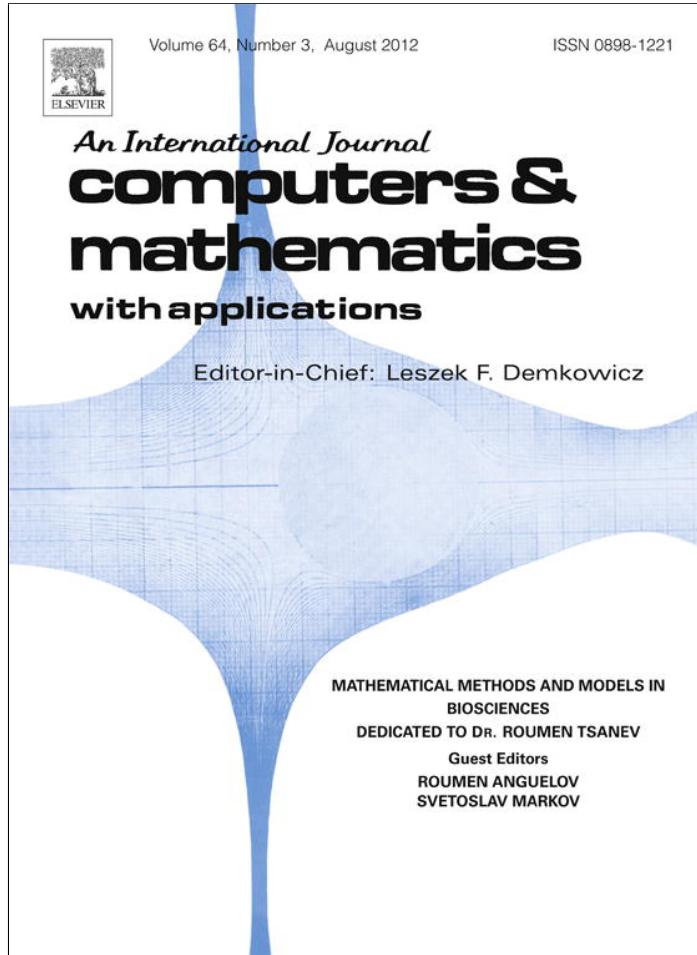


Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

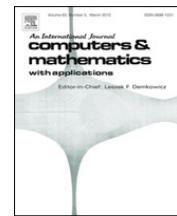
In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>



Contents lists available at SciVerse ScienceDirect

Computers and Mathematics with Applications

journal homepage: www.elsevier.com/locate/camwa

Mathematical modeling of sterile insect technology for control of *anopheles* mosquito

Roumen Anguelov^a, Yves Dumont^b, Jean Lubuma^{a,*}^a Department of Mathematics and Applied Mathematics, University of Pretoria, 0002 Pretoria, South Africa^b CIRAD, UMR AMAP, TA-A51/PS2, Boulevard de la Lironde, 34398 Montpellier Cedex 5, France

ARTICLE INFO

Keywords:

Sterile insect technology
Compartmental modeling
Mosquito control
Monotone operators

ABSTRACT

The Sterile Insect Technology (SIT) is a nonpolluting method of control of the invading insects that transmit disease. The method relies on the release of sterile or treated males in order to reduce the wild population of *anopheles* mosquito. We propose two mathematical models. The first model governs the dynamics of the *anopheles* mosquito. The second model, the SIT model, deals with the interaction between treated males and wild female *anopheles*. Using the theory of monotone operators, we obtain dynamical properties of a global nature that can be summarized as follows. Both models are dissipative dynamical systems on the positive cone \mathbb{R}_+^4 . The value $R = 1$ of the basic offspring number R is a forward bifurcation for the model of the *anopheles* mosquito, with the trivial equilibrium 0 being globally asymptotically stable (GAS) when $R \leq 1$, whereas 0 becomes unstable and one stable equilibrium is born with well determined basins of attraction when $R > 1$. For the SIT model, we obtain a threshold number $\hat{\lambda}$ of treated male mosquitoes above which the control of wild female mosquitoes is effective. That is, for $\lambda > \hat{\lambda}$ the equilibrium 0 is GAS. When $0 < \lambda \leq \hat{\lambda}$, the number of equilibria and their stability are described together with their precise basins of attraction. These theoretical results are rephrased in terms of possible strategies for the control of the *anopheles* mosquito and they are illustrated by numerical simulations.

© 2012 Elsevier Ltd. All rights reserved.

1. Introduction

Malaria is one of the most prevalent vector-host diseases, whereby the disease is not transmitted directly from host to host, but through a vector. Malaria is caused by a protozoa of the genus plasmodium and is transmitted by the female *anopheles* mosquito (vector). According to the World Health Organization (WHO), approximately one to three million people die of malaria every year, the vast majority of which are pregnant women and children who live mostly in Africa and in South America. Moreover, it is now acknowledged that northern countries and in particular those in the South of Europe such as France and Italy could become infected again by malaria. Therefore, the control of the *anopheles* mosquito, the vector responsible for the transmission of diseases, is a major prevention strategy.

Chemicals have been and are still extensively used all over the world to control wild mosquito populations. However, in the long run mosquitoes can develop resistance to chemical products. Besides, the WHO only allows a limited number of insecticides in view of polluting disasters. As a viable alternative, nonpolluting methods also known as biological control tools are more and more studied, with a special focus on the ecology and behavior of the involved species. One of the most promising methods is the Sterile Insect Technique/Technology. The SIT is indeed a nonpolluting method of insect

* Corresponding author. Tel.: +27 12 420 2222; fax: +27 12 420 3893.
E-mail address: jean.lubuma@up.ac.za (J. Lubuma).

control, which relies on the release of sterile males. Mating of released sterile males with wild females leads to nonhatching eggs or to reducing drastically the number of hatching eggs and this slowly drives the wild population to decline. Thus, releasing sufficiently many sterile males and/or doing this over a sufficiently long period of time can lead to local reduction or elimination of the wild population.

The SIT has been known for more than half a century [1,2]. It was first used in 1954 on the Island of Curaao in the Netherlands Antilles in order to control the new world screwworm fly (*Cochliomyia hominivora* (Coquerel)). Sterile males were released for six months after which, the pest was completely eliminated [3]. Among regions where other releases were done, we can mention Southern USA, Mexico, Central America [4], and Libya [5]. Since then, the SIT has been used successfully to almost eradicate various insect populations ranging from pest species (e.g. Mediterranean fruit fly), *Ceratitis capitata* Wiedeman [6], codling moth *Cydia pomonella* (L.) [7,8], tsetse fly *Glossina austeni* [8], *Culex quinquefasciatus* to the vector of Bancroftian filariasis [9]. The book [10] provides a comprehensive overview on the SIT and its applications.

As far as the *anopheles* vector is concerned, the largest SIT release program specifically against the *anopheles albimanus* took place in El Salvador in the 1970s [11], over a 5-month period. About 4.3 million mosquito pupae were mass-produced, sterilized, and released around Lake Apastepeque. The analysis of the data of the *anopheles albimanus* population [12] from the release and the nearby control area demonstrated how effective the sterile males were in preventing a normal seasonal rise in the vector density. Subsequently, a more extensive trial took place from 1977 to 1979 on the Pacific coast of El Salvador [13] with up to 0.5 million sterile males or 1.25 million sterile male pupae being released every day. Recently (2007) in Italy, Bellini [14], released sterile males, which contributed to reduce the wild population of *aedes albopictus* and to fight the Chikungunya virus [15] (see [16,17] for further details about Chikungunya). Furthermore, mosquitoes genetically modified by using the RIDL (Release of Insects carrying a Dominant Lethal) Technique, were released in the Caíman Island and in Malaysia, by the Oxitec Company to fight Dengue Fever (see [18] for an overview on the RIDL approach for *Aedes aegypti*).

Since the first field releases, various modeling and/or mathematical works have been done on SIT using either discrete models [19,20], or continuous temporal models with continuous release (see for instance [21–25,20,26] and references therein), with pulsed releases [15,27], or spatio-temporal models with a one-dimensional spatial component and continuous (proportional) releases [24,28,29]. See also [30] for an overview on SIT mathematical modeling.

The mathematical models investigated in this work are designed according to the approach in [31,32], where the transmission of malaria is modeled by including variability in population in such a way that both the human and the *anopheles* mosquito populations follow the logistic growth law. Though having the same compartmental structure as the SIT study in [23] regarding the control of *aedes aegypti*, also investigated in [26], the differential equations in our model are constructed differently. Furthermore, the equation for the sterile males is much simpler (for other models, see for instance [20]). The purpose of this work is twofold. Firstly, for the dynamical systems under consideration, we are interested in properties of global nature, including the dissipativity of the system, the global asymptotic stability of the trivial equilibrium and the precise description of the basins of attraction of multiple stable equilibria. This goal is achieved by an alternative approach, namely, the theory of monotone operators [33,34], which unlike many classical studies is not subjected to any Lyapunov function. The major advantage of the obtained global properties of dynamical systems is translated into the second purpose of the work. That is to systematically analyze the impact of the SIT, as a measure for the control of the *anopheles* mosquito population. We identify efficient strategies that lead to the reduction of the mosquito population below a certain threshold, which is epidemiologically relevant.

The rest of paper is organized as follows. In the next section, we give the properties of monotone operators that are relevant to our study. This is followed (Section 3) by the presentation of the basic mathematical model of wild *anopheles* mosquito population and by the discussion of its global dynamical properties. Section 4 is devoted to the study of the SIT mathematical model, where the key finding is the identification of a threshold number of treated male mosquitoes or sterile mosquitoes above which the control of wild female mosquitoes is effective. The theoretical results are discussed and supported by numerical simulations in Section 5. The decrease of the wild population of female mosquitoes upon the release of sterile male mosquitoes is further characterized in Section 6 in terms of the so-called yield number of the SIT, which is a certain measure of the reduction of the wild population. Concluding remarks as to how this work fits in the literature and can be extended are given in Section 7. For convenience, we have included Appendix for the proofs of the three main results, which as indicated earlier, are based on the theory of monotone operators [35].

2. Preliminaries on monotone operators

Consider the system of ODEs

$$\frac{dx}{dt} = g(t, x), \quad (1)$$

where $D \subseteq \mathbb{R}^n$ and $g : [0, +\infty) \times D \rightarrow \mathbb{R}^n$ is continuous. Typically D is assumed open to avoid complications. However, in view of the models in this paper we assume only that $D \subset \text{closure}(\text{interior}(D))$ and that for some $\delta > 0$ the vector fields defined by $g(t, \cdot)$, $t \in [0, \delta]$, are all directed inwards at the points of ∂D . This is enough to ensure that for every $a \in D$ there exists $T_a > 0$ such that the system (1) has a solution $x(a, t)$ on the interval $[0, T_a]$ which satisfies $x(a, 0) = a$. We further

assume that g is such that the solution initiated at a is unique. To avoid new notations we assume that $[0, T_a)$ is the maximal (nonnegative) interval of existence of $x(a, t)$.

Definition 1. The system (1) is called *cooperative* if for every $i, j \in \{1, 2, \dots, n\}$ such that $i \neq j$ the function $g_i(t, x_1, \dots, x_n)$ is monotone increasing with respect to x_j .

If g is differentiable and the domain D is convex then, equivalently, the system is cooperative if the Jacobian $\frac{dg(t,x)}{dx}$ is a Metzler matrix for every $t \in [0, +\infty)$ and $x \in D$. Let us recall that a matrix is called *Metzler* if its nondiagonal entries are nonnegative [36].

The following theorem is often referred to as Kamke's theorem, see e.g. [37].

Theorem 2. Let system (1) be cooperative. Then for every $a, b \in D$

$$a \leq b \implies x(a, t) \leq x(b, t), \quad t \in [0, \min\{T_a, T_b\}).$$

The condition on g in Definition 1 is sometimes called quasimonotonicity with respect to x . It is linked in [34] to the monotonicity of differential operators. Kamke's theorem follows from a more general inequality given in [34].

Theorem 3. If g is quasimonotone with respect to x then for any two differentiable functions $y, z : [0, T) \rightarrow D$ we have

$$\left. \begin{array}{l} y(0) \leq z(0) \\ y'(t) - g(t, y(t)) \leq z'(t) - g(t, z(t)), \quad t \in [0, T) \end{array} \right\} \implies y(t) \leq z(t), \quad t \in [0, T].$$

The inequalities between vectors are considered here in their usual coordinate-wise sense, that is, for any $a, b \in \mathbb{R}^n$,

$$a \leq b \iff a_i \leq b_i, \quad i = 1, \dots, n.$$

In addition, we use the relations

$$\begin{aligned} a < b &\iff a \leq b, \quad a \neq b, \\ a \ll b &\iff a_i < b_i, \quad i = 1, \dots, n. \end{aligned}$$

Most of the theory for cooperative systems is developed for the case of autonomous systems

$$\frac{dx}{dt} = f(x), \tag{2}$$

where the right hand side is independent of t . In this case, Theorem 2 equivalently means that the evolution semi-group operator $\varphi_t : D_t \rightarrow D$ defined by $\varphi_t(a) = x(a, t)$ is monotone increasing on its domain $D_t = \{a \in D : T_a > t\}$ for every $t > 0$. Hence also the name *monotone systems* [33]. A system of the form (2) is called *irreducible* if its Jacobian $\frac{df}{dx}$ is an irreducible matrix for every $x \in D$. For cooperative irreducible systems the Kamke's theorem admits a stronger form as stated below, see [33, Theorem 4.1.1].

Theorem 4. If the system (2) is cooperative and irreducible then for every $a, b \in D$

$$a < b \implies x(a, t) \ll x(b, t), \quad t \in [0, \min\{T_a, T_b\}).$$

The next theorem characterizes monotone solutions of cooperative systems and is part of [33, Proposition 3.2.1].

Theorem 5. Assume (2) is cooperative, and let $a \in D$ such that $f(a) \geq \mathbf{0}$ ($f(a) \leq \mathbf{0}$) then the solution $x(a, t)$ is a monotone increasing (decreasing) function of $t \in [0, T_a)$.

The combined application of the monotonicity of the evolution operator φ_t given in Theorems 2 and 4 and the monotonicity of the solutions given in Theorem 5 is an efficient tool for studying dynamical systems. Let us recall that (1) defines a dynamical system on D if $x(a, t)$ is defined for all $t \geq 0$ and $x(a, t) \in D$. In terms of the notation introduced earlier, this means that $T_a = \infty$ for all $a \in D$. Using the monotonicity theorems stated here, one can prove, for example, stability and attractiveness of equilibria without using the Jacobian of the right hand side. Furthermore, this approach provides a method for characterizing the basins of attraction and addressing other related issues. As usual we call an equilibrium asymptotically stable if it is both stable and attractive. An asymptotically stable equilibrium is called globally asymptotically stable if the basin of attraction is the whole domain D . Basins of attraction are often represented as n -dimensional intervals: given $a, b \in \mathbb{R}^n$ with $a \leq b$

$$[a, b] = \{x \in \mathbb{R}^n : a \leq x \leq b\}.$$

Theorem 6. Let $a, b \in D$ be such that $a < b$, $[a, b] \subseteq D$ and $f(b) \leq \mathbf{0} \leq f(a)$. Then (1) defines a (positive) dynamical system on $[a, b]$. Moreover, if $[a, b]$ contains a unique equilibrium p then p is globally asymptotically stable on $[a, b]$.

Proof. Under the stated assumptions it follows from [Theorem 5](#) that $x(a, t)$ and $x(b, t)$ are respectively monotone increasing and monotone decreasing. Moreover, [Theorem 2](#) implies that $x(a, t) \leq x(b, t)$, $t \in [0, \min\{T_a, T_b\}]$. Therefore, at least one of the solutions remains in $[a, b]$ in its maximal interval of existence. Then the compactness of $[a, b]$ implies that $T_a = T_b = \infty$ so that for any $z \in [a, b]$ we have $T_z = \infty$ and

$$a \leq x(a, t) \leq x(z, t) \leq x(b, t) \leq b, \quad t \in [0, \infty).$$

Therefore, (1) defines a (positive) dynamical system on $[a, b]$. The global asymptotic stability of a unique equilibrium $p \in [a, b]$ follows from a general theorem [38], but in this setting it also admits an elementary proof. Due to the monotonicity of system (2), both solutions converge to points of $[a, b]$ as $t \rightarrow \infty$. Since these limits are equilibria of the dynamical system and p is the only equilibrium in $[a, b] \cap D$, it follows that $\lim_{t \rightarrow \infty} x(a, t) = \lim_{t \rightarrow \infty} x(b, t) = p$. It remains to show the stability of p . Assume first that $a < p < b$. Let V be an open neighborhood of p in $[a, b]$. Then there exists $t_1 > 0$ such that $x(a, t) \in V$ and $x(b, t) \in V$ for all $t \geq t_1$. Clearly the set $W = (x(a, t_1), x(b, t_1))$ is an open neighborhood of p . An application of [Theorem 2](#) yields

$$x(a, t_1 + t) < x(z, t) < x(b, t_1 + t), \quad z \in W.$$

Therefore, $x(z, t) \in W \subset V$ for every $z \in W$, which proves the stability of p . When $a = p$ and $b = p$, a simplified version of the arguments above can be used. \square

3. Population dynamics of anopheles mosquito

The life cycle of a mosquito consists of two main stages: aquatic (egg, larva, pupa) and adult (with males and females). After emergence from pupa a female mosquito needs to mate and get a blood meal before it starts laying eggs. Then every 4–5 days it will take a blood meal and lay 100–150 eggs at different places (10–15 per place). For the mathematical description, we will consider two stages [22]: the aquatic stage and the adult stage. Furthermore, we split the adult stage into three sub-compartments, with females and males, which leads to the following compartments:

- A – population in aquatic stage
- Y – young females, not yet laying eggs
- F – fertilized and egg-laying females
- M – number of males.

The life cycle is described through the flow chart in [Fig. 1](#). The mathematical model is the system of ordinary differential equations (3)–(6).

$$\frac{dA}{dt} = \phi F - (\gamma + \mu_1 + \mu_2 A)A, \quad (3)$$

$$\frac{dY}{dt} = r\gamma A - (\beta + \mu_Y)Y, \quad (4)$$

$$\frac{dF}{dt} = \beta Y - \mu_F F, \quad (5)$$

$$\frac{dM}{dt} = (1 - r)\gamma A - \mu_M M. \quad (6)$$

Note that Eq. (3) can be considered as a logistic population with immigration. Following [31,32], it is formulated by using density dependent mortality rate, $-\mu_2 A^2$, rather than carrying capacity. A female needs to mate successfully only once. The eggs are laid in the so-called gonotrophic cycle. It consists of taking a blood meal, maturation of the eggs and oviposition. Before a female begins laying eggs, two essential events need to take place, mating and taking a blood meal, occurring in varying order. We consider a female to be in the Y compartment from its emergence from pupa until her gonotrophic cycle has began, that is the time of mating and taking the first blood meal, which takes typically 3–4 days. The death rate during that period reflects essentially only death from predators and adverse climatic conditions. Therefore, it is generally lower than the death rate for the F compartment. Typically the male mosquitoes are (depending on the temperature) about half or at least 40% of the total population. In the model the fraction of the emerging female mosquitoes is denoted by r , with $1 - r$ being the fraction of emerging male mosquitoes. Mating is a complex process that is not fully understood [39]. The male mosquito can mate practically through all its life. A female mosquito needs one successful mating to breed lifelong. It is admitted that mosquitoes locate themselves in space and time to ensure they are available to mate [39]. Therefore, it is reasonable to assume that in any case the immature female will mate and, thus, move to compartment F , or die. Thus $1/(\beta + \mu_Y)$ represents the mean time a female stays in compartment Y . Mathematically this means that Eq. (5) can be decoupled from the system. Sometimes β is referred to as “mating rate”, which, as explained above, can be a bit misleading and does not define well the boundary between compartments Y and F : the terminology contact rate would be better for β . We clearly fixed this boundary at the beginning of the first gonotrophic cycle of a female, that is immediately after the mating and first blood meal. Then the rate (per day) of laying eggs in the breeding sites is ϕF , where ϕ is the average amount of eggs

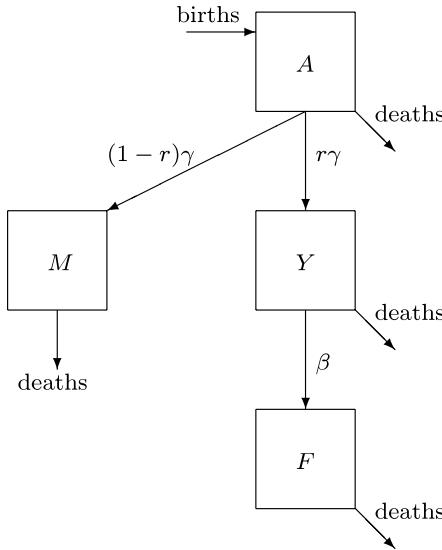


Fig. 1. Wild mosquito flow chart.

laid per fertilized female per day. In the model, we use a density dependent death rate for the aquatic stage since anophelis larvae are density sensitive, which imply an additional density mortality rate. In [23], the size of the population is also restricted only in the aquatic stage but in a different way by an explicit carrying capacity beyond which no eggs are laid. In Eq. (3) the parameters μ_1 and μ_2 denote, respectively, the density independent and the density dependent death rates of the aquatic stage. In Eqs. (4)–(6), μ with respective index refers to the death rate for a specific compartment (which is density independent). The system (3)–(6) has two equilibria: the origin $\mathbf{0}$ and the nontrivial equilibrium $x^{\#} = (A^{\#}, Y^{\#}, F^{\#}, M^{\#})'$ given by

$$\begin{aligned} A^{\#} &= \frac{\gamma + \mu_1}{\mu_2}(R - 1), & Y^{\#} &= \frac{r\gamma(\gamma + \mu_1)}{\mu_2(\beta + \mu_Y)}(R - 1), \\ F^{\#} &= \frac{r\gamma\beta(\gamma + \mu_1)}{\mu_2\mu_F(\beta + \mu_Y)}(R - 1), & M^{\#} &= \frac{(1 - r)\gamma(\gamma + \mu_1)}{\mu_2\mu_M}(R - 1), \end{aligned} \quad (7)$$

where

$$R = \frac{\phi\beta r\gamma}{(\beta + \mu_Y)(\gamma + \mu_1)\mu_F} \quad (8)$$

is the basic offspring number. The nontrivial equilibrium $x^{\#}$ is nonnegative, that is, it has a biological meaning if and only if $R \geq 1$.

Denoting $x = (A, Y, F, M)'$ the system (3)–(6) can be written in the form (2) where the function f is defined via the right hand side of (3)–(6). It is easy to see that the system is cooperative on $D = \mathbb{R}_+^4$. Moreover, f is continuous on D and the vector field defined by f is directed inwards on ∂D . Hence Theorems 2, 5 and 6 are applicable.

The essential properties of the model (3)–(6) as a dynamical system are summarized in the following theorem. A major point that differentiates this theorem and its proof from those in the literature (e.g. [23]) are the global nature of the properties and the irrelevance of the Lyapunov function. (For an alternative approach see [23].)

Theorem 7. *The set of ODEs (3)–(6) defines a dissipative dynamical system on $D = \mathbb{R}_+^4 = \{x \in \mathbb{R}^4 : x \geq \mathbf{0}\}$. Moreover,*

- (i) *If $R \leq 1$ then $\mathbf{0}$ is globally asymptotically stable on D .*
- (ii) *If $R > 1$ then the system has two equilibria $\mathbf{0}$ and $x^{\#}$ on D where $x^{\#}$ is stable with basin of attraction $D \setminus \{x = (A, Y, M, F) \in \mathbb{R}_+^4 : A = Y = F = 0\}$ and $\mathbf{0}$ is unstable with the nonnegative M -axis being a stable manifold.*

Proof. The inequality

$$\frac{\gamma + \mu_1 + \mu_2 A}{\gamma + \mu_1} > 4R \quad (9)$$

holds for all sufficiently large A . Let $m > 0$ and let A_m be so large that in addition to (9) the following inequalities also hold:

$$A_m \geq m, \quad (10)$$

$$F_m := \frac{(\gamma + \mu_1 + \mu_2 A_m)A_m}{2\phi} \geq m, \quad (11)$$

$$Y_m := \frac{\mu_F}{2\beta} F_m \geq m, \quad (12)$$

$$M_m := \frac{2(1-r)\gamma A_m}{\mu_M} \geq m. \quad (13)$$

Let $b_m = (A_m, Y_m, F_m, M_m)'$. Then

$$f(b_m) = \begin{pmatrix} -\phi F_m \\ r\gamma A_m \left(1 - \frac{\gamma + \mu_1 + \mu_2 A_m}{4R(\gamma + \mu_1)}\right) \\ -\beta Y_m \\ -\frac{1}{2}\mu_M M_m \end{pmatrix} < \mathbf{0}. \quad (14)$$

Applying [Theorem 6](#) with $a = \mathbf{0}$ and $b = b_m$ we obtain that (2) defines a dynamical system on $[\mathbf{0}, b_m]$. However, b_m can be selected larger than any $x \in \mathbb{R}_+^4$. Hence, (2) defines a dynamical system on $D = \mathbb{R}_+^4$.

(i) In this case the only equilibrium in D is the origin $\mathbf{0}$. It follows from [Theorem 6](#) that $\mathbf{0}$ is globally asymptotically stable on $[\mathbf{0}, b_m]$ for any $m > 0$. Hence it is globally asymptotically stable on D .

(ii) Since $R > 1$ the inequality

$$\frac{\gamma + \mu_1 + \mu_2 A}{\gamma + \mu_1} < \sqrt{R} \quad (15)$$

holds for all sufficiently small values of A . Let $\varepsilon > 0$ and let A_ε be so small that in addition to (15) the following inequalities also hold

$$A_\varepsilon \leq \varepsilon, \quad (16)$$

$$F_\varepsilon := \sqrt[4]{R} \frac{(\gamma + \mu_1 + \mu_2 A_\varepsilon) A_\varepsilon}{\phi} \leq \varepsilon, \quad (17)$$

$$Y_\varepsilon := \sqrt[4]{R} \frac{\mu_F}{\beta} F_\varepsilon \leq \varepsilon, \quad (18)$$

$$M_\varepsilon := \frac{(1-r)\gamma A_\varepsilon}{\mu_M \sqrt{R}} \leq \varepsilon. \quad (19)$$

Let $a_\varepsilon = (A_\varepsilon, Y_\varepsilon, F_\varepsilon, M_\varepsilon)'$. Then

$$f(a_\varepsilon) = \begin{pmatrix} \left(1 - \frac{1}{\sqrt[4]{R}}\right) \phi F_\varepsilon \\ r\gamma A_\varepsilon \left(1 - \frac{\gamma + \mu_1 + \mu_2 A_\varepsilon}{\sqrt{R}(\gamma + \mu_1)}\right) \\ \left(1 - \frac{1}{\sqrt[4]{R}}\right) \beta Y_\varepsilon \\ (\sqrt{R} - 1) \mu_M M_\varepsilon \end{pmatrix} > \mathbf{0}. \quad (20)$$

Hence it follows from [Theorem 6](#) that $x^\# = (A^\#, Y^\#, F^\#, M^\#)'$ is globally asymptotically stable on $[a_\varepsilon, b_m]$. Since a_ε can be selected to be smaller than any $x > \mathbf{0}$ and b_m can be selected to be larger than any $x > \mathbf{0}$ we have that $x^\#$ is asymptotically stable on $D = \mathbb{R}_+^4$ with a basin of attraction at least the interior of D . We prove that the basin of attraction is $\tilde{D} = D \setminus \{x = (A, Y, M, F) \in \mathbb{R}_+^4 : A = Y = F = 0\}$ by using that the system is irreducible on \tilde{D} , which can be seen easily. Let $z \in \tilde{D}$. Then $z > \mathbf{0}$ and it follows from [Theorem 4](#) that $x(z, t) \gg \mathbf{0}$ for $t > 0$. Hence by what has been proved already $\lim_{t \rightarrow +\infty} x(z, t) = x^\#$. Moreover, on the M -axis Eq. (5) is reduced to a decreasing equation. Hence all solutions converge to $\mathbf{0}$. Therefore, the basin of attraction of $x^\#$ is precisely \tilde{D} . This also implies that $\mathbf{0}$ is unstable with the M -axis being a stable manifold. \square

Note that the basic offspring number R does not depend on μ_2 while the equilibrium values of all compartments are inversely proportional to μ_2 . Having $\mu_2 > 0$ is essential for the dissipativity of the system. For $R > 1$ the equilibrium $x^\#$ has also the role of a carrying capacity although it does not appear explicitly in the formulation of the model.

4. The SIT model

The SIT is a nonpolluting method of insect control that relies on the release of sterile insects. Mating of released sterile males with wild females leads to nonhatching eggs. Thus, if males are released in sufficient numbers and/or over a sufficiently

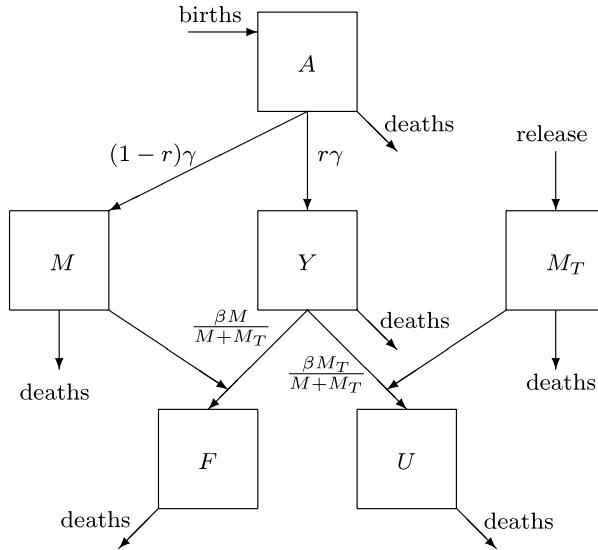


Fig. 2. SIT control of mosquito flow chart.

long period of time, it can lead to the local reduction or elimination of the wild population. Typically the aim is to lower this population under a certain threshold so that the entomological risk is low. Thus SIT can also be used as a preventive tool, or after a standard vector control campaign, with adulticide, larvicide or/and mechanical control. The success of the SIT is based on the fact that the sterile mosquito are in many ways the same as the wild ones, most importantly, they will mate with wild females. Nevertheless there are some differences. One for example is their distribution. Since they are distributed manually, the place of release depends on available roads and resources as well as on the level of knowledge about the distribution of wild mosquitoes (breeding sites, feeding grounds). Therefore we assume that only a fraction p of the released mosquito can join the wild mosquito population. A further difference is that some change in the biology, like the mating competitiveness of the sterile male mosquito, due to irradiation [40]. In general, this can be captured by a ratio q , representing the mean mating competitiveness of the sterile males [39]. Note that q could be less or greater than 1 [14,39]. We denote by M_T the number of “wild mosquitoes equivalent” of sterile mosquitoes. This means that the actual number of sterile mosquitoes is $\frac{1}{pq}M_T$. The death rate μ_T also depends on the procedure. Given that the sterile mosquitoes are released at a rate of $\psi(t)$ at time t , the population of treated males M_T is modeled by Eq. (26). Under the assumption that, after the stated adjustments, the mosquitoes in the compartments M and M_T are equally likely to mate, a female mating female mosquito has probability $\frac{M}{M+M_T}$ to be with a wild mosquito and probability $\frac{M_T}{M+M_T}$ to be with a sterile mosquito. Hence the transfer rate β from the compartment Y splits into transfer rate of $\frac{\beta M}{M+M_T}$ to compartment F and a transfer rate of $\frac{\beta M_T}{M+M_T}$ to compartment U of females that would be laying sterile (nonhatching) eggs. Note that the total mating rate $\frac{\beta M}{M+M_T} + \frac{\beta M_T}{M+M_T} = \beta$ remains unchanged by the introduction of the sterile mosquito. We should remark that the different strategy used in [23] results in the biologically unrealistic situation of lowering the mating rate due to the introduction of the sterile mosquitoes. A modified flow diagram involving sterile males also is given in Fig. 2. Then the mathematical model is represented as the system of 6 differential equations (21)–(26). Note that, in contrast to the model (3)–(6), neither M nor M_T can be decoupled. The effect of the introduction of the sterile mosquitoes is in the reduction of the Y to F transfer rate from β to $\frac{\beta M}{M+M_T}$. The females fertilized by sterile mosquitoes also lay eggs, but these eggs do not hatch. Therefore they have no effect on the aquatic stage of the population. Other techniques, like RID, lead to eggs which hatch and the larvae die only later, having a further negative impact on the wild larvae population by competing with it for resources, i.e. reducing the carrying capacity of the breeding sites. This is not the case with the SIT technique. Only the wild mosquito develop in the breeding sites. Let us note that in some previous models, e.g. [41], the sterile mosquito population is assumed to have a direct impact on the available carrying capacity for the wild population, which is biologically incorrect.

$$\frac{dA}{dt} = \phi F - (\gamma + \mu_1 + \mu_2 A)A, \quad (21)$$

$$\frac{dY}{dt} = r\gamma A - (\beta + \mu_Y)Y, \quad (22)$$

$$\frac{dF}{dt} = \frac{\beta M}{M + M_T} Y - \mu_F F, \quad (23)$$

$$\frac{dU}{dt} = \frac{\beta M_T}{M + M_T} Y - \mu_U U, \quad (24)$$

$$\frac{dM}{dt} = (1-r)\gamma A - \mu_M M, \quad (25)$$

$$\frac{dM_T}{dt} = pq\psi - \mu_T M_T. \quad (26)$$

The model (21)–(26) can be simplified in the following way. First, the equation for U can be decoupled from the system. Secondly, the size of M_T is controlled by human intervention and independent from the rest of the population. Indeed, given a continuous function $\psi(t)$ the linear equation (26) has the solution

$$M_T(t) = e^{-\mu_T t} \left(M_T(0) + \int_0^t e^{\mu_T s} pq\psi(s) ds \right). \quad (27)$$

Then, the mathematical model is a nonautonomous system of four differential equations as follows:

$$\frac{dA}{dt} = \phi F - (\gamma + \mu_1 + \mu_2 A)A, \quad (28)$$

$$\frac{dY}{dt} = r\gamma A - (\beta + \mu_Y)Y, \quad (29)$$

$$\frac{dM}{dt} = (1-r)\gamma A - \mu_M M, \quad (30)$$

$$\frac{dF}{dt} = \frac{\beta M}{M + M_T(t)} Y - \mu_F F. \quad (31)$$

In addition to having fewer equations, a major advantage of the system (28)–(31) is that its right hand side is quasi-monotone. This fact in turn explains why the badly needed global properties in Theorems 8 and 9 are obtained at low cost i.e. “no Lyapunov function”.

Theorem 8. Assume that $\psi(t)$ is a continuous nonnegative valued function of $t \in [0, \infty)$ so that $M_T = M_T(t)$ in (27) has the same property. Then the system of ODEs (28)–(31) defines a dissipative dynamical system on $D = \mathbb{R}_+^4$.

Proof. We use the notation as in the proof of Theorem 7. The system (28)–(31) is nonautonomous. Denoting its right hand side by $g(t, x)$ it assumes the form (1). The function g depends on t via $M_T(t)$, that is, it can be written as $g(t, x) = \Phi(M_T(t), x)$. It is easy to see that $g(t, x) = \Phi(M_T(t), x) \leq \Phi(0, x) = f(x)$ where f is the right hand side of (3)–(6). Let $z \in D$. Denote by $x(z, t)$ and $x_0(z, t)$ the solutions of (3)–(6) and (28)–(31), both initiated at z . As shown in Theorem 7, $x_0(z, t)$ is defined for all $t \geq 0$. Let $[0, T_z)$ be the maximal interval of existence of $x(z, t)$. We have

$$\frac{d}{dt}x(z, t) - f(x(z, t)) \leq \frac{d}{dt}x(z, t) - g(t, x(z, t)) = 0 = \frac{d}{dt}x_0(z, t) - f(x_0(z, t)).$$

Then it follows from Theorem 3 that $x(z, t) \leq x_0(z, t)$, $t \in [0, T_z)$. Furthermore, using that $\mathbf{0}$ is an equilibrium of (28)–(31) we obtain by Theorem 2 that $x(z, t) \geq \mathbf{0}$, $t \in [0, T_z)$. Now using the dissipativity of (3)–(6) as obtained in Theorem 7, it is easy to obtain that $T_z = +\infty$ and that $x(z, t)$ is eventually absorbed into a neighborhood of either $\mathbf{0}$ or $[\mathbf{0}, x^\#]$. \square

The dynamical system (28)–(31) is not autonomous. The right hand side depends directly on t via the function $M_T(t)$. In order to characterize the behavior of the solutions more specifically than in Theorem 8 we need further knowledge about the function M_T . In what follows we assume that the manual intervention $\psi(t)$ is such that the function in (27) satisfies:

$$\lim_{t \rightarrow \infty} M_T(t) = \lambda \quad \text{for some } \lambda \in (0, +\infty). \quad (32)$$

For sufficiently large values of t Eq. (31) can be replaced by the simpler equation

$$\frac{dF}{dt} = \frac{\beta M}{M + \lambda} Y - \mu_F F. \quad (33)$$

Moreover, in addition to providing approximation to (28)–(31) for large t the system (28)–(30), (33) has the same invariant sets and respective stability. Hence, we carry out our further analysis on the autonomous dynamical system (28)–(30), (33). Equating the right hand side to zero we obtain that at any equilibrium of this system the ratio $\alpha = \frac{M}{\lambda}$ satisfies the equation

$$\alpha^2 - (R - \lambda Q - 1)\alpha + \lambda Q = 0, \quad (34)$$

where R is the basic offspring number (8) of the wild mosquito population and

$$Q = \frac{\mu_2 \mu_M}{(\gamma + \mu_1)(1-r)\gamma}. \quad (35)$$

In view of [Theorem 7](#) we are only interested in the SIT model (28)–(30), (33) when $R > 1$ which we assume in the sequel. It is easy to see that $\hat{\lambda} = \frac{(\sqrt{R}-1)^2}{Q}$ is a threshold value of λ determining the number of positive roots of Eq. (34). More precisely, if $\lambda < \hat{\lambda}$ the equation has two positive roots α^* and α^{**} ($\alpha^* > \alpha^{**}$), if $\lambda = \hat{\lambda}$ it has one positive root $\hat{\alpha}$, and if $\lambda > \hat{\lambda}$ there are no positive roots. Let $\hat{x} = (\hat{A}, \hat{Y}, \hat{M}, \hat{F})'$, $x^* = (A^*, Y^*, M^*, F^*)'$ and $x^{**} = (A^{**}, Y^{**}, M^{**}, F^{**})'$ be the equilibria of the dynamical system (28)–(30), (33) corresponding to $\hat{\alpha}$, α^* and α^{**} , respectively. It is easy to see that $\mathbf{0} < \hat{x}, \mathbf{0} < x^* < x^{**}$ whenever these equilibria exist (see [Appendix](#) for detailed computations). The properties of the model as a dynamical system are summarized in the next theorem.

Theorem 9. *The Eqs. (28)–(30), (33) define a dissipative dynamical system on $D = \mathbb{R}_+^4$ for any $\lambda \in (0, +\infty)$. Moreover, we have that:*

- (a) *If $\lambda > \hat{\lambda}$ then $\mathbf{0}$ is globally asymptotically stable equilibrium.*
- (b) *If $\lambda = \hat{\lambda}$ the system has two equilibria $\mathbf{0}$ and \hat{x} . The set $\{x \in \mathbb{R}^4 : \mathbf{0} \leq x < \hat{x}\}$ is in the basin of attraction of $\mathbf{0}$ while $\{x \in \mathbb{R}^4 : x \geq \hat{x}\}$ is in the basin of attraction of \hat{x} .*
- (c) *If $0 < \lambda < \hat{\lambda}$ the system has three equilibria $\mathbf{0}$, x^* and x^{**} . The set $\{x \in \mathbb{R}^4 : \mathbf{0} \leq x < x^*\}$ is in the basin of attraction of $\mathbf{0}$, while $\{x \in \mathbb{R}^4 : x > x^*\}$ is in the basin of attraction of x^{**} .*

Proof. In the notation used in the proof of [Theorem 8](#), the system (28)–(30), (33) can be written as

$$\frac{dx}{dt} = \Phi(\lambda, x). \quad (36)$$

Denote by $x_\lambda(z, t)$ the solution of (36) satisfying $x_\lambda(z, 0) = z$. Consider the point b_m as given by (10)–(13). Using (14) we have

$$\Phi(\lambda, b_m) \leq \Phi(0, b_m) = f(b_m) < \mathbf{0}.$$

Then it follows from [Theorem 6](#) that (36) defines a dynamical system on $[\mathbf{0}, b_m]$.

(a) Let $\lambda > \hat{\lambda}$. In this case the system (36) has only one nonnegative equilibrium, namely $\mathbf{0}$. Therefore, by [Theorem 6](#), $\mathbf{0}$ is globally asymptotically stable on $[\mathbf{0}, b_m]$. Since b_m can be selected to be larger than any point in \mathbb{R}_+^4 , this implies that $\mathbf{0}$ is globally asymptotically stable on \mathbb{R}_+^4 .

(c) In this case $\lambda < \hat{\lambda}$ and the dynamical system (36) has three equilibria $\mathbf{0}$, x^* and x^{**} . For an arbitrary $0 < \delta < \alpha^* - \alpha^{**}$, let $c_\delta = (A_\delta, Y_\delta, M_\delta, F_\delta)'$ where

$$M_\delta = \frac{\lambda}{\alpha^* - \delta}, \quad (37)$$

$$A_\delta = \frac{\mu_M}{(1-r)\gamma} M_\delta, \quad (38)$$

$$Y_\delta = \frac{r\gamma}{\beta + \mu_Y} A_\delta = \frac{r\gamma\mu_M}{(\beta + \mu_Y)(1-r)\gamma} M_\delta, \quad (39)$$

$$F_\delta = \frac{\beta M_\delta}{\mu_F(M_\delta + \lambda)} Y_\delta = \frac{\beta r \gamma \mu_M}{(1+\alpha^*-\delta)\mu_F(\beta + \mu_Y)(1-r)\gamma} M_\delta. \quad (40)$$

Substituting in the expression for Φ we have

$$\Phi(\lambda, c_\delta) = \begin{pmatrix} \frac{\delta(\alpha^* - \alpha^{**} - \delta)}{(\alpha^* - \delta)(1 + \alpha^* - \delta)} \\ 0 \\ 0 \\ 0 \end{pmatrix}. \quad (41)$$

Let $\delta > 0$. Then $\Phi(\lambda, c_\delta) > \mathbf{0}$ and $c_\delta > x^*$. Applying [Theorem 6](#) with $a = c_\delta$ and $b = b_m$ we obtain that for m sufficiently large Eq. (36) defines a dynamical system on $[c_\delta, b_m]$ and that x^{**} is globally asymptotically stable on $[c_\delta, b_m]$. Using the fact that

$$M_\delta = M^* + \frac{\lambda\delta}{\alpha^*(\alpha^* - \delta)} \leq \frac{\delta}{Q},$$

it is easy to see that for any point $z > x^*$ one can find $\delta > 0$ so that $c_\delta < z$ (see [Appendix](#) for detailed computations). In addition, b_m can be larger than any point in \mathbb{R}_+^4 . Therefore, x^{**} is a stable equilibrium and $\{x \in \mathbb{R}_+^4 : x \gg x^*\}$ is in its basin of attraction. Using that the system (36) is irreducible one can replace \gg with $>$ by an application of [Theorem 4](#) as in the proof of [Theorem 7](#).

For $\delta < 0$ we have $\Phi(\lambda, c_\delta) < \mathbf{0}$ and $c_\delta < x^*$. Then following the same method we prove that $\mathbf{0}$ is stable and $\{x \in \mathbb{R}_+^4 : x < x^*\}$ is in its basin of attraction.

The proof of (b) is similar to (c) with respective modification to take into account that $\alpha = \hat{\alpha} = \alpha^* = \alpha^{**}$. \square

Table 1
Entomological parameters [32].

Parameters	Description	Value
ϕ	Number of eggs at each deposit per capita (per day)	50
γ	Maturation rate from larvae to adult (per day)	0.1
μ_1	Mortality rate of the aquatic stage	≈ 0.25
μ_2	Density mortality rate of the aquatic stage	10^{-5}
$1/\mu_T$	Average lifespan of sterile male (in days)	7
$1/\mu_M$	Average lifespan of male mosquitoes (in days)	7
$1/\mu_F$	Average lifespan of female mosquitoes (in days)	10
$1/(\beta + \mu_Y)$	Average time in compartment Y (in days)	3.33

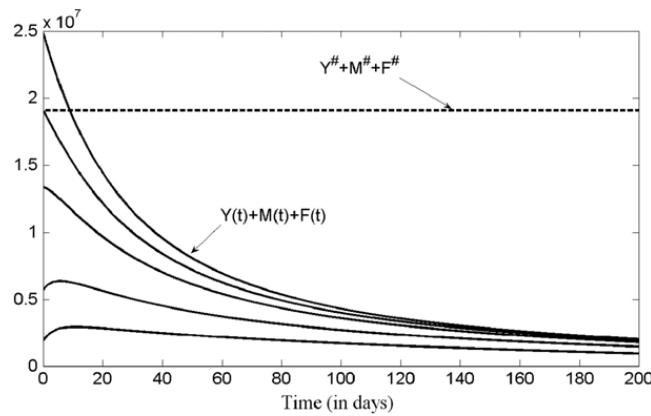


Fig. 3. $\lambda = 1.2\hat{\lambda}$.

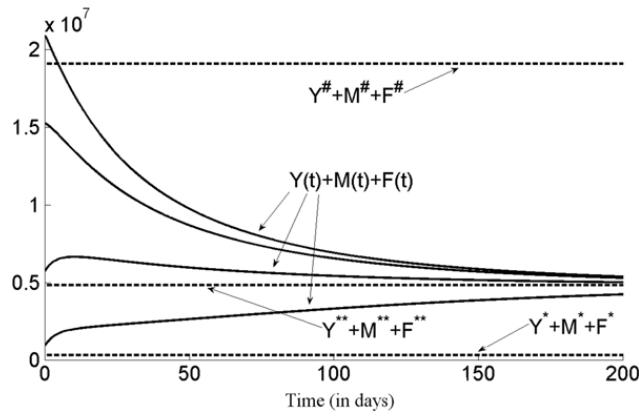


Fig. 4. $\lambda = 0.8\hat{\lambda}$, $x(0) > x^*$.

5. Discussion and simulations

It follows from [Theorem 9\(a\)](#) that a sufficiently large output of sterile mosquito, namely $M_T(t) = \lambda > \hat{\lambda}$, is an effective control of the mosquito population. The threshold number $\hat{\lambda}$ can be written in the form

$$\hat{\lambda} = \frac{\sqrt{R} - 1}{\sqrt{R} + 1} M^#. \quad (42)$$

Hence for large values of R , as in the case of *anopheles*, we have $\hat{\lambda} \approx M^#$. This indicates that for effective control using only the SIT method the output of sterile male mosquito need to be of similar magnitude as the equilibrium value of the male mosquito as determined by the environment. Further, we note that the qualitative behavior of the solutions of the model presented in [Theorem 9](#) is independent of the values of the parameters of the model as long as $R > 1$. Moreover, the threshold number $\hat{\lambda}$ depends on the parameters only via R and $M^#$, where both quantities are directly measurable in a practical setting. In the simulation presented in [Figs. 3–5](#), we use the parameter values in [Table 1](#) obtained from [32].

The dynamics of all compartments are very similar to each other. Hence, only the graphs of the total flying mosquito population, that is, $Y + M + F$ are presented in these figures. For these values of the parameters we have that $\hat{\lambda}$ is about 78% of $M^#$. In absolute terms it may turn out that $\hat{\lambda}$ is so large that it may not be practical to implement SIT with $\lambda > \hat{\lambda}$ and/or to

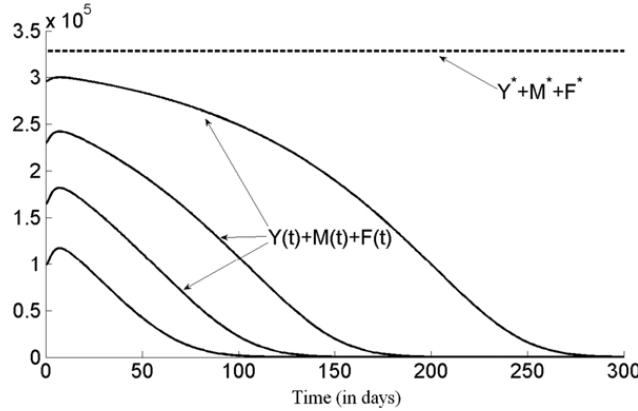


Fig. 5. $\lambda = 0.8\hat{\lambda}$, $x(0) < x^*$.

sustain it for a sufficiently long time. As demonstrated in Fig. 4, for sterile insect release $\lambda < \hat{\lambda}$ the equilibrium x^{**} attracts all trajectories with initial value higher than x^* . Thus, SIT reduces the mosquito population from the wild equilibrium x^* to a new equilibrium $x^{**} < x^*$.

A possible control strategy when $\lambda < \hat{\lambda}$ is suggested by point (c) in Theorem 9. It shows that even a small continuous release of sterile males makes $\mathbf{0}$ a locally asymptotically stable equilibrium. Hence if the mosquito population has not grown yet sufficiently or it has been reduced by some other measures, e.g. destroying the breeding places, it can be controlled by release of sterile males, see Fig. 5.

6. The yield of SIT

Our aim in this section is to quantify the controlling effect SIT has on the mosquito population. Without human intervention the wild mosquito population settles around its natural equilibrium x^* , which has coordinates $(A^*, Y^*, M^*, F^*)'$. If a sterile male mosquito is released, this results in certain decrease of the wild population. To quantify this decrease we need to make the basic assumption that the sterile mosquitoes are released at the same rate until the population settles around a new equilibrium. Then the reduction from x^* to the new equilibrium describes the effect of SIT. Assume first that $\lambda < \hat{\lambda}$. Then the new equilibrium is $x^{**} = (A^{**}, Y^{**}, M^{**}, F^{**})'$. Explicitly the equilibrium x^{**} is given by

$$M^{**} = \frac{\lambda}{\alpha^{**}}, \quad (43)$$

$$A^{**} = \frac{\mu_M}{(1-r)\gamma} M^{**}, \quad (44)$$

$$Y^{**} = \frac{r\gamma}{\beta + \mu_Y} A^{**} = \frac{r\mu_M}{(\beta + \mu_Y)(1-r)} M^{**}, \quad (45)$$

$$F^{**} = \frac{\beta M^{**}}{(M^{**} + \lambda)\mu_F} Y^{**} = \frac{\beta r \mu_M}{(1 + \alpha^{**})\mu_F (\beta + \mu_Y)(1-r)} M^{**}, \quad (46)$$

where

$$\alpha^{**} = \frac{1}{2} \left(R - 1 - \lambda Q - \sqrt{(R - 1 - \lambda Q)^2 - 4\lambda Q} \right).$$

It is easy to see from (7) that the coordinates of x^* can be represented in similar terms. More precisely, we have

$$M^* = \frac{R - 1}{Q}, \quad (47)$$

$$A^* = \frac{\mu_M}{(1-r)\gamma} M^*, \quad (48)$$

$$Y^* = \frac{r\mu_M}{(\beta + \mu_Y)(1-r)} M^*, \quad (49)$$

$$F^* = \frac{\beta r \mu_M}{\mu_F (\beta + \mu_Y)(1-r)} M^*. \quad (50)$$

Now one can see that the relative reduction of the compartments A , Y , M between the two equilibria is the same, that is

$$\frac{M^* - M^{**}}{M^*} = \frac{A^* - A^{**}}{A^*} = \frac{Y^* - Y^{**}}{Y^*}.$$

It is easy to see that $\frac{F^{\#}-F^{**}}{F^{\#}} \neq \frac{M^{\#}-M^{**}}{M^{\#}}$. However, we have to recall that with the SIT application the wild female mosquito is divided into the compartments F and U . It follows from (24) that

$$U^{**} = \frac{\beta\lambda}{(M^{**} + \lambda)\mu_F} Y^{**} = \frac{\alpha^{**}\beta r\mu_M}{(1 + \alpha^{**})\mu_F(\beta + \mu_Y)(1 - r)} M^{**}.$$

Thus we obtain

$$\frac{F^{\#}-F^{**}-U^{**}}{F^{\#}} = \frac{M^{\#}-M^{**}}{M^{\#}}.$$

Then the number

$$\varphi := \frac{M^{\#}-M^{**}}{M^{\#}} = \frac{A^{\#}-A^{**}}{A^{\#}} = \frac{Y^{\#}-Y^{**}}{Y^{\#}} = \frac{F^{\#}-F^{**}-U^{**}}{F^{\#}}$$

describes the reduction of the wild mosquito population both in its totality and per compartment. Shortly, the number φ will be called *SIT yield*. Using (43) and (47) we obtain

$$\begin{aligned} M^{**} &= \lambda \frac{1}{\alpha^{**}} = \lambda \frac{R-1-\lambda Q + \sqrt{(R-1-\lambda Q)^2 - 4\lambda Q}}{2\lambda Q} \\ &= \frac{1}{2} \left(M^{\#} - \lambda + \sqrt{(M^{\#} - \lambda)^2 - \frac{4}{R-1} M^{\#}} \right) \\ &= \frac{M^{\#}}{2} \left(1 - \xi + \sqrt{(1 - \xi)^2 - \frac{4\xi}{R-1}} \right), \end{aligned}$$

where $\xi = \frac{\lambda}{M^{\#}}$ is the release of sterile males as a fraction of the wild male natural equilibrium. Then we derive an explicit expression for φ as follows

$$\varphi = \frac{M^{\#}-M^{**}}{M^{\#}} = \frac{1}{2} \left(1 + \xi - \sqrt{(1 - \xi)^2 - \frac{4\xi}{R-1}} \right).$$

This is valid when $\lambda \leq \hat{\lambda}$ or equivalently

$$\xi \leq \hat{\xi} := \frac{\hat{\lambda}}{M^{\#}} = \frac{\sqrt{R}-1}{\sqrt{R}+1}.$$

For $\xi > \hat{\xi}$ the mosquito population decreases to **0**. So its relative reduction from $x^{\#}$ to the new equilibrium **0** is 1 so that the SIT yield is

$$\varphi(\xi) = \begin{cases} \frac{1}{2} \left(1 + \xi - \sqrt{(1 - \xi)^2 - \frac{4\xi}{R-1}} \right) & \text{if } \xi \leq \hat{\xi}, \\ 1 & \text{if } \xi > \hat{\xi}. \end{cases}$$

One should note that φ as a function of ξ depends on the parameters of the model only through the basic offspring number R . In particular, it is independent of the density dependent death rate μ_2 of the aquatic stage. Hence qualitatively the response of the mosquito population to SIT is independent of its size. The yield function for various values of R is graphically presented in Fig. 6.

Sterile male release such that $\lambda \leq \hat{\lambda}$, or equivalently $\xi \leq \hat{\xi}$, results in suppressing the mosquito population towards extinction only if at the beginning of the release process this population is relatively small, namely, less than y^* . The equilibrium y^* is obtained similarly to (43)–(46) with α^* instead of α^{**} . Then a sterile male mosquito release of $\lambda = \xi M^{\#}$ can suppress a population not exceeding $y = \eta y^*$ where

$$\eta := \frac{M^*}{M^{\#}} = \frac{A^*}{A^{\#}} = \frac{Y^*}{Y^{\#}} = \frac{F^*+U^*}{F^{\#}}.$$

Further, η can be obtained as a function of ξ in the form

$$\eta = \frac{1}{2} \left(1 - \xi - \sqrt{(1 - \xi)^2 - \frac{4\xi}{R-1}} \right).$$

The graph of the function $\eta = \eta(\xi)$ is presented in Fig. 7 for several values of R . One can observe that for the mosquito population for large R , as it is typically the case for a mosquito, the population size needs to be relatively quite small to be controlled via release $\xi < \hat{\xi}$. For example if $R = 40$, release of $\xi = 60\%$ can only control a mosquito population of about 4% of the wild equilibrium.

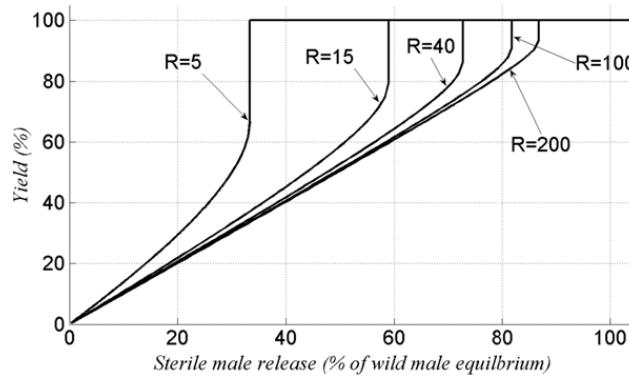


Fig. 6. SIT yield function.

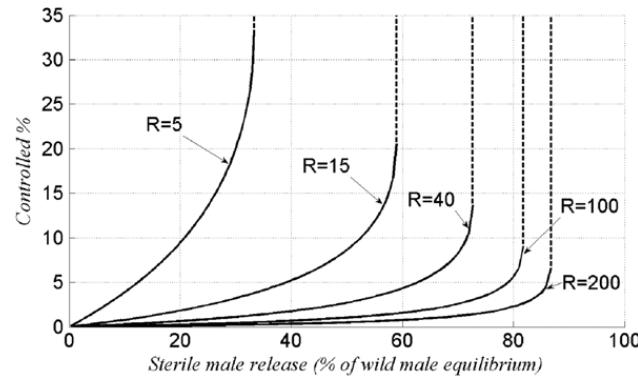


Fig. 7. SIT controlled population size.

Remark 10. In [17,15] the authors have considered mechanical control as an additional vector control tool for the Chikungunya Disease. Mechanical control consists in reducing breeding sites, that is in reducing egg deposits. In our model, mechanical control would modify the parameter ϕ . Indeed, let $c \in [0, 1]$ be the parameter that represents the mechanical control: when $c = 1$, there is no mechanical control, and when $c = 0$, the mechanical control is total (elimination of all breeding sites). Then the time evolution of the aquatic stage becomes

$$\frac{dA}{dt} = c\phi F - (\gamma + \mu_1 + \mu_2)A,$$

such that the new basic offspring number is given by $R_m = cR$. Thus following Figs. 6 and 7, it is also clear, that a combination of SIT and Mechanical Control can be helpful to improve the yield of the Control.

7. Conclusion

By establishing a relevant and simple mathematical model, we studied, through it, the life cycle of mosquitoes (from the aquatic stage to the adult stage that includes the female vectors). We establish, in terms of the basic offspring number, properties of global nature such as the stability of the equilibria and their basins of attraction. We added to this initial model a compartment of treated or sterile male mosquitoes in order to get the SIT model. We obtained a threshold number and established theoretically and computationally that the control of wild female mosquitoes is effective provided that the number of released sterile male mosquitoes is above this threshold number. Furthermore, below this number, we determined properties of a global nature for the equilibria of the system.

Our study reveals that the success of the SIT depends on the entomological parameters of the wild *anopheles* mosquito as well as on parameters related to the sterile males, i.e. p , q , ψ , and μ_T , which determine the said threshold number. This leads us to being interested in future work in combining the SIT with Mechanical Control, in order to improve the control. Comparing the SIT approach with standard chemical vector control is also of interest. Another possible extension would be to couple our SIT model with the epidemiological model studied in [42].

Acknowledgments

The second author (Y.D.) was supported by the SIT program (CRVOI, Réunion Island, France) and the French Ministry of Health, while the other authors (R.A. and J.L.) were supported by the National Research Foundation of South Africa. The

authors express their gratitude to the anonymous referees whose remarks and suggestions have contributed to improving the paper in many respects.

Appendix. Computations

A.1. Equilibria of the model (28)–(30), (33)

When equating the right hand side of the considered system of ODEs, from Eqs. (29) and (33) we have

$$F = \frac{\beta M}{(M + \lambda)\mu_F} Y = \frac{\beta M}{(M + \lambda)\mu_F} \frac{r\gamma}{\beta + \mu_Y} A.$$

Substituting into the right hand side of (28) we obtain

$$\phi \frac{\beta M}{(M + \lambda)\mu_F} \frac{r\gamma}{\beta + \mu_Y} A - (\gamma + \mu_1 + \mu_2 A)A = 0.$$

Excluding the trivial case $A = 0$ the equation simplifies to

$$\frac{\phi\beta r\gamma M}{\mu_F(\beta + \mu_Y)(M + \lambda)} - \gamma - \mu_1 - \mu_2 A = 0.$$

Using (30), we have $A = \frac{\mu_M M}{(1-r)\gamma}$, which implies the following equation about M

$$\frac{\phi\beta r\gamma M}{\mu_F(\beta + \mu_Y)(M + \lambda)} - \gamma - \mu_1 - \mu_2 \frac{\mu_M M}{(1-r)\gamma} = 0.$$

Substituting $\alpha = \frac{\lambda}{M}$ leads to

$$\frac{\phi\beta r\gamma}{\mu_F(\beta + \mu_Y)} \frac{1}{1 + \alpha} - \gamma - \mu_1 - \frac{\mu_2 \mu_M}{(1-r)\gamma} \frac{\lambda}{\alpha} = 0$$

or equivalently

$$\frac{\phi\beta r\gamma}{\mu_F(\beta + \mu_Y)(\gamma + \mu_1)} \frac{1}{1 + \alpha} - 1 - \frac{\mu_2 \mu_M}{(1-r)\gamma(\gamma + \mu_1)} \frac{\lambda}{\alpha} = 0. \quad (51)$$

The coefficient of $\frac{1}{1+\alpha}$ is exactly the basic offspring number R . Denote the coefficient of $\frac{\lambda}{\alpha}$ by Q . Then (51) is equivalent to the following quadratic equation with respect to α

$$\alpha^2 - (R - 1 - \lambda Q)\alpha + \lambda Q = 0. \quad (52)$$

As mentioned earlier it is assumed that $R > 1$. The discriminant is

$$\Delta = (R - 1 - \lambda Q)^2 - 4\lambda Q = (R + 1 - \lambda Q)^2 - 4R = ((\sqrt{R} - 1)^2 - \lambda Q)((\sqrt{R} + 1)^2 - \lambda Q).$$

The equation has two real positive roots iff $\Delta > 0$ and $R - 1 - \lambda Q > 0$. Then using that $(\sqrt{R} - 1)^2 < R - 1 < (\sqrt{R} + 1)^2$ and in view of the expression for Δ , Eq. (52) has two positive roots iff $(\sqrt{R} - 1)^2 - \lambda Q > 0$ or equivalently

$$\lambda < \hat{\lambda} := \frac{(\sqrt{R} - 1)^2}{Q}.$$

In this case the roots are

$$\begin{aligned} \alpha^* &= \frac{1}{2} \left(R - 1 - \lambda Q + \sqrt{(R - 1 - \lambda Q)^2 - 4\lambda Q} \right) \\ \alpha^{**} &= \frac{1}{2} \left(R - 1 - \lambda Q - \sqrt{(R - 1 - \lambda Q)^2 - 4\lambda Q} \right). \end{aligned}$$

Further, if $\lambda = \hat{\lambda}$ Eq. (52) has one positive root $\hat{\alpha} = \sqrt{R} - 1$ and it has no positive roots when $\lambda > \hat{\lambda}$.

Equilibria:

$$\begin{aligned} M^* &= \frac{\lambda}{\alpha^*} \\ A^* &= \frac{\mu_M}{(1-r)\gamma} M^* \\ Y^* &= \frac{r\gamma}{\beta + \mu_Y} A^* = \frac{r\gamma \mu_M}{(\beta + \mu_Y)(1-r)\gamma} M^* \\ F^* &= \frac{\beta M^*}{(M^* + \lambda)\mu_F} Y^* = \frac{\beta}{(1 + \alpha^*)\mu_F} \frac{r\gamma}{\beta + \mu_Y} A^* \\ &= \frac{\beta r\gamma \mu_M}{(1 + \alpha^*)\mu_F(\beta + \mu_Y)(1-r)\gamma} M^*. \end{aligned}$$

For x^{**} and \hat{x} one uses the above formulas with α^{**} and $\hat{\alpha}$.

A.2. Inequalities in the proof of Theorem 9

The first coordinate of the function Φ is

$$\begin{aligned}\Phi_1(\lambda, x) &= \frac{\phi\beta r\gamma}{\mu_F(\beta + \mu_Y)} \frac{1}{1+\alpha} - \gamma - \mu_1 - \frac{\mu_2\mu_M}{(1-r)\gamma} \frac{\lambda}{\alpha} \\ &= -\frac{\alpha^2 - (R - 1 - \lambda Q)\alpha + \lambda Q}{\alpha(\alpha + 1)} = \frac{(\alpha^* - \alpha)(\alpha - \alpha^{**})}{\alpha(\alpha + 1)}.\end{aligned}$$

Using that $0 < \delta < \alpha^* - \alpha^{**}$ we obtain

$$\Phi_1(\lambda, c_\delta) = \frac{\delta(\alpha^* - \delta - \alpha^{**})}{(\alpha^* - \delta)(\alpha^* - \delta + 1)} > 0.$$

The inequality $c_\delta > x^*$ is derived as follows:

$$\begin{aligned}M_\delta &= \frac{\lambda}{\alpha^* - \delta} > \frac{\lambda}{\alpha^*} = M^* \\ A_\delta &= \frac{\mu_M}{(1-r)\gamma} M_\delta > \frac{\mu_M}{(1-r)\gamma} M^* = A^* \\ Y_\delta &= \frac{r\gamma}{\beta + \mu_Y} A_\delta > \frac{r\gamma}{\beta + \mu_Y} A^* = Y^* \\ F_\delta &= \frac{\beta M_\delta}{(M_\delta + \lambda)\mu_F} Y_\delta = \frac{\beta}{(1 + \alpha^* - \delta)\mu_F} Y_\delta \\ &> \frac{\beta}{(1 + \alpha^*)\mu_F} Y_\delta > \frac{\beta}{(1 + \alpha^*)\mu_F} Y^* = F^*.\end{aligned}$$

Further, we also have

$$\begin{aligned}M_\delta - M^* &= \frac{\lambda}{\alpha^* - \delta} - \frac{\lambda}{\alpha^*} = \frac{\lambda\delta}{\alpha^*(\alpha^* - \delta)} \leq \frac{\lambda\delta}{\alpha^*\alpha^{**}} = \frac{\delta}{Q} \\ A_\delta - A^* &= \frac{\mu_M}{(1-r)\gamma} (M_\delta - M^*) \\ Y_\delta - Y^* &= \frac{r\gamma}{\beta + \mu_Y} (A_\delta - A^*) \\ F_\delta - F^* &= \frac{\beta}{(1 + \alpha^* - \delta)\mu_F} Y_\delta - \frac{\beta}{(1 + \alpha^*)\mu_F} Y^* \\ &= \left(\frac{\beta}{(1 + \alpha^* - \delta)\mu_F} - \frac{\beta}{(1 + \alpha^*)\mu_F} \right) Y_\delta + \frac{\beta}{(1 + \alpha^*)\mu_F} (Y_\delta - Y^*) \\ &= \frac{\delta\beta}{(1 + \alpha^{**})(1 + \alpha^*)\mu_F} Y_\delta + \frac{\beta}{(1 + \alpha^*)\mu_F} (Y_\delta - Y^*).\end{aligned}$$

Therefore c_δ is arbitrarily close to x^* .

References

- [1] E.F. Knipling, Possibilities of insect control or eradication through the use of sexually sterile males, *J. Econ. Entomol.* 48 (1955) 459.
- [2] L. Alphey, M. Benedict, R. Bellini, G.G. Clark, D.A. Dame, M.W. Service, S.L. Dobson, Sterile-insect method for control of mosquito-borne diseases, *Vector-Borne and Zoonotic Diseases* 10 (3) (2010) 295–311.
- [3] A.H. Baumhover, A.J. Graham, B.A. Bitter, D.E. Hopkins, W.D. New, F.H. Dudley, R.C. Bushland, Screwworm control through release of sterile flies, *J. Econ. Entomol.* 48 (1955) 462–466.
- [4] J.H. Wyss, Screw-worm eradication in the Americas overview, in: K.H. Tan (Ed.), *Area-Wide Control of Fruit Flies and Other Insect Pests*, Penerbit Universiti Sains Malaysia, Penang, 2000, pp. 79–86.
- [5] D.A. Lindquist, M. Abusowa, M.J. Hall, The New World screwworm fly in Libya: a review of its introduction and eradication, *Med. Vet. Entomol.* 6 (1) (1992) 2–8.
- [6] J. Hendrichs, G. Franz, P. Rendon, Increased effectiveness and applicability of the sterile insect technique through male-only releases for control of Mediterranean fruit flies during fruiting seasons, *J. Appl. Entomol.* 119 (1995) 371–377.
- [7] K.A. Bloem, S. Bloem, SIT for codling moth eradication in British Columbia, Canada, in: K.H. Tan (Ed.), *Area-Wide Control of Fruit Flies and Other Insect Pests*. Proc. Int. Conf. on Area-Wide Control of Insect Pests and the Fifth Int. Symp. on Fruit Flies of Economic Importance, Penerbit University Sains, Penang, Malaysia, 1998, pp. 207–214. 28 May–5 June.
- [8] A.R. Msangi, K.M. Saleh, N. Kiwia, Malele II, W.A. Mussa, F. Mramba, K.G. Juma, V.A. Dyck, M.J.B. Vreyen, A.G. Parker, et al., Success in Zanzibar: eradication of Tsetse, in: K.H. Tan (Ed.), *Area-Wide Control of Fruit Flies and Other Insect Pests*, Penerbit University Sains, Penang, Malaysia, 2000, pp. 57–66.
- [9] R.S. Patterson, R.E. Lowe, B.J. Smittle, D.A. Dame, M.D. Boston, A.L. Cameron, Release of radiosterilized males to control *Culex pipiens quinquefasciatus* (Diptera: culicidae), *J. Med. Entomol.* 14 (3) (1977) 299–304.

- [10] V.A. Dyck, J. Hendrichs, A.S. Robinson, *The Sterile Insect Technique, Principles and Practice in Area-Wide Integrated Pest Management*, Springer, Dordrecht, 2006, p. 787.
- [11] C.S. Lofgren, D.A. Dame, S.G. Breeland, D.E. Weidhaas, G. Jeffery, R. Kaiser, H.R. Ford, M.D. Boston, K.F. Baldwin, Release of chemosterilized males for the control of *Anopheles albimanus* in El Salvador. 3. Field methods and population control, *Am. J. Trop. Med. Hyg.* 23 (1974) 288–297.
- [12] M. Benedict, A. Robinson, The first releases of transgenic mosquitoes: an argument for the sterile insect technique, *Trends Parasitol.* 19 (2003) 349–355.
- [13] R.E. Lowe, D.L. Bailey, D.A. Dame, K. Savage, P.E. Kaiser, Efficiency of techniques for the mass release of sterile male *Anopheles albimanus* Wiedemann in El Salvador, *Am. J. Trop. Med. Hyg.* 29 (1980) 695–703.
- [14] R. Bellini, M. Calvitti, A. Medici, M. Carrieri, G. Celli, S. Maini, Use of the sterile insect technique against *Aedes albopictus* in Italy: first results of a pilot trial, in: M.J.B. Vreysen, A.S. Robinson, J. Hendrichs (Eds.), *Area-Wide Control of Insect Pests: From Research to Field Implementation*, Springer, Dordrecht, The Netherlands, 2007, pp. 505–515.
- [15] Y. Dumont, J.M. Tchuenche, Mathematical studies on the sterile insect technique for the Chikungunya disease and *Aedes albopictus*, *J. Math. Biol.*, <http://dx.doi.org/10.1007/s00285-011-0477-6> (in press).
- [16] Y. Dumont, F. Chiroleu, C. Domerg, On a temporal model for the Chikungunya disease: modeling, theory and numerics, *Math. Biosci.* 213 (2008) 70–81.
- [17] Y. Dumont, F. Chiroleu, Vector control for the Chikungunya disease, *Math. Biosci. Eng.* 7 (2) (2010) 315–348.
- [18] H.K. Phuc, M.H. Andreasen, R.S. Burton, C. Vass, M.J. Epton, G. Pape, G. Fu, K.C. Condon, S. Scaife, C.A. Donnelly, P.G. Coleman, H. White-Cooper, L. Alphey, Late-acting dominant lethal genetic systems and mosquito control, *BMC Biol.* (2007) 5–11.
- [19] A.A. Berryman, Mathematical description of the sterile male principle, *Can. Entomol.* 99 (1967) 858–865.
- [20] J. Li, Simple mathematical models for mosquito populations with genetically altered mosquitoes, *Math. Biosci.* 189 (2004) 39–59.
- [21] H.J. Barclay, M. Mackauer, The sterile insect release method for pest control: a density-dependent model, *Environ. Entomol.* 9 (6) (1980) 810–817.
- [22] H.J. Barclay, P. Van Den Driessche, A sterile release model for control of a pest with two life stages under predation, *Rocky Mountain J. Math.* 20 (4) (1990) 847–855.
- [23] L. Esteva, H.M. Yang, Mathematical model to assess the control of *Aedes aegypti* mosquitos by the sterile insect technique, *Math. Biosci.* 198 (2005) 132–147.
- [24] G.W. Harrison, H.J. Barclay, P. van den Driessche, Analysis of a sterile insect release model with predation, *J. Math. Biol.* 16 (1) (1982–1983) 33–48.
- [25] M.A. Lewis, P. van den Driessche, Wave extinction from sterile insect release, *Math. Biosci.* 116 (1993) 221–247.
- [26] R.C.A. Thomé, H.M. Yang, L. Esteva, Optimal control of *Aedes aegypti* mosquitoes by the sterile insect technique and insecticide, *Math. Biosci.* 223 (1) (2010) 12–23.
- [27] S.M. White, P. Rohani, S.M. Sait, Modelling pulsed releases for sterile insect techniques: fitness costs of sterile and transgenic males and the effects on mosquito dynamics, *J. Appl. Ecol.* 47 (6) (2010) 1329–1339.
- [28] V.S. Manoranjan, P. van den Driessche, On a diffusion model for sterile insect release, *Math. Biosci.* 79 (1986) 199–208.
- [29] R. Tyson, H. Thistlewood, G.J.R. Judd, Modelling dispersal of sterile male codling moths, *Cydia pomonella*, across orchard boundaries, *Ecol. Modell.* 205 (2007) 1–12.
- [30] H.J. Barclay, Mathematical models for the use of sterile insects, in: V.A. Dyck, J. Hendrichs, A.S. Robinson (Eds.), *Sterile Insect Technique. Principles and Practice in Area-Wide Integrated Pest Management*, Springer, Heidelberg, Germany, 2005, pp. 147–174.
- [31] N. Chitnis, J.M. Hyman, J.M. Cushing, Bifurcation analysis of a mathematical model for malaria transmission, *SIAM J. Appl. Math.* 67 (1) (2006) 24–45.
- [32] N. Chitnis, J.M. Hyman, J.M. Cushing, Determining important parameters in the spread through the sensitivity analysis of a mathematical model, *Bull. Math. Biol.* 70 (2008) 1272–1296.
- [33] H.L. Smith, *Monotone Dynamical Systems*, AMS, 1995.
- [34] W. Walter, *Differential and Integral Inequalities*, Springer-Verlag, Berlin, Heidelberg, New York, 1970.
- [35] R. Anguelov, Y. Dumont, J.M.-S. Lubuma, Monotone dynamical systems: application to population models, in: S. Margenov, S. Dimova, A. Slavova (Eds.), *Proceedings of the Annual Meeting of the Bulgarian Section of SIAM* (Sofia, 20–21 December, 2010), Demetra, Sofia, 2011, pp. 7–10.
- [36] A. Berman, R.J. Plemmons, *Nonnegative Matrices in the Mathematical Sciences*, in: *Classics in Applied Mathematics*, SIAM, 1994.
- [37] M.W. Hirsch, Systems of differential equations which are competitive or cooperative II: convergence almost everywhere, *SIAM J. Math. Anal.* 16 (1985) 423–439.
- [38] J.P. LaSalle, Stability theory for ordinary differential equations, *J. Differential Equations* 4 (1968) 57–65.
- [39] P.I. Howell, B.G.J. Knols, Male mating biology, *Malar. J.* 8 (Suppl. 2) (2009) S8. <http://dx.doi.org/10.1186/1475-2875-8-S2-S8>.
- [40] M.E.H. Helinski, A.G. Parker, B.G.J. Knols, Radiation biology of mosquitoes, *Malar. J.* 8 (Suppl. 2) (2009) S6. <http://dx.doi.org/10.1186/1475-2875-8-S2-S6>.
- [41] A. Maiti, B. Patra, G.P. Samanta, Sterile insect release method as a control measure of insect pests: a mathematical model, *J. Appl. Math. Comput.* 22 (3) (2006) 71–86.
- [42] R. Anguelov, Y. Dumont, J. Lubuma, E. Mureithi, Stability analysis and dynamics preserving non-standard finite difference schemes for a malaria model, University of Pretoria Technical Report, No. UPWT 2010/05, 23 pp., *Math. Popul. Stud.* (in press).