COMBINED TROJAN Y CHROMOSOME STRATEGY AND STERILE INSECT TECHNIQUE TO ELIMINATE MOSQUITOES: MODELLING AND ANALYSIS

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Abstract. Sterile insect technique has been successfully applied in the control of agricultural pests, however, it has a limited ability to control mosquitoes. A promising alternative approach is Trojan Y Chromosome strategy, which works by manipulating the sex ratio of a population through the introduction of feminized YY supermales that guarantee male offspring. A combined Trojan Y chromosome strategy and sterile insect technique (TYC-SIT) strategy is modeled with ordinary differential equations that allow the kinetics of the female population decline of mosquitoes to be evaluated under identical modeling conditions. The dynamical analysis leads to results on both local and global stabilities of this combined model. Optimal control analysis is also implemented to investigate the optimal mechanisms for extinction of mosquitoes. In particular, the numerical results affirm that the combined TYC-SIT enables near elimination of mosquitoes. The conclusion has great significance for pest controls.

Keywords: Sterile insect technique; Trojan Y chromosome strategy; equilibrium; Stability analysis; Optimal control; Extinction

1. INTRODUCTION

Mosquito-borne diseases are transmitted by mosquitoes infected with viruses, such as Zika virus, yellow fever virus, West Nile fever virus, and dengue fever virus [1]. The spread of mosquito-borne virus in humans is mainly through the bite of mosquitoes infected with the virus like Anopheles sinensis, Anopheles anthropophagus, Aedes aegypti, Aedes albopictus, Culex mosquitoes, and etc. [2, 3, 4]. Chemical treatments such as pesticides have been implemented for many years to eradicate mosquitoes. However, environmental problems caused by excessive use of pesticides [5], insecticide resistance [6, 7], and combined with the lack of vaccines [8, 9], have called for alternative environment-friendly and sustainable approaches.
such as radiation-based sterile insect technique (SIT) and Trojan Y chromosome strategy (TYC).

SIT works by releasing radiation-sterilized males to an existing population, to mate with wild females so that they have no viable offspring \[11, 10\]. SIT has been successfully applied in the control of several agricultural pests such as invasive fruit flies, lepidopteran and Hemiptera \[12, 13, 14\], however, it has a limited ability to control mosquitoes due to the decline in their mating competitiveness and survival \[15, 16, 17, 18\]. A promising alternative approach that has been proposed for eliminating mosquitoes is TYC, in which released feminized supermales (containing two Y chromosomes) into the field to mate with wild females, resulting in a sharp sex imbalance of subsequent generations \[19, 20, 21, 22\]. Figure 1 illustrates that an equal proportion of females and males are produced in the wild, however, the offspring is guaranteed to be male when a natural female mates with a feminized YY supermale. The gradual reduction in females may lead to eventual extinction of the targeted population after several generation cycles \[23\]. The TYC strategy is safe because it is reversible and has the advantage of targeting a specific species, thus preserving other beneficial species and avoiding non-target effects. Furthermore, no genetically engineered genes can be transferred to subsequent generations. Also, the strength of the effect can be controlled because we can decide how many supermales to be introduced to the population.

![Figure 1. Mating pedigrees of TYC. (a) Mating of a wild-type XX female (F\(_{XX}\)) and a wild-type XY male (M\(_{XY}\)); (b) Mating of a wild-type XX female (F\(_{XX}\)) and a feminized YY supermale (M\(_{YY}\)).](image)

In this manuscript, we will compare the TYC to SIT from both dynamics and optimal control aspects. To the best of our knowledge, it is the first mathematical investigation to compare theoretical TYC to SIT.

2. Materials and Methods

2.1. Mathematical Modelling. The population of mosquitoes in the wild tends to be numerous because their reproduction rates are high and matings occur constantly \[28\], therefore, continuous models of ordinary differential equations (ODEs) can be established to describe the population dynamics of mosquitoes. Parameters will be used in this work are firstly explained in Table 1.
Table 1. List of Parameters. All parameters are non-negative.

| Parameter | Description |
|-----------|-------------|
| $\beta$  | Birth coefficient proportional to the viability of progeny |
| $\delta$ | Death coefficient proportional to the death from predators, illness, etc. |
| $L$      | Logistic term (to limit the size of the population) |
| $K$      | Carrying capacity of the ecosystem |
| $\mu_1$  | Constant influx of radiation-based sterile males |
| $\mu_2$  | Constant influx of feminized $YY$ supermales |

The TYC-SIT model, in which both feminized $YY$ supermales and radiation-based sterile males are introduced, is described by a system of four ODEs for state variables: a wild-type $XX$ female ($f$), a wild-type $XY$ male ($m$), a sterile male ($s_1$), and a feminized $YY$ supermale ($s_2$). Half female and half male offspring are produced in the wild, however, only males can be produced if a wild female mates with a feminized $YY$ supermale, and no viable offspring can be produced if mates with a sterile male. Thusly, the set of equations that describe the system is:

\[
\begin{align*}
\frac{df}{dt} &= \frac{1}{2} fm\beta L \frac{m}{m + s_1 + s_2} - \delta f, \\
\frac{dm}{dt} &= \frac{1}{2} fm\beta L \frac{m}{m + s_1 + s_2} + fs_2\beta L \frac{s_2}{m + s_1 + s_2} - \delta m, \\
\frac{ds_1}{dt} &= \mu_1 - \delta s_1, \\
\frac{ds_2}{dt} &= \mu_2 - \delta s_2,
\end{align*}
\]

where $f, m, s_1, s_2$ define the number of individuals in each associated class, and

\[
L = 1 - \frac{f + m + s_1 + s_2}{K}.
\]

The intraspecies competition for female mates caused by the introduction of feminized $YY$ supermales and radiation-based sterile males is considered and modeled as

\[
\frac{m}{m + s_1 + s_2} \quad \text{and} \quad \frac{s_2}{m + s_1 + s_2}.
\]

If $s_1 = s_2 = 0$, there is no mating pressure on wild males ($\frac{m}{m + s_1 + s_2} = 1$). Obviously, the range of $\frac{m}{m + s_1 + s_2}$ and $\frac{s_2}{m + s_1 + s_2}$ is between 0 and 1. The larger the value of $\frac{m}{m + s_1 + s_2}$ is, the more competitive wild males are. Similarly, the larger the value of $\frac{s_2}{m + s_1 + s_2}$ is, the more competitive feminized $YY$ supermales are.

2.2. Equilibrium and Stability Analysis. The stability of the TYC-SIT model (1) is now investigated. There is one equilibrium, $(0, 0, \frac{\mu_1}{\delta}, \frac{\mu_2}{\delta})$, on the boundary. It’s clear $(0, 0, \frac{\mu_1}{\delta}, \frac{\mu_2}{\delta})$ is global stable. To get the positive interior equilibrium explicitly, i.e., $(f^*, m^*, s_1^*, s_2^*)$, it is equivalent to solve the following equations:
\[
\begin{align*}
\frac{1}{2} f^* \beta^* L^* \frac{m^*}{m^* + s_1^* + s_2^*} - \delta f^* &= 0, \\
\frac{1}{2} f^* \beta^* L^* \frac{m^*}{m^* + s_1^* + s_2^*} + f s_2^* \beta^* L^* \frac{s_2^*}{m^* + s_1^* + s_2^*} - \delta m^* &= 0, \\
\mu_1 - \delta s_1^* &= 0, \\
\mu_2 - \delta s_2^* &= 0, \\
L^* &= 1 - \frac{f^* + m^* + s_1^* + s_2^*}{K}.
\end{align*}
\] (4)

By solving these equations, we have

\[
\begin{align*}
f^* &= K - (m^* + s_1^* + s_2^*) - \frac{2\delta K (m^* + s_1^* + s_2^*)}{m^* \beta^*}, \\
s_1^* &= \frac{\mu_1}{\delta}, \\
s_2^* &= \frac{\mu_2}{\delta},
\end{align*}
\] (5)

and \(m^*\) can be calculated from

\[
\begin{align*}
2\beta m^* \delta s_2^2(s_1 + s_2 - K) m^* + 2 \left( K \delta + \beta s_2^2 \right) m^* + \\
\left[ 2\delta K (s_1 + s_2) + 2\beta s_2^2(s_1 + s_2 - 1) \right] m^* + 4K \delta s_2^2 (s_1 + s_2) &= 0.
\end{align*}
\] (6)

The Jacobian matrix of the model (1) about \((f^*, m^*, s_1^*, s_2^*)\) is given as

\[
J = \begin{bmatrix}
J_{11} & J_{12} & J_{13} & J_{14} \\
J_{21} & J_{22} & J_{23} & J_{24} \\
0 & 0 & J_{33} & 0 \\
0 & 0 & 0 & J_{44}
\end{bmatrix}
\] (7)

where
Theorem 2.1. Let \( \lambda > 0 \). The interior equilibrium \((f^*, m^*, s_1^*, s_2^*)\) is locally asymptotically stable if

\[
J_{11} = \frac{\beta Km^*L^* - \beta f^*m^2}{2K(m^* + s_1^* + s_2^*)} - \delta ,
\]
\[
J_{12} = \frac{(2KL - m^*)\beta f^*m^*}{2K(m^* + s_1^* + s_2^*)} - \frac{\beta f^*m^*L^*}{2s(m^* + s_1^* + s_2^*)^2} ,
\]
\[
J_{13} = -\frac{\beta f^*m^*L^*}{2(m^* + s_1^* + s_2^*)^2} - \frac{\beta f^*m^2}{2K(m^* + s_1^* + s_2^*)} ,
\]
\[
J_{14} = -\frac{\beta f^*m^*L^*}{2(m^* + s_1^* + s_2^*)^2} - \frac{\beta f^*m^2}{2K(m^* + s_1^* + s_2^*)} ,
\]
\[
J_{21} = \frac{\beta L^*(m^2 + 2s_1^*) - \beta f^*(m^2 + 2s_2^*)}{2K(m^* + s_1^* + s_2^*)} ,
\]
\[
J_{22} = \frac{\beta f^*L^*(m^2 + 2s_1^*)}{2(m^* + s_1^* + s_2^*)^2} + \frac{\beta f^*(2Km^*L^* - m^2 - 2s_2^*)}{2K(m^* + s_1^* + s_2^*)} - \delta ,
\]
\[
J_{23} = \frac{\beta f^*L^*(m^2 + 2s_1^*)}{2(m^* + s_1^* + s_2^*)^2} - \frac{b + f(m^2 + 2s_2^*)}{2K(m^* + s_1^* + s_2^*)} ,
\]
\[
J_{24} = \frac{\beta f^*L^*(m^2 + 2s_1^*)}{2(m^* + s_1^* + s_2^*)^2} + \frac{\beta f^*(4Ks_1^*L^* - m^2 - 2s_2^*)}{2K(m^* + s_1^* + s_2^*)} ,
\]
\[
J_{33} = -\delta ,
\]
\[
J_{44} = -\delta .
\]

The corresponding characteristic equation is

\[
\lambda^4 + R_1\lambda^3 + R_2\lambda^2 + R_3\lambda + R_4 = 0
\]

where

\[
R_1 = -(J_{11} + J_{22} + J_{33} + J_{44}),
\]
\[
R_2 = J_{11}J_{22} + J_{11}J_{33} + J_{11}J_{44} + J_{22}J_{33} + J_{22}J_{44} + J_{33}J_{44} - J_{12}J_{21},
\]
\[
R_3 = (J_{33} + J_{44})J_{12}J_{21} - (J_{11} + J_{22})J_{33}J_{44},
\]
\[
R_4 = J_{11}J_{22}J_{33}J_{44} - J_{12}J_{21}J_{33}J_{44}.
\]

**Theorem 2.2.** Let \( \mu > 0 \). The interior equilibrium \((f^*, m^*, s_1^*, s_2^*)\) is locally asymptotically stable if

\[
R_1 > 0, \quad R_3 > 0, \quad R_4 > 0, \quad R_1R_2R_3 - A_0 > R_2^2 + R_4^2.
\]

**Proof.** It follows from Routh Hurwitz stability criteria. \(\square\)

**Theorem 2.2.** In the case of \(\mu_1 = \mu_2 = 0\), the trivial equilibrium \((0, 0, 0, 0)\) of TYC-SIT model (1) is globally asymptotically stable if \(\beta < \frac{\delta}{K}\).

**Proof.** Consider the Lyapunov function \(V(f, m, s_1, s_2) = f + m + s_1 + s_2\). Note that \(V(f, m, s_1, s_2) \geq 0\) due to the positivity of its solutions and \(V(f, m, x)\) is radially bounded. It is left to show that \(V'(f, m, s_1, s_2) < 0\) for all \((f, m, s_1, s_2) \neq (0, 0, 0, 0)\). Taking the derivative of \(V(f, m, s_1, s_2)\) about \(t\) yields
We also hope the production of sterile males and feminized YY supermales is minimized. Herein, the following objective function is chosen:

\[ \text{Obj}(13) \]

The goal is to find the optimal controls \((\mu_1(t), \mu_2(t))\) such that

\[ \text{Obj}(\mu_1(t), \mu_2(t)) = \min_{\mu_1(t), \mu_2(t)} \int_0^T \frac{1}{2} f^2 + \frac{1}{2} \mu_1(t)^2 + \frac{1}{2} \mu_2(t)^2 dt \]

The existence of \(\mu_1^*(t), \mu_2^*(t)\) for minimization problem (15) is guaranteed in the literatures \([29, 30, 31]\).

**Theorem 2.3.** An optimal control \((\mu_1^*(t), \mu_2^*(t)) \in U\) of the system (1) that minimizes the objective function \(\text{Obj}\) is characterized by \((\mu_1^*(t), \mu_2^*(t)) = \left( \max_t \{0, -\lambda_3\}, \max_t \{0, -\lambda_4\} \right)\).

**Proof.** Here the Pontryagin’s minimum principle is used to derive the necessary conditions on this problem. The Hamiltonian \(H\) in this problem is
(16) \( H = \frac{1}{2} f^2 + \frac{1}{2} \mu_1(t)^2 + \frac{1}{2} \mu_2(t)^2 + \lambda_1 f' + \lambda_2 m' + \lambda_3 s_1' + \lambda_4 s_2' \)

The Hamiltonian is used to find the adjoint functions \((\lambda_i, i = 1, 2, 3, 4)\),

(17) \[
\begin{align*}
\lambda_1' &= -\frac{\partial H}{\partial f} = \lambda_1 \left( \delta + \frac{\beta m^2(f - KL)}{2K(m + s_1 + s_2)} \right) - \lambda_2 \left( \frac{\beta L (m^2 + 2s_2^2)}{2(m + s_1 + s_2)} + \frac{\beta f (m^2 + 2s_2^2)}{2K(m + s_1 + s_2)} \right) - f, \\
\lambda_2' &= -\frac{\partial H}{\partial m} = \lambda_1 \left( \frac{\beta fm^2L}{2(m + s_1 + s_2)^2} + \frac{\beta fm(m - 2KL)}{2K(m + s_1 + s_2)} \right) \\
&\quad + \lambda_2 \left( \delta - \frac{\beta fmL}{m + s_1 + s_2} + \frac{\beta fL(m^2 + 2s_2^2)}{2(m + s_1 + s_2)^2} + \frac{\beta f(m^2 + 2s_2^2)}{2K(m + s_1 + s_2)} \right), \\
\lambda_3' &= -\frac{\partial H}{\partial s_1} = \lambda_1 \left( \frac{\beta fm^2L}{2(m + s_1 + s_2)^2} + \frac{\beta fm^2}{2K(m + s_1 + s_2)} \right) \\
&\quad + \lambda_2 \left( \frac{2\beta fs_2L}{m + s_1 + s_2} + \frac{\beta fL(m^2 + 2s_2^2)}{2(m + s_1 + s_2)^2} + \frac{\beta f(m^2 + 2s_2^2)}{2K(m + s_1 + s_2)} \right) + \lambda_3 \delta \\
\lambda_4' &= -\frac{\partial H}{\partial s_2} = \lambda_1 \left( \frac{\beta fm^2L}{2(m + s_1 + s_2)^2} + \frac{\beta fm^2}{2K(m + s_1 + s_2)} \right) \\
&\quad + \lambda_2 \left( -\frac{2\beta fs_2L}{m + s_1 + s_2} + \frac{\beta fL(m^2 + 2s_2^2)}{2(m + s_1 + s_2)^2} + \frac{\beta f(m^2 + 2s_2^2)}{2K(m + s_1 + s_2)} \right) + \lambda_4 \delta
\end{align*}
\]

To find the optimal \((\mu_1^*(t), \mu_2^*(t))\), minimize \(H\) pointwise:

(18) \[
\frac{\partial H}{\partial \mu_1} = \mu_1 + \lambda_3, \quad \frac{\partial H}{\partial \mu_2} = \mu_2 + \lambda_4.
\]

Note that \(\frac{1}{2}\) cancels with the 2 which comes from the square of the controls \(\mu_1\) and \(\mu_2\). Furthermore, the problem is indeed minimization as

(19) \[
\frac{\partial^2 H}{\partial \mu_1^2} = 1 > 0, \quad \frac{\partial^2 H}{\partial \mu_2^2} = 1 > 0.
\]

Hence the optimal solutions are

(20) \[
\frac{\partial H}{\partial \mu_1} > 0 \Rightarrow \mu_1^*(t) = 0 \\
\frac{\partial H}{\partial \mu_1} = 0 \Rightarrow 0 \leq \mu_1^*(t) = -\lambda_3
\]

(21) \[
\frac{\partial H}{\partial \mu_2} > 0 \Rightarrow \mu_2^*(t) = 0 \\
\frac{\partial H}{\partial \mu_2} = 0 \Rightarrow 0 \leq \mu_2^*(t) = -\lambda_4
\]
A compact way of writing the optimal control \((\mu_1^*(t), \mu_2^*(t))\) is

\[(22) \quad \mu_1^*(t) = \max_t \{0, -\lambda_3\}, \quad \mu_2^*(t) = \max_t \{0, -\lambda_4\}.\]

Now the proof is completed. \(\square\)

2.4. Computational Methods. The numerical simulations are investigated by MATLAB R2019b with the values of initial conditions and parameters shown in Table 2. The ode15s solver was used to get numerical solutions of the combined TYC-SIT system. The TOMLAB Base Module and TOMLAB/SNOPT are also used to solve the optimal control problems of our dynamic systems.

| Initial Conditions | Parameters |
|--------------------|------------|
| \(f(0) = 100\)    | \(\beta = 0.01\) |
| \(m(0) = 100\)    | \(\delta = 0.04\) |
| \(s_1(0) = [0, 10, 20, 50, 100]\) | \(\mu_1 = [0, 5, 10, 15, 20]\) |
| \(s_2(0) = [0, 10, 20, 50, 100]\) | \(\mu_2 = [0, 5, 10, 15, 20]\) |

**Remark 1.** The range of initial conditions and parameters were selected for purely theoretical researches. The initial number of \(f, m, s_1, s_2\) can represent thousands, tens of thousands, etc. And extinction in this manuscript is defined as the female population is less than 0.5.

3. Results

The combined TYC-SIT system is modeled, and the initial conditions and parameters in Table 2 are utilized to observe the relative population decline of females \((f)\) in response to the addition of the radiation-based sterile males and feminized YY supermales.

Under the condition of \(\mu_1 = 0, \mu_2 = 0\), that is, sterile males or feminized YY supermales are added to the population only once at time \(t = 0\), and no additional will be introduced, it is observed that no matter how large the initial introduction of sterile males or feminized YY supermales are, the system of the combined TYC-SIT cannot achieve extinction, and instead leads to an equilibrium state. As shown in Figure 2, the population did decline for some time with large enough (i.e. purple/green star line) influx of sterile males or feminized YY supermales, however, the population recovers soon and reaches the equilibrium state at approximately 172, which can be also calculated from equations (4)-(5). Extinction can occur with continuous introducing modified males, two examples are provided in Figure 3.
Figure 2. The population change of females over time under $\mu_1 = 0, \mu_2 = 0$ with different number of initial introduction of sterile males and feminized YY supermales. They all reach a stable state.

Figure 3. The population change of females over time under continuous constant introduction of sterile males and feminized YY supermales.

If we solely continue adding sterile males (i.e. $\mu_2 = 0$) or solely continue adding feminized YY supermales (i.e. $\mu_1 = 0$) after the initial introduction of the both, how and how many modified males would be introduced has a great impact on
the population decline of mosquitoes. With a relatively low influx of modified males, purely introducing sterile males or feminized YY supermales cannot drive the population to extinction, however, the effectiveness of the continuous introduction of YY supermales is better because the population drops much more, see part (a) in Figure 4. As $\mu_1$ or $\mu_2$ is increased to 10, the initial decline rate with $\mu_2 = 10$ is faster than $mu_1 = 10$, but then the situation is reversed after the threshold point. As we can see in part (c) and (d) in Figure 4, the population decline rate with either $\mu_1 = 0$ or $\mu_2 = 0$ is similar if the influx of modified males is large enough.

Figure 4. Investigation of purely introducing sterile males or purely introducing feminized YY supermales after the initial introduction of the both. Blue star line is under $\mu_2 = 0$, and the orange star line is under $\mu_1 = 0$. Here, $s_1(0) = s_2(0) = 10$. (a) Compared $\mu_1 = 5, \mu_2 = 0$ with $\mu_1 = 0, \mu_2 = 5$; (b) Compared $\mu_1 = 10, \mu_2 = 0$ with $\mu_1 = 0, \mu_2 = 10$; (c) Compared $\mu_1 = 15, \mu_2 = 0$ with $\mu_1 = 0, \mu_2 = 15$; (d) Compared $\mu_1 = 20, \mu_2 = 0$ with $\mu_1 = 0, \mu_2 = 20$.

Considering the cost of the production of sterile males and feminized YY supermales, optimal strategies and its corresponding optimal states have also been numerically simulated, see Figures 5-6. The population can be driven to extinction with an optimal time controls $\mu_1(t)$ or $\mu_2(t)$ by using the combined TYC-SIT approach. Figure 5 shows the optimal strategy requires to introduce feminized YY supermales at 20% of the initial female population (or 5% of the carrying capacity) for a short time to bring the population of females below some threshold, then gradually drops to a relatively low level after introducing sterile males at time $t = 4$, as shown in the figure.
and finally turns off until the entire population vanishes. Figure 6 describes the cost of implementing TYC-SIT approach varies as increasing time. After $t=4$, the cost is decreasing.

**Figure 5.** The optimal control analysis of the combined TYC-SIT model. (a) Top panel: female population change with increasing time; (b) Bottom panel: optimal controls $\mu_1$ and $\mu_2$ varies with time.

**Figure 6.** Cost varies as increasing time with optimal controls.
4. Conclusions and Discussions

In this manuscript, we established a mathematical model of the combined TYC and SIT approaches. The population was divided by the following four state variables: wild female mosquitoes \( f \), wild male mosquitoes \( m \), radiation-based sterile males \( s_1 \), and feminized YY supermales \( s_2 \). Six parameters, the birth coefficient \( \beta \), the death coefficient \( \delta \), the logistic term \( L \), carrying capacity \( K \), the influx of sterile males \( \mu_1 \), and the influx of sterile males \( \mu_2 \), are included. The intraspecies competition for female mates caused by the introduction of modified male mosquitoes is especially considered, which is omitted in many studies. The dynamic analysis and optimal control analysis of TYC-SIT model is important to understand the efficiency of this combined strategy to eliminate mosquitoes. Numerical simulations indicate the combined TYC-SIT approach can indeed eliminate mosquitoes.

The combined TYC-SIT approach is safe because it is reversible and has the advantage of targeting a specific species, thus preserving other beneficial species. Furthermore, there is no genetically engineered genes can be transferred to subsequent generations. Also, the strength of the effect can be controlled because we can decide how many feminized YY supermales and sterile males to be introduced to the population. Unlike other strategy, TYC-SIT does not depend on eliminating all wild matings to influence the total population. Instead, it depends on the gradual reduction in wild females over several generation cycles. These results have great significance in biological control of pests.

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Abbreviations
The following abbreviations are used in this manuscript:

- SIT: Sterile Insect Technique
- TYC: Trojan Y Chromosome Strategy
- ODEs: Ordinary Differential Equations
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