Mathematical Biosciences and Engineering

http://www.aimspress.com/journal/MBE

Mathematical Biosciences and Engineering, 16(2): 572–602.
DOI: 10.3934/mbe.2019028
Received: 18 June 2018
Accepted: 03 October 2018
Published: 11 January 2019

Research article

Stage-structured discrete-time models for interacting wild and sterile mosquitoes with beverton-holt survivability

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Abstract: The sterile insect technique (SIT) is an effective weapon to prevent transmission of mosquito-borne diseases, in which sterile mosquitoes are released to reduce or eradicate the wild mosquito population. To study the impact of the sterile insect technique on the disease transmission, we formulate stage-structured discrete-time models for the interactive dynamics of the wild and sterile mosquitoes using Beverton-Holt type of survivability, based on difference equations. We incorporate different strategies for releasing sterile mosquitoes, and investigate the model dynamics. Numerical simulations are also provided to demonstrate dynamical features of the models.

Keywords: mathematical modeling; beverton-holt survivability; discrete-time models; sterile mosquitoes; vector-borne diseases; numerical simulations

1. Introduction

To prevent mosquito-borne diseases, the sterile insect technique (SIT) has been applied to reduce or eradicate the wild mosquitoes and has shown promising results in laboratory studies [1, 8, 38], but predicting the impact of releasing sterile mosquitoes into the field of wild mosquito populations is still challenging. Mathematical models have proven useful in gaining insights into interactive dynamics of wild and sterile mosquito populations, and there are models in the literature for such studies [4, 5, 6, 7, 13, 17, 18, 28, 29]. However, most of them assume homogeneous mosquito populations without distinguishing the metamorphic stages of mosquitoes.

Mosquitoes undergo complete metamorphosis, going through four distinct stages of development during a lifetime, egg, pupae, larva, and adult. After a female mosquito drinking blood, she can lay from 100 to 300 eggs at a time in standing water or very slow-moving water. In her lifetime, she can produce from 1000 to 3000 eggs [34]. Within a week, the eggs hatch into larvae, which will use their tubes to breathe air by poking above the surface of the water. Larvae eat a bit of floating organic matter and each other. Larvae molt four times totally as they grow and after the fourth molt, they are called pupae. Pupae also live near the surface of water and breathe through two horn-like tubes (called siphons) on their back. But pupae do not eat. When the skin splits after a few days from a pupae, an adult mosquito emerges. The adults live for only a few weeks and a full life-cycle of a mosquito takes about a month [2, 9].

To have more realistic modeling of mosquitoes, we need to include stage structure since the different stages have different responses to environment and regulating factors to the population [36]. While the interspecific competition and predation are rare events and could be discounted as major causes of larval mortality, the intraspecific competition could represent a major density dependent source. Thus the effect of crowding could be an important factor in the population dynamics of mosquitoes [15, 19, 35].

Moreover, since the first three stages in a mosquito's life time are aquatic and the major density dependent source comes from the larval stage, following the line in [24, 26], we group the three aquatic stages of mosquitoes into one class and divide the whole mosquito population into only two classes to keep our mathematical modeling as simple as possible. We call the class consisting of the first three stages larvae and the other class adult. We assume that the density dependence is based on larvae not the adults. We still simplify our models such that no male and female individuals are distinguished.

For the density-dependent mortality, most existing works in the literature, including our previous studies, have assumed the Ricker-type nonlinearity [24, 25, 27, 29, 31]. The dynamics of the Ricker-type nonlinearity are complex, causing, e.g. period-doubling bifurcations even without any other interactions. As the sterile mosquitoes are included, the model dynamics become more complex and it is not clear whether the complexity is from the baseline model without interaction already or from the interaction. Thus, we assume that the mosquito population follow the nonlinearity of Beverton-Holt type [11, 12] in this paper.

We first investigate the dynamics of the general stage-structured model with no releases of sterile mosquitoes in Section 2. We then introduce sterile mosquitoes into the model and formulate the interactive stage-structured models in Section 3. Similar to those in [4, 5, 13, 29], we consider three strategies of releases. The case of constant releases is studied in Section 3.1. Complete mathematical analysis for the model dynamics is given. We then formulate a model for the case where the number of sterile mosquito releases is proportional to the wild mosquito population size in Section 3.2. Mathematical analysis and numerical simulations are provided to demonstrate the complexity of the model dynamics. Considering different sizes of wild mosquito population, we consider a different releasing strategy as in [30, 31] in Section 3.3, where the releases of sterile mosquitoes are proportional to the wild mosquitoes size when the wild mosquitoes size is small but is saturated and approaches a constant as the wild mosquitoes size is sufficiently large. We provide complete mathematical analysis for the model dynamics. We finally provide a brief discussion on our findings, particularly on the impact of the three different strategies on the mosquito control measures in Section 4.

2. Stage-structured model basis without the presence of sterile mosquitoes

We first consider a stage-structured model of wild mosquitoes in the absence of sterile mosquitoes. Let x_n and y_n be the numbers of mosquito larvae and adults at generation n, respectively, and assume that population dynamics of the mosquitoes are described by the following system:

$$\begin{aligned} x_{n+1} &= f(x_n, y_n) y_n s_1(x_n, y_n), \\ y_{n+1} &= g(x_n, y_n) x_n s_2(x_n, y_n), \end{aligned}$$

where f is the number of the offspring produced per adult, s_1 is the survival probability of larvae or the fraction of larvae who survive, g is the progression rate of larvae or the adults emergence rate, and s_2 is the survival probability of adults.

We assume a constant birth rate and denote it as $f := a$. Since the intraspecific competition mainly takes place within the aquatic stages of mosquitoes, we assume that the death and the progression rates of larvae are density-dependent only on the larvae size, with the Beverton-Holt type of nonlinearity, such that $s_1(x_n, y_n) = \dfrac{k_1}{1 + \eta_1 x_n}$ and $g(x_n, y_n) = \dfrac{\gamma}{1 + \eta_2 x_n}$, where k_1 is the maximum survival probability, η_1 and η_2 are density-dependent factors, and γ is the maximum progression rate.

We assume that food is abundant for mosquito adults so that the adults survival rate is constant, denoted as $s_2(x_n, y_n) := s_2$. Then the model equations become

$$\begin{aligned} x_{n+1} &= \frac{a y_n}{1 + \eta_1 x_n}, \\ y_{n+1} &= \frac{\gamma x_n}{1 + \eta_2 x_n}, \end{aligned} \tag{2.1}$$

where we merge k_1 and s_2 into a and γ, respectively, but we still use a and γ for those parameters without confusion.

The origin $(0, 0)$ is a trivial fixed point of system (2.1). Define the intrinsic growth rate of the stage-structured mosquito population $r_0 := a\gamma$. The trivial fixed point is locally asymptotically stable if $r_0 < 1$ and is unstable if $r_0 > 1$.

2.1. *Existence and stability of positive fixed points*

The x component of a positive fixed point of system (2.1) satisfies

$$\eta_1 \eta_2 x^2 + (\eta_1 + \eta_2) x + 1 - r_0 = 0. \tag{2.2}$$

Clearly, the quadratic equation (2.2) has no positive root and hence system (2.1) has no positive fixed point if $r_0 \leq 1$. Equation (2.2) has a unique positive root and hence system (2.1) has a unique positive fixed point $\overline{E} := (\bar{x}, \bar{y})$ if $r_0 > 1$, with

$$\bar{x} = \frac{-(\eta_1 + \eta_2) + \sqrt{\Delta}}{2\eta_1 \eta_2}, \quad \bar{y} = \frac{\gamma(-(\eta_1 + \eta_2) + \sqrt{\Delta})}{2\eta_1 \eta_2 + \eta_2(-(\eta_1 + \eta_2) + \sqrt{\Delta})}, \tag{2.3}$$

where $\Delta = (\eta_1 - \eta_2)^2 + 4\eta_1 \eta_2 a\gamma$.

The Jacobian matrix of system (2.1) at $\overline{E}$ has the form

$$J_1 := \begin{pmatrix} -\dfrac{\eta_1 \bar{x}}{1+\eta_1 \bar{x}} & \dfrac{a}{1+\eta_1 \bar{x}} \\ \dfrac{\gamma}{(1+\eta_2 \bar{x})^2} & 0 \end{pmatrix}. \tag{2.4}$$

Fixed point $\overline{E}$ is locally asymptotically stable if

$$|\mathrm{tr} J_1| < 1 + \det J_1 < 2$$

[22, 33], that is,

$$\frac{\eta_1 \bar{x}}{1+\eta_1 \bar{x}} < 1 - \frac{1}{1+\eta_2 \bar{x}} < 2.$$

Thus fixed point $\overline{E}$ is locally asymptotically stable if

$$\eta_1 < \eta_2,$$

and is unstable if

$$\eta_1 > \eta_2.$$

2.2. Existence and stability of synchronous 2-cycles

System (2.1) may have periodic cycles of different periods. We first consider 2-cycles with $x_{n+2} = x_n \neq 0$ and $y_{n+2} = y_n \neq 0$, for all $n \geq 0$.

It follows from system (2.1) that

$$\begin{aligned} x_{n+2} &= \frac{a y_{n+1}}{1+\eta_1 x_{n+1}} = \frac{a\gamma x_n}{(1+\eta_2 x_n)(1+\eta_1 x_{n+1})}, \\ y_{n+2} &= \frac{\gamma x_{n+1}}{1+\eta_2 x_{n+1}} = \frac{a\gamma y_n}{(1+\eta_1 x_n)(1+\eta_2 x_{n+1})}. \end{aligned} \tag{2.5}$$

Then there exists a positive nontrivial 2-cycle if and only if

$$(1+\eta_2 x_n)(1+\eta_1 x_{n+1}) = (1+\eta_1 x_n)(1+\eta_2 x_{n+1}) = a\gamma,$$

which implies

$$(\eta_2 - \eta_1)(x_n - x_{n+1}) = 0,$$

for all $n \geq 0$.

If $\eta_1 \neq \eta_2$, there exist no positive 2-cycles. If $\eta_1 = \eta_2 := \eta$, there may exist positive nontrivial 2-cycles. Before we investigate their existence and dynamics, we consider nonnegative synchronous 2-cycles which are not strictly positive, but are non-negative with alternating zero and positive components [14]. In such a situation, the mosquito larvae and adults are synchronized in such a way as to appear and vanish alternately in one time unit.

Synchronous 2-cycles can be found by looking for nontrivial equilibria of system (2.5) which have one component equal to zero. It follows from

$$x_{n+2} = \frac{a\gamma x_n}{(1+\eta_2 x_n)(1+\eta_1 x_{n+1})}$$

that

$$x_* = \frac{a\gamma x_*}{(1+\eta_2 x_*)(1+\eta_1 \cdot 0)},$$

which yields

$$x_* = \frac{r_0 - 1}{\eta_2}. \tag{2.6}$$

Then it follows from

$$x_{n+2} = \frac{a y_{n+1}}{1+\eta_1 x_{n+1}},$$

that

$$x_* = \frac{a y_*}{1+\eta_1 \cdot 0},$$

which leads to

$$y_* = \frac{x_*}{a} = \frac{a\gamma - 1}{a\eta_2}. \tag{2.7}$$

Thus the system will undergo a unique synchronous 2-cycle as

$$\begin{pmatrix} x_* \\ 0 \end{pmatrix} \to \begin{pmatrix} 0 \\ y_* \end{pmatrix} \to \begin{pmatrix} x_* \\ 0 \end{pmatrix} \to \begin{pmatrix} 0 \\ y_* \end{pmatrix} \to \cdots,$$

where x_* is given in (2.6) and y_* is given in (2.7), for $r_0 > 1$.

At the synchronous 2-cycle, the Jacobian matrix is

$$J_2 := \begin{pmatrix} \frac{a\gamma}{(1+\eta_2 x_*)^2} & -\frac{a\eta_1 x_*}{1+\eta_1 x_*} \\ 0 & \frac{a\gamma}{1+\eta_1 x_*} \end{pmatrix} = \begin{pmatrix} \frac{1}{r_0} & -\frac{a\eta_1 x_*}{1+\eta_1 x_*} \\ 0 & \frac{r_0}{1+\eta_1 x_*} \end{pmatrix}.$$

Then, it follows from

$$\mathrm{tr} J_2 = \frac{1}{r_0} + \frac{r_0}{1+\eta_1 x_*}, \quad \det J_2 = \frac{1}{1+\eta_1 x_*},$$

that the unique synchronous 2-cycle is locally asymptotically stable if

$$\frac{1}{r_0} + \frac{r_0}{1+\eta_1 x_*} < 1 + \frac{1}{1+\eta_1 x_*},$$

that is,

$$\eta_1 > \eta_2.$$

2.3. *Existence and stability of positive 2-cycles*

We now assume $\eta_1 = \eta_2 := \eta$ to analyze the case of positive 2-cycles. Then the unique positive fixed point has the components

$$\bar{x}_0 = \frac{\sqrt{r_0} - 1}{\eta}, \quad \bar{y}_0 = \frac{\sqrt{\gamma}(\sqrt{r_0} - 1)}{\sqrt{a}\eta}, \tag{2.8}$$

whose stability is determined by the eigenvalues of the Jacobian matrix in (2.4). The eigenvalues are

$$\lambda_1 = -1, \quad \lambda_2 = \frac{1}{\sqrt{r_0}} < 1,$$

which implies the possibility of bifurcated 2-cycles. We now explore the existence of such 2-cycles.

It follows from system (2.1) that

$$\begin{aligned} x_{n+2} &= \frac{a\gamma x_n}{(1+\eta x_n)(1+\eta x_{n+1})} = \frac{r_0 x_n}{1+\eta x_n + a\eta y_n}, \\ y_{n+2} &= \frac{a\gamma y_n}{(1+\eta x_n)(1+\eta x_{n+1})} = \frac{r_0 y_n}{1+\eta x_n + a\eta y_n}. \end{aligned} \tag{2.9}$$

For a positive 2-cycle with initial values (x_0, y_0), it follows from (2.9) that the two components satisfy the following linear equation:

$$1 + \eta x_0 + a\eta y_0 = r_0. \tag{2.10}$$

Thus, if we let $x_0 \in \left(0, \frac{r_0-1}{\eta}\right)$ and $y_0 = \frac{r_0-1-\eta x_0}{a\eta}$, then a solution of (2.1) with such initial values is a positive 2-cycle.

Any positive 2-cycle has the form

$$\begin{pmatrix} x_1 \\ y_1 \end{pmatrix} \to \begin{pmatrix} x_2 \\ y_2 \end{pmatrix} \to \begin{pmatrix} x_1 \\ y_1 \end{pmatrix} \to \begin{pmatrix} x_2 \\ y_2 \end{pmatrix} \to \cdots$$

with (x_1, y_1) and (x_2, y_2) on the straight line given in (2.10). Hence there exists a continuum of positive 2-cycles of system (2.1). To determine the asymptotic behavior of these 2-cycles, we first show that for any initial point $(x_0 > 0, y_0 > 0)$, the distance between the point (x_k, y_k) and the straight line given in (2.10) after $k \geq 1$ steps is smaller and smaller until converges to zero.

If the initial point (x_0, y_0) is above the line given in (2.10), the distance between the line and the point (x_k, y_k) after k steps is

$$d_k = \frac{\eta x_k + a\eta y_k + 1 - r_0}{\sqrt{\eta^2 + (a\eta)^2}}.$$

Thus

$$d_{k+1} - d_k = \frac{\eta(x_{k+1} - x_k) + a\eta(y_{k+1} - y_k)}{\sqrt{\eta^2 + (a\eta)^2}},$$

where

$$x_{k+1} - x_k = \frac{a y_k - x_k(1+\eta x_k)}{1+\eta x_k}, \quad y_{k+1} - y_k = \frac{\gamma x_k - y_k(1+\eta x_k)}{1+\eta x_k}.$$

Therefore,

$$d_{k+1} - d_k = \frac{\eta x_k}{(1+\eta x_k)\sqrt{\eta^2 + (a\eta)^2}}\left(r_0 - (1 + \eta x_k + a\eta y_k)\right), \tag{2.11}$$

where $r_0 < 1 + \eta x_k + a\eta y_k$ since the point (x_k, y_k) is above the straight line $1 + \eta x + a\eta y = r_0$ for any positive k.

We use mathematical induction method to prove that (x_k, y_k) is above the straight line $1+\eta x+a\eta y = r_0$ given that (x_0, y_0) is above the same line. If the point (x_m, y_m) is above the line, then $1+\eta x_m+a\eta y_m > r_0$. For the point (x_{m+1}, y_{m+1}), we have

$$\begin{aligned} 1 + \eta x_{m+1} + a\eta y_{m+1} - r_0 &= 1 + \eta \frac{a y_m}{1+\eta x_m} + a\eta \frac{\gamma x_m}{1+\eta x_m} - r_0 \\ &= \frac{1+\eta x_m + a\eta y_m - r_0}{1+\eta x_m} > 0, \end{aligned}$$

which implies that the point (x_{m+1}, y_{m+1}) is also above the same line. Thus, for any positive k, the point (x_k, y_k) is always above the straight line $1 + \eta x + a\eta y = r_0$.

Then we have

$$d_{k+1} - d_k < 0,$$

which indicates that the distance $\{d_k\}$ is a nonnegative strictly decreasing sequence bounded below by zero. Thus, $\lim_{k\to\infty} d_k := d$ exists. Taking the limit in (2.11), we then have $\lim_{k\to\infty}(1 + \eta x_k + a\eta y_k) = r_0$, that is, (x_k, y_k) approaches the line given in (2.10) and thus $d = 0$.

Similarly, if the initial point is below the line, we can show that the distance $\{d_k\}$ is also a nonnegative strictly decreasing sequence with a limit equal to zero and (x_k, y_k) approaches the line given in (2.10) as well. Therefore, the line given in (2.10) is a global attractor and a continuum of positive 2-cycles of system (2.1) occurs, where each of the positive 2-cycle is locally stable. We give an example to demonstrate the existence of a positive 2-cycle in Example 1.

Example 1. *Given parameters*

$$a = 5, \quad \gamma = 0.4, \quad \eta_2 = 0.3, \tag{2.12}$$

there exists a continuum of positive 2-cycles of system (2.1) *if* $\eta_1 = 0.3$. *The line given in* (2.10) *is a global attractor. With initial values on the line, the solutions of* (2.1) *are positive 2-cycles, which are locally stable. Initial value* $(x_0, y_0) = (0.9524, 0.4762)$ *is on the line given in* (2.10) *and creates a positive 2-cycle as shown in the left figure in Figure 1. If* $\eta_1 = 0.5$, *there exists a unique synchronous 2-cycle with components* $x_* = 3.3333$ *and* $y_* = 0.6667$ *which is globally asymptotically stable as shown in the right figure in Figure 1.*

We would like to point out that if we define parameter $\Gamma := \frac{\eta_1}{\eta_2}$, it can be used as a bifurcation parameter. As $\Gamma < 1$, that is $\eta_1 < \eta_2$, there exists a unique positive fixed point which is globally asymptotically stable. It loses its stability when $\Gamma \geq 1$, that is $\eta_1 \geq \eta_2$. At $\Gamma = 1$, a continuum of positive 2-cycles is bifurcated and for $\Gamma > 1$, a unique asymptotically stable synchronous 2-cycle appears. A simple bifurcation diagram is given in Figure 2.

We further prove, in Appendix 4, that other $k-$cycles, for $k \geq 3$, do not exist, which indicates the chaotic phenomenon cannot occur [16]. We summarize our results as follows.

Theorem 2.1. *The trivial fixed point* $(0, 0)$ *for* (2.1) *is globally asymptotically stable if the intrinsic growth rate* $r_0 < 1$ *and unstable if* $r_0 > 1$. *System* (2.1) *has a unique positive fixed point* $\overline{E} = (\bar{x}, \bar{y})$ *given in* (2.3) *and a unique synchronous 2-cycle if* $r_0 > 1$. *The positive fixed point is globally asymptotically stable when* $\eta_1 < \eta_2$ *and is unstable when* $\eta_1 > \eta_2$. *The unique synchronous 2-cycle is globally asymptotically stable if* $\eta_1 > \eta_2$ *and unstable if* $\eta_1 < \eta_2$. *A continuum of positive 2-cycles with initial values on the straight line given in* (2.10) *appears when* $\eta_1 = \eta_2$. *The straight line is globally attractive and every positive 2-cycle with an initial value on the straight line in* (2.10) *is locally stable.*

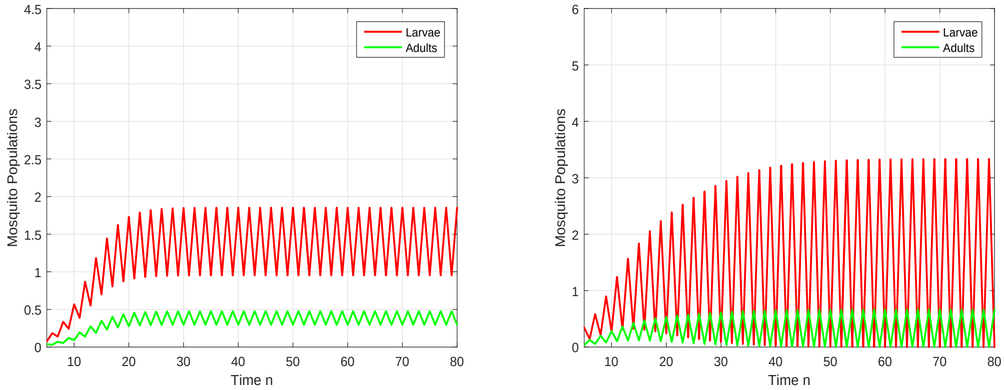

Figure 1. The parameters are given in (2.12). The line given in (2.10) is globally attractive if $\eta_1 = 0.3$. Initial value $(x_0, y_0) = (0.9524, 0.4762)$ is on the line and creates a positive 2-cycle as shown in the left figure. If $\eta_1 = 0.5$, there exists a unique synchronous 2-cycle with components $x_* = 3.3333$ and $y_* = 0.6667$ which is globally asymptotically stable as shown in the right figure.

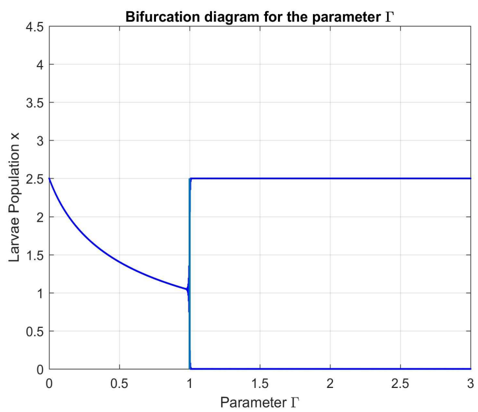

Figure 2. When $\eta_1 < \eta_2$, that is $\Gamma < 1$, there exists a unique positive fixed point which is globally asymptotically stable. At $\Gamma = 1$, a continuum of positive 2-cycles is bifurcated which is shown as the vertical line. When $\Gamma > 1$, that is, $\eta_1 > \eta_2$, the positive fixed point becomes unstable, and a unique asymptotically stable synchronous 2-cycle appears.

3. Stage-structured interactive model with sterile mosquitoes

Now suppose sterile mosquitoes are released into the field of wild mosquitoes. Since sterile mosquitoes do not reproduce, the birth input term will be their releases rate. Let B_n be the number of sterile mosquitoes released at generation n. After the sterile mosquitoes are released, the mating interaction between wild and sterile mosquitoes takes place. We assume harmonic means for matings such that the per capita birth rate is given by

$$b_n = C(N_n)\frac{ay_n}{y_n + B_n} = C(N_n)\frac{ay_n}{N_n},$$

where $C(N_n)$ is the number of matings per mosquito, per unit of time, with $N_n = y_n + B_n$ and a is the number of wild larvae produced per wild mosquito. The interactive dynamics of wild and sterile mosquitoes are then described by the following system:

$$\begin{aligned} x_{n+1} &= C(N_n)\frac{ay_n}{y_n + B_n}\frac{y_n}{1 + \eta_1 x_n}, \\ y_{n+1} &= \frac{\gamma x_n}{1 + \eta_2 x_n}. \end{aligned} \tag{3.1}$$

3.1. Constant releases

We first consider the case where $B_n := b$ is a constant which means sterile mosquitoes are constantly released for each generation, and assume that the number of matings $C(N_n)$ is a constant and is merged into the birth rate a with the same notation for convenience. Then the system (3.1) becomes

$$\begin{aligned} x_{n+1} &= \frac{ay_n}{y_n + b}\frac{y_n}{1 + \eta_1 x_n} = \frac{ay_n^2}{(y_n + b)(1 + \eta_1 x_n)}, \\ y_{n+1} &= \frac{\gamma x_n}{1 + \eta_2 x_n}. \end{aligned} \tag{3.2}$$

Clearly, the origin $(0, 0)$ is a fixed point and is always locally asymptotically stable. Let (x, y) be a positive fixed point. It satisfies the following equations:

$$\begin{aligned} x &= \frac{ay^2}{(y + b)(1 + \eta_1 x)}, \\ y &= \frac{\gamma x}{1 + \eta_2 x}, \end{aligned}$$

which lead to

$$\frac{ay}{(y + b)(1 + \eta_1 x)}\frac{\gamma}{1 + \eta_2 x} = 1.$$

Solving for b then yields

$$\begin{aligned} b &= \frac{a\gamma y}{(1 + \eta_1 x)(1 + \eta_2 x)} - y \\ &= \frac{\gamma x}{(1 + \eta_1 x)(1 + \eta_2 x)^2}\left(r_0 - (1 + \eta_1 x)(1 + \eta_2 x)\right) := \gamma H(x), \end{aligned} \tag{3.3}$$

for $(1 + \eta_1 x)(1 + \eta_2 x) \leq r_0$, i.e. $x \leq \bar{x}$, where $\bar{x}$ is given in (2.3).

Clearly, there exists no positive fixed point if $r_0 \leq 1$. For the existence of positive fixed point, function $H(x)$ first needs to satisfy $H(x) > 0$ for $r_0 > 1$. We then only consider $x \in \Omega$ where set Ω is defined by

$$\Omega := \{x : 0 < x < \bar{x}\}. \tag{3.4}$$

Since

$$H'(x) = \frac{1}{(1 + \eta_1 x)(1 + \eta_2 x)^3}\left(r_0(1 - \eta_2 x - \frac{\eta_1 x(1 + \eta_2 x)}{1 + \eta_1 x}) - (1 + \eta_1 x)(1 + \eta_2 x)\right), \tag{3.5}$$

we define $L(x) := r_0\left(1 - \eta_2 x - \dfrac{\eta_1 x(1+\eta_2 x)}{1+\eta_1 x}\right)$ and $F(x) := (1+\eta_1 x)(1+\eta_2 x)$. Then $H'(x) = 0$ for $x \geq 0$ if and only if $L(x) = F(x)$ for $x \geq 0$.

Since

$$L'(x) = r_0\left(-\eta_2 - \frac{\eta_1 + 2\eta_1\eta_2 x + \eta_1^2\eta_2 x^2}{(1+\eta_1 x)^2}\right) < 0,$$

$L(x)$ is decreasing in the set Ω and $L(0) = r_0 > 1$. Notice that $F(x)$ is increasing in Ω and $F(0) = 1$. Then there exists a unique intersection point between the curves of $F(x)$ and $L(x)$, denoted by x_c, with $0 < x_c \leq \bar{x}$ since $F(x_c) = L(x_c) < r_0$.

With this unique x_c, we have $H'(x)|_{x=x_c} = 0$. Clearly, $L(x) > F(x)$ for $0 < x < x_c$, and $L(x) < F(x)$ for $x_c < x < \bar{x}$. Thus

$$\begin{cases} H'(x) > 0 & 0 < x < x_c, \\ H'(x) < 0 & x_c < x < \bar{x}. \end{cases}$$

We define

$$b_c := \gamma H(x_c). \tag{3.6}$$

Then b_c determines the threshold value for releases of sterile mosquitoes such that system (3.2) has no positive fixed point, one positive fixed point (x, y), or two positive fixed points (x_i, y_i), $i = 1, 2$ with $x_1 < x_c < x_2$, if $b > b_c$, $b = b_c$, or $b < b_c$, respectively.

To investigate the existence of synchronous 2-cycles, we have such a form

$$\begin{pmatrix} x_* \\ 0 \end{pmatrix} \to \begin{pmatrix} 0 \\ y_* \end{pmatrix} \to \begin{pmatrix} x_* \\ 0 \end{pmatrix} \to \begin{pmatrix} 0 \\ y_* \end{pmatrix} \to \cdots,$$

where

$$x_* = \frac{a{y_*}^2}{b + y_*}, \qquad y_* = \frac{\gamma x_*}{1 + \eta_2 x_*}. \tag{3.7}$$

To solve for x_* and y_*, we have

$$a\eta_2 {y_*}^2 + (1 - r_0)y_* + b = 0. \tag{3.8}$$

Since $r_0 > 1$, the existence of positive solutions of (3.8) depends on the discriminant $\Delta = (r_0 - 1)^2 - 4a\eta_2 b$. Define the threshold value

$$b_1 := \frac{(r_0 - 1)^2}{4a\eta_2}. \tag{3.9}$$

Then there exists no, one synchronous 2-cycle with

$$y_* = \frac{r_0 - 1}{2a\eta_2},$$

or two synchronous 2-cycles with

$$y_*^{\{1\}} = \frac{r_0 - 1 - \sqrt{(r_0-1)^2 - 4a\eta_2 b}}{2a\eta_2}, \quad y_*^{\{2\}} = \frac{r_0 - 1 + \sqrt{(r_0-1)^2 - 4a\eta_2 b}}{2a\eta_2}, \tag{3.10}$$

if $b > b_1$, $b = b_1$, or $b < b_1$, respectively.

Now we claim $b_c < b_1$. Thus, if $b > b_1$, there exists neither synchronous 2-cycle nor positive fixed point thus no positive 2-cycles, which makes the trivial fixed point globally asymptotically stable. To this end, we define a function

$$P(x) := \gamma H(x) - b_1 = \frac{Q(x)}{4a\eta_2(1+\eta_1 x)(1+\eta_2 x)^2},$$

where

$$Q(x) := -Ax^3 - Bx^2 + Cx - (r_0 - 1)^2$$

with

$$\begin{aligned} A &= 4r_0\eta_1\eta_2^2 + \eta_1\eta_2^2(r_0-1)^2 > 0, \\ B &= 4r_0\eta_2(\eta_1+\eta_2) + \eta_2^2(r_0-1)^2 + 2\eta_1\eta_2(r_0-1)^2 > 0, \\ C &= 4r_0\eta_2(r_0-1) - 2\eta_2(r_0-1)^2 - \eta_1(r_0-1)^2. \end{aligned} \tag{3.11}$$

Then the function $P(x)$ has the same sign as $Q(x)$. If $C < 0$, then the function $Q(x)$ is negative for all $x \in \Omega$ since all of the coefficients are negative. Thus the function $P(x)$ is negative for all $x \in \Omega$, which implies $b_c < b_1$.

Assume $C > 0$. It follows from

$$Q'(x) = -3Ax^2 - 2Bx + C$$

that $Q(x)$ has a maximum value

$$Q(x_0) = -Ax_0^3 - Bx_0^2 + Cx_0 - (r_0-1)^2,$$

at

$$x_0 = \frac{\sqrt{B^2+3AC} - B}{3A} > 0,$$

where, A, B and C are given in (3.11).

Using η_1 as a variable, we have

$$Q(x_0) := q(\eta_1) = -A(\eta_1)\cdot x_0^3(\eta_1) - B(\eta_1)\cdot x_0^2(\eta_1) + C(\eta_1)\cdot x_0(\eta_1) - (r_0-1)^2,$$

where $\eta_1 \in (0, 1]$.

Taking the derivative of $q(\eta_1)$ with respect to η_1, we have

$$\begin{aligned} q'(\eta_1) =& (-3A(\eta_1)x_0^2(\eta_1) - 2B(\eta_1)x_0(\eta_1) + C(\eta_1))\cdot x_0'(\eta_1) \\ &+ (-A'(\eta_1)x_0^3(\eta_1) - B'(\eta_1)x_0^2(\eta_1) + C'(\eta_1)x_0(\eta_1)) \\ =& -A'(\eta_1)x_0^3(\eta_1) - B'(\eta_1)x_0^2(\eta_1) + C'(\eta_1)x_0(\eta_1) \end{aligned}$$

since

$$-3Ax_0^2 - 2Bx_0 + C = Q'(x_0) = 0.$$

Notice that

$$A'(\eta_1) = 4r_0\eta_2^2 + \eta_2^2(r_0-1)^2 > 0,$$

$$B'(\eta_1) = 4r_0\eta_2 + 2\eta_2(r_0 - 1)^2 > 0,$$
$$C'(\eta_1) = -(r_0 - 1)^2 < 0.$$

Thus $q'(\eta_1) < 0$ for $\eta_1 \in (0, 1]$, and then $q(\eta_1)$ is monotone decreasing.

Moreover, it follows from $A(0) = 0$, $B(0) = \eta_2^2(r_0 + 1)^2$, and $C(0) = 2\eta_2(r_0^2 - 1)$ that

$$x_0(\eta_1)|_{\eta_1 \to 0} = \lim_{\eta_1 \to 0} x_0(\eta_1) = \frac{C(0)}{2B(0)},$$

and thus

$$\begin{aligned}\lim_{\eta_1 \to 0} q(\eta_1) &= -B(0)x_0^2(0) + C(0)x_0(0) - (r_0 - 1)^2 \\ &= -B(0)\frac{C^2(0)}{4B^2(0)} + C(0)\frac{C(0)}{2B(0)} - (r_0 - 1)^2 \\ &= \frac{C^2(0)}{4B(0)} - (r_0 - 1)^2 = \frac{1}{4B(0)}(C^2(0) - 4B(0)(r_0 - 1)^2) = 0.\end{aligned}$$

Hence $q(\eta_1) < 0$ for $\eta_1 \in (0, 1]$, that is, $Q(x_0) < 0$, and then $P(x) < 0$ for all $x \in \Omega$. Therefore $b_c < b_1$.

We next investigate the stability of the positive fixed points and the synchronous 2-cycles.

The Jacobian matrix evaluated at a positive fixed point has the form

$$J := \begin{pmatrix} -\dfrac{\eta_1 x}{1 + \eta_1 x} & \dfrac{x}{y}\dfrac{y + 2b}{y + b} \\ \dfrac{y}{x}\dfrac{1}{1 + \eta_2 x} & 0 \end{pmatrix}.$$

Since

$$\mathrm{tr}J = -\frac{\eta_1 x}{1 + \eta_1 x}, \qquad \det J = -\frac{y + 2b}{(y + b)(1 + \eta_2 x)},$$

a positive fixed point (x, y) is locally asymptotically stable if

$$\frac{\eta_1 x}{1 + \eta_1 x} + \frac{y + 2b}{(y + b)(1 + \eta_2 x)} < 1,$$

which is equivalent to

$$b(1 + 2\eta_1 x - \eta_2 x) - (\eta_2 - \eta_1)xy < 0. \tag{3.12}$$

If $\eta_2 < \eta_1$, then $b(1 + 2\eta_1 x - \eta_2 x) - (\eta_2 - \eta_1)xy = b(1 + (2\eta_1 - \eta_2)x + (\eta_1 - \eta_2)xy > 0$, which implies that all positive points are unstable if they exist.

We then assume $\eta_2 > \eta_1$ such that the wild mosquitoes maintain a locally steady state before the sterile mosquitoes are released. Since the component x of a positive fixed point (x, y) is a solution of $b = \gamma H(x)$ in (3.3), condition (3.12) is equivalent to

$$\begin{aligned}&\gamma H(x) \cdot (1 + 2\eta_1 x - \eta_2 x) - (\eta_2 - \eta_1)x\frac{\gamma x}{1 + \eta_2 x} \\ =&\frac{\gamma x}{(1 + \eta_1 x)(1 + \eta_2 x)}(r_0(1 + 2\eta_1 x - \eta_2 x) - (1 + \eta_1 x)^2(1 + \eta_2 x)) < 0.\end{aligned}$$

Define the following function $h(x)$ to determine the stability of positive fixed points

$$h(x) := r_0(1 + 2\eta_1 x - \eta_2 x) - (1 + \eta_1 x)^2(1 + \eta_2 x).$$

Thus, the positive fixed point (x, y) is locally asymptotically stable if $h(x) < 0$ and unstable if $h(x) > 0$.

For $b = b_c$, there exists a unique positive fixed point (x_c, y_c) where $H'(x_c) = 0$ from (3.5) and hence

$$(1 + \eta_1 x_c)(1 + \eta_2 x_c) = r_0\left(1 - \eta_2 x_c - \frac{\eta_1 x_c(1 + \eta_2 x_c)}{1 + \eta_1 x_c}\right).$$

Then we have

$$\begin{aligned} h(x_c) &= r_0(1 + 2\eta_1 x_c - \eta_2 x_c) - (1 + \eta_1 x_c) r_0\left(1 - \eta_2 x_c - \frac{\eta_1 x_c(1 + \eta_2 x_c)}{1 + \eta_1 x_c}\right) \\ &= r_0(1 + 2\eta_1 x_c - \eta_2 x_c) - r_0\left((1 + \eta_1 x_c) - \eta_2 x_c(1 + \eta_1 x_c) - \eta_1 x_c(1 + \eta_2 x_c)\right) \\ &= r_0(2\eta_1 x_c + 2\eta_1\eta_2 x_c^2) = 2r_0\eta_1 x_c(1 + \eta_2 x_c) > 0, \end{aligned}$$

and thus this unique positive fixed point (x_c, y_c) is unstable.

For $b < b_c$, there exist two positive fixed points (x_i, y_i), $i = 1, 2$, with $x_1 < x_2$, where $H'(x_1) > 0$ and $H'(x_2) < 0$.

We first consider the positive fixed point (x_1, y_1), with $H'(x_1) > 0$ which is equivalent to

$$(1 + \eta_1 x_1)(1 + \eta_2 x_1) < r_0\left(1 - \eta_2 x_1 - \frac{\eta_1 x_1(1 + \eta_2 x_1)}{1 + \eta_1 x_1}\right).$$

Then we have

$$\begin{aligned} h(x_1) &> r_0(1 + 2\eta_1 x_1 - \eta_2 x_1) - (1 + \eta_1 x_1) r_0\left(1 - \eta_2 x_1 - \frac{\eta_1 x_1(1 + \eta_2 x_1)}{1 + \eta_1 x_1}\right) \\ &= r_0(1 + 2\eta_1 x_1 - \eta_2 x_1) - r_0((1 + \eta_1 x_1) - \eta_2 x_1(1 + \eta_1 x_1) - \eta_1 x_1(1 + \eta_2 x_1)) \\ &= r_0(2\eta_1 x_1 + 2\eta_1\eta_2 x_1^2) = 2r_0\eta_1 x_1(1 + \eta_2 x_1) > 0, \end{aligned}$$

and thus fixed point (x_1, y_1) is unstable.

Next we consider the positive fixed point (x_2, y_2) with $H'(x_2) < 0$. Simple calculation shows that $h(x_2)$ can be negative or positive. We then define a threshold value x_s satisfying $h(x_s) = 0$, that is,

$$h(x_s) = -\eta_1^2\eta_2 x_s^3 - (\eta_1^2 + 2\eta_1\eta_2)x_s^2 + (r_0(2\eta_1 - \eta_2) - 2\eta_1 - \eta_2)x_s + (r_0 - 1) = 0.$$

Notice that $h(x) = 0$ is a cubic equation and $r_0 - 1 > 0$. Then it follows from Descartes' rule of sign that there exists a unique positive solution to $h(x) = 0$. Moreover, since

$$h(\bar{x}) = r_0(\eta_1 - \eta_2)\bar{x} < 0$$

and $h(x_1) > 0$, the threshold value x_s satisfies $x_1 < x_s < \bar{x}$, and $h(x) > 0$ for $x_1 < x < x_s$ and $h(x) < 0$ for $x_s < x < \bar{x}$.

Then, the positive fixed point (x_2, y_2) is locally asymptotically stable if $x_2 > x_s$ with $h(x_2) < 0$ and unstable if $x_2 < x_s$ with $h(x_2) > 0$. We define the corresponding threshold value of releases for the stability of (x_2, y_2) as

$$b_s := \gamma H(x_s), \tag{3.13}$$

where $H(x)$ is defined in (3.3). Then positive fixed point (x_2, y_2) is locally asymptotically stable if $b < b_s$ and unstable if $b > b_s$. Notice that $b_s < b_c$ since b_c is the maximum value of the function $\gamma H(x)$.

For the stability of the synchronous 2-cycles with components x_* and y_* given in (3.7), the corresponding Jacobian matrix has the form

$$\begin{pmatrix} \lambda & 0 \\ 0 & 0 \end{pmatrix},$$

where

$$\lambda = \frac{2r_0 y_*}{(1+\eta_2 x_*)(b+y_*)} - \frac{2a\eta_2 {y_*}^2}{(1+\eta_2 x_*)(b+y_*)} - \frac{r_0 {y_*}^2}{(1+\eta_2 x_*)^2(b+y_*)^2}.$$

Since $r_0 y_* = (1+\eta_2 x_*)(b+y_*)$ at the synchronous 2-cycles,

$$\lambda = \frac{2r_0 y_*}{r_0 y_*} - \frac{2a\eta_2 {y_*}^2}{r_0 y_*} - \frac{r_0 {y_*}^2}{r_0^2 {y_*}^2} = 2 - \frac{2\eta_2}{\gamma} y_* - \frac{1}{r_0}.$$

If $b < b_1$, there exist two synchronous 2-cycles with components $x_*^{\{1\}} < x_*^{\{2\}}$ and $y_*^{\{1\}} < y_*^{\{2\}}$ in (3.10). The corresponding eigenvalues are

$$\lambda^{\{1\}} = 2 - \frac{r_0 - \sqrt{(r_0-1)^2 - 4ba\eta_2}}{r_0} = \frac{r_0 + \sqrt{(r_0-1)^2 - 4ba\eta_2}}{r_0} > 1,$$

at $\left(x_*^{\{1\}}, y_*^{\{1\}}\right)$, and

$$\lambda^{\{2\}} = 2 - \frac{r_0 + \sqrt{(r_0-1)^2 - 4ba\eta_2}}{r_0} = \frac{r_0 - \sqrt{(r_0-1)^2 - 4ba\eta_2}}{r_0} < 1,$$

at $\left(x_*^{\{2\}}, y_*^{\{2\}}\right)$, respectively. Thus synchronous 2-cycle $\left(x_*^{\{1\}}, y_*^{\{1\}}\right)$ is unstable and synchronous 2-cycle $\left(x_*^{\{2\}}, y_*^{\{2\}}\right)$ is locally asymptotically stable.

We summarize our results in the following theorem and Table 1.

Theorem 3.1. *The trivial fixed point* $(0, 0)$ *is always locally asymptotically stable for system* (3.2). *Suppose the intrinsic growth rate of the stage-structured mosquito population* $r_0 > 1$. *We define the threshold values for the releases of the sterile mosquitoes* b_c *in* (3.6), b_1 *in* (3.9), *and* b_s *in* (3.13), *respectively, with* $b_s < b_c < b_1$. *System* (3.2) *has no, one, or two positive fixed points if* $b > b_c$, $b = b_c$, *or* $b < b_c$, *and has no, one, or two synchronous 2-cycles if* $b > b_1$, $b = b_1$, *or* $b < b_1$ *respectively. If* $b > b_1$, *the trivial fixed point is globally asymptotically stable, which makes the population of the wild mosquitoes to go extinct when sufficient sterile mosquitoes are released. If* $b_c < b < b_1$, *there exist no positive fixed points and two synchronous 2-cycles, where the one with larger components is locally asymptotically stable and the other is unstable. If* $b < b_c$, *it depends on the relation of* η_1 *and* η_2. *If* $\eta_2 < \eta_1$, *there exist two positive fixed points, where both of them are unstable, and two synchronous 2-cycles, where the one with larger components is locally asymptotically stable and the other is unstable. Suppose* $\eta_1 < \eta_2$. *If* $b_s < b < b_c$, *there exist two positive fixed points, but both are unstable, and two synchronous 2-cycles, where the one with larger components is locally asymptotically stable and the other is unstable. If* $0 < b < b_s$, *there exist two positive fixed points and two synchronous 2-cycles. The positive fixed point with larger components and the synchronous 2-cycle with larger components are both locally asymptotically stable, and the other positive fixed point and the other synchronous 2-cycle are both unstable.*

Table 1. Summary table for the existence of positive fixed points and synchronous 2-cycles with $r_0 > 1$.
(PFP stands for positive fixed point and STC stands for synchronous 2-cycle.)

<table>
<tr><th></th><th>$b < b_s$</th><th>$b_s < b < b_c$</th><th>$b_c < b < b_1$</th><th>$b_1 < b$</th></tr>
<tr><td rowspan="2">$\eta_1 < \eta_2$</td><td>Two PFP
One stable
One unstable</td><td>Two PFP
both unstable</td><td colspan="2">No PFP</td></tr>
<tr><td colspan="3">Two STC
One stable
One unstable</td><td>No STC</td></tr>
<tr><td rowspan="2">$\eta_2 < \eta_1$</td><td colspan="2">Two PFP
both unstable</td><td colspan="2">No PFP</td></tr>
<tr><td colspan="3">Two STC
One stable
One unstable</td><td>No STC</td></tr>
</table>

We then give the following example to demonstrate the results in Theorem 3.1, but only address the case of $\eta_1 < \eta_2$.

Example 2. *Choosing the following parameters*

$$a = 25, \quad \gamma = 0.8, \quad \eta_1 = 0.2, \quad \eta_2 = 0.7, \tag{3.14}$$

we have $r_0 = a\gamma = 20 > 1$ and $\eta_1 < \eta_2$. The threshold values of releases are $b_c = 4.1523$, $b_1 = 5.1571$ and $b_s = 2.9252$. For $b = 1$, there exist two positive fixed points $E_1 = (0.0741, 0.0564)$ and $E_2 = (5.1949, 0.8964)$, where E_1 is unstable and E_2 is locally asymptotically stable since $b < b_s$. For the same release value $b = 1$, there also exist two synchronous 2-cycles with components $\left(x_*^{\{1\}}, 0\right) \rightarrow \left(0, y_*^{\{1\}}\right)$ and $\left(x_*^{\{2\}}, 0\right) \rightarrow \left(0, y_*^{\{2\}}\right)$, where the synchronous 2-cycle with bigger components $x_*^{\{2\}} = 13.0700$ and $y_*^{\{2\}} = 1.0302$ is locally asymptotically stable while the one with smaller components $x_*^{\{1\}} = 0.0728$ and $y_*^{\{1\}} = 0.0554$ is unstable. Notice that the origin $(0, 0)$ is always locally asymptotically stable. Therefore, for $b = 1$, solutions approach the origin, positive fixed point E_2, or synchronous 2-cycle with components $x_*^{\{2\}}$ and $y_*^{\{2\}}$, depending on their initial values, as shown in the upper left, upper right, or the lower figure in Figure 3, respectively.

3.2. Releases proportional to the wild mosquito population size

Instead of constant releases of sterile mosquitoes, we assume that the releases are proportional to the population size of the wild mosquitoes such that the number of releases is $B(\cdot) := by$ where b is a constant [13].

We assume that there is no mating difficulty for mosquitoes. Then the model dynamics are governed

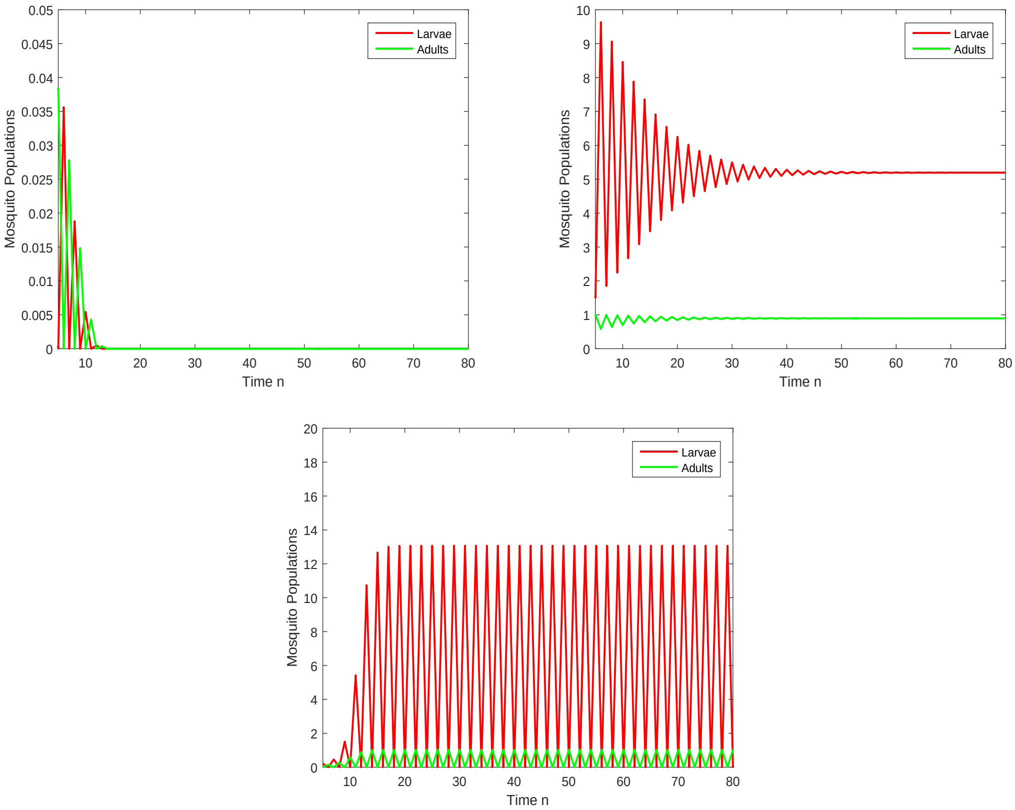

Figure 3. With the parameters given in (3.14), the threshold values of releases are $b_c = 4.1523$, $b_1 = 5.1571$, and $b_s = 2.9252$. For $b = 1$, there exist two positive fixed points $E_1 = (0.0741, 0.0564)$ and $E_2 = (5.1949, 0.8964)$, where E_1 is unstable and E_2 is locally asymptotically stable since $b < b_s$. For the same release value $b = 1$, there also exist two synchronous 2-cycles with components $\left(x_*^{\{1\}}, 0\right) \to \left(0, y_*^{\{1\}}\right)$ and $\left(x_*^{\{2\}}, 0\right) \to \left(0, y_*^{\{2\}}\right)$, where the synchronous 2-cycle with bigger components $x_*^{\{2\}} = 13.0700$ and $y_*^{\{2\}} = 1.0302$ is locally asymptotically stable while the one with smaller components $x_*^{\{1\}} = 0.0728$ and $y_*^{\{1\}} = 0.0554$ is unstable. Notice that the origin $(0, 0)$ is always locally asymptotically stable. Solutions approach the origin, positive fixed point E_2, or synchronous 2-cycle $(x_*^{\{2\}}, 0) \to (0, y_*^{\{2\}})$, depending on their initial values, as shown in upper left, upper right, or the lower figure, respectively.

by the following system:

$$
\begin{aligned}
x_{n+1} &= \frac{ay_n}{y_n + by_n} \cdot \frac{y_n}{1+\eta_1 x_n} = \frac{ay_n}{(1+b)(1+\eta_1 x_n)} = \frac{\bar{a}y_n}{1+\eta_1 x_n}, \\
y_{n+1} &= \frac{\gamma x_n}{1+\eta_2 x_n},
\end{aligned} \tag{3.15}
$$

where $\bar{a} = \frac{a}{1+b}$.

Mathematically, the system is the same as system (2.1). It follows from Theorem 2.1 that if $\bar{r_0} = \bar{a}\gamma > 1$, the trivial fixed point is globally asymptotically stable. We define the sterile mosquitoes release threshold value by

$$b_c := a\gamma - 1 = r_0 - 1.$$

Then the trivial fixed point is globally asymptotically stable if $b > b_c$ and unstable if $b < b_c$.

If $b < b_c$, there exists a unique positive fixed point $E^* := (x^*, y^*)$ with

$$
\begin{aligned}
x^* &= \frac{-(\eta_1+\eta_2) + \sqrt{\Delta}}{2\eta_1\eta_2}, \\
y^* &= \frac{\gamma x^*}{1+\eta_2 x^*} = \frac{\gamma(-(\eta_1+\eta_2)+\sqrt{\Delta})}{2\eta_1\eta_2 + \eta_2(-(\eta_1+\eta_2)+\sqrt{\Delta})},
\end{aligned} \tag{3.16}
$$

where $\Delta = (\eta_1 - \eta_2)^2 + \dfrac{4\eta_1\eta_2 r_0}{1+b}$, and a unique synchronous 2-cycle

$$\begin{pmatrix} x_* \\ 0 \end{pmatrix} \to \begin{pmatrix} 0 \\ y_* \end{pmatrix} \to \begin{pmatrix} x_* \\ 0 \end{pmatrix} \to \begin{pmatrix} 0 \\ y_* \end{pmatrix} \to \cdots \tag{3.17}$$

with $x_* = \frac{r_0-(1+b)}{\eta_2(1+b)} > 0$ and $y_* = \frac{r_0-(1+b)}{r_0\eta_2} > 0$. It follows from Theorem 2.1 that the positive fixed point E^* is globally asymptotically stable if $\eta_1 < \eta_2$ and the synchronous 2-cycle is globally asymptotically stable if $\eta_1 > \eta_2$. In summary, we have the following theorem.

Theorem 3.2. *The trivial fixed point* $(0, 0)$ *for system* (3.15) *is globally asymptotically stable if $b > b_c$ and is unstable if $b < b_c$ where the sterile mosquito release threshold $b_c := r_0 - 1$. If $b < b_c$, there exist a unique positive fixed point and a unique synchronous 2-cycle. The unique positive fixed point E^*, given in* (3.16)*, is globally asymptotically stable if $\eta_1 < \eta_2$ and unstable if $\eta_1 > \eta_2$. The synchronous 2-cycle, given in* (3.17)*, is globally asymptotically stable if $\eta_1 > \eta_2$ and unstable if $\eta_1 < \eta_2$. A continuum of locally stable positive 2-cycles exists if and only if $\eta_1 = \eta_2$.*

It follows from Theorem 3.2 that if $b > b_c$ such that sufficient sterile mosquitoes are released, wild mosquitoes can be wiped out. On the other hand, if $b < b_c$ such that not enough sterile mosquitoes are released, the two types of mosquitoes coexist. In such a case, although the stability condition remains the same as in system (2.1) even we have released sterile mosquitoes, it follows from (3.16) that x^* becomes smaller for larger b. Moreover, since y^* is a strictly increasing function of x^*, y^* becomes smaller with smaller x^*. That is to say, increasing the releases of sterile mosquitoes can reduce the population size of the wild mosquitoes. We demonstrate our findings in Example 3.

Example 3. *Given the parameters*

$$a = 5, \quad \gamma = 0.8, \tag{3.18}$$

we have threshold value $b_c = 3$. *For* $b = 4 > 3$, *the trivial fixed point is globally asymptotically stable as shown in the upper left figure in Figure 4. For* $b = 0.5 < b_c = 3$, *the trivial fixed point is unstable and there exist a unique positive fixed point* $E^* = (2.5519, 1.1563)$ *and a unique synchronous 2-cycle with components* $x_* = 5.5556$ *and* $y_* = 1.1111$. *The synchronous 2-cycle is unstable and the positive fixed point* E^* *is globally asymptotically stable when* $\eta_1 = 0.2 < \eta_2 = 0.3$ *as shown in the upper right figure in Figure 4. With the same values* η_1 *and* η_2, *as the threshold value of releases of sterile mosquitoes is increased to* $b = 1.5$, *the unique positive fixed point* $E^* = (1.0642, 0.6453)$ *is still globally asymptotically stable but has smaller magnitudes of x and y compared to those for* $b = 0.5$ *as shown in the lower left figure in Figure 4. If we change the parameter values to* $\eta_1 = 0.5 > \eta_2 = 0.3$, *the unique positive fixed point* $E^* = (0.6667, 0.4444)$ *is unstable and the unique synchronous 2-cycle with* $x_* = 2$ *and* $y_* = 1.25$ *becomes globally asymptotically stable as shown in the lower right figure in Figure 4.*

3.3. Proportional releases with saturation

Compared to the case of constant releases, the proportional releases may be a good strategy when the size of the wild mosquito population is small since the size of releases is also small. However, if the wild mosquito population size is significantly large, the release size would be large as well, which may exceed our affordability. Then, as in [13], we consider a different strategy where the number of releases is proportional to the wild adult mosquito population size when it is small, but it is saturated and approaches a constant when the wild adult mosquito population size is sufficiently large. To this end, we let the releases be of Holling-II type [21] such that $B(\cdot) := \frac{by}{1+y}$. Then we consider the following system of equations:

$$\begin{aligned} x_{n+1} &= \frac{ay_n}{y_n + \dfrac{by_n}{1+y_n}} \cdot \frac{y_n}{1+\eta_1 x_n} = \frac{ay_n(1+y_n)}{(1+b+y_n)(1+\eta_1 x_n)}, \\ y_{n+1} &= \frac{\gamma x_n}{1+\eta_2 x_n}. \end{aligned} \tag{3.19}$$

We assume $r_0 = a\gamma > 1$ and define an initial sterile mosquitoes release threshold value $b_0 := r_0 - 1$ such that the origin $(0, 0)$ is locally asymptotically stable if $b > b_0$ and unstable if $b < b_0$.

A positive fixed point $E = (x, y)$ satisfies

$$\frac{a(1+y)}{(1+b+y)(1+\eta_1 x)} \cdot \frac{\gamma}{1+\eta_2 x} = 1,$$

that is,

$$b = \left(1 + \frac{\gamma x}{1+\eta_2 x}\right)\left(\frac{r_0}{(1+\eta_1 x)(1+\eta_2 x)} - 1\right) =: G(x). \tag{3.20}$$

Let $x \in \Omega$ where set Ω is defined in (3.4). It follows from

$$G'(x) = \frac{A_1 x^3 + A_2 x^2 + A_3 x + A_4}{(1+\eta_1 x)^2 (1+\eta_2 x)^3}, \tag{3.21}$$

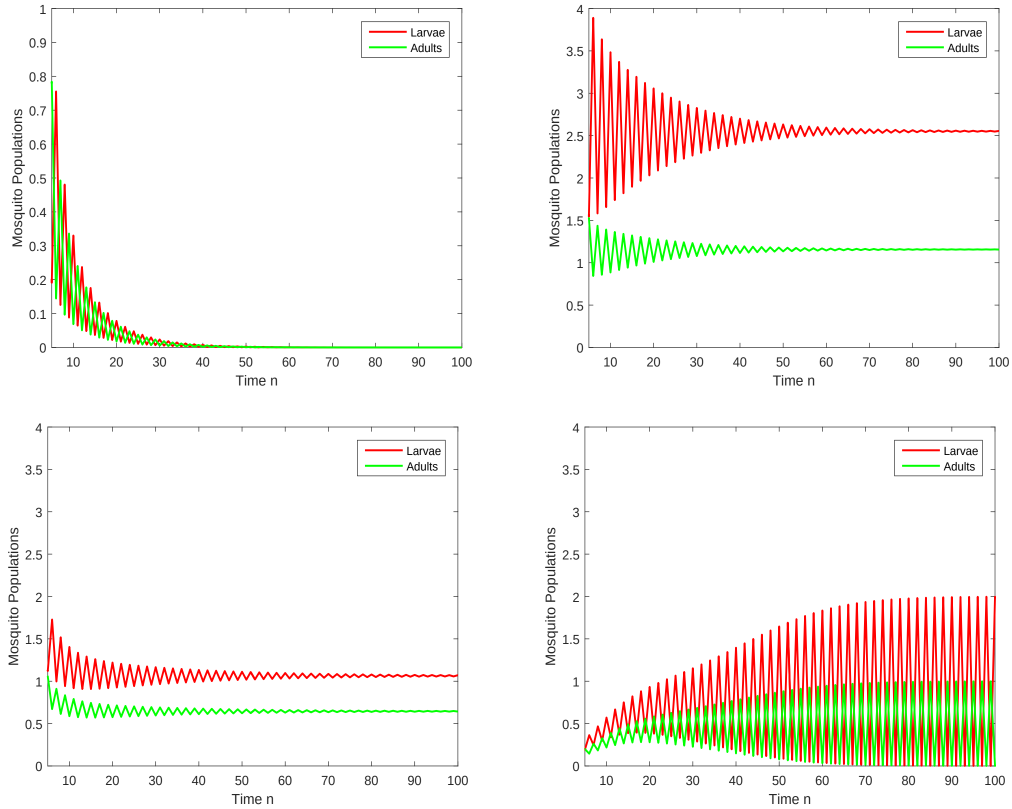

Figure 4. The parameters are given in (3.18). We have threshold value $b_c = 3$. For $b = 4$, the origin is globally asymptotically stable as shown in the upper left figure. For $b = 0.5$, we choose $\eta_1 = 0.2 < \eta_2 = 0.3$, the unique positive fixed point $E^* = (2.5519, 1.1563)$ is globally asymptotically stable as shown in the upper right figure. For $b = 1.5$, the unique positive fixed point $E^* = (1.0642, 0.6453)$ is still globally asymptotically stable but has smaller magnitudes of x and y compared to those for $b = 0.5$ as shown in the lower left figure. When η_1 and η_2 are changed to $\eta_1 = 0.5 > \eta_2 = 0.3$, the unique positive fixed point $E^* = (0.6667, 0.4444)$ is unstable and the unique synchronous 2-cycle with $x_* = 2$ and $y_* = 1.25$ is globally asymptotically stable as shown in the lower right figure.

where

$$
\begin{aligned}
A_1 &= -\eta_1^2\eta_2\gamma < 0, \\
A_2 &= -2\eta_1\eta_2^2 r_0 - 2\eta_1\eta_2\gamma r_0 - \eta_1^2\gamma - 2\eta_1\eta_2\gamma < 0, \\
A_3 &= -3\eta_1\eta_2 r_0 - \eta_2^2 r_0 - \eta_2\gamma r_0 - 2\eta_1\gamma - \eta_2\gamma < 0, \\
A_4 &= \gamma((a\gamma - a\eta_2) - (1 + a\eta_1)),
\end{aligned}
$$

that if $A_4 < 0$, that is, $a\gamma - a\eta_2 < 1 + a\eta_1$, then $G'(x) < 0$ for all $x \in \Omega$. Thus $G(x)$ is decreasing with the maximum value $G(0) = b_0 = r_0 - 1$, and hence there exists no, or one positive fixed point if $b > b_0$, or $b < b_0$.

Next we assume $A_4 > 0$, that is, $a\gamma - a\eta_2 > 1 + a\eta_1$. Then $G'(0) = A_4 > 0$ and function $G(x)$ is increasing for x positive and near 0. It is clear that the numerator of $G'(x)$ has only one positive root, denoted by x_c, according to Descartes rule of sign [3, 20]. Since the denominator of $G'(x)$ is positive, $G'(x) = 0$ has a unique positive solution at x_c, and hence $G(x)$ has a unique maximum value at $x = x_c$. We write $b_c := G(x_c)$. Then function $G(x)$ is increasing for $x \in (0, x_c)$, starting with the point $(0, b_0)$, and decreasing for $x \in (x_c, \bar{x})$, ending with the point $(\bar{x}, 0)$ where $G(\bar{x}) = 0$ as above. Write $x_1 = G^{-1}(b_0) > 0$. Then for each $b \in (0, b_0)$, there exists a unique $x \in (x_1, \bar{x})$ such that $G(x) = b$. On the other hand, for each $b \in (b_0, b_c)$, there exist two $x \in (0, x_1)$ such that $G(x) = b$. Therefore, with these two threshold values $b_0 < b_c$, there exists no positive fixed point if $b > b_c$, one positive fixed point if $b = b_c$ or $0 \le b \le b_0$, or two positive fixed points if $b_0 < b < b_c$.

The existence of the positive fixed points, based on the release value of the sterile mosquitoes b, is illustrated in Figure 5 where the x−axis is b.

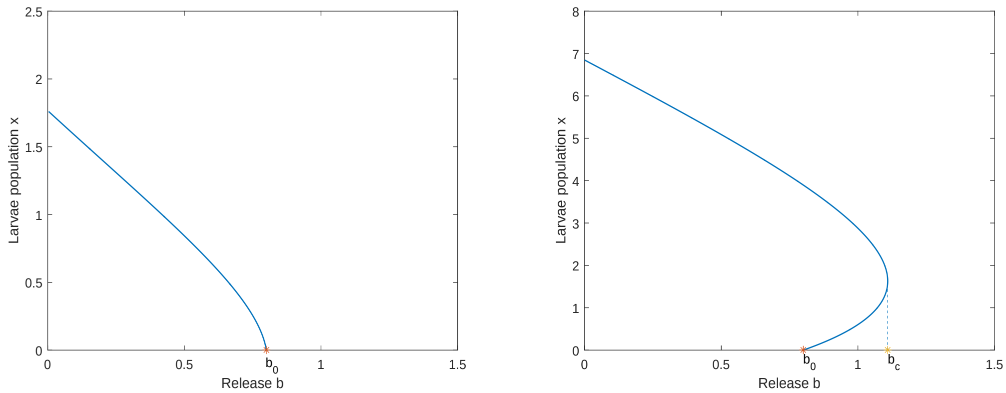

Figure 5. In the left figure, we have $a = 2.25$, $\gamma = .8$, $\eta_1 = .1$, and $\eta_2 = .3$ such that $A_4 = -0.08 < 0$. Thus there exists no positive fixed point, or one positive fixed point if $b > b_0$, or $b < b_0$, respectively. In the right figure, we have $a = 2.25$, $\gamma = .8$, $\eta_1 = .01$, and $\eta_2 = .1$ such that $A_4 = 0.44 > 0$. Then there exists no positive fixed point if $b > b_c$, one positive fixed point if $b = b_c$ or $0 \le b \le b_0$, or two positive fixed points if $b_0 < b < b_c$.

The system may also have positive cycles of different periods. We only consider synchronous 2-cycles with components $(x_*, 0)$ and $(0, y_*)$. It follows from

$$\begin{pmatrix} x_* \\ 0 \end{pmatrix} \to \begin{pmatrix} 0 \\ y_* \end{pmatrix} \to \begin{pmatrix} x_* \\ 0 \end{pmatrix} \to \begin{pmatrix} 0 \\ y_* \end{pmatrix} \to \cdots$$

that

$$x_* = \frac{a y_* (1 + y_*)}{1 + b + y_*},$$
$$y_* = \frac{\gamma x_*}{1 + \eta_2 x_*},$$

where

$$a\eta_2 {y_*}^2 - (b_0 - a\eta_2) y_* + b - b_0 = 0. \tag{3.22}$$

If $b_0 - a\eta_2 < 0$, that is, $a\gamma - a\eta_2 < 1$, there exists no or one synchronous 2-cycle if $b \ge b_0$ or $b < b_0$. If $b_0 - a\eta_2 > 0$, that is, $a\gamma - a\eta_2 > 1$, the existence of positive solutions depends on the discriminant of the quadratic equation (3.22). We define the threshold value

$$b_1 := \frac{(b_0 + a\eta_2)^2}{4a\eta_2} \geq b_0.$$

Then there exists no synchronous 2-cycle if $b > b_1$, one synchronous 2-cycle if $b = b_1$ or $0 \leq b \leq b_0$, or two synchronous 2-cycles if $b_0 < b < b_1$, respectively. Similarly as in Section 3.1, the two threshold values b_c and b_1 have $b_c < b_1$.

We illustrate our results in Table 2.

Table 2. Summary table for the existence of positive fixed points and synchronous 2-cycles. (PFP stands for positive fixed point and STC stands for synchronous 2-cycle.)

	$b < b_0$	$b_0 < b < b_c$	$b_c < b < b_1$	$b_1 < b$
$a(\gamma - \eta_2) < 1$	One PFP	No PFP		
	One STC	No STC		
$1 < a(\gamma - \eta_2) < 1 + a\eta_1$	One PFP	No PFP		
	One STC	Two STC	No STC	
$1 + a\eta_1 < a(\gamma - \eta_2)$	One PFP	Two PFP	No PFP	
	One STC	Two STC		No STC

We next investigate the stability of the positive fixed points. The Jacobian matrix at a positive fixed point $E = (x, y)$ has the form

$$\bar{J} := \begin{pmatrix} -\dfrac{\eta_1 x}{1 + \eta_1 x} & \dfrac{\left(b(1 + 2y) + (y + 1)^2\right)(1 + \eta_2 x)}{\gamma(1 + y)(1 + y + b)} \\ \dfrac{\gamma}{(1 + \eta_2 x)^2} & 0 \end{pmatrix}.$$

Since

$$\mathrm{tr}\bar{J} = -\frac{\eta_1 x}{1 + \eta_1 x}, \quad \det \bar{J} = -\frac{b(1 + 2y) + (y + 1)^2}{(1 + \eta_2 x)(1 + y + b)(1 + y)},$$

E is locally asymptotically stable if

$$\frac{b(1 + 2y) + (y + 1)^2}{(1 + \eta_2 x)(1 + y + b)(1 + y)} < 1 - \frac{\eta_1 x}{1 + \eta_1 x},$$

that is,

$$[(1 + \eta_1 x)(1 + 2y) - (1 + \eta_2 x)(1 + y)]\, b < (\eta_2 - \eta_1)x(1 + y)^2. \tag{3.23}$$

Substituting $y = \dfrac{\gamma x}{1 + \eta_2 x}$ for y in (3.23), we then define function

$$\begin{aligned}\Phi(x) &:= [(1 + \eta_1 x)(1 + 2y) - (1 + \eta_2 x)(1 + y)]\, b - (\eta_2 - \eta_1)x(1 + y)^2 \\ &= \frac{\gamma x(\eta_2 x + \gamma x + 1)}{(1 + \eta_1 x)(1 + \eta_2 x)^3} \cdot \phi(x),\end{aligned}$$

where

$$\phi(x) = -\eta_1^2\eta_2 x^3 - (\eta_1^2 + 2\eta_1\eta_2)x^2 + (\eta_1(2b_0 + a\eta_2) - \eta_2(r_0 + 1 + a\eta_2))x + b_0 - a\eta_2 + a\eta_1.$$

Thus the positive fixed point is locally asymptotically stable if $\phi(x) < 0$ and unstable if $\phi(x) > 0$.

It is clear from (3.23) that if $\eta_2 < \eta_1$, a positive fixed point is unstable. We then assume $\eta_1 < \eta_2$. If $b_0 - a\eta_2 + a\eta_1 < 0$, that is, $a\gamma - a\eta_2 < 1 - a\eta_1$, the coefficient of the linear term in $\phi(x)$ becomes

$$\begin{aligned}\eta_1(2b_0 + a\eta_2) - \eta_2(r_0 + 1 + a\eta_2) &< \eta_1(2b_0 + a\eta_2) - \eta_2(r_0 + 1 + b_0 + a\eta_1)\\ &= 2b_0\eta_1 - 2(b_0 + 1)\eta_2\\ &= 2b_0(\eta_1 - \eta_2) - 2\eta_2 < 0,\end{aligned}$$

which implies that $\phi(x) < 0$, for all $x \in \Omega$, and there exists a unique positive fixed point for $b < b_0$. Hence this unique positive fixed point is always locally asymptotically stable.

If $b_0 - a\eta_2 + a\eta_1 > 0$, that is, $a\gamma - a\eta_2 > 1 - a\eta_1$, there exists a unique positive solution to $\phi(x) = 0$ from Descartes' rule of sign. Denote it as x_s such that $\phi(x_s) = 0$, and define

$$b_s := G(x_s),$$

where $G(x)$ is defined in (3.20). Then a positive fixed point (x, y) is locally asymptotically stable if $x > x_s$ and unstable if $x < x_s$.

For the case of $1 - a\eta_1 < a\gamma - a\eta_2 < 1 + a\eta_1$, it follows from table 2 that there exists a unique positive fixed point if $b < b_0$, where b_0 is the maximum value of function $G(x)$ and $b_s < b_0$. Then this positive fixed point is locally asymptotically stable if $b < b_s$ and unstable if $b > b_s$.

For the case of $a\gamma - a\eta_2 > 1 + a\eta_1$ with $b_s < b_0$, there exists one or two positive fixed points if $b < b_0$ or $b_0 < b < b_c$, respectively. Then the unique positive fixed point is locally asymptotically stable if $b < b_s$ and unstable if $b_s < b < b_0$. The two positive fixed points are unstable if $b_0 < b < b_c$.

For the case of $a\gamma - a\eta_2 > 1 + a\eta_1$ with $b_s > b_0$. If $b < b_0$, the unique positive fixed point is always locally asymptotically stable. If $b_0 < b < b_s$, there exist two positive fixed points (x_i, y_i), $i = 1, 2$, with $x_1 < x_s < x_2$. Thus the positive fixed point with larger components, (x_2, y_2), is locally asymptotically stable while the one with smaller components, (x_1, y_1), is unstable. If $b_s < b < b_c$, we claim $x_c < x_s$. Then the two positive fixed points (x_i, y_i), $i = 1, 2$, are both unstable since $x_1 < x_c < x_2 < x_s$.

To prove $x_c < x_s$ we denote the numerator of $G'(x)$ in (3.21) by

$$d_G(x) := A_1x^3 + A_2x^2 + A_3x + A_4,$$

where $d_G(x_c) = 0$ since $G'(x_c) = 0$. It follows from

$$\begin{aligned}&\gamma\phi(x) - d_G(x)\\ =&(2\eta_1\eta_2^2 r_0 + 2\eta_1\eta_2\gamma r_0)x^2 + (4\eta_1\eta_2 r_0 + 2\eta_1\gamma r_0)x + 2r_0\eta_1 > 0,\end{aligned}$$

for all $x \in \Omega$, that $\gamma\phi(x_c) > d_G(x_c) = 0$, which implies $\phi(x_c) > 0$. Thus $x_c < x_s$ since $\phi(x)$ is monotone decreasing for positive x and $\phi(x_s) = 0$.

We use Table 3 to summarize our results, and give Example 4 to demonstrate the existence and stability results for the positive fixed point of system (3.19).

Table 3. Summary table for the stability of positive fixed points.
(PFP stands for positive fixed point and L.A.S stands for locally asymptotically stable.)

$a(\gamma-\eta_2)<1-a\eta_1$	$b<b_0$	$b_0<b$		
	One PFP L.A.S.	No PFP -		
$1-a\eta_1<a(\gamma-\eta_2)<1+a\eta_1$	$b<b_s$	$b_s<b<b_0$	$b_0<b$	
	One PFP L.A.S.	One PFP unstable	No PFP -	
$1+a\eta_1<a(\gamma-\eta_2)$ with $b_s<b_0$	$b<b_s$	$b_s<b<b_0$	$b_0<b<b_c$	$b_c<b$
	One PFP L.A.S.	One PFP unstable	Two PFP both unstable	No PFP -
$1+a\eta_1<a(\gamma-\eta_2)$ with $b_0<b_s$	$b<b_0$	$b_0<b<b_s$	$b_s<b<b_c$	$b_c<b$
	One PFP L.A.S.	Two PFP larger one L.A.S.	Two PFP both unstable	No PFP -

Example 4. *With the following parameters,*

$$a=2.25,\quad \gamma=0.8,\quad \eta_1=0.1,\quad \eta_2=0.3, \tag{3.24}$$

we have $b_0=0.8$*,* $b_s=0.6957$ *and* $1-a\eta_1=0.775<a(\gamma-\eta_2)=1.125<1+a\eta_1=1.225$*. There exists no positive fixed point and no synchronous 2-cycles if* $b>b_0$*, which implies that the trivial fixed point is globally asymptotically stable. For* $b=1>b_0$*, the trivial fixed point is globally asymptotically stable as shown in the upper left figure in Figure 6. For* $b=0.79<b_0$*, there exists a unique positive fixed point* $(0.0822, 0.0641)$*, which is unstable since* $b>b_s$ *and a unique synchronous 2-cycle with components* $x_*=0.3380$ *and* $y_*=0.2455$*, which is locally asymptotically stable, as shown in the upper right figure in Figure 6. For* $b=0.5<b_s$*, there exists a unique positive fixed point* $(0.8428, 0.5382)$*, which is locally asymptotically stable as shown in the lower figure in Figure 6.*

Example 5. *Given the following parameters,*

$$a=2.25,\quad \gamma=0.8,\quad \eta_1=0.1,\quad \eta_2=0.2, \tag{3.25}$$

we have the threshold values $b_1=0.8681$*,* $b_s=0.5505<b_0=0.8000$*,* $b_c=0.8061$ *and* $a(\gamma-\eta_2)=1.350>1+a\eta_1=1.225$*. For* $b=0.3<b_s$*, there exists a unique positive fixed point* $(1.6967, 1.0135)$*, which is locally asymptotically stable as shown in the upper left figure in Figure 7. For* $b=0.7<b_0$*, there exists a unique positive fixed point* $(0.7306, 0.5100)$*, which is unstable since* $b>b_s$ *and a unique synchronous 2-cycle with* $x_*=1.6667$ *and* $y_*=1.0000$*, which is locally asymptotically stable as shown in the upper right figure in Figure 7. For* $b_0<b=0.803<b_c$*, there exist two positive fixed points* $(0.0353, 0.0281)$ *and* $(0.2176, 0.1668)$*, which are both unstable, and two synchronous 2-cycles, where the one with larger components* $x_*=1.1902$ *and* $y_*=0.7691$ *is locally asymptotically stable as shown in the lower figure in Figure 7.*

Example 6. *With the following parameters,*

$$a=2.25,\quad \gamma=0.8,\quad \eta_1=0.02,\quad \eta_2=0.1, \tag{3.26}$$

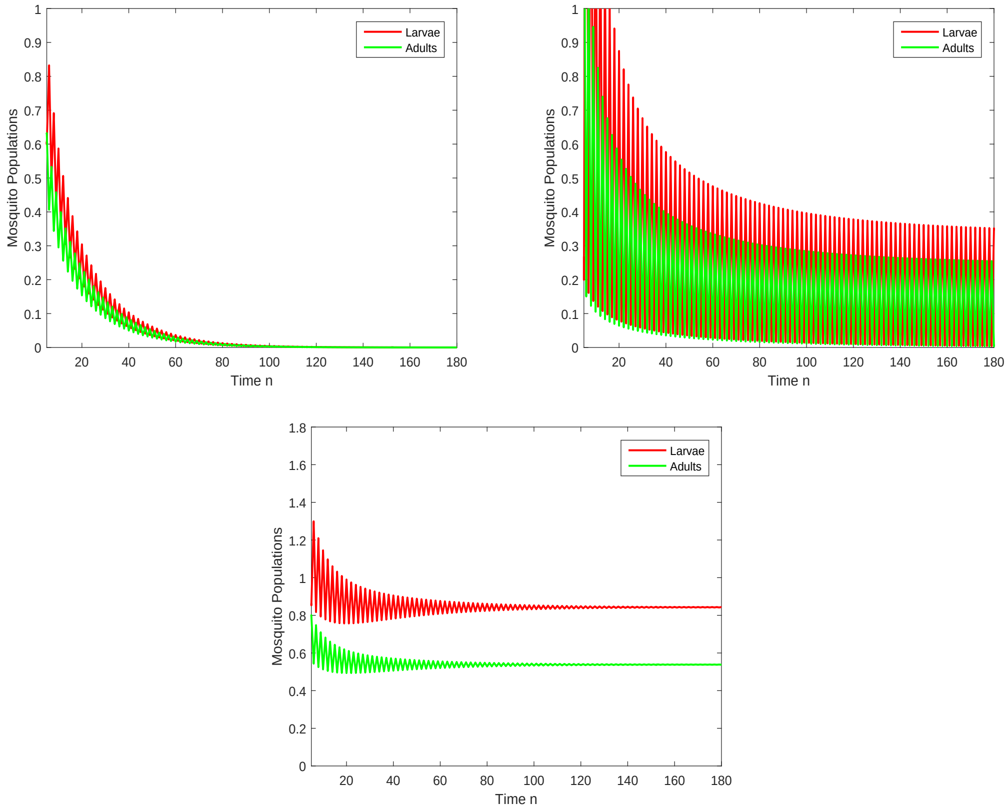

Figure 6. With the parameters given in (3.24), we have $b_0 = 0.8$, $b_s = 0.6957$ and $1 - a\eta_1 = 0.775 < a(\gamma - \eta_2) = 1.125 < 1 + a\eta_1 = 1.225$. For $b = 1 > b_0$, the trivial fixed point is globally asymptotically stable as shown in the upper left figure. For $b = 0.79 < b_0$, there exists a unique positive fixed point $(0.0822, 0.0641)$, which is unstable since $b > b_s$ and a unique synchronous 2-cycle with components $x_* = 0.3380$ and $y_* = 0.2455$, which is locally asymptotically stable as shown in the upper right figure. For $b = 0.5 < b_s$, there exists a unique positive fixed point $(0.8428, 0.5382)$, which is locally asymptotically stable as shown in the lower figure.

we have the threshold values $b_1 = 1.1674$, $b_s = 1.0034 > b_0 = 0.8$, $b_c = 1.0625$ *and* $a(\gamma - \eta_2) = 1.575 > 1 + a\eta_1 = 1.045$. *For* $b = 0.6 < b_0$, *there exists a unique positive fixed point* $(4.0936, 2.3237)$, *which is locally asymptotically stable as shown in the upper left figure in Figure 8. For* $b = 0.9 > b_0$, *there exist two positive fixed points* $(0.2713, 0.2113)$ *and* $(2.8617, 1.7800)$, *where smaller one is unstable while the larger one* $(2.8617, 1.7800)$ *is locally asymptotically stable since* $b < b_s$ *as shown in the upper right figure in Figure 8. For* $b = 1.03 > b_s$, *the two positive fixed points* $(0.8742, 0.6431)$ *and* $(2.0203, 1.3446)$ *are both unstable and there are two synchronous 2-cycles exist, where the one with larger components* $x_* = 3.4660$ *and* $y_* = 2.0591$ *is locally asymptotically stable as shown in the lower figure in Figure 8.*

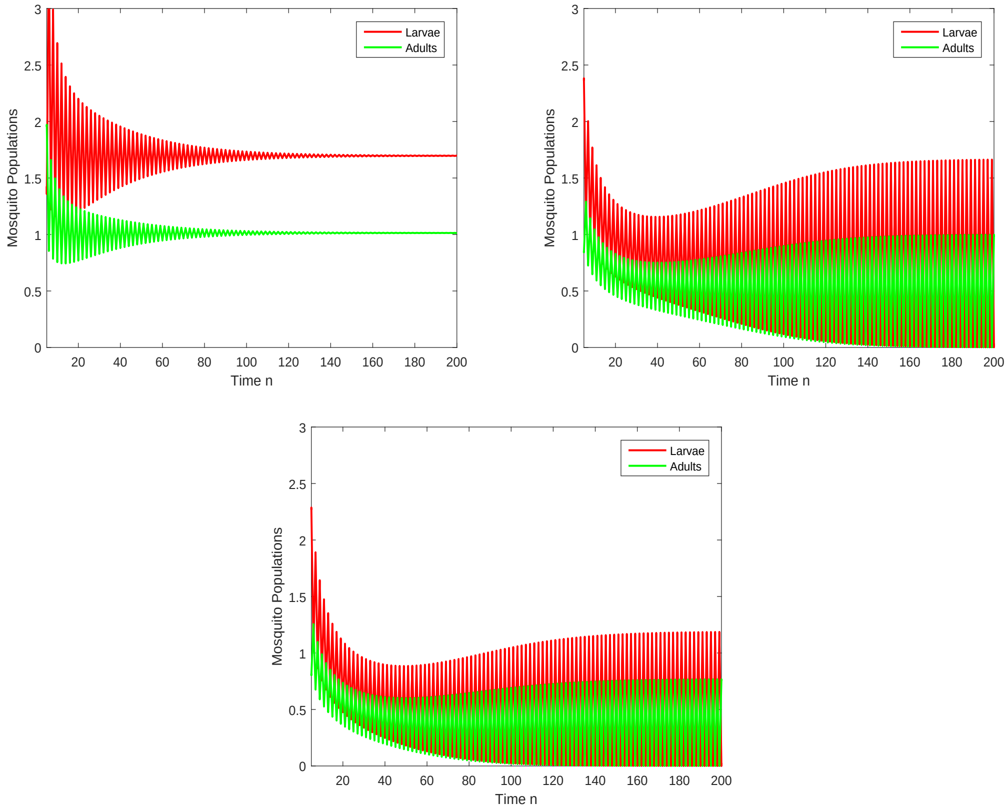

Figure 7. With the parameters given in (3.25), we have $b_1 = 0.8681$, $b_s = 0.5505 < b_0 = 0.8000$, $b_c = 0.8061$ and $a(\gamma - \eta_2) = 1.350 > 1 + a\eta_1 = 1.225$. For $b = 0.3 < b_s$, there exists a unique positive fixed point $(1.6967, 1.0135)$, which is locally asymptotically stable as shown in the upper left figure. For $b = 0.7 < b_0$, there exists a unique positive fixed point $(0.7306, 0.5100)$, which is unstable since $b > b_s$ and a unique synchronous 2-cycle with $x_* = 1.6667$ and $y_* = 1.0000$, which is locally asymptotically stable as shown in the upper right figure. For $b_0 < b = 0.803 < b_c$, there exist two positive fixed points $(0.0353, 0.0281)$ and $(0.2176, 0.1668)$, which are both unstable, and two synchronous 2-cycles, where the one with larger components $x_* = 1.1902$ and $y_* = 0.7691$ is locally asymptotically stable as shown in the lower figure.

4. Concluding remarks

In this paper, we first formulated a discrete-time stage-structured mosquito model where the mosquito population is divided into two groups, the larvae and the adults. We assume that the survivability and progression of larvae are both of Beverton-Holt type nonlinearity. We determined the existence and stability for the positive fixed points and the synchronous 2-cycles, respectively. When the intrinsic growth rate of the population $r_0 < 1$, the trivial fixed point is the only nonnegative fixed point and is globally asymptotically stable. If $r_0 > 1$, the trivial fixed point is unstable, and the model dynamics depend also on parameters η_1 and η_2. If $\eta_1 < \eta_2$, there exists a unique positive fixed point, which is globally asymptotically stable; if $\eta_1 = \eta_2$, there exists a continuum of positive 2-cycles, each

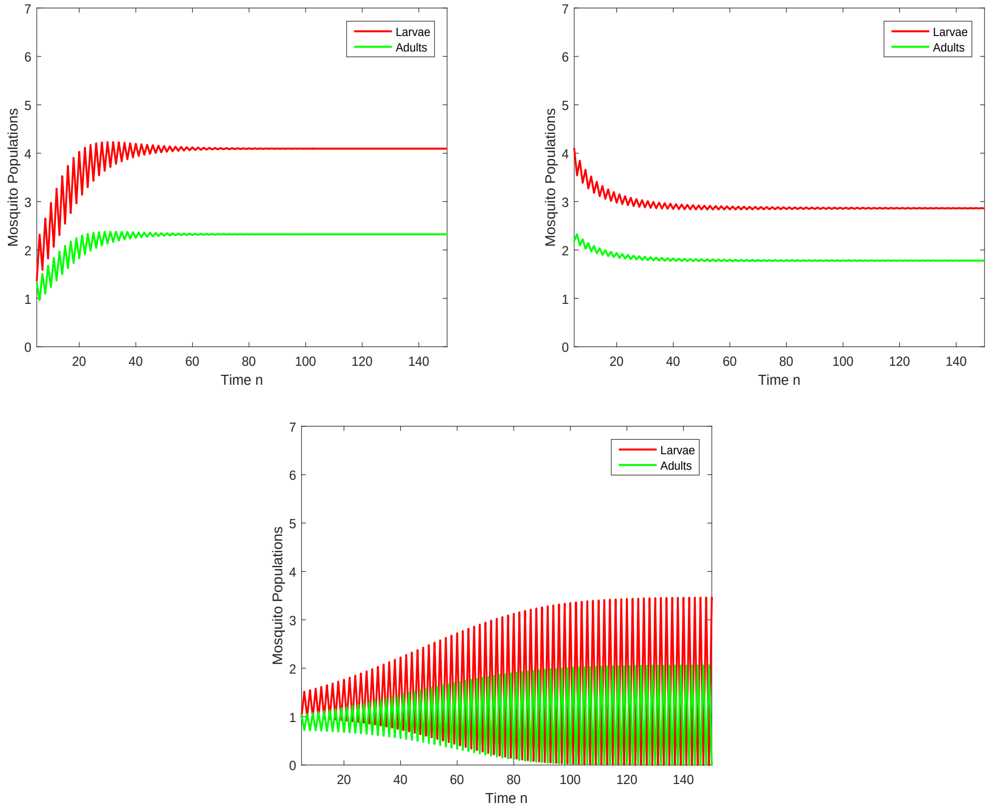

Figure 8. With the parameters given in (3.26), we have $b_1 = 1.1674$, $b_s = 1.0034 > b_0 = 0.8$, $b_c = 1.0625$ and $a(\gamma - \eta_2) = 1.575 > 1 + a\eta_1 = 1.045$. For $b = 0.6 < b_0$, there exists a unique positive fixed point $(4.0936, 2.3237)$, which is locally asymptotically stable as shown in the upper left figure. For $b = 0.9 > b_0$, there exist two positive fixed points $(0.2713, 0.2113)$ and $(2.8617, 1.7800)$, where the one with smaller components is unstable and the one with larger components $(2.8617, 1.7800)$ is locally asymptotically stable since $b < b_s$ as shown in the upper right figure. For $b = 1.03 > b_s$, the two positive fixed points $(0.8742, 0.6431)$ and $(2.0203, 1.3446)$ are both unstable, and there are two synchronous 2-cycles, where the one with larger components $x_* = 3.4660$ and $y_* = 2.0591$ is locally asymptotically stable as shown in the lower figure.

of which is locally stable; and if $\eta_1 > \eta_2$, the positive fixed point becomes unstable, and there exists a unique synchronous 2-cycle, which is globally asymptotically stable.

We then introduced sterile mosquitoes in the stage-structured wild mosquito population and considered three different strategies for the releases of sterile mosquitoes in model system (3.2) where the sterile mosquitoes are released constantly, (3.15) where the releases are proportional to the size of the wild mosquitoes, and (3.19) where the releases are of Holling-II type, respectively. We established threshold value b_c and b_1 for the existence of the positive fixed points or synchronous 2-cycles, and threshold value b_s for the stability of the positive fixed points or synchronous 2-cycles for each of the model systems. If $b > b_c$, there exists no positive fixed point for all of the three model systems. If $b < b_c$, there exist two positive fixed points for system (3.2) and (3.19), and a unique positive fixed point for system (3.15). A positive fixed point is locally asymptotically stable if $b < b_s$, and unstable if $b > b_s$. We also defined threshold value b_1 for the existence of synchronous 2-cycle with $b_1 > b_c$ for system (3.2) and (3.19). If $b < b_1$, there exist two synchronous 2-cycles, where the one with bigger components is locally asymptotically stable and the one with smaller components is unstable. If $b > b_1$, there exist no synchronous 2-cycles and no positive fixed points. Thus the trivial fixed point is globally asymptotically stable. Details can be found in Theorems 3.1 and 3.2 and Tables 1, 2, and 3.

We note that, in the absence of sterile mosquitoes, if the density-dependent death has less effect than the density-dependent progression from the larvae, that is, $\eta_1 x_n < \eta_2 x_n$, the structured population tends to be more stable in the sense that the positive fixed point is globally asymptotically stable while the unique synchronous 2-cycle is unstable. On the other hand, if the density-dependent death has more effect than the density-dependent progression from the larvae, that is, $\eta_1 x_n > \eta_2 x_n$, the structured population tends to be less stable such that the positive fixed point becomes unstable and it tends asymptotically to the oscillatory state, that is, the synchronous 2-cycle.

Such dynamical features are similarly carried out when the sterile mosquitoes are released constantly or proportionally. More specifically, with the constant release rate and in the case of $b < b_s$, there are two positive fixed points. When the density-dependent death has less effect than the density-dependent progression from the larvae such that $\eta_1 x_n < \eta_2 x_n$, one of the two positive fixed points is asymptotically stable, whereas the two positive fixed points are both unstable when the density-dependent death has more effect than the density-dependent progression from the larvae such that $\eta_1 x_n > \eta_2 x_n$. The picture for the proportional releases with saturation is not as clear as for the other two release strategies. Other parameters play a role as well.

For any of the three release strategies, it is not surprising that the amount of releases changes the model dynamics. As small amounts of sterile mosquitoes are released, there exist stable positive fixed points or synchronous 2-cycles. When the release amount is gradually increasing greater than the stability thresholds, first positive fixed points or synchronous 2-cycles become unstable, and then all disappear leading to the extinction of wild mosquitoes.

We would also like to point out that the outcomes from the models studied in this paper seem to be similar to those with the Ricker-type nonlinearity in [27]. However, it is well known that the Beverton-Holt nonlinearity excludes the possibility of the period doubling bifurcation and chaotic feature for the models without stage structure. When stage structure is included, the relatively simple dynamics with no period doubling bifurcation and chaotic feature are carried out, which makes the analysis more tractable. Such model structure has been applied to the discrete-time malaria transmission models incorporating releases of sterile mosquitoes in [32].

Acknowledgments

The authors thanks the two anonymous reviewers for their careful reading and valuable comments and suggestions.

Conflict of interest

All authors declare no conflicts of interest in this paper.

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appendix

The proof of non-existence of $k-$cycles for $k \geq 3$

Proof. To prove that there exist no positive $k-$ cycles for system (2.9), we consider $k = 3$ first. The model (2.9) then becomes

$$\begin{aligned} x_{n+3} &= \frac{a^2 \gamma y_n}{1 + a\eta y_n + \eta(r_0 + 1)x_n}, \\ y_{n+3} &= \frac{a\gamma^2 x_n}{1 + a\eta y_n + \eta(r_0 + 1)x_n}. \end{aligned} \tag{4.1}$$

Any point (x, y) on a 3-cycle should satisfy $x \neq \dfrac{\sqrt{r_0} - 1}{\eta}$, $1+\eta x+a\eta y \neq r_0$ and $y = \sqrt{\dfrac{\gamma}{a}}x$. According to the first equation of (4.1), we have

$$1 + a\eta y + \eta(r_0 + 1)x = a^2\gamma\frac{y}{x}.$$

Plugging $y = \sqrt{\dfrac{\gamma}{a}}x$ into it, we have

$$x = \frac{\sqrt{r_0} - 1}{\eta},$$

which is exactly the fixed point from (2.8). Thus 3-cycles do not exist and as a consequence, any $(2n + 1)$-cycles do not exist with integer $n > 0$.

We next check for 4-cycles. If $k = 4$, the model (2.9) becomes

$$\begin{aligned} x_{n+4} &= \frac{r_0^2 x_n}{1 + \eta(r_0 + 1)x_n + a\eta(r_0 + 1)y_n}, \\ y_{n+4} &= \frac{r_0^2 y_n}{1 + \eta(r_0 + 1)x_n + a\eta(r_0 + 1)y_n}. \end{aligned} \tag{4.2}$$

For a point (x, y) on 4-cycle, it satisfies

$$r_0^2 = 1 + \eta(r_0 + 1)x + a\eta(r_0 + 1)y.$$

Equivalently, we can write it in this form

$$r_0^2 - 1 = (r_0 + 1)(\eta x + a\eta y),$$

that is,

$$r_0 = 1 + \eta x + a\eta y.$$

It is exactly the positive 2-cycle from (2.10). Thus there exist no 4-cycles, and as a consequence, there exist no $2n$-cycles for integer $n > 1$.

Therefore, there exist no positive $k-$cycles for $k \geq 3$. □