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## Differential equations models for interacting wild and transgenic mosquito populations

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We formulate and study continuous-time models, based on systems of ordinary differential equations, for interacting wild and transgenic mosquito populations. We assume that the mosquito mating rate is either constant, proportional to total mosquito population size, or has a Holling-II-type functional form. The focus is on the model with the Holling-II-type functional mating rate that incorporates Allee effects, in order to account for mating difficulty when the size of the total mosquito populations is small. We investigate the existence and stability of both boundary and positive equilibria. We show that the Holling-II-type model is the more realistic and, by means of numerical simulations, that it exhibits richer dynamics.

**Keywords:** population models; Holling-II-type mating rates; transgenic mosquitoes; stability; non-hyperbolic equilibrium; mosquito-borne diseases

*AMS Subject Classifications:* 34C60; 34D99; 92D15; 92D25; 92D40

### 1. Introduction

Mosquito-borne diseases, such as malaria, dengue fever, and West Nile, are considerable public health concerns worldwide. These diseases are transmitted between humans by blood-feeding mosquitoes. To prevent and control mosquito-borne diseases, genetically altered or transgenic mosquitoes provide a new and potentially effective weapon against malaria [7,10,15] and possibly other mosquito-borne diseases.

However, as transgenic mosquitoes are released to the field, they are, naturally, introduced into an existing population of wild mosquitoes at which time ‘interspecific’ matings between wild and transgenic types take place. The gene distributions of the offspring or of the ensuing generations of mosquitoes reproduced through such matings are complicated. As transgenic mosquitoes are first released, they are all homozygous. When they mate with wild type, all the progeny will be heterozygous. However, from then on, the number of copies or type of the gene per generation depends on the types of the individuals in the mating pair. Matings among heterozygous mosquitoes produce homozygous transgenic, homozygous wild, and heterozygous transgenic mosquitoes. Matings among heterozygous transgenic and homozygous wild or transgenic mosquitoes produce

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heterozygous transgenic mosquitoes and homozygous wild or transgenic mosquitoes [11,18]. Such iterated gene distributions after several generations and the gene structure of the progeny of late generations can be complex.

In [13], we formulated discrete-time models in order to gain insight into this kind of complex process. In those models, we grouped mosquitoes into two classes, ignoring zygosity: wild and transgenic. In this paper, we study continuous time, differential equation models based on the same group scheme. We include density dependence in both birth and death functions as in [13]. The fundamental goal of this study is to investigate the genetic distributions in all generations of the mosquitoes populations. Because such distributions are mainly contributed by the offspring produced by the ‘interspecific’ mating between transgenic and wild mosquitoes, we focus on the birth functions and consider three cases of density-dependent mating rates. Specifically, we consider the following three cases: the mating rate (or the number of encounters per individual) is constant (Section 3), is proportional to total mosquito population size (Section 4), or has a Holling-II-type functional form (Section 5). While we explore the existence of all possible equilibria and study the stability of those equilibria for all models, we give a more complete analysis of the Holling-II-type model, which we supplement with numerical simulations that demonstrate some of the complex dynamics possible with this model. We give brief discussions of our findings in Section 6.

## 2. General model formulation

Let  $x$  and  $y$  be the numbers of wild and transgenic mosquitoes, and assume that the dynamics of the interacting mosquitoes populations are of Kolmogorov type with the model equations

$$\begin{aligned}\frac{dx}{dt} &= x(b_1(x, y) - d_1(x, y)), \\ \frac{dy}{dt} &= y(b_2(x, y) - d_2(x, y)),\end{aligned}$$

where  $b_i$ ,  $i = 1, 2$ , are per-capita birth rates, that is, the per-capita rates of offspring production, and  $d_i$ ,  $i = 1, 2$ , the per-capita death rates.

We assume that the death rates are linear functions of the form  $d_i(x, y) = \mu_i + \xi_i(x + y)$ , where the constants  $\mu_i > 0$  and  $\xi_i \geq 0$ ,  $i = 1, 2$ , characterize the density-independent and dependent death rates, respectively. As was pointed out in [13], the study of fitness of the transgenic mosquitoes with the SM1 transgene shows no fitness difference between the transgenic and wild mosquitoes and that the SM1 transgene does not impose a fitness load to the mosquitoes; that is, the transgenes do not affect some mosquitoes’ longevity and egg production [10,11,16,19]. These facts make it reasonable to assume in our models that both wild and transgenic mosquitoes have the same death rate, and hence the same survival rate such that  $\xi_1 = \xi_2 := \xi$  and  $\mu_1 = \mu_2 := \mu$ .

We assume that the birth functions satisfy  $b_i(0, 0) = 0$ ,  $i = 1, 2$ , and the harmonic mean for  $x \geq 0$ ,  $y \geq 0$ ,  $(x, y) \neq (0, 0)$  [3,12].

Let  $c(N)$  be the total number of encounters or matings per individual, per unit of time, where  $N = x + y$ . Then the number of matings that are with wild or transgenic mosquitoes is  $c(N)x/N$  or  $c(N)y/N$ , respectively. Let  $\alpha_1$  and  $\beta_1$  be the numbers of wild offspring that a wild mosquito produces, through a mating with a wild and a transgenic mosquito, and  $\alpha_2$  and  $\beta_2$  be the numbers of offspring with the transgene that are produced by a transgenic mosquito, through a mating with a wild and a transgenic mosquito, respectively. Then, we have the general formulas for the

density-dependent birth rates

$$b_1 = c(N) \frac{\alpha_1 x + \beta_1 y}{N}, \quad b_2 = c(N) \frac{\alpha_2 x + \beta_2 y}{N},$$

for  $x \geq 0, y \geq 0$ , and  $(x, y) \neq (0, 0)$ .

With the assumptions described above, the dynamics of the interacting wild and transgenic mosquitoes populations are governed by the equations

$$\begin{aligned} \frac{dx}{dt} &= x \left( c(N) \frac{\alpha_1 x + \beta_1 y}{N} - (\mu + \xi(x + y)) \right), \\ \frac{dy}{dt} &= y \left( c(N) \frac{\alpha_2 x + \beta_2 y}{N} - (\mu + \xi(x + y)) \right), \end{aligned} \tag{1}$$

for  $x \geq 0, y \geq 0$ , and  $(x, y) \neq (0, 0)$ .

The density-dependent mating rate,  $c(N)$ , plays an important role on the dynamics of the interactive populations. When the total mosquito population size is large, the number of matings becomes saturated, and hence the mating rate is approximately constant. On the other hand, when the total population size is small, the number of matings is heavily density-dependent and is proportional to the population size. This is due to mating difficulty, as we studied in [13]. In a more realistic situation, however, the effect of population size on the number of matings falls between these two extreme cases. In this case, the Holling-II-type functional form is more appropriate for the mating rate [6,9]. We study all the three cases, respectively, in the following sections.

### 3. Constant mating rate

Within sufficiently large populations, mosquitoes can more easily find their mates. For example, mating contacts for mosquitoes of the genus Anopheline are usually associated with swarming in relatively open areas [4]. To model mosquito dynamics under such circumstances, we assume the mating rate to be constant, denoted by  $c(N) := c$ , for all  $N$  [13]. Let  $a_i := c\alpha_i$  and  $b_i := c\beta_i$ ,  $i = 1, 2$ , be the numbers of offspring produced per mosquito through *all* matings with wild or transgenic mosquitoes, per unit of time, respectively. The model equations become

$$\begin{aligned} \frac{dx}{dt} &= x \left( \frac{a_1 x + b_1 y}{x + y} - (\mu + \xi(x + y)) \right), \\ \frac{dy}{dt} &= y \left( \frac{a_2 x + b_2 y}{x + y} - (\mu + \xi(x + y)) \right), \end{aligned} \tag{2}$$

for  $x \geq 0, y \geq 0$ , and  $(x, y) \neq (0, 0)$ .

We assume

$$a_1 > \mu \quad \text{and} \quad b_2 > \mu, \tag{3}$$

such that the origin is a repeller for all solutions of system (2).

System (2) has two positive boundary equilibria,

$$E_1 = \left( \frac{a_1 - \mu}{\xi}, 0 \right), \quad E_2 = \left( 0, \frac{b_2 - \mu}{\xi} \right), \tag{4}$$

if and only if  $a_1 > \mu$  and  $b_2 > \mu$ .

Linearization on the boundary equilibrium  $E_1$  shows that it is a locally asymptotically stable node if  $a_2 - \mu - \xi x = a_2 - a_1 < 0$ , and an unstable saddle if  $a_2 - a_1 > 0$ . Similarly, the boundary equilibrium  $E_2$  is a locally asymptotically stable node if  $b_1 - \mu - \xi y = b_1 - b_2 < 0$ , and an unstable saddle if  $b_1 - b_2 > 0$ .

System (2) may have a positive equilibrium, that is to say, an equilibrium both of whose components are positive. The components of a positive equilibrium of Equation (2) satisfy the equations

$$\begin{aligned} a_1x + b_1y &= (x + y)(\mu + \xi(x + y)), \\ a_2x + b_2y &= (x + y)(\mu + \xi(x + y)), \end{aligned} \quad (5)$$

which leads to

$$(a_1 - a_2)x = (b_2 - b_1)y. \quad (6)$$

Hence there exists a positive solution of Equation (5) only if

$$(a_1 - a_2)(b_2 - b_1) > 0. \quad (7)$$

Suppose condition (7) is satisfied. Writing  $y$  in terms of  $x$ , we have

$$y = Ax \quad \text{and} \quad x + y = (1 + A)x, \quad (8)$$

where

$$A := \frac{a_1 - a_2}{b_2 - b_1}.$$

Substituting Equation (8) into (5) yields

$$\xi(1 + A)x = \frac{a_1 + b_1A}{1 + A} - \mu. \quad (9)$$

Hence by substituting  $A$  into Equation (9), we have

$$x = \frac{((a_1b_2 - b_1a_2) - \mu(a_1 - a_2 + b_2 - b_1))(b_2 - b_1)}{(a_1 - a_2 + b_2 - b_1)^2\xi}, \quad (10)$$

and then

$$y = \frac{((a_1b_2 - b_1a_2) - \mu(a_1 - a_2 + b_2 - b_1))(a_1 - a_2)}{(a_1 - a_2 + b_2 - b_1)^2\xi}. \quad (11)$$

Notice that for the existence of the positive equilibrium, we need

$$((a_1b_2 - b_1a_2) - \mu(a_1 - a_2 + b_2 - b_1))(b_2 - b_1) > 0.$$

Then, under condition (7), if  $b_2 > b_1$ , we need  $(a_1b_2 - b_1a_2) - \mu(a_1 - a_2 + b_2 - b_1) > 0$ , which implies

$$\frac{a_1b_2 - b_1a_2}{a_1 - a_2 + b_2 - b_1} > \mu,$$

and if  $b_2 < b_1$ , we need  $(a_1b_2 - b_1a_2) - \mu(a_1 - a_2 + b_2 - b_1) < 0$ , which also implies

$$\frac{a_1b_2 - b_1a_2}{a_1 - a_2 + b_2 - b_1} > \mu.$$

**THEOREM 3.1** Define the net reproductive number  $R := (a_1b_2 - b_1a_2)/((a_1 - a_2 + b_2 - b_1)\mu)$ . Then there exists a unique positive equilibrium of system (2), given by Equations (10) and (11), if and only if the conditions

$$(a_1 - a_2)(b_2 - b_1) > 0 \quad \text{and} \quad R > 1 \tag{12}$$

are both satisfied.

We now investigate the local stability of the positive equilibrium by linearization. Write  $\Delta_i := a_i - b_i, i = 1, 2$ , and  $P := (x + y)^2$ , where  $x$  and  $y$  are evaluated at the positive equilibrium. Then the Jacobian matrix can be written as

$$J_1 = \frac{1}{P} \begin{pmatrix} x(\Delta_1y - \xi P) & x(-\Delta_1x - \xi P) \\ y(\Delta_2y - \xi P) & y(-\Delta_2x - \xi P) \end{pmatrix}. \tag{13}$$

Straightforward algebra leads to

$$\text{tr} J_1 = -\frac{1}{P}((\Delta_2 - \Delta_1)xy + \xi S(x + y)), \quad \det J_1 = \frac{\xi xy}{P}(x + y)(\Delta_2 - \Delta_1),$$

and

$$(\text{tr} J_1)^2 - 4 \det J_1 = \frac{1}{P^2}((\Delta_2 - \Delta_1)xy - \xi P(x + y))^2 \geq 0.$$

Thus, all eigenvalues of  $J_1$  are real numbers.

If  $\Delta_2 < \Delta_1$ , the determinant of  $J_1$  is negative, which implies that there exist two real eigenvalues of  $J_1$  with opposite signs. Hence the positive equilibrium is an unstable saddle.

If  $\Delta_2 > \Delta_1$ , then the determinant of  $J_1$  is positive and the trace of  $J_1$  is negative. Hence the eigenvalues of  $J_1$  are both real and negative, and the equilibrium is a locally asymptotically stable node.

**THEOREM 3.2** Suppose conditions (12) in Theorem 3.1 are satisfied so that there exists a unique positive equilibrium. Then

- (1) if  $a_2 - a_1 + b_1 - b_2 < 0$ , the positive equilibrium is an unstable saddle;
- (2) if  $a_2 - a_1 + b_1 - b_2 > 0$ , the positive equilibrium is a locally asymptotically stable node.

Notice that if  $a_1 > a_2, a_1 > \mu$  and  $b_2 > b_1, b_2 > \mu$ , so that the boundary equilibria  $E_1$  and  $E_2$  both exist and are stable nodes, then the positive equilibrium either does not exist or is an unstable saddle. On the other hand, if  $a_2 > a_1 > \mu$  and  $b_1 > b_2 > \mu$  so that the boundary equilibria  $E_1$  and  $E_2$  both exist and are unstable saddles, then it is easy to show that conditions in Equation (12) are both satisfied.

#### 4. Mating rate proportional to the total population

To prevent malaria or other mosquito-borne diseases, intensive efforts have been made for many years to reduce mosquito populations by massive spraying of insecticides or diminution of breeding sites. As pointed out in [13], if spraying strategies are used on a wild population before the release of a transgenic population (in order to lower the size of transgenic population needed to be an effective control), then the wild population will be reduced in size and, as a result, not satisfy the assumption of saturated mating made in Section 3. To investigate the dynamics of interacting mosquitoes in such a situation, we assume that the mating rate is proportional to the

total mosquito population such that  $c(N) := cN$ . Again we let  $a_i := c\alpha_i$  and  $b_i := c\beta_i$ ,  $i = 1, 2$ . The model equations become

$$\begin{aligned} \frac{dx}{dt} &= x(a_1x + b_1y - (\mu + \xi(x + y))) = x((a_1 - \xi)x + (b_1 - \xi)y - \mu), \\ \frac{dy}{dt} &= y(a_2x + b_2y - (\mu + \xi(x + y))) = y((a_2 - \xi)x + (b_2 - \xi)y - \mu), \end{aligned} \tag{14}$$

for  $x \geq 0$  and  $y \geq 0$ .

The trivial solution  $E_0 := (0, 0)$  is a stable node. There are only the following three biologically feasible cases that we need to consider:

- (1)  $\xi < a_i, \xi < b_i, i = 1, 2$ ,
- (2)  $a_1 < \xi < a_2, b_2 < \xi < b_1$ ,
- (3)  $a_2 < \xi < a_1, b_1 < \xi < b_2$ .

We illustrate below that there exist unrealistic or undesirable dynamic consequences implied by model (14), and skip the details of the analysis.

In case (21), the wild and transgenic mosquito populations become ‘cooperative’. In the absence of interactions between the two mosquito populations, either population goes extinct or becomes unbounded. With such a ‘cooperation’, the dynamics are similar when the interaction between the two populations occurs.

In case (2), the interaction is also ‘cooperative’. Depending on the initial population size, both populations go extinct, or one or two of the mosquito populations becomes unbounded.

In case (3), the two populations are competing when the interaction occurs. There exists a separatrix such that solutions from different subregions, separated by the separatrix, either approach the origin or become unbounded.

In any of the above three cases, there is one or more separatrices dividing the first quadrant into subregions such that both wild and transgenic mosquitoes can become unbounded from some subregions. This unrealistic phenomenon indeed comes from the nature of the model for each of the two mosquito populations in the absence of interaction. That is, there is an extinction threshold for the model such that if the mosquito population is below the threshold, the population goes extinct, and if the population exceeds the threshold, it grows unboundedly. This feature can be shown by the equation

$$\frac{dx}{dt} = x(a_1x - \mu),$$

where  $\mu/a_1$  is a threshold such that if  $x(0) < \mu/a_1$ ,  $\lim_{t \rightarrow \infty} x(t) = 0$ , and if  $x(0) > \mu/a_1$ ,  $\lim_{t \rightarrow \infty} x(t) = \infty$ . The unbounded growth is undesirable from modelling perspectives [8].

### 5. Holling-II-type functional mating rate

A more realistic assumption is that matings occur in a manner between the two extreme cases studied in Sections 3 and 4. Towards this end, we assume that the mating rate is proportional to the total size of the two mosquito populations when the total size is small, and approximately constant when the total size is sufficiently large. Using the form of the Holling-II-type functional response [9], we assume the mating rate to be  $c(N) = kN/(\varepsilon + N)$ , where  $k$  is the maximum mating rate and  $\varepsilon$  the half-saturation constant. This assumption incorporates Allee effects into the model formulation [1,6,14]. Note that if  $\varepsilon = 0$ , the mating rate becomes constant, as in Section 3. We assume  $\varepsilon > 0$  in this section.

With this Holling-II-type functional mating rate, the model equations have the form

$$\begin{aligned} \frac{dx}{dt} &= x \left( \frac{a_1x + b_1y}{\varepsilon + x + y} - (\mu + \xi(x + y)) \right), \\ \frac{dy}{dt} &= y \left( \frac{a_2x + b_2y}{\varepsilon + x + y} - (\mu + \xi(x + y)) \right), \end{aligned} \tag{15}$$

for  $x \geq 0$  and  $y \geq 0$ , where we let  $a_i := k\alpha_i$  and  $b_i := k\beta_i$ ,  $i = 1, 2$ .

By rescaling  $x$  and  $y$  to  $x/\varepsilon$  and  $y/\varepsilon$ , respectively, system (15) can be transformed to the system

$$\begin{aligned} \frac{dx}{dt} &= x \left( \frac{a_1x + b_1y}{1 + x + y} - (\mu + \eta(x + y)) \right), \\ \frac{dy}{dt} &= y \left( \frac{a_2x + b_2y}{1 + x + y} - (\mu + \eta(x + y)) \right), \end{aligned} \tag{16}$$

where, for convenience, we still use  $x$  and  $y$  as the dependent variables, and write  $\eta := \xi\varepsilon$ .

The trivial solution  $(0, 0)$  is a locally asymptotically stable node. Our goal is to study boundary and positive equilibria of system (16).

### 5.1. Boundary equilibria

System (16) may have boundary equilibria  $E_1 := (x, 0)$ , where  $x > 0$ , and  $E_2 := (0, y)$ , where  $y > 0$ . We only investigate the existence and stability of  $E_1$ . The investigations for  $E_2 = (0, y)$  are similar.

At the boundary equilibrium  $E_1$ , the components  $x$  are the positive roots of the function

$$\frac{a_1x}{1 + x} - (\mu + \eta x) = \frac{a_1x - (\mu + (\mu + \eta)x + \eta x^2)}{1 + x} = -\frac{\eta x^2 + (\mu + \eta - a_1)x + \mu}{1 + x},$$

which are the positive solutions of the quadratic equation

$$\eta x^2 + (\mu + \eta - a_1)x + \mu = 0, \tag{17}$$

whose solutions are given by

$$x = \frac{(a_1 - \mu - \eta) \pm \sqrt{(a_1 - \mu - \eta)^2 - 4\mu\eta}}{2\eta}. \tag{18}$$

It is clear that there exists no positive solution of Equation (17) if  $a_1 \leq \mu + \eta$ . We suppose  $a_1 > \mu + \eta$ . Then Equation (17) has two positive solutions if  $(a_1 - \mu - \eta)^2 > 4\mu\eta$ , a unique positive solution if  $(a_1 - \mu - \eta)^2 = 4\mu\eta$ , and no positive solution if  $(a_1 - \mu - \eta)^2 < 4\mu\eta$ .

Notice that if  $a_1 - \mu - \eta > 0$ , then  $(a_1 - \mu - \eta)^2 \geq 4\mu\eta$  is equivalent to  $a_1 - \mu - \eta \geq 2\sqrt{\mu\eta}$ , or  $a_1 - (\mu + 2\sqrt{\mu\eta} + \eta) = (\sqrt{a_1})^2 - (\sqrt{\mu} + \sqrt{\eta})^2 \geq 0$ , which holds if and only if  $\sqrt{a_1} \geq \sqrt{\mu} + \sqrt{\eta}$ . On the other hand, if  $\sqrt{a_1} \geq \sqrt{\mu} + \sqrt{\eta}$ , then  $a_1 - \mu - \eta \geq 0$ .

**THEOREM 5.1** *There exist*

- (1) *no boundary equilibrium with  $x > 0$  and  $y = 0$  if  $\sqrt{a_1} < \sqrt{\mu} + \sqrt{\eta}$ ;*
- (2) *a unique boundary equilibrium with  $x > 0$  and  $y = 0$ , if  $\sqrt{a_1} = \sqrt{\mu} + \sqrt{\eta}$ ; or*
- (3) *two boundary equilibria with  $x > 0$  and  $y = 0$  if  $\sqrt{a_1} > \sqrt{\mu} + \sqrt{\eta}$ .*

Similarly, there exist

- (i) no boundary equilibrium with  $x = 0$  and  $y > 0$  if  $\sqrt{b_2} < \sqrt{\mu} + \sqrt{\eta}$ ;
- (ii) a unique boundary equilibrium with  $x = 0$  and  $y > 0$  if  $\sqrt{b_2} = \sqrt{\mu} + \sqrt{\eta}$ ; or
- (iii) two boundary equilibria with  $x = 0$  and  $y > 0$  if  $\sqrt{b_2} > \sqrt{\mu} + \sqrt{\eta}$ .

We now study the local stability of the boundary equilibria and again use linearization. The Jacobian matrix of Equation (16) at  $E_1$  has the form

$$\begin{pmatrix} \frac{1}{1+\bar{x}}(\mu - \eta\bar{x}^2) & \cdot \\ 0 & \frac{a_2 - a_1}{a_1}(\mu + \eta\bar{x}) \end{pmatrix}. \tag{19}$$

Let  $\bar{x} = (a_1 - \mu - \eta)/2\eta$ . It follows from Equation (17) that, at  $E_1$ ,  $\mu - \eta\bar{x}^2 = (a_1 - \mu - \eta)\bar{x} - 2\eta\bar{x}^2 = 2\eta\bar{x}(\bar{x} - \bar{x})$ .

Suppose that there are two boundary equilibria  $E_1^{(1)} = (x^{(1)}, 0)$  and  $E_1^{(2)} = (x^{(2)}, 0)$ . Then  $x^{(1)} < \bar{x} < x^{(2)}$ . Hence  $\mu - \eta(x^{(1)})^2 = 2\eta x^{(1)}(\bar{x} - x^{(1)}) > 0$  and  $\mu - \eta(x^{(2)})^2 = 2\eta x^{(2)}(\bar{x} - x^{(2)}) < 0$ . Therefore, if  $a_2 > a_1$ ,  $E_1^{(1)}$  is an unstable node and  $E_1^{(2)}$  is an unstable saddle, and if  $a_2 < a_1$ ,  $E_1^{(1)}$  is an unstable saddle and  $E_1^{(2)}$  a stable node.

The stability of boundary equilibria  $E_2^{(i)}$ ,  $i = 1, 2$ , can be analysed similarly.

In the case where there exists a unique boundary equilibrium  $E_1 = (x, 0)$ ,  $x = \bar{x}$  and the Jacobian matrix at this unique boundary equilibrium has a zero eigenvalue. Hence  $E_1$  is a nonhyperbolic equilibrium, and the linearization cannot determine its stability.

Let  $u_1 = x - \bar{x}$  and  $u_2 = y$ . The system (16) is transformed to

$$\frac{du_1}{dt} = g_1(u_1, u_2), \quad \frac{du_2}{dt} = g_2(u_1, u_2), \tag{20}$$

where

$$\begin{aligned} g_1(u_1, u_2) &:= (u_1 + \bar{x}) \left( \frac{a_1\bar{x} + a_1u_1 + b_1u_2}{1 + \bar{x} + u_1 + u_2} - (\mu + \eta\bar{x} + \eta(u_1 + u_2)) \right) \\ &= \bar{x} \left( \frac{b_1 + (b_1 - a_1)\bar{x}}{(1 + \bar{x})^2} - \eta \right) u_2 + \left( \frac{b_1 + (b_1 - a_1)\bar{x}}{(1 + \bar{x})^2} - \eta \right) u_1 u_2 + \mathcal{O}(|(u_1, u_2)|^2), \\ g_2(u_1, u_2) &:= u_2 \left( \frac{a_2\bar{x} + a_2u_1 + b_2u_2}{1 + \bar{x} + u_1 + u_2} - (\mu + \eta\bar{x} + \eta(u_1 + u_2)) \right) \\ &= u_2 \left( \frac{a_2 - a_1}{a_1}(\mu + \eta\bar{x}) + \left( \frac{a_2}{(1 + \bar{x})^2} - \eta \right) u_1 \right. \\ &\quad \left. + \frac{a_2\bar{x}}{(1 + \bar{x})^3} u_2(u_1 + u_2)^2 + \mathcal{O}(|(u_1, u_2)|^2) \right). \end{aligned}$$

Note that  $g_2(u, 0) = 0$ . Then we let

$$G(u) := g_1(u, 0) = (u + \bar{x}) \left( \frac{a_1\bar{x} + a_1u}{1 + \bar{x} + u} - (\mu + \eta\bar{x} + \eta u) \right).$$

It is easy to check that

$$G(0) = \bar{x} \left( \frac{a_1\bar{x}}{1 + \bar{x}} - (\mu + \eta\bar{x}) \right) = 0, \quad G'(0) = \bar{x} \left( \frac{a_1}{(1 + \bar{x})^2} - \eta \right) = 0, \quad G''(0) = -\frac{2a_1\bar{x}}{(1 + \bar{x})^3}.$$

Then

$$g_1(u, 0) = -\frac{a_1 \bar{x}}{(1 + \bar{x})^3} u^2 + \mathcal{O}(u^3).$$

Thus the unique boundary equilibrium, if exists, is an unstable saddle node [2,17].

Similarly, we can investigate the stability of the boundary equilibrium  $E_2 = (0, y)$ . Hence we have the following.

**THEOREM 5.2** *If there exists a unique boundary equilibrium  $E_1 = (x > 0, 0)$ , where  $x = (a_1 - \mu - \eta)/2\eta$ , or a unique boundary equilibrium  $E_2 = (0, y > 0)$ , where  $y = (b_2 - \mu - \eta)/2\eta$ , the unique boundary equilibrium  $E_1$ , or  $E_2$ , is an unstable saddle node.*

*If there exist two boundary equilibria  $E_1^{(1)} = (x^{(1)}, 0)$  and  $E_1^{(2)} = (x^{(2)}, 0)$ , with  $x^{(1)} < \bar{x} < x^{(2)}$  where  $\bar{x} = (a_1 - \mu - \eta)/2\eta$ , then  $E_1^{(1)}$  is an unstable saddle and  $E_1^{(2)}$  a locally stable node if  $a_2 < a_1$ . The boundary equilibrium  $E_1^{(1)}$  is an unstable node and  $E_1^{(2)}$  an unstable saddle if  $a_2 > a_1$ . Similarly, if there exist two boundary equilibria  $E_2^{(1)} = (0, y^{(1)})$  and  $E_2^{(2)} = (0, y^{(2)})$ , with  $y^{(1)} < \bar{y} < y^{(2)}$  where  $\bar{y} = (b_2 - \mu - \eta)/2\eta$ , then  $E_2^{(1)}$  is an unstable saddle and  $E_2^{(2)}$  a locally stable node if  $b_1 < b_2$ . The Boundary equilibrium  $E_2^{(1)}$  is an unstable node and  $E_2^{(2)}$  an unstable saddle if  $b_1 > b_2$ .*

### 5.2. Positive equilibria

We explore the existence and stability of the positive equilibria of system (16) as follows.

#### 5.2.1. Existence of positive equilibria

The components of a positive equilibrium of system (16),  $x$  and  $y$ , satisfy

$$\frac{a_1 x + b_1 y}{1 + x + y} = \mu + \eta(x + y) = \frac{a_2 x + b_2 y}{1 + x + y}. \tag{21}$$

Hence, similarly as in Section 3, there exists a positive equilibrium only if

$$(a_1 - a_2)(b_2 - b_1) > 0. \tag{22}$$

Suppose condition (22) is satisfied. Then we have

$$y = \frac{a_1 - a_2}{b_2 - b_1} x = Ax. \tag{23}$$

Substituting Equation (23) into (21), we obtain the following quadratic equation for  $x$ :

$$\eta(A + 1)^2 x^2 + ((A + 1)(\mu + \eta) - (a_1 + b_1 A))x + \mu = 0. \tag{24}$$

Write

$$W := \frac{a_1 + b_1 A}{1 + A} = \frac{a_1 b_2 - b_1 a_2}{a_1 - a_2 + b_2 - b_1},$$

and let

$$\begin{aligned} \Delta &:= a_1 + b_1 A - (\mu + \eta)(1 + A) = (1 + A) \left( \frac{a_1 + b_1 A}{1 + A} - (\mu + \eta) \right) \\ &= (1 + A)(W - (\mu + \eta)). \end{aligned}$$

Then solutions of Equation (24) are given by  $x = (\Delta \pm \sqrt{\Delta^2 - 4\mu\eta(1 + A)^2}) / (2\eta(1 + A)^2)$ . If  $\Delta < 0$ , there exists no positive equilibrium for system (16).

We assume  $\Delta \geq 0$ . Then, it follows from

$$\Delta^2 - 4\mu\eta(1 + A)^2 = (\Delta + 2\sqrt{\mu\eta}(1 + A))(\Delta - 2\sqrt{\mu\eta}(1 + A)) \tag{25}$$

that there exist two positive equilibria,  $E_*^{(1)}$  and  $E_*^{(2)}$ , if  $\Delta > 2\sqrt{(\mu\eta)}(1 + A)$ , and a unique positive equilibrium  $E_* = (x, y)$  with  $x = \Delta / (2\eta(1 + A)^2)$  if  $\Delta = 2\sqrt{(\mu\eta)}(1 + A)$ .

The inequality  $\Delta \geq 2\sqrt{(\mu\eta)}(1 + A)$  is equivalent to

$$(1 + A)(W - (\mu + \eta) - 2\sqrt{\mu\eta}) = (1 + A)(W - (\sqrt{\mu} + \sqrt{\eta})^2) \geq 0$$

or

$$W \geq (\sqrt{\mu} + \sqrt{\eta})^2. \tag{26}$$

We write  $S := (\sqrt{\mu} + \sqrt{\eta})^2$  and define the net reproductive number  $R := W/S$ . Then we have the following existence results for positive equilibria.

**THEOREM 5.3** *There exists no positive equilibrium if  $(a_1 - a_2)(b_2 - b_1) \leq 0$ . Assume  $(a_1 - a_2)(b_2 - b_1) > 0$ . Then there exist two positive equilibria if  $R > 1$ ,*

*Remark 5.4* Notice that

$$W = \frac{a_1 + b_1A}{1 + A} = \frac{a_1x + b_1y}{x + y},$$

where  $x$  and  $y$  are evaluated at a positive equilibrium. Hence it is a measurement of the number of offspring produced per wild mosquito per unit of time through all matings at a steady state. It follows from Equation (21) that we also have

$$W = \frac{a_2x + b_2y}{x + y},$$

which measures the number of offspring produced per transgenic mosquito per unit of time through all matings at a steady state.

We also note that  $S$  measures the death rate of mosquito populations. Then  $R$  is a net reproductive number of both wild and transgenic mosquitoes [5]. Therefore, if the net reproductive number for both wild and transgenic mosquitoes is larger than 1, the coexistence of both mosquitoes may occur. If this net reproductive number is less than 1, the coexistence of both mosquitoes becomes impossible.

*Remark 5.5* We can further show that if condition (22) is satisfied, and  $a_i > S$  and  $b_i > S$ , for  $i = 1, 2$ , then the net reproductive number is greater than 1. Indeed, we need only to consider  $a_2 > a_1 > S$  and  $b_1 > b_2 > S$ , or  $a_1 > a_2 > S$  and  $b_2 > b_1 > S$ . Suppose  $a_2 > a_1 > S$  and  $b_1 > b_2 > S$ . We can write  $a_2 = a_1 + d_1$  and  $b_1 = b_2 + d_2$ , where  $d_1$  and  $d_2$  are positive. Then

$$W = \frac{a_1b_2 - b_1a_2}{a_1 - a_2 + b_2 - b_1} = \frac{a_1d_2 + b_2d_1 + d_1d_2}{d_1 + d_2} > \frac{a_1d_2 + b_2d_1}{d_1 + d_2} > S.$$

The proof for the case of  $a_1 > a_2 > S$  and  $b_2 > b_1 > S$  is similar.

Likewise, we can show that if condition (22) is satisfied and  $a_i < S$  and  $b_i < S$ , for  $i = 1, 2$ , then the net reproductive number is less than 1. The details are omitted.

5.2.2. Stability of positive equilibria

The Jacobian matrix at a positive equilibrium  $E_* = (x, y)$  has the form of

$$J_2 = \begin{pmatrix} x \left( \frac{a_1 + (a_1 - b_1)y}{(1 + x + y)^2} - \eta \right) & x \left( \frac{b_1 + (b_1 - a_1)x}{(1 + x + y)^2} - \eta \right) \\ y \left( \frac{a_2 + (a_2 - b_2)y}{(1 + x + y)^2} - \eta \right) & y \left( \frac{b_2 + (b_2 - a_2)x}{(1 + x + y)^2} - \eta \right) \end{pmatrix}. \tag{27}$$

The trace of the Jacobian matrix  $J_2$  satisfies

$$\begin{aligned} \frac{(1 + (1 + A)x)^2 \operatorname{tr} J_2}{x} &= \frac{(1 + x + y)^2}{x} \left( \frac{a_1x + b_2y + (a_1 - a_2 + b_2 - b_1)xy}{(1 + x + y)^2} - \eta(x + y) \right) \\ &= a_1 + b_2A + (a_1 - a_2 + b_2 - b_1)Ax - \eta(1 + A)(1 + (1 + A)x)^2 \\ &= (a_1 - a_2)(1 + (1 + A)x) + (1 + A) \left( W - \eta(1 + (1 + A)x)^2 \right), \end{aligned} \tag{28}$$

where we use the  $A$  defined in Equation (23) such that  $(b_2 - b_1)A = a_1 - a_2$  and  $(a_1 - a_2 + b_2 - b_1)A = (a_1 - a_2)(1 + A)$ . The determinant of  $J_2$  satisfies  $(\det J_2)/(xy) = D_1 + D_2$ , where

$$\begin{aligned} D_1 &:= \frac{(a_1b_2 - b_1a_2) + ((a_1(b_2 - a_2) - a_2(b_1 - a_1))x + (b_2(a_1 - b_1) - (b_1(a_2 - b_2))y)}{(1 + x + y)^4} \\ &= \frac{a_1b_2 - b_1a_2}{(1 + x + y)^3} \end{aligned}$$

and

$$\begin{aligned} D_2 &:= \eta \frac{a_2 - a_1 + b_1 - b_2 + (b_1 - a_1)x + (a_2 - b_2)y - (a_1 - b_1)y - (b_2 - a_2)x}{(1 + x + y)^2} \\ &= \frac{\eta(a_2 - a_1 + b_1 - b_2)}{1 + x + y}. \end{aligned}$$

Hence

$$\begin{aligned} \frac{\det J_2}{x^2} &= A \frac{a_1b_2 - b_1a_2 + \eta(b_1 - b_2 + a_2 - a_1)(1 + x + y)^2}{(1 + x + y)^3} \\ &= \frac{(a_1 - a_2)(1 + A)}{(1 + (1 + A)x)^3} \left( W - \eta(1 + (1 + A)x)^2 \right), \end{aligned} \tag{29}$$

and

$$\begin{aligned} &\frac{(1 + (1 + A)x)^2}{x^2} \left( (\operatorname{tr} J_2)^2 - 4 \det J_2 \right) \\ &= \left( (a_1 - a_2)(1 + (1 + A)x) - (1 + A)(W - \eta(1 + (1 + A)x)^2) \right)^2 \geq 0. \end{aligned} \tag{30}$$

Therefore, all eigenvalues of the Jacobian matrix  $J_2$  are real numbers.

We next consider the cases of either two positive equilibria or a unique positive equilibrium.

*Two positive equilibria.* Suppose the net reproductive number is greater than 1 so that there exist two positive equilibria  $E_*^{(1)} = (x_*^{(1)}, y_*^{(1)})$  and  $E_*^{(2)} = (x_*^{(2)}, y_*^{(2)})$ . At equilibrium  $E_*^{(1)}$ ,

$$\begin{aligned} W - \eta(1 + (1 + A)x_*^{(1)})^2 &= W - \eta \left( 1 + \frac{\Delta - \sqrt{\Delta^2 - 4\mu\eta(1 + A)^2}}{2\eta(1 + A)} \right)^2 \\ &> W - \eta \left( 1 + \frac{2\mu(1 + A)}{\Delta} \right)^2 \\ &= W - (\sqrt{\mu} + \sqrt{\eta})^2 > 0. \end{aligned} \tag{31}$$

Then if  $a_1 < a_2$  and  $b_2 < b_1$ , it follows from Equation (29) that  $\det J_2 < 0$ . Hence  $E_*^{(1)}$  is an unstable saddle. If  $a_1 > a_2$  and  $b_2 > b_1$ , then it follows from Equations (28) and (29) that the trace and the determinant of  $J_2$  are both positive. Hence  $E_*^{(1)}$  is an unstable node. At  $E_*^{(2)}$ ,

$$\begin{aligned} W - \eta(1 + (1 + A)x_*^{(2)})^2 &= W - \eta \left( 1 + \frac{\Delta + \sqrt{\Delta^2 - 4\mu\eta(1 + A)^2}}{2\eta(1 + A)} \right)^2 \\ &< W - \eta \left( 1 + \frac{\Delta}{2\eta(1 + A)} \right)^2 \\ &= \frac{1}{4\eta} (4\eta W - (W + \eta - \mu)^2). \end{aligned} \tag{32}$$

Note that

$$4\eta W - (W + \eta - \mu)^2 = -(W - (\sqrt{\mu} + \sqrt{\eta})^2)(W - (\sqrt{\mu} - \sqrt{\eta})^2). \tag{33}$$

Hence, it follows from  $R = W/S > 1$  that

$$W - \eta(1 + (1 + A)x_*^{(2)})^2 < 0.$$

If  $a_1 > a_2$  and  $b_2 > b_1$ , then it follows from Equation (29) that the determinant of  $J_2$  is negative. Hence  $E_*^{(2)}$  is an unstable saddle. If  $a_1 < a_2$  and  $b_2 < b_1$ , then it follows from Equations (28) and (29) that the trace of  $J_2$  is negative and the determinant of  $J_2$  is positive. Hence  $E_*^{(2)}$  is a stable node.

*Unique positive equilibrium.* It rarely happens that the net reproductive number equals 1. It can be shown, however, that in this nongeneric case, the unique equilibrium is an unstable saddle node [2,17].

**THEOREM 5.6** *Suppose that there exist two positive equilibria  $E_*^{(1)}$  and  $E_*^{(2)}$ , with  $x_*^{(1)} < x_*^{(2)}$ . Then if  $a_1 < a_2$  and  $b_2 < b_1$ ,  $E_*^{(1)}$  is an unstable saddle and  $E_*^{(2)}$  a locally asymptotically stable node. If  $a_1 > a_2$  and  $b_2 > b_1$ , then  $E_*^{(1)}$  is an unstable node and  $E_*^{(2)}$  an unstable saddle. If there exists a unique positive equilibrium, it is an unstable saddle node.*

**5.3. Summary of the results and numerical examples for system (16)**

We first note that system (16) is of Kolmogorov type and hence the positive quadrant of the  $xy$  plane is forward invariant under the flow defined by Equation (16). We then note that for either  $x$  or  $y$  sufficiently large, both  $dx/dt$  and  $dy/dt$  are negative.

The trivial solution,  $E_0$ , of system (16) is a locally asymptotically stable node for all parameter settings. If

$$a_2 \leq a_1 < S \quad \text{or} \quad a_1 \leq a_2 < S, \tag{34}$$

there exist no boundary equilibria  $E_1^{(i)}, i = 1, 2$ . If

$$b_1 \leq b_2 < S \quad \text{or} \quad b_2 \leq b_1 < S, \tag{35}$$

there exist no boundary equilibria  $E_2^{(i)}, i = 1, 2$ . In particular, if we assume

$$\text{either} \quad \begin{cases} a_2 \leq a_1 < S \\ b_1 \leq b_2 < S \end{cases} \quad \text{or} \quad \begin{cases} a_1 \leq a_2 < S, \\ b_2 \leq b_1 < S, \end{cases} \tag{36}$$

then there exist no boundary nor positive equilibria. The trivial solution  $E_0$  is a globally asymptotically stable node.

If

$$a_1 < S < a_2, \tag{37}$$

there exist no boundary equilibria  $E_1^{(i)}, i = 1, 2$ , and if

$$b_2 < S < b_1, \tag{38}$$

there exist no boundary equilibria  $E_2^{(i)}, i = 1, 2$ . If both conditions (37) and (38) are satisfied, there exists no boundary equilibrium. There may or may not exist a positive equilibrium depending on the net reproductive number greater than or equal to 1. If there exists no positive equilibrium,  $E_0$  is globally asymptotically stable. If there exist two positive equilibria,  $E_*^{(1)}$  is a saddle and  $E_*^{(2)}$  a locally asymptotically stable node. The unstable manifold of  $E_*^{(1)}$  forms a separatrix that separates the first quadrant such that solutions approach either  $E_0$  or  $E_*^{(2)}$ , depending on their initial values. We demonstrate the dynamics of both the cases in Figure 1.

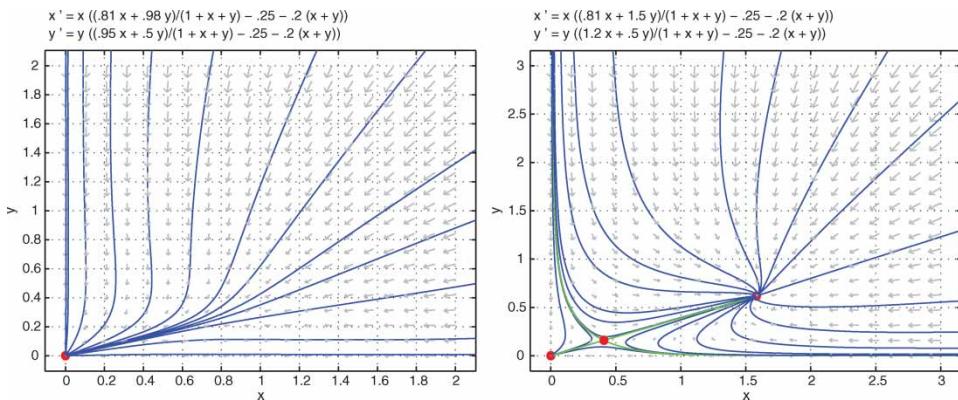


Figure 1. For both figures,  $\mu = 0.25$  and  $\eta = 0.2$ . The parameters are  $a_1 = 0.81, b_1 = 0.98, a_2 = 0.95$ , and  $b_2 = 0.5$  for the left figure, and  $a_1 = 0.81, b_1 = 1.5, a_2 = 1.2$ , and  $b_2 = 0.5$  for the right figure. In both cases, conditions (37) and (38) are satisfied. There exist no boundary equilibria. There exists no positive equilibrium so that  $E_0$  is globally asymptotically stable in the left figure. There exist two positive equilibria  $E_*^{(i)}, i = 1, 2$ , in the right figure. The positive equilibrium  $E_*^{(1)}$  is a saddle and  $E_*^{(2)}$  a stable node. The stable manifold of  $E_*^{(1)}$  separates the first quadrant such that solutions approach either  $E_0$  or  $E_*^{(2)}$ , depending on their initial values.

In the case of

$$a_2 < S < a_1 \tag{39}$$

or

$$b_1 < S < b_2, \tag{40}$$

boundary equilibria  $E_1^{(i)}$ , or  $E_2^{(i)}$ ,  $i = 1, 2$ , exist and  $E_1^{(2)}$ , or  $E_2^{(2)}$ , is a locally asymptotically stable node. There exist two or no positive equilibria again depending on whether the net reproductive number is greater or less than 1. If there exist two positive equilibria, they are both saddles. Solutions approach  $E_0$ ,  $E_1^{(2)}$ , or  $E_2^{(2)}$ , depending on their initial values, as shown in Figure 2.

Suppose that all parameters  $a_i$  and  $b_i$  satisfy

$$a_i > S \quad \text{and} \quad b_i > S, \quad i = 1, 2.$$

Then the dynamics of system (16) depend on the orders of these parameters, shown as follows.

- (1) If  $a_2 < a_1$  and  $b_2 < b_1$ , then there exist four boundary equilibria  $E_1^{(i)}$ , and  $E_2^{(i)}$ ,  $i = 1, 2$ , but no positive equilibrium. The boundary equilibrium  $E_1^{(1)}$  is a saddle,  $E_1^{(2)}$  a stable node,  $E_2^{(1)}$  an unstable node, and  $E_2^{(2)}$  a saddle.
- (2) If  $a_1 < a_2$  and  $b_1 < b_2$ , then the dynamics of Equation (16) are similar to the situation in case (1), except that the boundary equilibrium  $E_1^{(1)}$  is an unstable node,  $E_1^{(2)}$  a saddle,  $E_2^{(1)}$  a saddle, and  $E_2^{(2)}$  a stable node.
- (3) If  $a_2 < a_1$  and  $b_1 < b_2$ , then there exist four boundary equilibria  $E_1^{(i)}$ ,  $E_2^{(i)}$ , and two positive equilibria  $E_*^{(i)}$ ,  $i = 1, 2$ . Boundary equilibria  $E_1^{(1)}$  and  $E_2^{(1)}$  are both saddles, and  $E_1^{(2)}$  and  $E_2^{(2)}$  are both stable nodes. The positive equilibrium  $E_*^{(1)}$  is an unstable node and  $E_*^{(2)}$  a saddle. Solutions may approach  $E_0$ ,  $E_1^{(2)}$ , or  $E_2^{(2)}$ , depending on their initial values.

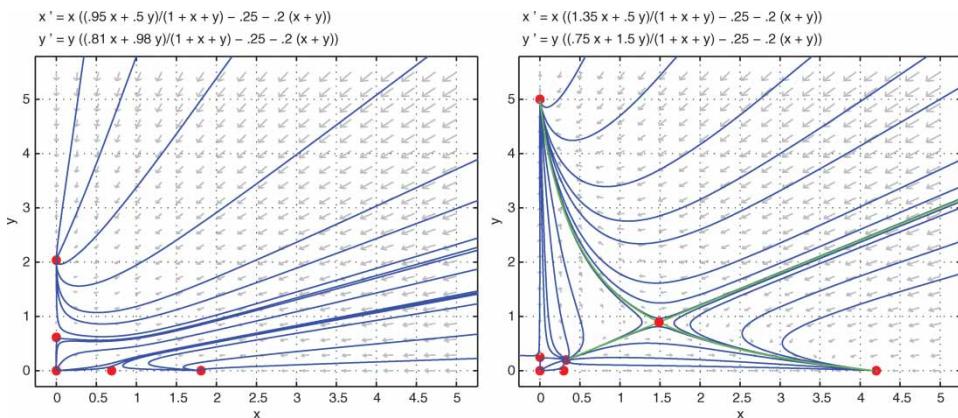


Figure 2. For both figures,  $\mu = 0.25$  and  $\eta = 0.2$ . For the left figure, other parameters are  $a_1 = 0.95$ ,  $b_1 = 0.5$ ,  $a_2 = 0.81$ , and  $b_2 = 0.98$ , such that conditions (39) and (40) are satisfied, and  $R < 1$ . All boundary equilibria  $E_1^{(i)}$  and  $E_2^{(i)}$ ,  $i = 1, 2$ , exist. The boundary equilibria  $E_1^{(1)}$  and  $E_2^{(1)}$  are both saddles, and  $E_1^{(2)}$  and  $E_2^{(2)}$  are both locally asymptotically stable nodes. No positive equilibria exist. The stable manifolds of  $E_1^{(1)}$  and  $E_2^{(1)}$  form separatrices of the positive quadrant. Solutions approach  $E_0$ ,  $E_1^{(2)}$ , or  $E_2^{(2)}$ , depending on their initial values. For the right figure, other parameters are  $a_1 = 1.35$ ,  $b_1 = 0.5$ ,  $a_2 = 0.75$ , and  $b_2 = 1.5$  such that conditions (39) and (40) are satisfied, and  $R > 1$ . All boundary and positive equilibria exist. Boundary equilibria  $E_1^{(1)}$  and  $E_2^{(1)}$  are both saddles, and  $E_1^{(2)}$  and  $E_2^{(2)}$  are both locally asymptotically stable nodes. The positive equilibrium  $E_*^{(1)}$  is an unstable node and  $E_*^{(2)}$  a saddle. Separatrices consisting of the stable and unstable manifolds of  $E_1^{(1)}$ ,  $E_2^{(1)}$ , and  $E_*^{(2)}$  divide the positive quadrant into subregions such that solutions approach  $E_0$ ,  $E_1^{(2)}$ , or  $E_2^{(2)}$ , depending on where their initial values are.

- (4) If  $a_1 < a_2$  and  $b_2 < b_1$ , there also exist four boundary equilibria  $E_1^{(i)}, E_2^{(i)}$ , and two positive equilibria  $E_*^{(i)}, i = 1, 2$ . Boundary equilibria  $E_1^{(1)}$  and  $E_2^{(1)}$  are both unstable nodes, and  $E_1^{(2)}$  and  $E_2^{(2)}$  are both saddles. The positive equilibrium  $E_*^{(1)}$  is a saddle and  $E_*^{(2)}$  a stable node. Solutions may approach  $E_0$ , or  $E_*^{(2)}$ , depending on their initial values.

We demonstrate the above four cases in Figure 3.

If  $(a_1 - a_2)(b_2 - b_1) > 0$  and the net reproductive number equals 1, then there exists a unique positive equilibrium. This unique positive equilibrium is an unstable saddle node with a hyperbolic sector. There may or may not exist a boundary equilibrium. We provide two examples, where there exist either no boundary equilibrium or four boundary equilibria, respectively, in Figure 4.

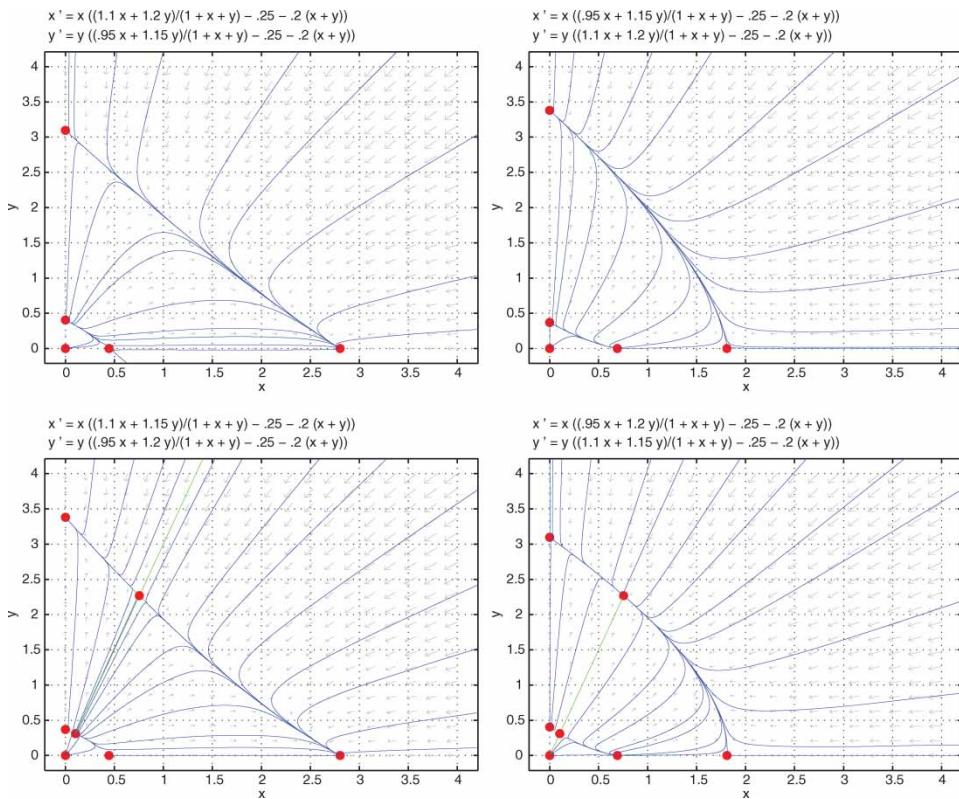


Figure 3. The parameters  $\mu = 0.25$  and  $\eta = 0.2$  are the same, and  $a_i$  and  $b_i$  satisfy  $a_i, b_i > S, i = 1, 2$ , for all the four figures. In the upper left figure, the parameters are  $a_1 = 1.1, b_1 = 1.2, a_2 = 0.95,$  and  $b_2 = 1.15$  such that  $a_2 < a_1$  and  $b_2 < b_1$ . There exists no positive equilibrium. The boundary equilibrium  $E_1^{(1)}$  is a saddle,  $E_1^{(2)}$  a stable node,  $E_2^{(1)}$  an unstable node, and  $E_2^{(2)}$  a saddle. In the upper right figure, the parameters are  $a_1 = 0.95, b_1 = 1.15, a_2 = 1.1,$  and  $b_2 = 1.2$  such that  $a_1 < a_2$  and  $b_1 < b_2$ . No positive equilibrium exists. The boundary equilibrium  $E_1^{(1)}$  is an unstable node,  $E_1^{(2)}$  a saddle,  $E_2^{(1)}$  a saddle, and  $E_2^{(2)}$  a stable node. In the lower left figure, the parameters are  $a_1 = 1.1, b_1 = 1.15, a_2 = 0.95,$  and  $b_2 = 1.2$  such that  $a_2 < a_1$  and  $b_1 < b_2$ . Boundary equilibria  $E_1^{(1)}$  and  $E_2^{(1)}$  are both saddles, and  $E_1^{(2)}$  and  $E_2^{(2)}$  are both stable nodes. Two positive equilibria exist. The positive equilibrium  $E_*^{(1)}$  is an unstable node and  $E_*^{(2)}$  a saddle. Solutions approach  $E_0, E_1^{(2)}$ , or  $E_2^{(2)}$ , depending on their initial values. In the lower right figure, parameters are  $a_1 = 0.95, b_1 = 1.2, a_2 = 1.1,$  and  $b_2 = 1.15$  such that  $a_1 < a_2$  and  $b_2 < b_1$ . Boundary equilibria  $E_1^{(1)}$  and  $E_2^{(1)}$  are both unstable nodes, and  $E_1^{(2)}$  and  $E_2^{(2)}$  are both saddles. Two positive equilibria exist. The positive equilibrium  $E_*^{(1)}$  a saddle and  $E_*^{(2)}$  is a stable node. Solutions approach  $E_0$  or  $E_*^{(2)}$ , depending on their initial values.

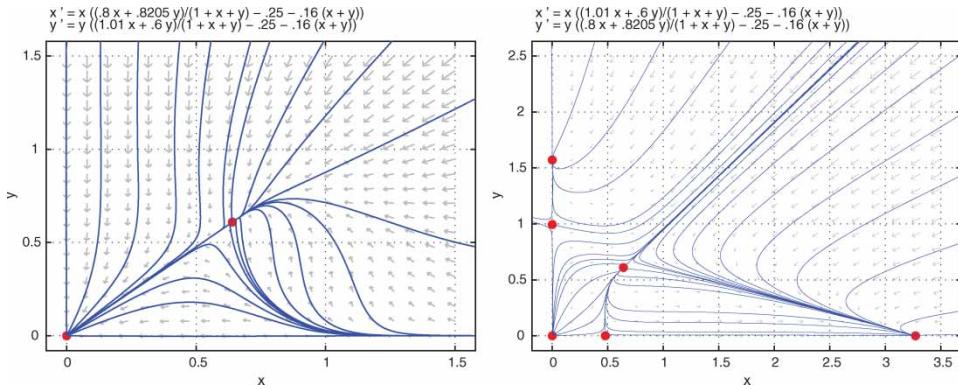


Figure 4. Parameters are  $\mu = 0.25$  and  $\eta = 0.2$  for both figures. The other parameters are  $a_1 = 0.8$ ,  $b_1 = 0.8205$ ,  $a_2 = 1.01$ , and  $b_2 = 0.6$  for the left figure and  $a_1 = 1.01$ ,  $b_1 = 0.6$ ,  $a_2 = 0.8$ , and  $b_2 = 0.8205$  for the right figure, so that the net reproductive number equals 1. In the left figure, there exist no boundary equilibria, but a unique positive equilibrium  $E_* = (0.6402, 0.6097)$  exists. The unique positive equilibrium  $E_*$  is an unstable saddle node with a hyperbolic sector. In the right figure, there exist, in addition to a unique positive equilibrium, four boundary equilibria. Boundary equilibria  $E_1^{(1)}$  and  $E_2^{(1)}$  are both saddles, and  $E_1^{(2)}$  and  $E_2^{(2)}$  are both stable nodes. The unique positive equilibrium is also an unstable saddle node with a hyperbolic sector.

## 6. Concluding remarks

To prevent and control mosquito-borne diseases – in particular, malaria – transgenic mosquitoes that are resistant to malaria infection provide a new and effective weapon. As the transgenic mosquitoes are released into the field with wild mosquitoes, the interactions between the two populations and ‘inter-specific’ matings between the wild and transgenic mosquitoes take place. The gene distributions after several generations and the gene structures of the progeny of late generations can be complex. To better understand the impact of releasing transgenic mosquitoes and the contributions different modelling structures can make, we formulated continuous-time models, based on differential equations, and explored the dynamics of these models.

As in [13], we assumed different functional forms for the mating rates. If the mating rate is constant (Section 3), the model dynamics are relatively simple. If the number of wild (or transgenic) offspring is greater than the number of transgenic (or wild) offspring produced by a wild (or transgenic) mosquito through all matings, and is greater than the natural death rate, the wild (or transgenic) mosquitoes survive and drive the transgenic (or wild) mosquitoes to extinction locally through the interaction. In either case, there exists either no positive equilibrium or a unique unstable positive equilibrium. Whether wild or transgenic mosquitoes go extinct depends on the initial sizes of the two mosquitoes populations.

We also considered the case when the mating rate is proportional to the total mosquito populations and illustrated the unrealistic or undesirable features of model (14) in Section 4. More specifically, the positive quadrant is always divided by separatrices consisting of the manifolds of the boundary or positive equilibria such that mosquito populations can become extinct or unbounded, depending on their initial sizes. These unrealistic or undesirable features are due to the fact that when the population sizes are sufficiently large, the numbers of wild and transgenic offspring per mosquito also become sufficiently large. This assumption is biologically unrealistic.

To make the functional forms for the mating rates more realistic and also to incorporate Allee effects into the modelling formulation, which reflects the mating difficulty as population sizes are relatively small, we assumed a Holling-II-type functional form for the mating rates in Section 5. This functional form implies that mating rates are approximately proportional to the total mosquito

populations when the population sizes are small, but approach constant for large populations. The resulting model, described by system (16), has much richer dynamics.

All solutions are bounded and the origin is a locally asymptotically stable node, *i.e.*, mosquito populations go extinct if their sizes are sufficiently small. If the number of offspring produced by either wild or transgenic mosquitoes per unit of time is not large enough to compromise their death ( $a_i < S$  or  $b_i < S$ ,  $i = 1, 2$ ), no matter whether the number of wild offspring is greater than the number of transgenic offsprings or vice versa, both populations go extinct regardless of their initial sizes. However, if the number of offspring of either wild or transgenic mosquitoes per unit of time exceeds a threshold of the death rates ( $S < a_i$  or  $S < b_i$ ,  $i = 1, 2$ ), the dynamics of the interaction of the two mosquito populations can be complex and several possibilities exist. Either wild or transgenic mosquitoes can survive and drive the other population to extinction, or both coexist. In distinction from the models in Sections 3 and 4, there may exist no, one, or two boundary equilibria on each axis, and there may also exist no, one, or two positive equilibria, depending on whether the net reproductive number is less than, equal to, or greater than 1. Although the boundary or positive equilibrium with smaller components is always unstable (either an unstable node or a saddle), the boundary or positive equilibrium with larger components can be a saddle or a stable node in different parameter regions. The separatrices composed by the stable or unstable manifolds of the equilibria divide the positive quadrant into several regions from which the populations can lead to extinction of wild or transgenic mosquitoes, or the coexistence of two populations. Therefore, in this case, it would be important to introduce sufficient numbers of reproductive transgenic mosquitoes, or to find more dominant transgenes, so as to eventually wipe out the mosquitoes without malaria-resistant genes.

The examples shown in Figure 4 with a unique positive equilibrium for model (16) may rarely happen in biology because the parameters need to satisfy exactly the net reproductive number equal to 1. Nevertheless, they provide interesting mathematical examples for the existence of an unstable nonhyperbolic saddle node with a hyperbolic sector in a 2D dynamical system.

Finally, we need to point out that the models formulated in this paper are approximations for the study of the dynamics of interacting wild and transgenic mosquitoes. We assume density-dependent deaths based on the total mosquito populations. In reality, it would be more appropriate to assume density-dependent deaths for mosquito larvae. Moreover, the total size of mosquito populations is usually regulated by the emergence rate of new adult mosquitoes. Therefore, a more accurate model necessitates the inclusion of mosquito life-cycle stages in its formulation. This, naturally, introduces more complexity into both the model and its analysis. We plan to investigate such models in the future.

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