mu_2}{D} \left( 2 - \left( \frac{\alpha C}{\mu_F} - \frac{1}{\bar{\gamma}} \right) M \right).
 \end{aligned} \tag{4.15}$$

Suppose  $b < b_p$  such that there exist two positive equilibria. Then from (4.8), we can rewrite  $M_p^\mp$  as

$$M_p^\mp = \frac{B \mp \sqrt{B^2 - 4AC}}{2A},$$

where  $A := \alpha \bar{C}(1 + P) > 0$ ,  $B := K(\alpha \bar{C} - \mu_F) > 0$ , and  $C := \mu_F K \bar{\gamma} > 0$  for short, and  $B^2 > 4AC$  from  $b < b_p$ . Then

$$\begin{aligned}
 2 - \left( \frac{\alpha C}{\mu_F} - \frac{1}{\bar{\gamma}} \right) M_p^\mp &= 2 - \frac{\alpha \bar{C} - \mu_F}{\mu_F \bar{\gamma}} M_p^\mp = 2 - \frac{B}{C} M_p^\mp \\
 &= \frac{1}{C} (2C - B M_p^\mp) = \frac{1}{C} \left( 2C - B \frac{B \mp \sqrt{B^2 - 4AC}}{2A} \right) \\
 &= \frac{1}{2AC} (4AC - B^2 \pm B \sqrt{B^2 - 4AC}) \\
 &= \frac{\sqrt{B^2 - 4AC}}{2AC} (\pm B - \sqrt{B^2 - 4AC}).
 \end{aligned} \tag{4.16}$$

Hence

$$\det J_2|_{E_p^-} = \frac{\mu_F \mu_M \mu_2}{D} \frac{\sqrt{B^2 - 4AC}}{2AC} (B - \sqrt{B^2 - 4AC}) > 0,$$

and

$$\det J_2|_{E_p^+} = \frac{\mu_F \mu_M \mu_2}{D} \frac{\sqrt{B^2 - 4AC}}{2AC} (-B - \sqrt{B^2 - 4AC}) < 0.$$

An immediate conclusion is that the positive equilibrium  $E_p^-$  is unstable.

For the stability of  $E_p^+$ , we employ the Routh-Hurwitz stability criterion as follows.

Let the characteristic polynomial of  $J_2$  be

$$P(\lambda) = \lambda^3 + a_1(M)\lambda^2 + a_2(M)\lambda + a_3(M).$$

Straight calculations yield

$$\begin{aligned} a_1(M) &= -\text{tr}J_2 = -J_{11} + \mu_2 - J_{22}, \\ a_2(M) &= \sum_{i=1}^3 D_i = -\mu_F J_{22} - \mu_F P J_{21} - \mu_2 J_{22} - b J_{23} - J_{11} \mu_2, \\ a_3(M) &= -\det J_2 = -\mu_F \mu_2 (J_{22} + P J_{21} + \frac{b}{\mu_2} J_{23}), \end{aligned} \quad (4.17)$$

where  $D_i$ ,  $i = 1, 2, 3$ , are the  $2 \times 2$  principal minors of  $J_2$ , and we write  $J_{11} = \frac{-\alpha C F M}{K D}$ .

It is clear that  $a_1(M_p^+) > 0$  and we have previously shown  $a_3(M) > 0$ . Thus the stability of  $E_p^+$  is determined by whether  $a_1(M_p^+)a_2(M_p^+) > a_3(M_p^+)$ . We write

$$\begin{aligned} a_2(M) &= -\mu_2(J_{11} + J_{22}) - \left( \mu_F \left( J_{22} + P J_{21} + \frac{1}{\mu_2} b J_{23} \right) + \left( 1 - \frac{\mu_F}{\mu_2} \right) b J_{23} \right) \\ &= -\mu_2(J_{11} + J_{22}) + \frac{1}{\mu_2} a_3(M) - \left( 1 - \frac{\mu_F}{\mu_2} \right) b J_{23} \end{aligned} \quad (4.18)$$

and  $H(M) = a_1(M)a_2(M) - a_3(M)$ . Then it follows from  $J_{11} < 0$ ,  $J_{22} < 0$ ,  $J_{23} < 0$ ,  $a_1(M_p^+) > 0$ , and  $a_3(M_p^+) > 0$  that if we assume  $\mu_2 \geq \mu_F$ ,

$$H(M_p^+) = -\mu_2(J_{11} + J_{22})a_1(M_p^+) - \frac{J_{11} + J_{22}}{\mu_2} a_3(M_p^+) - (\mu_2 - \mu_F) \frac{b J_{23}}{\mu_2} a_1(M_p^+) > 0. \quad (4.19)$$

Therefore, positive equilibrium  $E_p^+$  is locally asymptotically stable under the assumption of  $\mu_2 \geq \mu_F$ .

In summary, we have the following results.

**Theorem 4.1.** Define the threshold  $b_p$  in (4.7) for the release of sterile mosquitoes for system (4.1). Then

1. If  $b > b_p$ , there is no positive equilibrium and the origin  $(0, 0, 0)$  is globally asymptotically stable.
2. If  $b = b_p$ , there exists one positive equilibrium  $E^*$  which is unstable, and the origin  $(0, 0, 0)$  is locally asymptotically stable.
3. If  $b < b_p$ , there exist two positive equilibrium  $E_p^-$  and  $E_p^+$ . Equilibrium  $E_p^-$  is always an unstable saddle and  $E_p^+$  is locally asymptotically stable under the assumption of  $\mu_2 \geq \mu_F$ .

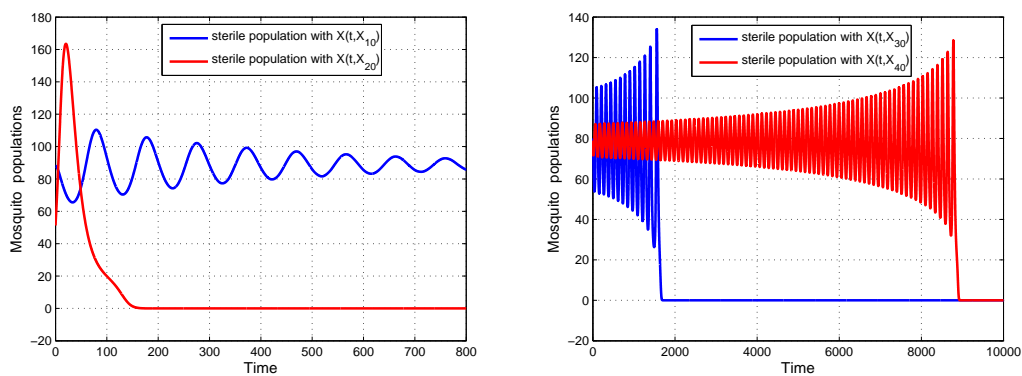
Notice that the model dynamics become more complex when  $\mu_2 < \mu_F$ . Equilibrium  $E_p^-$  is still always an unstable saddle, but  $E_p^+$  is no longer necessarily locally asymptotically stable. Even though we have been unable to find stable or unstable closed orbits when  $E_p^+$  is unstable, solutions initially close to it can eventually approach the origin spirally. Example 2 demonstrates the dynamical complexity of system (4.1).



*Example 2.* Parameters are given as

$$\alpha = 0.4, C = 10, \mu_F = 0.2, \mu_M = 0.2, \mu_2 = 0.16, K = 20, \beta = 0.3, \quad (4.20)$$

so that the release threshold is  $b_p = 8.7563$ . For  $b = 8.3 < b_p$ , there exist two positive equilibria  $E_p^- = (0.2336, 0.3505, 18.1801)$  and  $E_p^+ = (1.1414, 1.7120, 88.8121)$ . Equilibrium  $E_p^-$  is an unstable saddle and  $E_p^+$  is a stable spiral. Solutions approach either the origin or  $E_p^+$  oscillatorily, as shown in the left figure in Figure 2. However, for  $b = 8.448$ , which is still less than  $b_p$ , although there still exist two positive equilibria  $E_p^- = (0.2676, 0.4015, 21.1972)$  and  $E_p^+ = (0.9964, 1.4945, 78.9116)$  and equilibrium  $E_p^-$  is still an unstable saddle,  $E_p^+$  becomes an unstable spiral. Solutions all approach the origin as shown in the right figure in Figure 2.



**Figure 2.** Parameters are given in (4.20) and the release threshold is  $b_p = 8.7563$ . For  $b = 8.3 < b_p$ , there exist two positive equilibria  $E_p^- = (0.2336, 0.3505, 18.1801)$ , which is an unstable saddle, and  $E_p^+ = (1.1414, 1.7120, 88.8121)$ , which is a stable spiral. The solution initially starting from  $X_{10} = (1, 1.7, 88)$  spirals towards  $E_p^+$  and the solution initially starting from  $X_{20} = (1, 1.7, 51.2)$  approaches the origin as both shown in the left figure. With the same parameters but  $b = 8.448 < b_p$  however, there still exist two positive equilibria  $E_p^- = (0.2676, 0.4015, 21.1972)$  and  $E_p^+ = (0.9964, 1.4945, 78.9116)$ . Equilibrium  $E_p^-$  is still an unstable saddle, but  $E_p^+$  becomes an unstable spiral. As shown in the right figure, the solution initially starting from  $X_{30} = (0.9, 1.5, 80)$  oscillates first, and then approaches the origin for  $t$  sufficiently large. Another solution initially starting from  $X_{40} = (1, 1.3, 79)$  has similar dynamics, but approaches the origin much faster than the first solution.

## 5. Concluding remarks

We formulated sex-structured models for interactive wild and sterile mosquitoes, following [9, 26], and studied the models dynamics with different sterile mosquito release strategies. We analyzed models without sterile mosquitoes, including a model with Allee effect, as well as models with male sterile mosquitoes that are released at a constant rate or a rate that is proportional to the wild male mosquitoes. We then studied the dynamics of interactive wild and sterile mosquitoes, more specifically, the existence and stability of all equilibria. We established threshold values,  $b_c$  and  $b_p$ , for the two model systems (3.1) and (4.1), respectively. We showed that, for the case of constant releases, if the release

rate is greater than the threshold, that is,  $b > b_c$ , there exists no positive equilibrium and the boundary equilibrium where the two components for the wild mosquitoes are both zero and the component for the sterile mosquitoes is positive, is globally asymptotically stable. Thus, all wild mosquitoes will be wiped out eventually. If, on the other hand,  $b < b_c$ , the boundary equilibrium is locally asymptotically stable and there exist two positive equilibria, one of which is unstable and the other is locally asymptotically stable. Either all wild mosquitoes will go extinct or the two types of mosquitoes coexist, depending on their initial values. There is no closed orbit for the model system with constant releases.

The dynamics for the releases proportional to the size of wild male mosquitoes are relatively similar to those of constant releases, except that the origin  $(0, 0, 0)$  is an equilibrium and there is no boundary equilibrium. If  $b > b_p$ , there exists no positive equilibrium and the origin is globally asymptotically stable. If  $b < b_p$ , the origin is locally asymptotically stable and there exist two positive equilibria. One of the two positive equilibria is always unstable and the other can be either locally asymptotically stable or unstable. If it is locally asymptotically stable, solutions approach either the origin or the stable positive equilibrium. Thus, either all mosquitoes go extinct eventually or the two types of mosquitoes coexist, depending on their initial sizes. If the other positive equilibrium is unstable, on the other hand, all the wild female and male mosquitoes are eventually wiped out. Note that this unstable positive equilibrium can be a spiral and there might possibly exist closed orbits. However, we unfortunately haven't been able to find any although we are unable to prove their nonexistence yet.

We considered, using parameter  $\beta$ , the competition between wild and sterile male mosquitoes for their wild female mates in this study. It plays a role in determining the release thresholds and the wild mosquito components when the two types of mosquitoes coexist. According to Davis et al. [11] radio-sterilized male mosquitoes are not as competitive as normal males in mating with normal females. (See also [23].) So, increasing the mating competitiveness of sterilized male mosquitoes is essential to achieve sterility in a substantial part of the total population. It follows from the formulas for the thresholds in (3.3) and (4.7), the two thresholds are proportional to the reciprocal of  $\beta$  such that they are reduced as  $\beta$  increases. Following from the formulas for the wild mosquito components at the stable positive equilibria for the constant releases of sterile mosquitoes in (3.4), we have

$$\alpha C \mu_F \mu_2 K \beta (1 + P)(b_c - b) = K_1 - K_2 \beta,$$

and then

$$M_c^+ = A_1 + A_2 \sqrt{K_1 - K_2 \beta},$$

where  $A_1$ ,  $A_2$ ,  $K_1$  and  $K_2$  are all positive constants, independent of  $\beta$ . Hence,  $M_c^+$ , if exists, decreases as  $\beta$  increases. Similarly, we can also show that  $M_p^+$ , if exists, decreases linearly as  $\beta$  increases. Thus, as the sterile male mosquitoes are more capable to compete for female wild mates, the required release thresholds of sterile mosquitoes are reduced and, if the number of releases is less than the threshold such that the wild mosquitoes still exist, the wild components for the wild mosquitoes at the stable positive equilibria are reduced too for both of the two release strategies. Therefore, it seems that more attention needs to be given to increasing the competitiveness of sterile mosquitoes before they are released.

We notice that the dynamics of the sexual-structured model systems with different strategies of releases investigated in this paper are similar to the dynamics of the model systems in [26] where all mosquitoes are assumed homogeneous without distinguishing their gender. That is, based on the threshold values of releases and under certain other conditions, there exist two positive equilibria,

one of which is unstable and one of which is locally asymptotically stable for both of the two model systems. System (3) has a boundary equilibrium  $(0, 0, g^0)$  and system (4) has the trivial equilibrium  $(0, 0, 0)$  other than the positive equilibria. Solutions approach either the boundary (or the trivial) equilibrium or the stable positive equilibrium, depending on their initial values. Nevertheless, the analysis is more difficult for the three-dimensional systems in this paper than the two-dimensional systems in [26]. As is illustrated above, the inclusion of the mosquitoes' sexual structure is necessary from the biology of mosquitoes and the modeling perspective. On the other hand, we have also learned once more from this study, as has been well described in many other existing studies as well, that simplified models may not necessarily lose key features that the more complicated models exhibit. Therefore, the assumption of homogeneous populations are valid in many biological situations and we may start with relatively simple models when we work on real world problems.

We would like to finally point out that while the studies of the dynamics of sex-structured mosquitoes models with different releasing strategies such as the constant releases and the proportional release of the sterile male mosquito population are important, any efforts directed at controlling mosquitoes to prevent the spread of diseases is desirable. In the future, we will pay more attention on the dynamics of mosquitoes populations combined with the population evolution induced by the biological control.

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### Conflict of interest

The authors declare no conflict of interest in this paper.

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