

DYNAMICS OF MOSQUITOES POPULATIONS WITH DIFFERENT STRATEGIES FOR RELEASING STERILE MOSQUITOES*

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Abstract. To prevent the transmissions of malaria, dengue fever, or other mosquito-borne diseases, one of the effective weapons is the sterile insect technique in which sterile mosquitoes are released to reduce or eradicate the wild mosquito population. To study the impact of the sterile insect technique on disease transmission, we formulate continuous-time mathematical models for the interactive dynamics of the wild and sterile mosquitoes, incorporating different strategies in releasing sterile mosquitoes. We investigate the model dynamics and compare the impact of the different release strategies. Numerical examples are also given to demonstrate rich dynamical features of the models.

Key words. mosquito-borne diseases, sterile mosquitoes, releasing strategies, Allee effects, stability, limit cycles

AMS subject classifications. 34D20, 34D23, 92D25, 92D40, 93D05

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1. Introduction. Mosquito-borne diseases, such as malaria and dengue fever, are a considerable public health concern worldwide. These diseases are transmitted between humans by blood-feeding mosquitoes. No vaccines are available and an effective way to prevent these mosquito-borne diseases is to control mosquitoes. Among the mosquitoes control measures, genetic approaches have been proven to be useful and effective. Mosquito transgenesis and paratransgenesis are two novel strategies that aim at rendering the vector incapable of sustaining *Plasmodium* development, and hence interfering with parasite transmission of the diseases. The transgenesis strategy is to introduce the refractory genes into the mosquito population and to genetically modify the mosquito for midgut expression of effector genes, whose products inhibit parasite development. The paratransgenesis strategy is to introduce genes into bacteria of the mosquito midgut, instead of into the mosquito itself, and to genetically modify the bacteria, whose products also inhibit parasite development. Both of these techniques aim to replace the wild mosquitoes by disease resistant mosquitoes [8, 14, 22, 25].

In the meantime, the sterile insect technique (SIT) has also been applied to reduce or eradicate the wild mosquitoes. SIT is a method of biological control in which the natural reproductive process of mosquitoes is disrupted. Utilizing radical or other chemical or physical methods, male mosquitoes are genetically modified to be sterile so that they are incapable of producing offspring despite being sexually active. These sterile male mosquitoes are then released into the environment to mate with the wild mosquitoes that are present in the environment. A wild female that mates with a

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sterile male will either not reproduce, or produce eggs, but the eggs will not hatch. Repeated releases of genetically modified mosquitoes or releasing a significantly large number of sterile mosquitoes may eventually wipe out a wild mosquito population, although it is often more realistic to consider controlling the population rather than eradicating it [3, 7, 26].

The transgenic approach and the SIT bring effective weapons to fight vector-borne diseases, and have shown to be promising in laboratory studies. Nevertheless, the investigation and assessment of the impact of releasing genetically modified or sterile mosquitoes into the field of wild mosquito populations are still challenging tasks.

Mathematical models have proven useful in gaining insights into such challenging questions in population dynamics and epidemiology. There are mathematical models in the literature formulated to study the interactive dynamics of mosquito populations or the control of mosquitoes [4, 5, 6, 9, 12, 13, 15, 16, 17, 19, 20, 21]. Models for vector-borne diseases, incorporating transgenic or sterile mosquitoes, are also formulated to study the disease transmission dynamics in [1, 10, 11, 18, 24].

We focus on the dynamics of the interactive wild and sterile mosquitoes and explore the impact of different strategies of releasing sterile mosquitoes in this paper. We consider homogeneous mosquito populations without distinguishing male or female individuals, and assume that the mosquito populations follow the logistic growth in the absence of interactions and that the birth rate of the sterile mosquitoes is their release rate. We first formulate a model, similar to that in [4, 6], where the release rate of sterile mosquitoes is constant, but we assume distinct fitness for the wild and sterile mosquitoes in section 2. Complete mathematical analysis is given for the model. We then formulate a model for the case where the release rate of sterile mosquitoes is proportional to the wild mosquito population size and an Allee effect to the population dynamics of the wild mosquitoes is considered in section 3. Mathematical analysis and numerical examples are presented to show the complexity of the model dynamics. To provide a different releasing strategy, we assume, in section 4, that the release rate is of Holling-II type such that it is proportional to the wild mosquito population size when the wild mosquito population size is small but is saturated and approaches a constant as the wild mosquito population size is sufficiently large. We also provide a complete mathematical analysis of the model. We finally give brief discussions on our findings, particularly on the impact of the three different strategies on the mosquito control measures in section 5.

2. Constant release rate. Let $w(t)$ and $g(t)$ be the numbers of wild and sterile mosquitoes at time t , respectively. We assume that the dynamics of the wild and sterile mosquito populations, in the absence of interactions, both follow logistic growth, where the birth rate of sterile mosquitoes is their release rate.

After the sterile mosquitoes are released into the wild mosquito population, the interactive dynamics are then governed by the following system:

$$(2.1) \quad \begin{aligned} \frac{dw}{dt} &= \left(C(N) \frac{aw}{w+g} - (\mu_1 + \xi_1(w+g)) \right) w, \\ \frac{dg}{dt} &= B(\cdot) - (\mu_2 + \xi_2(w+g))g, \end{aligned}$$

where $C(N)$ is the number of matings per individual, per unit of time, with $N = w+g$; a is the number of wild offspring produced per mate; μ_i and ξ_i , $i = 1, 2$, are the density independent and dependent death rates of the wild and sterile mosquitoes, respectively; and $B(\cdot)$ is the release rate of the sterile mosquitoes. We assume that

mating rate $C(N) = c$ is constant and merge c and a to write it as a . We assume $a > \mu_1$ so that the wild mosquito population approaches its carrying capacity. We further assume that the release rate is constant with $B = b$ in this section so that system (2.1) becomes

$$(2.2) \quad \begin{aligned} \frac{dw}{dt} &= \left(\frac{aw}{w+g} - (\mu_1 + \xi_1(w+g)) \right) w, \\ \frac{dg}{dt} &= b - (\mu_2 + \xi_2(w+g))g. \end{aligned}$$

Remark 1. We notice that if $\mu_1 = \mu_2$ and $\xi_1 = \xi_2$, system (2.2) has the same form as those in [4, 6], but the analysis given here is different from those in [4, 6].

It follows from (2.2) that

$$(2.3) \quad \frac{dN}{dt} = \frac{aw^2}{N} + b - \mu_1 w - \mu_2 g - \xi_1 N w - \xi_2 N g.$$

Write the right-hand side of (2.3) as $H(w, g)$. Then

$$H(w, g) \geq b - (\mu_0 + \xi_0 N)N \geq b - (\mu_0 + \xi_0)N > 0 \quad \forall 0 < N < \min \left\{ 1, \frac{b}{\mu_0 + \xi_0} \right\},$$

and

$$H(w, g) \leq aN + b - (\tilde{\mu} + \tilde{\xi}N)N = (b - \tilde{\mu}N) + (a - \tilde{\xi}N)N < 0 \quad \forall N > \max \left\{ b/\tilde{\mu}, a/\tilde{\xi} \right\},$$

where $\mu_0 := \max\{\mu_1, \mu_2\}$, $\tilde{\mu} := \min\{\mu_1, \mu_2\}$, $\xi_0 := \max\{\xi_1, \xi_2\}$, and $\tilde{\xi} := \min\{\xi_1, \xi_2\}$.

Letting F_1 and F_2 denote the functions of the right-hand sides in (2.2), we have

$$F_1(0, g) = 0 \quad \forall g > 0, \quad F_2(w, 0) = b > 0.$$

We conclude that the positive g -axis is an invariant set of (2.2), and for any two fixed constants K_1 and K_2 such that $0 < K_1 < \min\{1, b/(\mu_0 + \xi_0)\}$ and $K_2 > \max\{b/\tilde{\mu}, a/\tilde{\xi}\}$, the set

$$\Omega_1 := \{(w, g) : K_1 < w + g < K_2\}$$

is a positively invariant and attracting set for the flows of (2.2) in the positive quadrant. We then focus our analysis only in set Ω_1 in this section.

2.1. Existence of equilibria. It is clear that the only boundary equilibrium of system (2.2), with one component positive and one component zero, is $E_0(0, g^0)$, where

$$(2.4) \quad g^0 = \frac{\sqrt{\mu_2^2 + 4b\xi_2} - \mu_2}{2\xi_2} > 0.$$

For a positive equilibrium of (2.2), its components satisfy

$$\frac{aw}{w+g} = \mu_1 + \xi_1(w+g), \quad \frac{b}{g} = \mu_2 + \xi_2(w+g),$$

which leads to

$$(2.5) \quad aw = N(\mu_1 + \xi_1 N), \quad ag = \frac{ab}{\mu_2 + \xi_2 N}.$$

Adding these two equations yields

$$(2.6) \quad aN = N(\mu_1 + \xi_1 N) + \frac{ab}{\mu_2 + \xi_2 N}.$$

Define

$$(2.7) \quad \begin{aligned} P(N) &:= N(\mu_1 + \xi_1 N)(\mu_2 + \xi_2 N) - aN(\mu_2 + \xi_2 N) + ab \\ &= \xi_1 \xi_2 N^3 - (\xi_2(a - \mu_1) - \xi_1 \mu_2)N^2 - (a - \mu_1)\mu_2 N + ab. \end{aligned}$$

Then (w, g) is a positive equilibrium of (2.2) if and only if $N = w + g$ is a positive solution of $P(N) = 0$.

It follows from

$$P'(N) = 3\xi_1 \xi_2 N^2 - 2(\xi_2(a - \mu_1) - \xi_1 \mu_2)N - (a - \mu_1)\mu_2,$$

that if $\bar{N} > 0$ is a critical point of $P(N)$ with $P'(\bar{N}) = 0$, then

$$(2.8) \quad \bar{N} = \frac{1}{3\xi_1 \xi_2} \left(\sqrt{(\xi_2(a - \mu_1) - \xi_1 \mu_2)^2 + 3\xi_1 \xi_2(a - \mu_1)\mu_2 + \xi_2(a - \mu_1) - \xi_1 \mu_2} \right).$$

Notice that

$$2P(\bar{N}) = 2P(\bar{N}) - P'(\bar{N})\bar{N} = -\xi_1 \xi_2 \bar{N}^3 - (a - \mu_1)\mu_2 \bar{N} + 2ab.$$

Hence if we define the threshold release value of sterile mosquitoes as

$$(2.9) \quad b_0 := \frac{1}{2a} (\xi_1 \xi_2 \bar{N}^2 + (a - \mu_1)\mu_2) \bar{N},$$

then $P(\bar{N}) < 0$ if and only if $b < b_0$. Thus it follows from $P(0) = ab > 0$ and $\lim_{N \rightarrow \infty} P(N) = \infty$ that there exists a unique positive solution $N^* = \bar{N}$ of (2.7) if and only if $b = b_0$, and two positive solutions, N_1^* and N_2^* with $N_1^* < \bar{N} < N_2^*$, if and only if $b < b_0$. We summarize our existence results for the equilibria as follows.

THEOREM 2.1. *Boundary equilibrium $E_0(0, g^0)$, where g^0 is given in (2.4), is the only equilibrium of system (2.2) if and only if $b > b_0$. System (2.2) has a unique positive equilibrium $E^*(w^*, g^*)$, where*

$$(2.10) \quad w^* = \frac{\bar{N}(\mu_1 + \xi_1 \bar{N})}{a}, \quad g^* = \frac{b}{\mu_2 + \xi_2 \bar{N}}$$

with \bar{N} given in (2.8), if and only if $b = b_0$. It has two positive equilibria $E_1^*(w_1^*, g_1^*)$ and $E_2^*(w_2^*, g_2^*)$, corresponding to N_1^* and N_2^* with

$$(2.11) \quad \begin{aligned} w_1^* &= \frac{N_1^*(\mu_1 + \xi_1 N_1^*)}{a} < w_2^* = \frac{N_2^*(\mu_1 + \xi_1 N_2^*)}{a}, \\ g_2^* &= \frac{b}{\mu_2 + \xi_2 N_2^*} < g_1^* = \frac{b}{\mu_2 + \xi_2 N_1^*}, \end{aligned}$$

if and only if $b < b_0$.

Notice that it follows from (2.8) that the expression of \bar{N} is independent of b , and hence the formula for the threshold release value b_0 is independent of b . If the amount

of releases of the sterile mosquitoes exceeds the threshold, the wild mosquitoes become extinct eventually.

2.2. Stability of the equilibria. We now investigate the stability of the equilibria of system (2.2).

The Jacobian matrix of system (2.2) at boundary equilibrium E_0 is

$$\begin{pmatrix} -(\mu_1 + \xi_1 g^0) & 0 \\ -\xi_2 g^0 & -(\mu_2 + 2\xi_2 g^0) \end{pmatrix}.$$

Hence E_0 is always a locally asymptotically stable node. In the case of $b > b_0$, since E_0 is the only equilibrium in Ω_1 , and system (2.2) is a monotone system, then it follows from the Poincaré–Bendixson theorem that the ω -limit set of every solution in Ω_1 is E_0 , which implies the globally asymptotic stability of E_0 .

Suppose $b \leq b_0$. The Jacobian matrix of system (2.2) at a positive equilibrium point has the following form:

$$J_1 = \begin{pmatrix} \left(\frac{ag}{(w+g)^2} - \xi_1 \right) w & - \left(\frac{aw}{(w+g)^2} + \xi_1 \right) w \\ -\xi_2 g & -\mu_2 - \xi_2(w+2g) \end{pmatrix}.$$

The determinant of J_1 is

$$\begin{aligned} \det J_1 &= \left(\xi_1 w - \frac{agw}{N^2} \right) (\mu_2 + \xi_2 N + \xi_2 g) - \xi_2 g \left(\frac{aw^2}{N^2} + \xi_1 w \right) \\ &= (\mu_2 + \xi_2 N) \left(\xi_1 w - \frac{agw}{N^2} \right) - \frac{a\xi_2 gw}{N}. \end{aligned} \quad (2.12)$$

It follows from (2.5) and (2.6) that

$$\begin{aligned} \det J_1 &= \frac{w}{N^2} (\xi_1 N^2 (\mu_2 + \xi_2 N) - ag(\mu_2 + 2\xi_2 N)) \\ &= \frac{w}{N^2} \left(\xi_1 N^2 (\mu_2 + \xi_2 N) - ab \frac{\mu_2 + 2\xi_2 N}{\mu_2 + \xi_2 N} \right) \\ &= \frac{w}{N^2} (\xi_1 N^2 (\mu_2 + \xi_2 N) + N(\xi_1 N - (a - \mu_1))(\mu_2 + 2\xi_2 N)) \\ &= \frac{w}{N} (3\xi_1 \xi_2 N^2 + 2(\xi_1 \mu_2 - \xi_2(a - \mu_1))N - (a - \mu_1)\mu_2) = \frac{w}{N} P'(N). \end{aligned}$$

From $P'(N_1^*) < 0$ and $P'(N_2^*) > 0$ it follows that $\det J_1(E_1^*) < 0$ and $\det J_1(E_2^*) > 0$. Thus equilibrium E_1^* is a saddle point.

Furthermore, it follows from (2.12) that, to have $\det J_1(E_2^*) > 0$, the term $\frac{ag_2^* w_2^*}{N_2^{*2}} - \xi_1 w_2^*$ must be negative, which yields $\text{tr} J_1(E_2^*) < 0$. Hence, equilibrium E_2^* is a locally asymptotically stable node or spiral. Notice that system (2.2) is a monotone system. Then E_2^* cannot be a spiral and hence is a stable node. Moreover, there exist no closed orbits for system (2.2). In summary, we have the following stability results.

THEOREM 2.2. *If $b > b_0$ such that boundary equilibrium E_0 is the only equilibrium for system (2.2) in Ω_1 , it is globally asymptotically stable. If $b < b_0$, boundary equilibrium E_0 is a locally asymptotically stable node, positive equilibrium E_1^* is a*

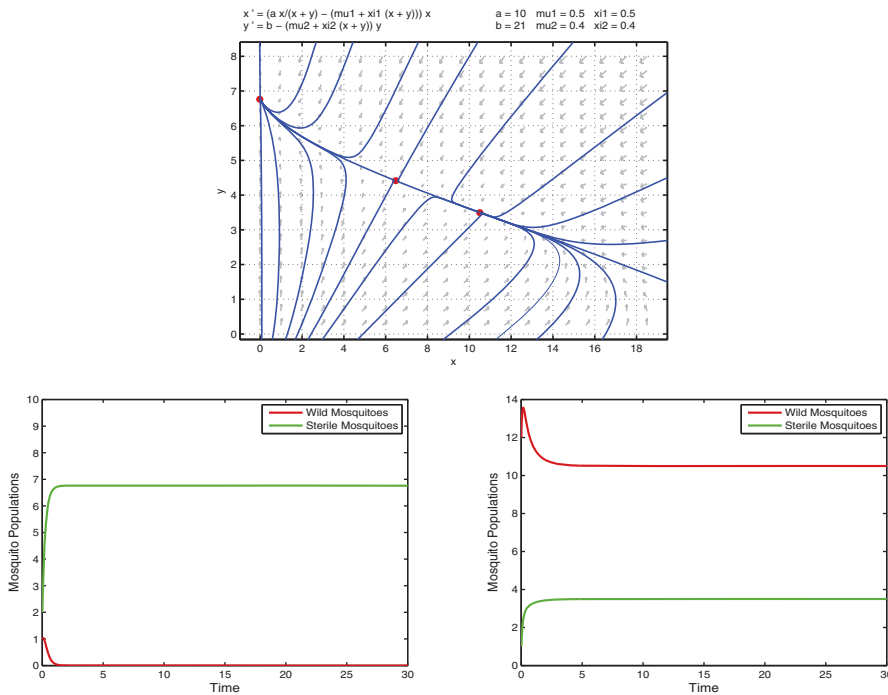


FIG. 1. The parameters are given in (2.13). For $b = 21 < b_0 = 21.935161$, there exist three nontrivial equilibria. Boundary equilibrium $E_0 = (0, 6.7629)$ is a locally asymptotically stable node. Positive equilibrium $E_1^* = (6.472, 4.416)$ is a saddle point, and positive equilibrium $E_2^* = (10.5, 3.5)$ is a locally asymptotically stable node, as shown in the upper figure. Solutions approach either E_0 or E_2^* depending on their initial values, as shown in the lower left and right figures.

saddle point, and E_2^* is a stable node. If $b = b_0$, the unique positive equilibrium with E^* given in (2.10) is an unstable saddle node. Moreover, system (2.2) has no closed orbits in Ω_1 .

We now present a numerical example to confirm the results in Theorems 2.1 and 2.2 as follows.

Example 1. We use the following parameters in this example:

$$(2.13) \quad a = 10, \quad \mu_1 = 0.5, \quad \xi_1 = 0.5, \quad \mu_2 = 0.4, \quad \xi_2 = 0.4.$$

The threshold release value is $b_0 = 21.935161$. For a small release rate $b = 21 < b_0$, $E_0 = (0, 6.7629)$ is a locally asymptotically stable node. There exist two positive equilibria $E_1^* = (6.472, 4.416)$ which is a saddle point, and $E_2^* = (10.5, 3.5)$ which is a locally asymptotically stable node. The phase plane dynamics of system (2.2) are shown in the upper figure in Figure 1. Trajectories may approach either E_0 or E_2^* , depending on their initial conditions. Solutions with different initial values approach either E_0 or E_2^* as shown in the lower left and right figures in Figure 1, respectively. That is, 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.

As the release rate b increases, the two positive equilibria are getting closer. They collide at $b = b_0$ and become a unique saddle-node point. Boundary equilibrium E_0 is then a globally asymptotically stable node for $b = b_0$ or $b > b_0$.

3. Release rate proportional to the wild mosquito population size. To have a more optimal and economically effective strategy for releasing sterile mosquitoes in an area where the population size of wild mosquitoes is relatively small, instead of keeping the release rate constantly fixed, we may consider to keep closely sampling or surveilling the wild mosquitoes and let the release rate be proportional to the population size of the wild mosquitoes. We then let the release rate be $B = bw$, where b is a constant. In the meantime, in a situation where a small mosquito population size may cause possible difficulty in finding mates, we assume an Allee effect such that the mating rate takes the form of $C(N) = c_0N/(1 + N)$, where c_0 is the maximum mating rate [2, 23]. Under these assumptions and after we merge c_0 into the birth rate and still write it as a , the dynamics of the interacting mosquitoes are governed by the following system:

$$(3.1) \quad \begin{aligned} \frac{dw}{dt} &= \left(\frac{aw}{1+w+g} - (\mu_1 + \xi_1(w+g)) \right) w, \\ \frac{dg}{dt} &= bw - (\mu_2 + \xi_2(w+g))g. \end{aligned}$$

Define set Ω_2 as

$$\Omega_2 := \left\{ (w, g) : 0 \leq w \leq a/\xi_1, 0 \leq g \leq \frac{ba}{\mu_2\xi_1} \right\}.$$

Then Ω_2 is a positive invariant set for system (3.1) and, in the following, we only consider $(w, g) \in \Omega_2$.

3.1. Existence of equilibria. Different from system (2.2), system (3.1) has the origin $(0, 0)$ as a trivial equilibrium. It follows from the second equation in (3.1) that if $w = 0$, then $g = 0$, and if $g = 0$, then $w = 0$. Hence there exists no boundary equilibrium for system (3.1).

We then consider a positive equilibrium of (3.1), whose components satisfy the following equations:

$$(3.2) \quad \frac{aw}{1+w+g} = \mu_1 + \xi_1(w+g), \quad bw = (\mu_2 + \xi_2(w+g))g.$$

Equations in (3.2) can be written, in terms of N , as

$$aw = (1+N)(\mu_1 + \xi_1N), \quad ag = \frac{abw}{\mu_2 + \xi_2N} = \frac{b(1+N)(\mu_1 + \xi_1N)}{\mu_2 + \xi_2N}.$$

Thus

$$aN = (1+N)(\mu_1 + \xi_1N) \left(1 + \frac{b}{\mu_2 + \xi_2N} \right),$$

that is,

$$(3.3) \quad aN(\mu_2 + \xi_2N) = (1+N)(\mu_1 + \xi_1N)(b + \mu_2 + \xi_2N).$$

Define

$$(3.4) \quad \begin{aligned} F(N) &:= (1+N)(\mu_1 + \xi_1N)(b + \mu_2 + \xi_2N) - aN(\mu_2 + \xi_2N) \\ &= \xi_1\xi_2N^3 + (\xi_1(b + \mu_2) + \xi_2(\mu_1 + \xi_2 - a))N^2 \\ &\quad + (\mu_1\xi_2 + b(\mu_1 + \xi_1) + (\mu_1 + \xi_1 - a)\mu_2)N + \mu_1(b + \mu_2). \end{aligned}$$

Then there exists a positive equilibrium of system (3.1) if and only if there exists a positive solution N to the equation $F(N) = 0$. Notice $\lim_{N \rightarrow -\infty} F(N) = -\infty$ and $F(0) > 0$. Thus there exist at most two positive solutions to $F(N) = 0$, that is, at most two positive equilibria of (3.1).

From (3.3) it also follows that the existence of a positive solution to $F(N) = 0$ is equivalent to the existence of a positive solution to the following equation:

$$\frac{((1 + N)(\mu_1 + \xi_1 N) - aN)(\mu_2 + \xi_2 N)}{(1 + N)(\mu_1 + \xi_1 N)} + b = 0.$$

Or, by defining the function

$$G(N) := \frac{(aN - (1 + N)(\mu_1 + \xi_1 N))(\mu_2 + \xi_2 N)}{(1 + N)(\mu_1 + \xi_1 N)},$$

there exists a positive equilibrium of (3.1) if and only if there exists a positive solution N to the equation $G(N) = b$.

The quadratic equation

$$aN - (1 + N)(\mu_1 + \xi_1 N) = -(\xi_1 N^2 - (a - \mu_1 - \xi_1)N + \mu_1) = 0$$

has two positive roots

$$(3.5) \quad N_{1,2} = \frac{1}{2\xi_1} \left((a - \mu_1 - \xi_1) \pm \sqrt{(a - \mu_1 - \xi_1)^2 - 4\mu_1\xi_1} \right)$$

if

$$a - \mu_1 - \xi_1 > 0 \quad \text{and} \quad (a - \mu_1 - \xi_1)^2 - 4\mu_1\xi_1 > 0,$$

or, equivalently,

$$(3.6) \quad a > \mu_1 + \xi_1 + 2\sqrt{\mu_1\xi_1} = (\sqrt{\mu_1} + \sqrt{\xi_1})^2.$$

Suppose condition (3.6) is satisfied, and let \bar{N} be the point in (N_1, N_2) such that $G'(\bar{N}) = 0$. We then define the threshold release value of sterile mosquitoes as

$$(3.7) \quad b_0 = G(\bar{N}).$$

Thus, $b_0 > 0$, and $G(N) = b$ has two positive roots $N_1^* < N_2^*$, lying in $[N_1, N_2]$, if and only if $b < b_0$, and a unique positive root $N_1^* = N_2^* = \bar{N}$ if $b = b_0$.

In summary, we have the following existence results for the positive equilibria of system (3.1).

THEOREM 3.1. *Assume condition (3.6) holds. Then system (3.1) has no positive equilibrium if $b > b_0$, a unique positive equilibrium $E^*(w^*, g^*)$, given by*

$$(3.8) \quad w^* = \frac{1}{a}(1 + \bar{N})(\mu_1 + \xi_1 \bar{N}), \quad g^* = \frac{b(1 + \bar{N})(\mu_1 + \xi_1 \bar{N})}{a(\mu_2 + \xi_2 \bar{N})}$$

if $b = b_0$, and two positive equilibria $E_1^*(w_1^*, g_1^*)$ and $E_2^*(w_2^*, g_2^*)$, given by

$$(3.9) \quad w_i^* = \frac{1}{a}(1 + N_i^*)(\mu_1 + \xi_1 N_i^*), \quad g_i^* = \frac{b(1 + N_i^*)(\mu_1 + \xi_1 N_i^*)}{a(\mu_2 + \xi_2 N_i^*)}, \quad i = 1, 2,$$

if $b < b_0$. Here b_0 is defined in (3.7), \bar{N} satisfies $G'(\bar{N}) = 0$, N_i^* , $i = 1, 2$, satisfy $G(N) = b$, and $N_1 < N_1^* < \bar{N} < N_2^* < N_2$ with N_i given in (3.5).

Remark 2. Even though the threshold release value b_0 is determined only implicitly in (3.7), we have the estimate

$$(3.10) \quad b_0 \leq b_c := \frac{(a - (\sqrt{\mu_1} + \sqrt{\xi_1})^2)(\mu_2 + \xi_2 N_2)}{(\sqrt{\mu_1} + \sqrt{\xi_1})^2}$$

provided (3.6) holds, where N_2 is given in (3.5).

In fact, let

$$G_1(N) := \frac{aN}{(1+N)(\mu_1 + \xi_1 N)} - 1.$$

Then it follows from

$$G'_1(N) = a \frac{(1+N)(\mu_1 + \xi_1) - N(\mu_1 + \xi_1 + 2\xi_1 N)}{(1+N)^2(\mu_1 + \xi_1 N)^2} = a \frac{\mu_1 - \xi_1 N^2}{(1+N)^2(\mu_1 + \xi_1 N)^2}$$

that G_1 reaches its global maximum at $N_0 = \sqrt{\mu_1(\xi_1)^{-1}} \in (N_1, N_2)$,

$$G_1(N_0) = \frac{a\sqrt{\mu_1(\xi_1)^{-1}}}{(1 + \sqrt{\mu_1(\xi_1)^{-1}})(\mu_1 + \sqrt{\mu_1\xi_1})} - 1 = \frac{a - (\sqrt{\mu_1} + \sqrt{\xi_1})^2}{(\sqrt{\mu_1} + \sqrt{\xi_1})^2},$$

and it follows from

$$b_c \leq G_1(N_0)(\mu_2 + \xi_2 N_2)$$

that estimate (3.10) holds. Thus, if $b \geq b_c$, all solutions approach the origin; that is, all wild mosquitoes are eventually wiped out which also implies no more sterile mosquito releases are needed.

3.2. Stability of the equilibria. It is trivial to show, from the linearization of system (3.1), that the origin $(0, 0)$ is a locally asymptotically stable node. Furthermore, if $b > b_0$ such that there exists no positive equilibrium in set Ω_2 , the origin is globally asymptotically stable since Ω_2 is positively invariant for system (3.1).

We then investigate the stability of the positive equilibria. The Jacobian matrix at a positive equilibrium is given as

$$J_2 = \begin{pmatrix} \frac{aw(1+g)}{(1+N)^2} - \xi_1 w & -\left(\frac{aw}{(1+N)^2} + \xi_1\right)w \\ b - \xi_2 g & -\mu_2 - \xi_2(N+g) \end{pmatrix}.$$

We first have, after tedious calculations,

$$(3.11) \quad \det J_2 = \frac{w}{1+N} F'(N),$$

where F is defined in (3.4). (The details are given in Appendix A.)

Since $F'(N_1^*) < 0$ and $F'(N_2^*) > 0$, it follows that

$$\det J_2(E_1^*) < 0, \quad \det J_2(E_2^*) > 0.$$

Hence, positive equilibrium E_1^* is a saddle point for any parameter setting, and E_2^* can be a node or a spiral.

Next we compute the trace of J_2 . Since, from (3.8) or (3.9),

$$\frac{aw(1+g)}{(1+N)^2} = \frac{aw}{1+N} \left(1 - \frac{w}{1+N}\right) = \frac{aw}{1+N} - \frac{aw^2}{(1+N)^2} = \mu_1 + \xi_1 N - \frac{aw^2}{(1+N)^2},$$

we can rewrite J_2 as

$$(3.12) \quad J_2 = \begin{pmatrix} \mu_1 + \xi_1 N - \left(\frac{aw}{(N+1)^2} + \xi_1\right)w & -\left(\frac{aw}{(N+1)^2} + \xi_1\right)w \\ b - \xi_2 g & -\mu_2 - \xi_2(N+g) \end{pmatrix}.$$

Thus

$$\begin{aligned} \text{tr} J_2 &= \mu_1 + \xi_1 N - \left(\frac{aw}{(N+1)^2} + \xi_1\right)w - \mu_2 - \xi_2(N+g) \\ &= \mu_1 - \mu_2 + (\xi_1 - 2\xi_2)N - \left(\frac{\mu_1 + \xi_1 N}{N+1} + \xi_1 - \xi_2\right)w \\ &= \mu_1 - \mu_2 + (\xi_1 - \xi_2)N - \frac{1}{a}(\mu_1 + \xi_1 N)^2 - \frac{1}{a}(\xi_1 - \xi_2)(1+N)(\mu_1 + \xi_1 N) - \xi_2 N \\ &= \frac{1}{a}A(N), \end{aligned}$$

where we define the function

$$(3.13) \quad \begin{aligned} A(N) &:= (a(\mu_1 - \mu_2) + \mu_1(\xi_2 - \xi_1 - \mu_1)) + (a(\xi_1 - 2\xi_2) \\ &\quad + \xi_1(\xi_2 - \xi_1) + \mu_1(\xi_2 - 3\xi_1))N + \xi_1(\xi_2 - 2\xi_1)N^2. \end{aligned}$$

Therefore, E_2^* is locally asymptotically stable if $\text{tr} J_2(E_2^*) = \frac{1}{a}A(N_2^*) < 0$.

On the other hand, if we assume $\mu_1 \leq \mu_2$ and $\xi_1 \leq 2\xi_2$, then it follows from (3.12) that

$$\begin{aligned} \text{tr} J_2 &= \mu_1 - \mu_2 + (\xi_1 - \xi_2)N - \xi_1 w - \xi_2 g - \frac{aw^2}{(1+N)^2} \\ &= \mu_1 - \mu_2 + (\xi_1 - 2\xi_2)N - (\xi_1 - \xi_2)w - \frac{aw^2}{(1+N)^2} < 0, \end{aligned}$$

which also leads to the local stability of E_2^* .

Moreover, by using the Dulac function $D(w, g) = \frac{1}{w^2}$ and writing the right-hand side of system (3.1) as $f_1(w, g)$ and $f_2(w, g)$, respectively, direct calculations yield

$$\frac{\partial(Df_1)}{\partial w} + \frac{\partial(Df_2)}{\partial g} = -\frac{a}{(1+N)^2} - \frac{\xi_1 - \xi_2}{w} + \frac{(\mu_1 - \mu_2) + (\xi_1 - 2\xi_2)N}{w^2} < 0,$$

provided $\mu_1 \leq \mu_2$ and $\xi_1 \leq 2\xi_2$, which implies that system (3.1) has no closed orbits in the interior of Ω_2 .

We summarize the stability results for the equilibria of system (3.1) as follows.

THEOREM 3.2. *The trivial equilibrium $(0, 0)$ is locally asymptotically stable for any parameter setting. If condition (3.6) holds, then we have the following results.*

1. *If $b > b_0$, where b_0 is defined in (3.7), the unique trivial equilibrium $(0, 0)$ is globally asymptotically stable.*

2. If $b = b_0$, the unique positive equilibrium E^* , given in (3.8), is an unstable saddle node and the trivial equilibrium $(0, 0)$ is globally asymptotically stable.
3. If $b < b_0$, positive equilibrium E_1^* , given in (3.9), is a saddle point and positive equilibrium E_2^* , given in (3.9), is locally asymptotically stable if $\mu_1 \leq \mu_2$ and $\xi_1 \leq 2\xi_2$, or $A(N_2^*) < 0$, where A is given in (3.13) and N_2^* is given in (3.5).
4. If $\mu_1 \leq \mu_2$ and $\xi_1 \leq 2\xi_2$, system (3.1) has no closed orbits.

Results 1 and 2 in Theorem 3.2 are easy to follow. Numerical demonstrations for 3 are given in Example 2.

Example 2. With the parameters

$$(3.14) \quad \mu_1 = 0.5, \quad \mu_2 = 0.4, \quad \xi_1 = 10, \quad \xi_2 = 8, \quad a = 25,$$

condition (3.6) is satisfied. The two solutions in (3.5) or to $G(N) = 0$ are $N_1 = 0.03534$ and $N_2 = 1.41466$. The solution to $G'(N) = 0$ is $\bar{N} = 0.58114$ and hence the threshold release value is $b_0 = G(\bar{N}) = 2.301778$. There exist two positive equilibria for $0 < b < 2.301778$, and no positive equilibrium if $b > 2.301778$. Set $b = 2$. The two positive roots of $G(N) = b$ are $N_1^* = 0.35505$ and $N_2^* = 0.84495$ such that the two positive equilibria of system (3.1) are $E_1^* = (0.21955, 0.13551)$ which is a saddle point, and $E_2^* = (0.66045, 0.18449)$. Moreover, since $A(N_2^*) = A(0.84495) = -162.88450 < 0$, E_2^* is a locally asymptotically stable node. The stable manifolds of E_1^* form a separatrix dividing the first quadrant into subregions. Solutions approach either the origin or E_2^* depending on their initial conditions as shown in the lower left and right figures in Figure 2. That is, the wild and sterile mosquitoes can both go extinct or coexist, depending on their initial sizes. The phase plane is given in the upper figure in Figure 2.

3.3. Oscillations and limit cycles. If there exist two positive equilibria, E_1^* is always unstable, but E_2^* can be either locally asymptotically stable or unstable. Solutions may approach the origin or E_2^* as shown in Example 2 or there may exist limit cycles so that sustained oscillations appear. We provide two examples as follows to show such possible complexity of the model dynamics. While our preliminary analysis via the Hopf bifurcation theorem has confirmed the existence of these limit cycles, further analysis is to appear in a separate study.

Example 3. Given the parameters

$$(3.15) \quad \mu_1 = \mu_2 = 1, \quad \xi_1 = 4, \quad \xi_2 = 0.51, \quad a = 20, \quad b = 1.51,$$

there exist two positive equilibria $E_1^* = (0.2101, 0.2563)$ and $E_2^* = (0.5, 0.5)$ for system (3.1). Equilibrium E_1^* is a saddle point and E_2^* is a stable spiral. Since set Ω_2 is a positively invariant set for system (3.1), it follows from the Poincaré–Bendixson theorem that there exists at least one unstable limit cycle, enclosing E_2^* , in Ω_2 . The stable and unstable manifolds of E_1^* form a separatrix for the subregions. Solutions approach the stable origin if they initially start from outside the cycle, or the stable spiral point E_2^* if they initially start from inside the cycle. We notice that the real part of the eigenvalues of the Jacobian matrix at E_2^* has the absolute value 0.0075. It is so small that the convergence to E_2^* is very slow. The dynamics are shown in Figure 3.

Example 4. In this example, parameters are given as

$$(3.16) \quad \mu_1 = 1, \quad \mu_2 = 2, \quad \xi_1 = 11, \quad \xi_2 = 0.95, \quad a = 48, \quad b = 2.95.$$

There exist two positive equilibria $E_1^* = (0.0645, 0.0887)$ and $E_2^* = (0.5, 0.5)$ for system (3.1). Equilibrium E_1^* is a saddle point and E_2^* is an unstable spiral. Similarly

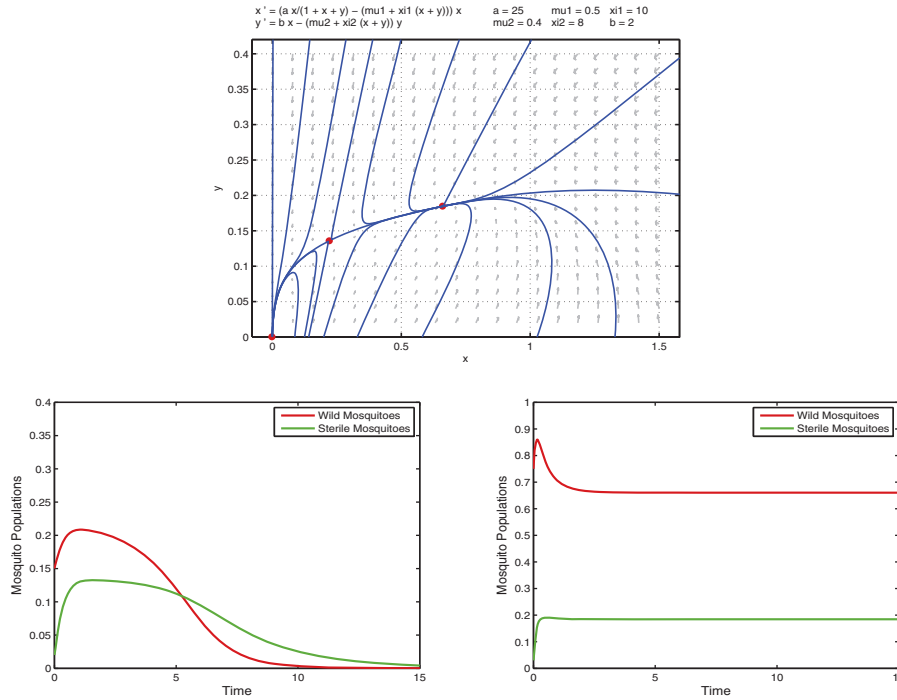


FIG. 2. The parameters are given in (3.14). There exist two positive equilibria $E_1^* = (0.21955, 0.13551)$, which is an unstable saddle point, and $E_2^* = (0.66045, 0.18449)$, which is a locally asymptotically stable node. The origin is also locally asymptotically stable. The phase plane is shown in the upper figure. Solutions approach either the origin or E_2^* depending on their initial values, as shown in the lower left and right figures, respectively.

as above, it follows from the Poincaré–Bendixson theorem that there exists at least one stable limit cycle, enclosing E_2^* , in Ω_2 . The stable and unstable manifolds of E_1^* form a separatrix dividing the positive quadrant into two regions one of which is adjacent to the origin and one of which encloses the limit cycle. Solutions approach the stable origin as they initially start from the region adjacent to the origin. Solutions approach the stable limit cycle as they initially start from inside the cycle or from outside the cycle but in the region that encloses the cycle. The dynamics are shown in Figure 4.

4. Proportional release rate with saturation. The proportional release rate introduced in section 3 seems economically optimal when the wild mosquito population size w is small, but not necessary when w is big since the number of releases is supposed to be big as well. Then we propose a new strategy such that the release rate is proportional to w when w is small, but is saturated and approaches a constant when w is sufficiently large. To this end, we let the release rate be of Holling-II type such that $B = \frac{bw}{1+w}$. We also consider an Allee effect such that the mosquito contact rate is the same as in section 3. Then we have the following system for the interactive dynamics of the mosquitoes:

$$(4.1) \quad \begin{aligned} \frac{dw}{dt} &= \left(\frac{aw}{1+w+g} - (\mu_1 + \xi_1(w+g)) \right) w, \\ \frac{dg}{dt} &= \frac{bw}{1+w} - (\mu_2 + \xi_2(w+g))g. \end{aligned}$$

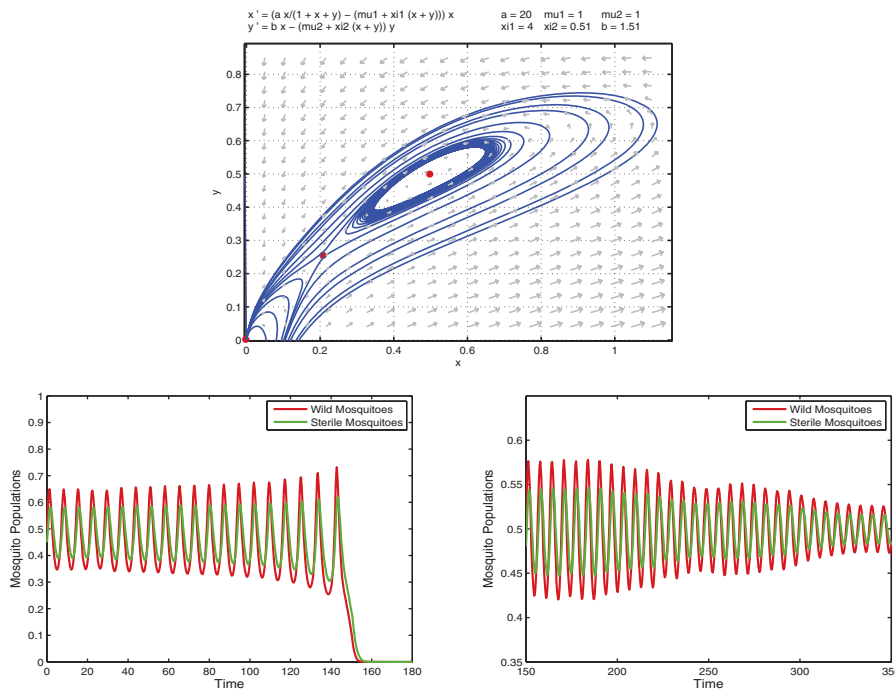


FIG. 3. The parameters are given in (3.15). There exist two positive equilibria $E_1^* = (0.2101, 0.2563)$ and $E_2^* = (0.5, 0.5)$ for system (3.1). Equilibrium E_1^* is a saddle point and E_2^* is a spiral sink. While a limit cycle exists, it is unstable. The phase plane is shown in the upper figure. The solutions approach the stable origin if they initially start from outside the cycle as shown in the lower left figure. The solutions approach the spiral sink if they initially start from inside the cycle, but the convergence is very slow as shown in the lower right figure.

If we define set Ω_3 as

$$\Omega_3 := \left\{ (w, g) : 0 \leq w \leq \frac{a}{\xi_1}, 0 \leq g \leq \frac{b}{a} \right\},$$

then Ω_3 is a positive invariant set for system (4.1), and we only consider $(w, g) \in \Omega_3$ in this section. Moreover, similarly as for system (3.1), by using the same Dulac function $D(w, g) = \frac{1}{w^2}$, it is easy to see that system (4.1) has no periodic solutions if $\mu_1 \leq \mu_2$ and $\xi_1 \leq 2\xi_2$.

The origin $(0, 0)$ is a locally asymptotically stable equilibrium for (4.1). System (4.1) has no boundary equilibrium. A complete analysis for the dynamical features of its positive equilibria, however, does not seem to be mathematically tractable. Hence we only consider the case where $\mu_1 = \mu_2 := \mu$ and $\xi_1 = \xi_2 := \xi$ such that the sterile mosquitoes have the same survivability as wild mosquitoes. System (4.1) then becomes

$$(4.2) \quad \begin{aligned} \frac{dw}{dt} &= \left(\frac{aw}{1+w+g} - (\mu + \xi(w+g)) \right) w, \\ \frac{dg}{dt} &= \frac{bw}{1+w} - (\mu + \xi(w+g))g. \end{aligned}$$

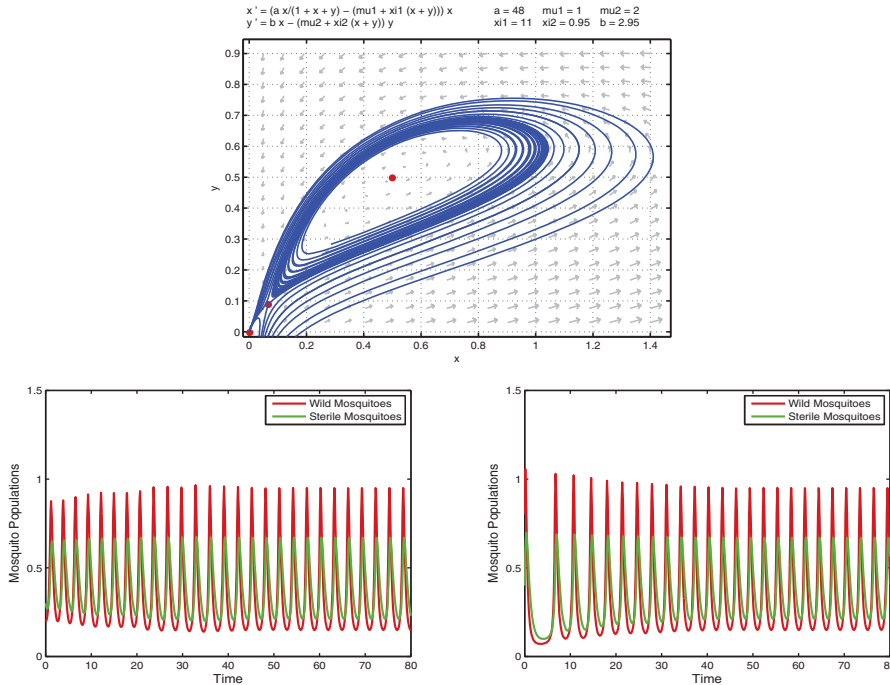


FIG. 4. The parameters are given in (3.15). There exist two positive equilibria $E_1^* = (0.0645, 0.0887)$ and $E_2^* = (0.5, 0.5)$ for system (3.1). Equilibrium E_1^* is a saddle point and E_2^* is a spiral source. A stable limit cycle exists. The phase plane is shown in the upper figure. The stable and unstable manifolds of E_1^* form a separatrix dividing the positive quadrant into two regions one of which is adjacent to the origin and one of which encloses the limit cycle. Solutions approach the stable limit cycle as they initially start from outside the cycle but inside the region enclosing the cycle as shown in the lower left figure, or from inside the cycle as shown in the lower right figure.

4.1. Existence of positive equilibria. At a positive equilibrium, with $N = w + g$, we have

$$w = \frac{1}{a}(1 + N)(\mu + \xi N), \quad g = \frac{b(1 + N)}{a + (1 + N)(\mu + \xi N)}.$$

For notational convenience, we merge a into μ , ξ , and b , respectively, and keep the same notation without confusion. Then N satisfies, at a positive equilibrium,

$$N = (1 + N)(\mu + \xi N) + \frac{b(1 + N)}{1 + (1 + N)(\mu + \xi N)},$$

that is,

$$(4.3) \quad (N - (1 + N)(\mu + \xi N))(1 + (1 + N)(\mu + \xi N)) = b(1 + N).$$

Notice that (4.3) is a polynomial equation of degree four, which, in general, may have four positive roots. However, we show that (4.3) has at most two positive roots as follows.

Let

$$W(N) := (1 + N)(\mu + \xi N).$$

It satisfies the following quadratic equation

$$W^2 + (1 - N)W + b(1 + N) - N = 0,$$

which has solutions

$$W_1(N) := \frac{1}{2}(N - 1 - \Delta), \quad W_2(N) := \frac{1}{2}(N - 1 + \Delta).$$

The two solutions $W_i(N)$, $i = 1, 2$, are both defined for all $N \geq 0$ if $b < 1/4$, and for all $N \geq 4b - 1$ if $b \geq 1/4$, where $\Delta := \sqrt{(N+1)(N+1-4b)}$. Then a positive equilibrium of (4.2) corresponds to a positive solution of

$$W(N) = W_1(N) \quad \text{or} \quad W(N) = W_2(N).$$

It follows from $\sqrt{(N+1)(N+1-4b)} < N+1-2b$ for all $N \geq 0$ if $b < 1/4$, and for all $N \geq 4b - 1$ if $b \geq 1/4$, that

$$W_1'(N) = \frac{1}{2} \left(1 - \frac{N+1-2b}{\Delta} \right) < 0 < W_2'(N) = \frac{1}{2} \left(1 + \frac{N+1-2b}{\Delta} \right),$$

and

$$W_1''(N) = \frac{2b^2}{\Delta^3} > 0 > W_2''(N) = -\frac{2b^2}{\Delta^3}.$$

In the case of $b < 1/4$, since $W_1(0) = -(1 + \sqrt{1-4b})/2 < 0$, $W_1'(N) < 0$, and $W(N) > 0$ for all $N \geq 0$, there is no positive solution to $W(N) = W_1(N)$, which implies that the positive solutions of (4.3) corresponds to the positive solutions of $W(N) = W_2(N)$.

In the case of $b \geq 1/4$, since $W_1(4b-1) = W_2(4b-1)$ if $W_i(4b-1) > W(4b-1)$, there are two positive solutions N , with $N > 4b-1$, from the intersections between $W(N)$ and $W_1(N)$ and between $W(N)$ and $W_2(N)$, respectively. On the other hand, if $W_i(4b-1) < W(4b-1)$, it is similar to the case of $b < 1/4$ that the positive solutions of (4.3) correspond to the positive solutions of $W(N) = W_2(N)$.

Then for the equation $W(N) = W_2(N)$, since $W'(N) > 0$, $W''(N) > 0$, $W_2'(N) > 0$, and $W_2''(N) < 0$, there are at most two positive solutions. Therefore, we conclude that, in any case, system (4.2) may have and only have zero, one, or two positive equilibria.

We next establish conditions for the existence of positive equilibria for system (4.2).

Define

$$(4.4) \quad Q_1(N) := \frac{1}{a}(aN - (1+N)(\mu + \xi N)), \quad Q_2(N) := \frac{a + (1+N)(\mu + \xi N)}{1+N}.$$

Then (4.3) becomes

$$(4.5) \quad Q_1(N)Q_2(N) = b,$$

and the positive equilibria of (4.2) are determined by the positive roots of (4.5).

Since $Q_2(N) > 0$ for all $N \geq 0$, $Q_1(0) = -\mu < 0$, and $Q_1(N)$ is a quadratic facing down, it follows that for (4.5) to have a positive root, it is necessary that the vertex

of quadratic Q_1 lies in the first quadrant; that is, the equation $Q_1(N) = 0$ has two positive roots, given by

$$(4.6) \quad \hat{N}_{1,2} = \frac{1}{2\xi} \left((a - \mu - \xi) \pm \sqrt{(a - \mu - \xi)^2 - 4\mu\xi} \right),$$

if $a > \mu + \xi$ and $(a - \mu - \xi)^2 - 4\mu\xi > 0$, or

$$(4.7) \quad \sqrt{\mu} + \sqrt{\xi} < \sqrt{a}.$$

Hence system (4.2) has a positive equilibrium only if condition (4.7) is satisfied, and it is clear that at any positive equilibrium, its corresponding N lies in (\hat{N}_1, \hat{N}_2) .

Moreover, since there are only two positive roots to (4.5) as proved above, the curve for $Q_1(N)Q_2(N)$ should have a similar shape as that for $Q_1(N)$ which implies that function $Q_1(N)Q_2(N)$ has a unique maximum value on interval (\hat{N}_1, \hat{N}_2) that determines the threshold release value b_0 . In summary, we have the following existence results.

THEOREM 4.1. *System (4.2) has no positive equilibrium if $\sqrt{\mu} + \sqrt{\xi} \geq \sqrt{a}$. Suppose condition (4.7) is satisfied and let the threshold release value be given as*

$$(4.8) \quad b_0 := \max_{N \in (\hat{N}_1, \hat{N}_2)} \{Q_1(N)Q_2(N)\},$$

where $Q_i, i = 1, 2$, are given in (4.4), and $\hat{N}_i, i = 1, 2$, are given in (4.6). Then system (4.2) has no positive equilibrium if $b > b_0$. It has one positive equilibrium $E^*(w^*, g^*)$ with

$$(4.9) \quad w^* = \frac{1}{a} (1 + N^*) (\mu + \xi N^*), \quad g^* = \frac{b(1 + N^*)}{a + (1 + N^*) (\mu + \xi N^*)}$$

if $b = b_0$, where N^* is the unique positive root of (4.5), or two positive equilibria $E_1^*(w_1^*, g_1^*)$ and $E_2^*(w_2^*, g_2^*)$ with

$$(4.10) \quad w_{1,2}^* = \frac{1}{a} (1 + N_{1,2}^*) (\mu + \xi N_{1,2}^*), \quad g_{1,2}^* = \frac{b(1 + N_{1,2}^*)}{a + (1 + N_{1,2}^*) (\mu + \xi N_{1,2}^*)}$$

if $b < b_0$, where $N_1^* < N_2^*$ are the two positive roots of (4.5).

Remark 3. Similarly as in section 3, although the threshold release value b_0 is determined implicitly in (4.8), we can obtain its estimate as follows.

Solving $Q_1'(N) = 0$, we obtain the critical point $N_{1c} = \frac{a - (\mu + \xi)}{2\xi}$, and thus $\max_{N \in (\hat{N}_1, \hat{N}_2)} \{Q_1(N)\} = Q_1(N_{1c})$. It follows from $Q_2''(N) > 0$ that $\max_{N \in (\hat{N}_1, \hat{N}_2)} \{Q_2(N)\} = \max\{Q_2(\hat{N}_1), Q_2(\hat{N}_2)\} = a$. Let

$$(4.11) \quad \sigma_1 := aQ_1(N_{1c}) = \left(\frac{(a - \mu - \xi)^2 - 4\mu\xi}{4\xi} \right).$$

Then $b_0 \leq \sigma_1$. Similarly, $(1 + N)Q_2(N)$, as a function of N , is an increasing function. Then

$$\max_{N \in (\hat{N}_1, \hat{N}_2)} \{(1 + N)Q_2(N)\} \leq (1 + N_2)Q_2(N_2).$$

We then define the function

$$Q_3(N) := \frac{Q_1(N)}{1+N},$$

which has its maximum at $N_{2c} = (\sqrt{a} - \sqrt{\xi})/\sqrt{\xi}$. Let

$$\sigma_2 := (1 + N_2)Q_2(N_2)Q_3(N_{2c}),$$

then $b_0 \leq \sigma_2$, and simple calculation yields

$$(4.12) \quad \sigma_2 = \frac{a - \mu - \xi + \sqrt{(a - \mu - \xi)^2 - 4\mu\xi}}{2\xi} \left((\sqrt{a} - \sqrt{\xi})^2 - \mu \right).$$

Combining (4.11) and (4.12), we have the following estimate:

$$(4.13) \quad b_0 \leq b_c := \min\{\sigma_1, \sigma_2\}.$$

If $b \geq b_c$, all solutions approach the origin; that is all mosquitoes are eventually wiped out, which also implies no more sterile mosquito releases are needed.

4.2. Stability of the positive equilibria. We now determine the stability of the positive equilibria for system (4.2). For notational convenience, we merge a into μ , ξ , and b , respectively, again and keep the same notation. The Jacobian matrix of system (4.2) at a positive equilibrium with $N = w + g > 0$ has the form

$$J_3 = \begin{pmatrix} \left(\frac{1+g}{(1+N)^2} - \xi \right) w & - \left(\frac{w}{(1+N)^2} + \xi \right) w \\ \frac{b}{(1+w)^2} - \xi g & -\mu - \xi N - \xi g \end{pmatrix}.$$

It follows from $\frac{w}{1+N} = \mu + \xi N$ that, at a positive equilibrium, we have

$$\begin{aligned} \text{tr} J_3 &= \frac{(1+g)w}{(1+N)^2} - \mu - 2\xi N = \frac{1+g}{1+N} (\mu + \xi N) - \mu - 2\xi N \\ &= (\mu + \xi N) \left(\frac{1+g}{1+N} - 1 \right) - \xi N = -\frac{(\mu + \xi N)w}{1+N} - \xi N < 0. \end{aligned}$$

Thus, the stability is determined by the determinant of J_3 .

After tedious calculations, we have

$$(4.14) \quad \det J_3 = -\frac{w(\mu + \xi N)}{1+w} \frac{d(Q_1 Q_2)}{dN},$$

where $Q_i(N)$, $i = 1, 2$, are given in (4.4) with $a = 1$. (The details are given in Appendix B.)

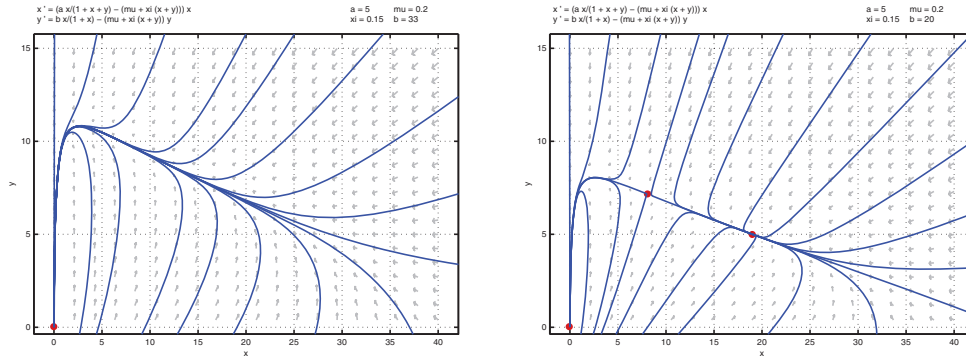


FIG. 5. The parameters are given in (4.15). For $b = 33 > b_0$, the origin is the only equilibrium of system (4.2) which is a globally asymptotically stable node. All solutions approach the origin, regardless of their initial values, as shown in the left figure. For $b = 20 < b_0$, there exist two positive equilibria $E_1^* = (8.0551, 7.1652)$ and $E_2^* = (19, 5)$. Equilibrium E_1^* is a saddle point and E_2^* is a nodal source. The stable manifolds of E_1^* form a separatrix such that solutions approach the stable origin or E_2^* as shown in the right figure.

Suppose there are two positive equilibria of (4.2), $E_1^*(w_1^*, g_1^*)$ and $E_2^*(w_2^*, g_2^*)$, associated with the two positive solutions of (4.5), $N_1^* < N_2^*$. As shown in Appendix B, we have

$$\left. \frac{d(Q_1 Q_2)}{dN} \right|_{N=N_2^*} < 0 < \left. \frac{d(Q_1 Q_2)}{dN} \right|_{N=N_1^*}.$$

Hence

$$\det J_3|_{N=N_1^*} < 0 < \det J_3|_{N=N_2^*}.$$

In summary, we have the following stability results.

THEOREM 4.2. Assume that there exist two positive equilibria of system (4.2), $E_1^*(w_1^*, g_1^*)$ and $E_2^*(w_2^*, g_2^*)$, given in (4.10), corresponding to the two positive roots $N_1^* < N_2^*$. Then E_1^* is a saddle point and E_2^* is a locally asymptotically stable node or spiral.

We provide an example to confirm the results in Theorems 4.1 and 4.2 as follows.

Example 5. Let the parameters in system (4.2) be given by

$$(4.15) \quad \mu_1 = \mu_2 = 0.2, \quad \xi_1 = \xi_2 = 0.15, \quad a = 5.$$

The threshold release value for the sterile mosquitoes is $b_0 = 22.5545$. For $b = 33 > b_0$, the origin is the only equilibrium of system (4.2) which is a globally asymptotically stable node. All solutions approach the origin, regardless of their initial values, as shown in the left figure in Figure 5. For $b = 20 < b_0$, system (4.2) has two positive equilibria, a saddle point $E_1^* = (8.0551, 7.1652)$ and a stable node $E_2^* = (19, 5)$. The stable manifolds of E_1^* form a separatrix such that solutions approach either the stable origin or E_2^* , depending on their initial values, as shown in the right figure in Figure 5.

5. Concluding remarks. While mosquito transgenesis and paratransgenesis are two novel strategies among the mosquitoes control measures, the sterile insect technique has also been applied to reduce or eradicate wild mosquitoes which transmit mosquito-borne diseases. Nevertheless, the interactive dynamics of wild and

sterile mosquitoes are so complex that investigations and assessments of the impact of releasing sterile mosquitoes into the field are very challenging. To have a better understanding of the complexity of the interactive dynamics and provide useful guidance for good strategies for releasing sterile mosquitoes, we introduced mathematical models with different release functions $B(\cdot)$ of the sterile mosquitoes in this study. The release function is assumed to be constant, proportional to w , or of Holling-II type, for model system (2.2), (3.1), or (4.1), respectively. In addition, we assumed Allee effects for models (3.1) and (4.1), considering possible mating difficulty, which is not necessary for model (2.2) due to the constant releases of sterile mosquitoes.

We explored the existence of all possible equilibria and the stability of these equilibria for all of the three model systems. We established a threshold release value explicitly for model (2.2) such that there exist no, one, or two positive equilibria as the release parameter is above, equal to, or below the threshold. We further showed, for model (2.2), that if the threshold is exceeded, all solutions approach globally a boundary equilibrium with the wild mosquito component equal to zero. On the other hand, if the threshold is not reached, while the boundary equilibrium is still locally asymptotically stable, there exist two positive equilibria, one of which is a saddle point and one of which is an asymptotically stable node or spiral. For model (3.1), however, the dynamics are not so simple. We still managed to determine a threshold release value, but only implicitly. As the release parameter is above the threshold, all solutions approach the origin regardless of their initial values, whereas if the release parameter is below the threshold, there also exist two positive equilibria one of which is also a saddle point, but the other positive equilibrium can be stable or unstable. By varying certain bifurcation parameters, unstable or stable limit cycles appear. An unstable limit cycle may not show stable dynamics for the model system, but it creates a larger attracting region of initial values for the origin, which enhances the efficiency of the control measures. In the meantime, a stable limit cycle describes the sustained oscillations which helps to explain the real observations and also provides useful guidelines in the mosquitoes control and disease prevention.

Model (4.1) has even more complex dynamical features which forced us to only focus on a special case where $\mu_1 = \mu_2$ and $\xi_1 = \xi_2$ where the same fitness for the sterile and wild mosquitoes is assumed. Then we were able to fulfill a relatively complete analysis for the model system. We obtained a threshold release value implicitly and showed that the dependence of the existence of positive equilibria on the threshold release value is similar to the dependence for the other models. We also showed that the stability feature for model (4.1) is similar to that for model (2.2) such that if there exist two positive equilibria, one must be a saddle point and one is an asymptotically stable node or spiral.

The qualitative features of the three model systems look similar such that all have the same number of positive equilibria and similar stability in some cases. However, their biological dynamics are different. More specifically, suppose that the release threshold is exceeded and hence there exists no positive equilibrium which means wild mosquitoes will be eventually wiped out for all of the models. The solutions approach the boundary equilibrium where the component of the sterile mosquitoes, g , is positive for model (2.2), whereas the component of the sterile mosquitoes for models (3.1) and (4.1) approaches zero. That is, even though wild mosquitoes go extinct, there are still sterile mosquitoes around in model (2.2). This is not surprising due to the constant releases of sterile mosquitoes no matter whether the wild mosquito population size is large or small. This apparently does not seem to be the best strategy economically

even though the model has an explicit formula for the threshold release value. In contrast, the strategy leading to model (3.1) has the releases of sterile mosquitoes being proportional to the current wild mosquito population size, which can be done with monitoring or surveillance of the wild mosquitoes in the field. As the amount of releases of sterile mosquitoes exceeds the threshold, all solutions approach the origin, not any boundary equilibrium, which means no more releases of sterile mosquitoes are needed in the long run. This has its advantage and is more economic particularly when the wild mosquito population size is small. Nevertheless, if the wild mosquito population size is significantly large in the field, the amount of the releases needs to be large as well which shows its disadvantage economically. As a compromise, we consider the release function to have the form of Holling-II type in model (4.1). It has the advantage of model (3.1) when wild mosquito population size is small, but the releases are saturated and approach its upper limit as the wild mosquito population is large. The model dynamics become even closer to those of model (2.2) for the special case we considered. Moreover, by comparing models (3.1) and (4.1), the release rates satisfy $b_2w/(1+w) > b_1w$ only if $b_2 > b_1$ and $w < (b_2 - b_1)/b_1$. Thus the strategy in model (4.1) seems more economically optimal. We use an example to demonstrate the difference of the three strategies below.

We fix the following parameters

$$(5.1) \quad a = 10, \quad \mu_1 = 0.5, \quad \xi_1 = 0.5, \quad \mu_2 = 0.4, \quad \xi_2 = 0.4,$$

and compare the results from the three different models with the release value b less than but close to their threshold release values.

The threshold release values b_0 are 21.9352 for model (2.2), approximately 4.42 for model (3.1), and 20.8 for model (4.1), respectively. As b exceeds the respective threshold release values, all solutions approach the boundary equilibrium for model (2.2), and the origin for models (3.1) and (4.1) globally, regardless of their initial values. We then let b be less than but close to the threshold release values for the three models. All of the three models have two positive equilibria, one saddle point and one locally asymptotically stable node. The stable manifolds of the saddle point form a separatrix for each of the models. Solutions approach either the boundary equilibrium $(0, 6.9213)$ or the positive equilibrium $(8.6266, 4.0181)$ for model (2.2), either the origin or the positive equilibrium $(1.0742, 2.5609)$ for model (3.1), and the positive equilibrium $(7.7856, 3.6928)$ for model (4.1), respectively, depending on their initial values. The phase dynamics are shown in Figure 6. The difference between model (2.2) and model (3.1) or (4.1) is clear as described above. For models (3.1) and (4.1), while both have solutions approaching the origin or the stable node, we particularly notice that the attracting region of the origin for model (4.1) is larger than that for (3.1). This implies that the likelihood of getting wild mosquitoes wiped out with the strategy implemented in model (4.1) is higher than that in model (3.1).

While the findings seem exciting and promising, yet there are still more tasks to be finished in our research. Numerical examples showing the existence of limit cycles for model (3.1) are provided, but complete investigations and bifurcation analysis have not been accomplished. We have a complete analysis for the interactive dynamics of the wild and sterile mosquitoes for model (4.2) in the special case of $\mu_1 = \mu_2$ and $\xi_1 = \xi_2$, but the dynamics may be quite different if their death rates are different, which needs to be explored. The mosquito population in this paper has been assumed to be homogeneous without distinguishing their genders. Models with separate male and female wild mosquito components incorporating with releasing male sterile mosquitoes

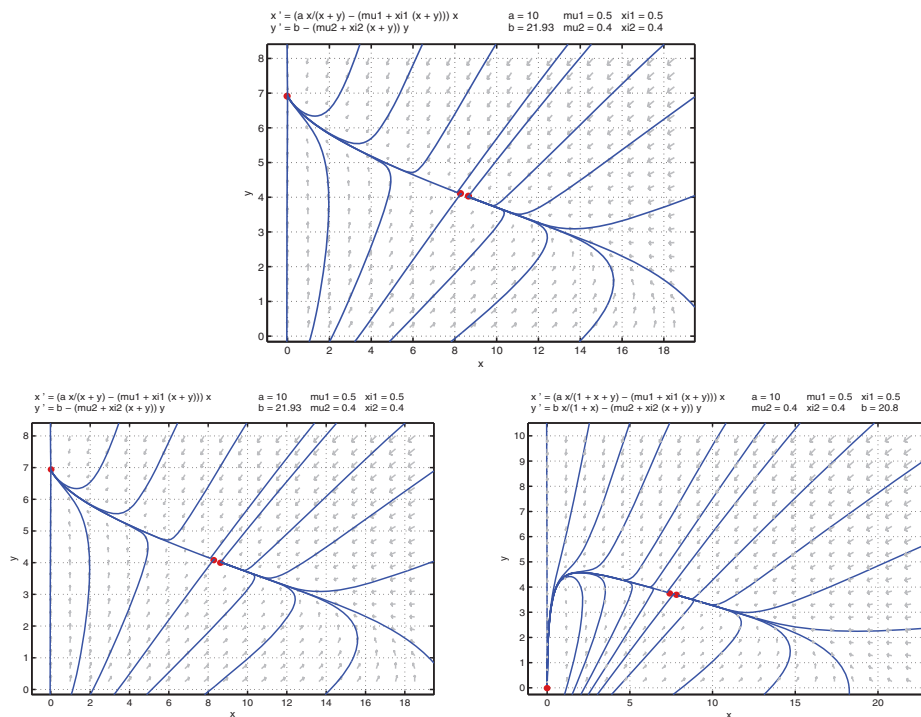


FIG. 6. The parameters are given in (5.1). The release parameter b is less than the threshold for all of the three models. There exist two positive equilibria for each of the three models, one of which is a saddle point and one of which is a locally asymptotically stable node. The stable manifolds of the saddle point form a separatrix for each of the models. Solutions approach either the boundary equilibrium or the stable positive node for model (2.2) as shown in the upper figure, and either the origin or the stable positive node for models (3.1) and (4.1) as shown in the lower left and right figures, respectively.

are needed to gain further insight into the interactive dynamics and impact of SIT on the mosquitoes control and disease transmission. All of these tasks are being undertaken or planned in our other projects.

Appendix A. The computation of determinant $\det J_2$ in (3.11). Let $\Delta_1 := \frac{(1+N)^2}{w} \det J_2$. It follows from

$$\begin{aligned}
 \det J_2 &= \left(\xi_1 w - \frac{aw(1+g)}{(1+N)^2} \right) (\mu_2 + \xi_2 g + \xi_2 N) + (b - \xi_2 g) \left(\xi_1 w + \frac{aw^2}{(N+1)^2} \right) \\
 &= (\mu_2 + \xi_2 N) \left(\xi_1 w - \frac{aw(1+g)}{(1+N)^2} \right) - \xi_2 g \frac{aw(1+g)}{(1+N)^2} + \frac{baw^2}{(1+N)^2} \\
 &\quad + b\xi_1 w - \frac{a\xi_2 gw^2}{(1+N)^2} \\
 &= (\mu_2 + \xi_2 N)\xi_1 w - \frac{aw((1+g)(\mu_2 + \xi_2 N) - bw)}{(1+N)^2} - \frac{a\xi_2 wg}{1+N} + b\xi_1 w \\
 &= (\mu_2 + \xi_2 N)\xi_1 w - \frac{aw(\mu_2 + \xi_2 N)}{(1+N)^2} - \frac{a\xi_2 wg}{1+N} + b\xi_1 w
 \end{aligned}$$

and (3.3) that

$$\begin{aligned} \Delta_1 &= \xi_1(\mu_2 + \xi_2 N)(1 + N)^2 - a(\mu_2 + \xi_2 N) - b\xi_2(1 + N)^2 \frac{\mu_1 + \xi_1 N}{\mu_2 + \xi_2 N} + b\xi_1(1 + N)^2 \\ &= \xi_1(\mu_2 + \xi_2 N)(1 + N)^2 - a(\mu_2 + \xi_2 N) \\ &\quad - \xi_2(1 + N)(aN - (1 + N)(\mu_1 + \xi_1 N)) + b\xi_1(1 + N)^2 \\ &= 2\xi_1\xi_2 N^3 + (\mu_2\xi_1 + 2\xi_1\xi_2 - a\xi_2 + \mu_1\xi_2 + 2\xi_1\xi_2 + b\xi_1)N^2 \\ &\quad + (2\mu_2\xi_1 + 2\xi_1\xi_2 - 2a\xi_2 + 2\mu_1\xi_2 + 2b\xi_1)N + \mu_2\xi_1 - a\mu_2 + \mu_1\xi_2 + b\xi_1. \end{aligned}$$

Adding $F(N) = 0$ to the right-hand side above then yields

$$\begin{aligned} \Delta_1 &= 3\xi_1\xi_2 N^3 + (\mu_2\xi_1 + 2\xi_1\xi_2 - a\xi_2 + \mu_1\xi_2 + 2\xi_1\xi_2 + b\xi_1 + b\xi_1 + \xi_1\xi_2 + \xi_1\mu_2 \\ &\quad + \xi_2(\mu_1 - a))N^2 + (2\mu_2\xi_1 + 2\xi_1\xi_2 - 2a\xi_2 + 2\mu_1\xi_2 + 2b\xi_1 + \mu_1\xi_2 + \mu_2\xi_1 \\ &\quad + b\xi_1 + b\mu_1 + (\mu_1 - a)\mu_2)N + \mu_2\xi_1 - a\mu_2 + \mu_1\xi_2 + b\xi_1 + b\mu_1 + \mu_1\mu_2 \\ &= 3\xi_1\xi_2 N^2(1 + N) + (2\mu_2\xi_1 + 2\xi_1\xi_2 + 2b\xi_1 + 2\xi_2(\mu_1 - a))N(1 + N) \\ &\quad + (\mu_1\xi_2 + \mu_2\xi_1 + b\xi_1 + b\mu_1 + (\mu_1 - a)\mu_2)(1 + N) = (1 + N)F'(N). \end{aligned}$$

Hence (3.11) follows.

Appendix B. The computation of determinant $\det J_3$ in (4.14). We first have

$$\begin{aligned} \frac{1}{w} \det J_3 &= \left(\xi - \frac{1 + g}{(1 + N)^2} \right) (\mu + \xi N + \xi g) + \left(\frac{w}{(N + 1)^2} + \xi \right) \left(\frac{b}{(1 + w)^2} - \xi g \right) \\ &= \left(\xi - \frac{1 + g}{(1 + N)^2} \right) (\mu + \xi N) - \frac{\xi g(1 + g)}{(1 + N)^2} + \left(\frac{w}{(N + 1)^2} + \xi \right) \frac{b}{(1 + w)^2} \\ &\quad - \frac{\xi g w}{(N + 1)^2} \\ &= \left(\xi - \frac{1 + g}{(1 + N)^2} \right) (\mu + \xi N) + \left(\frac{w}{(N + 1)^2} + \xi \right) \frac{b}{(1 + w)^2} - \frac{\xi g}{1 + N} \\ &= \left(\xi - \frac{1 + g}{(1 + N)^2} \right) (\mu + \xi N) + \frac{w}{(N + 1)^2} \frac{b}{(1 + w)^2} - \frac{\xi b w}{(1 + w)^2} \\ &= \left(\xi - \frac{1 + g}{(1 + N)^2} \right) (\mu + \xi N) + \left(\frac{1}{(N + 1)^2} - \xi \right) \frac{(\mu + \xi N)g}{1 + w}. \end{aligned}$$

Then writing $\Delta_2 := \det J_3 / (w(\mu + \xi N))$, we have

$$\begin{aligned} \Delta_2 &= \frac{1}{w(\mu + \xi N)} \det J_3 = \xi - \frac{1 + g}{(1 + N)^2} + \left(\frac{1}{(N + 1)^2} - \xi \right) \frac{g}{1 + w} \\ \text{(B.1)} \quad &= \left(\xi - \frac{1}{(1 + N)^2} \right) \left(1 - \frac{g}{1 + w} \right) - \frac{g}{(1 + N)^2}. \end{aligned}$$

It follows from (4.4) that $Q_2(N) = \frac{1+w}{1+N}$, at a positive equilibrium, and then

$$1 + w = (1 + N)Q_2, \quad g = N - w = (1 + N)(1 - Q_2).$$

Hence

$$\text{(B.2)} \quad 1 - \frac{g}{1 + w} = 1 - \frac{(1 + N)(1 - Q_2)}{(1 + N)Q_2} = \frac{1}{Q_2} (2Q_2 - 1)$$

and

$$(B.3) \quad -\frac{g}{(1+N)^2} = \frac{Q_2 - 1}{1+N}.$$

Noticing $Q'_2(N) = \xi - \frac{1}{(1+N)^2}$ and substituting (B.2) and (B.3) into (B.1), we have

$$(1+w)\Delta_2 = (1+w) \left(Q'_2 \frac{1}{Q_2} (2Q_2 - 1) + \frac{Q_2 - 1}{1+N} \right) = (1+N)Q'_2(2Q_2 - 1) + Q_2(Q_2 - 1).$$

On the other hand, we notice that $Q_1(N) = (1+N)(1 - Q_2(N))$ and then

$$\frac{d}{dN}(Q_1 Q_2) = \frac{d}{dN}((1+N)(1 - Q_2)Q_2) = (1 - Q_2)Q_2 + (1+N)(1 - 2Q_2)Q'_2.$$

Hence

$$\det J_3 = -\frac{w(\mu + \xi N)}{1+w} \frac{d(Q_1 Q_2)}{dN}.$$

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