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Assessing the Influence of Quiescence Eggs on the Dynamics of Mosquito *Aedes aegypti*

Hyun Mo Yang

UNICAMP, IMECC, DMA Praça Sérgio Buarque de Holanda, Campinas, Brazil
Email: hyunyang@ime.unicamp.br

Abstract

The anthropophilic and peridomestic female *Aedes aegypti* bites humans to suck blood to maturate fertilized eggs, which are laid in appropriate recipients (breeding sites). These eggs can hatch in contact with water releasing larvae, or can be stored in a dormant state (quiescence), which last for extended periods. Taking into account this ability of eggs of *A. aegypti* mosquitoes, mathematical model is developed taking into account four successive quiescence stages. The analysis of the model shows that the ability of the eggs surviving in dormant state in adverse abiotic conditions, depending on the model parameters, can increase the fitness of mosquito population; in other words, the capacity of the mosquitoes generating offsprings is increased.

Keywords

1. Introduction

The population dynamics of mosquitoes *Aedes aegypti* is clearly dependent on abiotic factors, with serious implications for dengue transmission. By using estimated entomological parameters dependent on temperature, including the dependency of these parameters on rainfall, the seasonally varying population size of mosquito *A. aegypti* was evaluated by a mathematical model [1]. However, eggs are known to be the most resistant stages during development, allowing a long survival of the mosquitoes under unfavorable climatic conditions, such as lower temperatures and dry seasons [2] [3].

The eggs of the mosquito *A. aegypti* possess the ability to undergo an extended quiescence hosting a fully developed 1st instar larvae within the chorion, and this life history traitpharate larvae can withstand months of quiescence inside the egg where they depend on stored maternal reserves. Therefore, the duration of quiescence

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*Corresponding author.

and extent of nutritional depletion may affect the physiology and survival of larvae that hatch in a suboptimal habitat [4].

Silva and Silva [5] carried out laboratorial experiments in order to determine the influence of the quiescence eggs on the life cycle of *A. aegypti*. Their experiments allow classifying the quiescence eggs in roughly four categories according to their ability to hatch larvae (see Section 4 for details). In this paper, these four stages of quiescence eggs are included in the modelling of the dynamics of *A. aegypti* [6], aiming to assess their influences on the size of mosquito population. This assessment is performed by determining the improvement of the fitness of mosquito population due to the quiescence eggs.

The paper is structured as follows. In Section 2, a model for *A. aegypti* population is formulated encompassing quiescence eggs, and in Section 3 the model is analyzed, determining the equilibrium points, and performing the stability analysis of these points. Section 4 presents discussion, and conclusion is given in Section 5.

2. Model Formulation

Embryonic development of the eggs of the mosquito *A. aegypti* is completed approximately within 3 days after oviposition, and a fully developed 1st instar larva resides within the chorion of the egg in a dormant state referred to as quiescence. Pharate 1st instar quiescent larvae will hatch out immediately upon exposure to the appropriate stimulus; in this way quiescence differs from diapause, which is a hormonally controlled and pre-programmed state of developmental arrest in which the larvae are refractory to hatching stimuli for an extended period of time. As a result of this life history trait, *A. aegypti* produce eggs that, in addition to being desiccation resistant, can withstand months of dormancy depending on stored maternal reserves [4]. The influence of these quiescence eggs on the population dynamics of *A. aegypti* mosquitoes is assessed by mathematical modelling.

The life cycle of *A. aegypti* encompasses an aquatic phase (egg, larva and pupa) followed by winged (adult) form. In Yang *et al.* [6], a mathematical model considering the compartments of aquatic phase (encompassing larvae and pupae) and adult mosquitoes was analyzed. However, the model developed here takes into account the compartment of eggs. Hence, the dynamics of mosquito population encompasses three phases in the life cycle of *A. aegypti*: eggs, aquatic phase and adult mosquitoes. The model considers only female mosquitoes (F), and two different stages of eggs (the quiescence eggs E^s and hatchable eggs E), distributed in four compartments according to the period of time they are quiescence (E_i^s and E_i, for $i = 1, \cdots, 4$), while aquatic phase comprises larva and pupa stages (A). The passage from E_i^s to E_i is dictated by external stimuli (such as temperature, humidity, nutrients, etc.) and is irreversible. See the flow chart in **Figure 1**.

In the modelling, it is assumed that all eggs laid by mosquitoes enter in the first quiescence stage, which number at time t is designated as E_1^s. The rate at which eggs are produced is given by ϕ, the oviposition rate, and among them a fraction f will originate female mosquitoes. These eggs are transferred to second quiescence stage E_2^s after a period of time α_1^{-1}, where α_1 is the transition rate from E_1^s to E_2^s; or, they enter to hatchable state E_1 at rate ε_1. The eggs in the hatchable state E_1 hatch as larvae at eclosion rate σ_1, and enter to the aquatic phase A. Another route is the death (inviabilization) of hatchable eggs at mortality rate μ_1, but
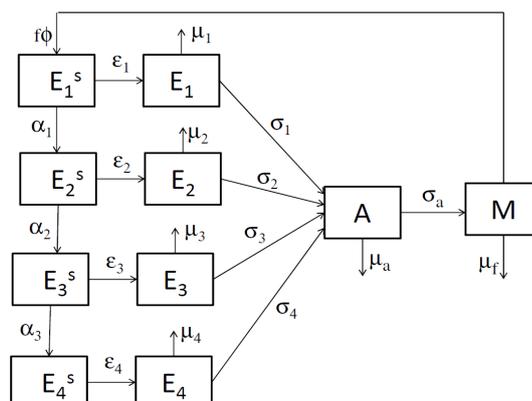
Figure 1. The flow chart of mosquito's life cycle including quiescence eggs.

it is assumed that the eggs in quiescence stage E_1^s are not under mortality. The number of aquatic forms is constrained by breeding sites and nutrients, which is designated by k, the carrying capacity. In aquatic phase, larvae develop to pupae, and emerge as adult (M) at rate σ_a, or they (in larval and pupal phases) die at mortality rate μ_a. Finally, the adult mosquitoes die at mortality rate μ_f. Notice that the inverse of the mortality rate $\mu_\bullet^{-1}$ is the average period of surviving in the state $\bullet$, where $\bullet$ stands for all compartments except quiescence stages; and the mating between male and female mosquitoes is not considered in the modelling [7].

The above descriptions are also valid for the quiescence eggs E_i^s and hatchable eggs E_i, for $i = 2,3,4$. The definitions of the parameters are the same described above, changing the subscript for 2, 3 or 4. Being the fourth stage of eggs the last, $\alpha_4 = 0$. The entomological parameters $(i = 1, \cdots, 4)$ ε_i, μ_i, σ_i, μ_a, σ_a, μ_f and ϕ are strongly dependent on temperature (consequently on time t), but α_i do not.

Based on the foregoing descriptions of model parameters and variables, the dynamics of mosquito population encompassing quiescence eggs is described by the system of differential Equations

$$
\begin{cases}
\dfrac{\mathrm{d}}{\mathrm{d}t} E_1^s = f\phi M - (\alpha_1 + \varepsilon_1) E_1^s \\[2mm]
\dfrac{\mathrm{d}}{\mathrm{d}t} E_1 = \varepsilon_1 E_1^s - (\mu_1 + \sigma_1) E_1 \\[2mm]
\dfrac{\mathrm{d}}{\mathrm{d}t} E_2^s = \alpha_1 E_1^s - (\alpha_2 + \varepsilon_2) E_2^s \\[2mm]
\dfrac{\mathrm{d}}{\mathrm{d}t} E_2 = \varepsilon_2 E_2^s - (\mu_2 + \sigma_2) E_2 \\[2mm]
\dfrac{\mathrm{d}}{\mathrm{d}t} E_3^s = \alpha_2 E_2^s - (\alpha_3 + \varepsilon_3) E_3^s \\[2mm]
\dfrac{\mathrm{d}}{\mathrm{d}t} E_3 = \varepsilon_3 E_3^s - (\mu_3 + \sigma_3) E_3 \\[2mm]
\dfrac{\mathrm{d}}{\mathrm{d}t} E_4^s = \alpha_3 E_3^s - \varepsilon_4 E_4^s \\[2mm]
\dfrac{\mathrm{d}}{\mathrm{d}t} E_4 = \varepsilon_4 E_4^s - (\mu_4 + \sigma_4) E_4 \\[2mm]
\dfrac{\mathrm{d}}{\mathrm{d}t} A = (\sigma_1 E_1 + \sigma_2 E_2 + \sigma_3 E_3 + \sigma_4 E_4)\left(1 - \dfrac{A}{k}\right) - (\mu_a + \sigma_a) A \\[2mm]
\dfrac{\mathrm{d}}{\mathrm{d}t} M = \sigma_a A - \mu_f M.
\end{cases}
\tag{1}
$$

This system of equations is analyzed in the steady state. A simplified version of this modelling is given in Appendix.

3. Analysis of the Model

The system of Equations (1) is dealt with determining the equilibrium points, and assessing the stability of these points.

3.1. Equilibrium Points

Before determining the equilibrium points, let the following parameters be defined. The quiescence eggs at stage i can go to next quiescence stage $i+1$ or to hatchable state i, with probabilities of transition from quiescence stage i to stage $i+1$ (a_i) and to hatchable stage i (b_i) being given by

$$
\begin{cases}
a_i = \dfrac{\alpha_i}{\alpha_i + \varepsilon_i} \\[3mm]
b_i = \dfrac{\varepsilon_i}{\alpha_i + \varepsilon_i},
\end{cases}
\tag{2}
$$

for $i = 1, \cdots, 4$, with $a_i + b_i = 1$. Notice that $a_4 = 0$ and $b_4 = 1$, due to $\alpha_4 = 0$. The average periods of time that eggs stay at quiescence (d_i) and hatchable (g_i) stages i are

$$
\begin{cases}
d_i = \dfrac{1}{\alpha_i + \varepsilon_i} \\
g_i = \dfrac{1}{\mu_i + \sigma_i},
\end{cases}
\tag{3}
$$

for $i = 1, \cdots, 4$. Finally, the probability of eggs surviving the hatchable stage i and hatch as larvae (c_i), and the probability of aquatic forms (larvae and pupae) surviving the aquatic phase and emerging as adult mosquitoes (c_a) are

$$
\begin{cases}
c_i = \dfrac{\sigma_i}{\mu_i + \sigma_i} \equiv \sigma_i g_i \\
c_a = \dfrac{\sigma_a}{\mu_a + \sigma_a},
\end{cases}
\tag{4}
$$

for $i = 1, \cdots, 4$.

There are two equilibrium points. The first equilibrium is the absence of mosquito population, designated by P^0, given by

$$
P^0 = \left(\left[\left(\bar{E}_i^s = 0, \bar{E}_i = 0 \right), i = 1, \cdots, 4 \right], \bar{A} = 0, \bar{M} = 0 \right),
$$

which is referred to the trivial equilibrium point.

The second equilibrium is the mosquito population being well established in a region (or community), the non-trivial equilibrium P^*, given by

$$
P^* = \left(\left[\left(\bar{E}_i^s = E_i^{s*}, \bar{E}_i = E_i^* \right), i = 1, \cdots, 4 \right], \bar{A} = A^*, \bar{M} = M^* \right).
$$

The coordinates of the non-trivial equilibrium are written in terms of the previously defined parameters, which are

$$
\begin{cases}
E_1^{s*} = d_1 f \phi M^* \\
E_1^* = b_1 g_1 f \phi M^* \\
E_2^{s*} = d_2 a_1 f \phi M^* \\
E_2^* = b_2 a_1 g_2 f \phi M^* \\
E_3^{s*} = d_3 a_2 a_1 f \phi M^* \\
E_3^* = b_3 a_2 a_1 g_3 f \phi M^* \\
E_4^{s*} = d_4 a_3 a_2 a_1 f \phi M^* \\
E_4^* = a_3 a_2 a_1 f \phi M^* \\
A^* = \dfrac{\mu_f}{\sigma_a} M^*,
\end{cases}
$$

and the number of adult mosquitoes M^* is

$$
M^* = \frac{\sigma_a}{\mu_f} k \left(1 - \frac{1}{Q_0} \right),
$$

where Q_0 is the basic offspring number defined by

$$
Q_0 = q_0 c_a \frac{f \phi}{\mu_f},
\tag{5}
$$

with q_0 being given by

$$q_0 = b_1 c_1 + b_2 a_1 c_2 + b_3 a_2 a_1 c_3 + a_3 a_2 a_1 c_4, \tag{6}$$

which is the overall production of larvae by all compartments of eggs. Clearly, the non-trivial equilibrium point is biologically feasible if $Q_0 > 1$.

Let Q_0 be interpreted biologically. Suppose that a fertilized female mosquito is introduced in a region completely free of mosquitoes. The term $f\phi/\mu_f$ is the average number of (female) eggs produced by this mosquito. These eggs are spread out among the four compartment with different probabilities of hatching according to the period of time they are stored as quiescence stage. Average number of eggs that survive these compartments and hatch as larvae is given by q_0, which must survive also the aquatic phase and emerge as adult (female) mosquitoes, with probability c_a. Hence, Q_0 is the average number of offsprings originated by a single female mosquito introduced in a region free of mosquitoes.

The overall production of eggs q_0 also deserves interpretation. All eggs enter into the class E_1^s. Among these eggs, a fraction b_1 enters to the hatchable state E_1 and, when surviving this stage with probability c_1, become larvae, resulting in $b_1 c_1$ aquatic forms produced by the eggs following the route E_1^s and E_1. But, the complementary fraction a_1 is transferred to quiescence stage E_2^s. Among these eggs, b_2 enters to the hatchable state E_2 and complementary fraction a_2 is transferred to quiescence stage E_3^s. Following previously definition, $b_2 a_1 c_2$ is the average number of larvae produced by eggs that remained quiescence without entering in the first hatchable state (a_1), but entered in the second hatchable state (b_2) and survived this state (c_2). This is the path of eggs following the route E_1^s, E_2^s and E_2 before hatching. The third ($b_3 a_2 a_1 c_3$, following the route E_1^s, E_2^s, E_3^s and E_3 before hatching) and fourth ($a_3 a_2 a_1 c_4$, following the route E_1^s, E_2^s, E_3^s, E_4^s and E_4 before hatching) terms follow similar interpretation. Hence q_0 is the overall production of aquatic forms by the four quiescence and hatchable compartments.

3.2. Stability Analysis of the Equilibrium Points

The stability analysis of the equilibrium points P^0 and P^* are assessed by the application of Routh-Hurwitz criteria to the characteristic Equation corresponding to the Jacobian matrix of Equation (1).

The Jacobian matrix evaluated at the equilibrium point P^*, named $J = J(P^*)$, results in

$$J = \begin{bmatrix} J_1 & J_2 \\ J_3 & J_4 \end{bmatrix},$$

where the 5×5 matrices J_i, with $i = 1, \cdots, 4$, are

$$J_1 = \begin{bmatrix} -j_1 & 0 & 0 & 0 & 0 \\ \varepsilon_1 & -j_2 & 0 & 0 & 0 \\ \alpha_1 & 0 & -j_3 & 0 & 0 \\ 0 & 0 & \varepsilon_2 & -j_4 & 0 \\ 0 & 0 & \alpha_2 & 0 & -j_5 \end{bmatrix},$$

with $j_1 = \alpha_1 + \varepsilon_1$, $j_2 = \mu_1 + \sigma_1$, $j_3 = \alpha_2 + \varepsilon_2$, $j_4 = \mu_2 + \sigma_2$ and $j_5 = \alpha_3 + \varepsilon_3$,

$$J_2 = \begin{bmatrix} 0 & 0 & 0 & 0 & f\phi \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \end{bmatrix},$$

$$J_3 = \begin{bmatrix} 0 & 0 & 0 & 0 & \varepsilon_3 \\ 0 & 0 & 0 & 0 & \alpha_3 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & \sigma_1 j_6 & 0 & \sigma_2 j_6 & 0 \\ 0 & 0 & 0 & 0 & 0 \end{bmatrix},$$

with $j_6 = 1 - \dfrac{A^*}{k}$, and

$$J_4 = \begin{bmatrix} -j_7 & 0 & 0 & 0 & 0 \\ 0 & -\varepsilon_4 & 0 & 0 & 0 \\ 0 & \varepsilon_4 & -j_8 & 0 & 0 \\ \sigma_3 j_6 & 0 & \sigma_4 j_6 & -\dfrac{j_9}{j_6} & 0 \\ 0 & 0 & 0 & \sigma_a & -\mu_f \end{bmatrix},$$

with $j_7 = \mu_3 + \sigma_3$, $j_8 = \mu_4 + \sigma_4$ and $j_9 = \mu_a + \sigma_a$. The local stability of the equilibrium points is assessed by the eigenvalues of the characteristic Equation $\Lambda(\lambda)$ [8], or

$$\Lambda(\lambda) = \det(J - \lambda I) = 0,$$

which can be written as

$$\Lambda(\lambda) = \left[(\alpha_1 + \varepsilon_1) + \lambda \right]\left[(\mu_1 + \sigma_1) + \lambda \right]\left[(\alpha_2 + \varepsilon_2) + \lambda \right]\left[(\mu_2 + \sigma_2) + \lambda \right]\left[(\alpha_3 + \varepsilon_3) + \lambda \right]\left[(\mu_3 + \sigma_3) + \lambda \right]$$

$$\times \left[(\mu_4 + \sigma_4) + \lambda \right](\varepsilon_4 + \lambda)(\mu_f + \lambda)\left(\frac{\mu_a + \sigma_a}{1 - \dfrac{A^*}{k}} + \lambda \right) - f\phi\sigma_a \left(1 - \frac{A^*}{k} \right)\left\{ \varepsilon_1 \sigma_1 \left[(\alpha_2 + \varepsilon_2) + \lambda \right]\left[(\mu_2 + \sigma_2) + \lambda \right] \right.$$

$$\times (\varepsilon_4 + \lambda) + \alpha_1 \varepsilon_2 \sigma_2 \left[(\alpha_3 + \varepsilon_3) + \lambda \right]\left[(\mu_3 + \sigma_3) + \lambda \right]\left[(\mu_4 + \sigma_4) + \lambda \right]\left[(\mu_1 + \sigma_1) + \lambda \right]\left[(\alpha_3 + \varepsilon_3) + \lambda \right]$$

$$\times \left[(\mu_3 + \sigma_3) + \lambda \right]\left[(\mu_4 + \sigma_4) + \lambda \right](\varepsilon_4 + \lambda) + \alpha_2 \alpha_1 \varepsilon_3 \sigma_3 \left[(\mu_1 + \sigma_1) + \lambda \right]\left[(\mu_2 + \sigma_2) + \lambda \right]$$

$$\times \left. \left[(\mu_4 + \sigma_4) + \lambda \right](\varepsilon_4 + \lambda) + \alpha_3 \alpha_2 \alpha_1 \varepsilon_4 \sigma_4 \left[(\mu_1 + \sigma_1) + \lambda \right]\left[(\mu_2 + \sigma_2) + \lambda \right]\left[(\mu_3 + \sigma_3) + \lambda \right] \right\},$$

a polynomial of 10th degree.

The independent term of the characteristic Equation, designated by Λ_0, which is given by $\Lambda_0 = \Lambda(0) = \det(J)$, is written as

$$\Lambda_0 = \theta \left[1 - \left(1 - \frac{A^*}{k} \right)^2 Q_0 \right],$$

where $\theta > 0$ is given by

$$\theta = (\alpha_1 + \varepsilon_1)(\mu_1 + \sigma_1)(\alpha_2 + \varepsilon_2)(\mu_2 + \sigma_2)(\alpha_3 + \varepsilon_3)(\mu_3 + \sigma_3)(\mu_4 + \sigma_4)\varepsilon_4 \mu_f \frac{\mu_a + \sigma_a}{1 - \dfrac{A^*}{k}}.$$

For the trivial equilibrium P^0, $A^* = 0$, and for the non-trivial equilibrium P^*, $A^* = k(1 - 1/Q_0)$, resulting in

$$\Lambda_0 = \begin{cases} \theta(1 - Q_0), & \text{for } P^0 \\ \theta\left(1 - \dfrac{1}{Q_0} \right), & \text{for } P^*. \end{cases}$$

Hence, according to Leite et al. [9], the trivial equilibrium point P^0 is locally asymptotically stable for $Q_0 \le 1$, and the non-trivial equilibrium P^* is stable for $Q_0 > 1$.

4. Discussion

The results obtained in previous section are dealt with to assess the influence of the quiescence eggs in the size

of *A. aegypti* population. First, the study is done qualitatively, and, then, the results are confronted with experimental data.

4.1. Assessing Qualitatively the Effects of Quiescence

The basic offspring number Q_0, given by Equation (5), is the average number of offsprings generated by a single fertilized mosquito considering four different stages of quiescence. Let this threshold parameter be compared with Q_0^1, the basic offspring number without quiescence stages, which is given by

$$Q_0^1 = c_1 c_a \frac{f\phi}{\mu_f} = \frac{\sigma_1}{\mu_1 + \sigma_1} \frac{\sigma_a}{\mu_a + \sigma_a} \frac{f\phi}{\mu_f}. \tag{7}$$

Notice that this is obtained by letting $\alpha_1 = 0$ (consequently, $b_1 = 1$) in Equation (5). The difference between Q_0 and Q_0^1 is taken as a measure of fitness of mosquito population by adopting the strategy of quiescence: If $Q_0 - Q_0^1 > 0$, then there is a gain in the fitness promoted by quiescence eggs; if not, there is loss of fitness.

Let first be defined the productivity of each hatchable stage E_i, with $i = 1, \cdots, 4$. Suppose an initial number of hatchable eggs n_i is in the stage *i*, and there is no influx. Hence, the number of eggs at time t is given by $E_i = n_i e^{-(\mu_i + \sigma_i)t}$. The number of eggs hatching to larvae between t and $t + \mathrm{d}t$ is given by $\sigma_i E_i \mathrm{d}t$, as well as the number of died eggs is $\mu_i E_i \mathrm{d}t$. The quocient between the total numbers of production of larvae and died eggs p_i is

$$p_i = \frac{\int_0^\infty \sigma_i E_i \mathrm{d}t}{\int_0^\infty \mu_i E_i \mathrm{d}t} = \frac{\sigma_i}{\mu_i}, \tag{8}$$

$i = 1, \cdots, 4$, which is called the productivity index of hatchable state E_i. This index does not reflect the velocity of transitions from hatchable state to aquatic phase, but only the ratio between eclosion and mortality of eggs.

The difference between Q_0 and Q_0^1, Equations (5) and (7), is

$$Q_0 - Q_0^1 = \delta \frac{\alpha_1 \mu_1}{\theta_1} c_a \frac{f\varphi}{\mu_f},$$

where $\theta_1 > 0$ is given by

$$\theta_1 = (\alpha_1 + \varepsilon_1)(\mu_1 + \sigma_1)(\alpha_2 + \varepsilon_2)(\alpha_3 + \varepsilon_3)(\mu_3 + \sigma_3)(\mu_4 + \sigma_4),$$

and δ is given by

$$\delta = -\mu_4(\mu_3 + \sigma_3)(p_1 - p_4)(\alpha_2 + \alpha_2^*)\alpha_3 - \mu_3(\mu_4 + \sigma_4)(p_1 - p_3)(\alpha_2 + \alpha_2^\#)\varepsilon_3,$$

where

$$\begin{cases} \alpha_2^* = \dfrac{\mu_2(\mu_4 + \sigma_4)(p_1 - p_2)}{\mu_4(\mu_2 + \sigma_2)(p_1 - p_4)}\varepsilon_2 \\[3mm] \alpha_2^\# = \dfrac{\mu_2(\mu_3 + \sigma_3)(p_1 - p_2)}{\mu_3(\mu_2 + \sigma_2)(p_1 - p_3)}\varepsilon_2 \\[3mm] \alpha_3^{th} = -\dfrac{\mu_3(\mu_4 + \sigma_4)(p_1 - p_3)(\alpha_2 + \alpha_2^\#)}{\mu_4(\mu_3 + \sigma_3)(p_1 - p_4)(\alpha_2 + \alpha_2^*)}\varepsilon_3, \end{cases} \tag{9}$$

with α_3^{th} being the solution of $\delta = 0$. Hence, the signal of $Q_0 - Q_0^1$ will be determined by the signal of δ.

Notice that the parameters α_1, ε_1 and ε_4 do not appear in δ, showing that these parameters do not affect in the change of fitness of the mosquito population. (These parameters affects in the magnitude of the difference $Q_0 - Q_0^1$.) The parameters α_2^*, $\alpha_2^\#$ and α_3^{th} can be increased by increasing the parameters ε_2 and ε_3, and

$$\frac{1}{\alpha_2^*} - \frac{1}{\alpha_2^\#} = \frac{\alpha_2^\# - \alpha_2^*}{\alpha_2^* \alpha_2^\#} = \frac{\mu_3 \mu_4 \left(\mu_1 + \sigma_1\right)\left(\mu_2 + \sigma_2\right)\left(p_3 - p_4\right)}{\mu_1 \mu_2 \left(\mu_3 + \sigma_3\right)\left(\mu_4 + \sigma_4\right)\left(p_1 - p_2\right)} \frac{1}{\varepsilon_2}. \tag{10}$$

There are four hatchable states E_i, originating from quiescence stages of eggs E_i^s, with different productivity of larvae p_i. The gain in the fitness promoted by quiescence eggs is studied taking into account the productivity index p_i. When E_1 changes the productivity with any other state E_i, $i = 2,3,4$, it is assumed that E_1 remains producing more larvae than other two stages.

A. $p_1 > p_2$, $p_1 > p_3$ and $p_1 > p_4$ —The first hatchable state E_1 is the most proficuous in larvae production. In this case, $\alpha_2^* > 0$ and $\alpha_2^\# > 0$, resulting in $\delta < 0$. Hence $Q_0^1 > Q_0$, and the quiescence eggs decrease the fitness of mosquito population.

B. $p_2 > p_1$, $p_1 > p_3$ and $p_1 > p_4$ —The second hatchable state E_2 is the most proficuous in larvae production.

In this case, $\alpha_2^* < 0$ and $\alpha_2^\# < 0$, resulting in two possibilities:

B.1. $p_3 > p_4$ —the third hatchable state E_3 is more proficuous than E_4.

In this case, $\left|\alpha_2^\#\right| > \left|\alpha_2^*\right|$, according to Equation (10), and the threshold of α_2 is defined by $\alpha_2^{th} = \left|\alpha_2^\#\right|$. In this case,

$$\delta > 0 \Leftrightarrow \begin{cases} \alpha_2 < \left|\alpha_2^*\right| \\ \text{or} \\ \left|\alpha_2^*\right| < \alpha_2 < \alpha_2^{th} \quad \text{and} \quad \alpha_3 < \alpha_3^{th}. \end{cases} \tag{11}$$

Hence, the quiescence eggs increase the fitness of mosquito population $\left(Q_0 > Q_0^1\right)$ in two situations: 1) when the influx is at lower level $\left(\alpha_2 < \left|\alpha_2^*\right|\right)$ in quiescence stage E_3^s, and 2) the influx is at moderate level $\left(\left|\alpha_2^*\right| < \alpha_2 < \alpha_2^{th}\right)$ and the outflux is lower $\left(\alpha_3 < \alpha_3^{th}\right)$ in quiescence stage E_3^s.

B.2. $p_4 > p_3$ —The fourth hatchable state E_4 is more proficuous than E_3.

In this case, $\left|\alpha_2^*\right| > \left|\alpha_2^\#\right|$, according to Equation (10), and the threshold of α_2 is defined by $\alpha_2^{th} = \left|\alpha_2^*\right|$. In this case,

$$\delta > 0 \Leftrightarrow \begin{cases} \alpha_2 < \left|\alpha_2^\#\right| \\ \text{or} \\ \left|\alpha_2^\#\right| < \alpha_2 < \alpha_2^{th} \quad \text{and} \quad \alpha_3 > \alpha_3^{th}. \end{cases} \tag{12}$$

Hence, the quiescence eggs increase the fitness of mosquito population $\left(Q_0 > Q_0^1\right)$ in two situations: 1) when the influx is at lower level $\left(\alpha_2 < \left|\alpha_2^\#\right|\right)$ in quiescence stage E_3^s, and 2) the influx is at moderate level $\left(\left|\alpha_2^\#\right| < \alpha_2 < \alpha_2^{th}\right)$ and the outflux is higher $\left(\alpha_3 > \alpha_3^{th}\right)$ in quiescence stage E_3^s.

C. $p_1 > p_2$, $p_3 > p_1$ and $p_1 > p_4$ —The third hatchable state E_3 is the most proficuous in larvae production.

In this case, $\alpha_2^* > 0$ and $\alpha_2^\# < 0$, and the threshold of α_2 is given by $\alpha_2^{th} = \left|\alpha_2^\#\right|$. In this case,

$$\delta > 0 \Leftrightarrow \alpha_2 > \alpha_2^{th} \quad \text{and} \quad \alpha_3 < \alpha_3^{th}. \tag{13}$$

Hence, the quiescence eggs increase the fitness of mosquito population $\left(Q_0 > Q_0^1\right)$ when the influx is at higher level $\left(\alpha_2 > \alpha_2^{th}\right)$ but the outflux is lower $\left(\alpha_3 < \alpha_3^{th}\right)$ in quiescence stage E_3^s.

D. $p_1 > p_2$, $p_1 > p_3$ and $p_4 > p_1$ —The fourth and last hatchable state E_4 is the most proficuous in larvae production.

In this case, $\alpha_2^* < 0$ and $\alpha_2^\# > 0$, and the threshold of α_2 is given by $\alpha_2^{th} = \left|\alpha_2^*\right|$. In this case,

$$\delta > 0 \Leftrightarrow \alpha_2 > \alpha_2^{th} \quad \text{and} \quad \alpha_3 > \alpha_3^{th}. \tag{14}$$

Hence, the quiescence eggs increase the fitness of mosquito population $\left(Q_0 > Q_0^1\right)$ when both influx $\left(\alpha_2 > \alpha_2^{th}\right)$ and outflux $\left(\alpha_3 > \alpha_3^{th}\right)$ in quiescence stage E_3^s are at higher levels.

Summarizing, the quiescence eggs increase the fitness of mosquito population if one of hatchable stages from E_2, E_3 and E_4 is more proficuous (higher productivity index p) than E_1. Besides the productivity indexes

p_i, the parameters α_2 and α_3, which are the influx and outflux rates in the quiescence stage E_3^s, play important role in the fitness. The quiescence eggs increase the fitness of mosquito population if: a) the second hatchable state E_2 is the most proficuous in larvae production, and α_2 assumes lower values and α_3 assumes lower or higher values according to the relative productivities of E_3 and E_4, Equations (11) and (12); b) the third hatchable state E_3 is the most proficuous in larvae production, and α_2 assumes higher values, while α_3 assumes lower values, Equation (13); and c) the fourth hatchable state E_4 is the most proficuous in larvae production, and α_2 and α_3 assume higher values, Equation (14).

The transition parameters ε_i, with $i = 1, \cdots, 4$, depend strongly on the abiotic factors. In contrast, α_i, with $i = 1, \cdots, 4$, are fixed. However, the corresponding thresholds of α_2 and α_3 are allowed to vary by varying ε_2 and ε_3 according to Equation (9). For this reason the threshold parameters α_2^{th} (which can be $\left|\alpha_2^*\right|$ or $\left|\alpha_2^\#\right|$) and α_3^{th} are varied in order to α_2 and α_3 be situated at higher or lower values with respect to corresponding thresholds. Hence, the thresholds of ε_2 and ε_3 are obtained for fixed values of α_2 and α_3, that is, letting $\alpha_2^* = \alpha_2^\# = \alpha_2$ and $\alpha_3^{th} = \alpha_3$ in Equation (9). The resulting thresholds of ε_2 and ε_3 are

$$\begin{cases} \varepsilon_2^* = \dfrac{\mu_4(\mu_2 + \sigma_2)(p_1 - p_4)}{\mu_2(\mu_4 + \sigma_4)(p_1 - p_2)}\alpha_2 \\[2mm] \varepsilon_2^\# = \dfrac{\mu_3(\mu_2 + \sigma_2)(p_1 - p_3)}{\mu_2(\mu_3 + \sigma_3)(p_1 - p_2)}\alpha_2 \\[2mm] \varepsilon_3^{th} = -\dfrac{\mu_4(\mu_3 + \sigma_3)(p_1 - p_4)(\alpha_2 + \alpha_2^*)}{\mu_3(\mu_4 + \sigma_4)(p_1 - p_3)(\alpha_2 + \alpha_2^\#)}\alpha_3. \end{cases} \tag{15}$$

Hence, depending on the productivity index p_i, the parameters ε_2 and ε_3 can be settle below or above the thresholds ε_2^{th} which can be $\left|\varepsilon_2^*\right|$ or $\left|\varepsilon_2^\#\right|$) and ε_3^{th}, in order to the thresholds α_2^{th} and α_3^{th} be situated above or below the values of α_2 and α_3, respectively. If one of the conditions given by Equations (11), (12), (13) and (14) is satisfied, then the quiescence eggs increase the fitness of *A. aegypti* population.

4.2. Comparing with Experimental Data

The theoretical results obtained in foregoing section are compared with the results of the experiments carried out by Silva and Silva [5], which are reproduced in **Table 1**. The laboratory experiments to determine the influence of different periods of quiescence on eclosion of eggs to larvae were performed in a biological chamber kept at 28°C, 80% relative humidity and 12 hours of photophase.

Table 1. Reproduction of the results obtained by silva and silva [1].

Experiment number	Quiescence (days)	Number of eggs	Eclosion (eggs × days^{-1})	Eclosion (%)
1	3	807	86.1	85.4
2	32	698	5.3	41.1
3	63	586	6.4	36.0
4	91	738	12.1	47.7
5	121	749	13.2	97.2
6	154	800	1.6	1.3
7	273	612	8.6	4.3
8	337	611	1.0	0.3
9	427	842	5.6	10.9
10	462	800	1.0	0.5
11	492	1708	1.0	0.2

Based on **Table 1**, **Table 2** presents the estimation of the per-capita eclosion and mortality rates according to $\sigma = \Sigma/N$ and $\mu = \sigma(100 - ep)/ep$, where Σ, N and ep are, respectively, the number of eggs, total eclosion rate and percentage of eclosion (columns 3rd, 4th and 5th of **Table 1**).

Observing the last column of **Table 1**, the 11 experiments can be clustered as follows: Experiment number 1 as quiescence stage 1, experiment numbers 2 to 4 as quiescence stage 2, experiment number 5 as quiescence stage 3, and, finally, experiment numbers 7 to 11 as quiescence stage 4. In **Table 3**, the mean eclosion (σ_i) and mortality (μ_i) rates, the productivity index (p_i), transition rate (α_i) and hatchable rate (ε_i) are presented. With respect to transition rate, it is assumed that the average periods of time (days) in quiescence stages are $\alpha_1^{-1} = 5$, $\alpha_2^{-1} = 110$ and $\alpha_3^{-1} = 30$ (notice that $\alpha_4^{-1} = \infty$, since this is the last stage). With respect to hatchable rate, it is set arbitrarily as $\varepsilon_i = \mu_i + \sigma_i$ (see appendix). Notice that the third quiescence stage is the most proficuous in larvae production $(p_3 > p_1 > p_2 > p_4)$, which was also observed by other authors [10] [11], and it corresponds to the case C shown in preceding section.

The estimated eclosion (σ_a) and mortality (μ_a) rates of aquatic phase, the mortality rate of adult female mosquitoes (μ_f) and the oviposition rate per female (ϕ) are given in **Table 4** [6]. These rates are given for two different temperatures (16˚C and 28˚C), in order to mimic favorable (summer or wet) and unfavorable (winter or dry) seasons. To the favorable seasons, the temperature of 28˚C was chosen due to the laboratorial experiments in [5].

Table 2. Calculation of the per-capita eclosion and mortality rates.

Experiment number	Per-capita eclosion rate (days^{-1})	Per-capita mortality rate (days^{-1})
1	0.1067	0.0182
2	0.007593	0.0109
3	0.01092	0.0194
4	0.01640	0.0180
5	0.01762	0.00051
6	0.002	0.1518
7	0.01405	0.3127
8	0.00164	0.5439
9	0.00665	0.05437
10	0.00125	0.2488
11	0.000585	0.2922

Table 3. Estimation of the parameters σ_i, μ_i, calculation of the productivity indexes $p_i = \sigma_i/\mu_i$, α_i and ε_i, for $i = 1, \cdots, 4$.

Stage—i	σ_i (days^{-1})	μ_i (days^{-1})	p_i	α_i (days^{-1})	ε_i (days^{-1})
1	0.10669	0.01824	5.85	0.2	0.1249
2	0.01164	0.01609	0.72	0.0091	0.02773
3	0.01762	0.0005077	34.7	0.0333	0.01813
4	0.00436	0.26730	0.016	0	0.27166

Table 4. The estimated values of the parameters σ_a, μ_a, μ_f and ϕ for 16 and 28 degree Celsius (˚C) [2].

Temperature	σ_a (days^{-1})	μ_a (days^{-1})	μ_f (days^{-1})	ϕ (eggs × days^{-1})
16˚C	0.02615	0.01397	0.03642	0.69714
28˚C	0.11612	0.06001	0.02877	8.29500

Table 5 presents the values of the critical parameters and the basic offspring number. Using values of parameters given in **Table 3** and **Table 4**, the threshold values ($days^{-1}$) of α_2 and α_3 are $\alpha_2^{th} = \left|\alpha_2^{\#}\right| = 0.102$ and $\alpha_3^{th} = -0.01$ (second column), and the corresponding basic offspring number is $Q_0 = 54.787$. Since $\alpha_3^{th} < 0$, from the case **C** described above, $\delta < 0$ for all α_3, resulting in $Q_0^1 > Q_0$, where $Q_0^1 = 81.158$ was calculated using Equation (7). Hence, using $\varepsilon_2 = 0.02773$ and $\varepsilon_3 = 0.01813$ (**Table 3**), the quiescence eggs decrease the fitness of mosquito population.

Table 5 additionally shows that the threshold values ($days^{-1}$) of ε_2 and ε_3 are $\varepsilon_2^{th} = \left|\varepsilon_2^{\#}\right| = 0.00247$ and $\varepsilon_3^{th} = -0.0597$. Remembering that the values of α_2 and α_3 are fixed, while ε_2 and ε_3 are allowed to vary, the thresholds α_2^{th} and α_3^{th} changed appropriately in order to satisfy $\delta > 0$, which is true if the conditions $\alpha_2 > \alpha_2^{th}$ and $\alpha_3 < \alpha_3^{th}$ are verified, according to Equation (13). From the case **C** described above, $Q_0 > Q_0^1$ (the quiescence eggs increase the fitness of mosquito population) is possible when $\alpha_2 > \alpha_2^{th}$ and $\alpha_3 < \alpha_3^{th}$. Since ε_2 and ε_3 are arbitrary values, the first condition $\left(\alpha_2 > \alpha_2^{th}\right)$ is satisfied for all ε_2 that satisfy $\varepsilon_2 < \varepsilon_2^{th}$. For this reason, only the value of ε_2 is changed in **Table 3**, or $\varepsilon_2 = 0.001$ $days^{-1}$, in order to decrease α_2^{th} and to satisfy the first condition. In this case, the new threshold ($days^{-1}$) is $\alpha_2^{th} = \left|\alpha_2^{\#}\right| = 0.0037$ (other critical values are given in the third column of **Table 5**), and the corresponding basic offspring number is $Q_0 = 52.230$, smaller than the previous case. Similarly, the second condition is satisfied if $\varepsilon_3 > \varepsilon_3^{th}$, which is the reason to choose $\varepsilon_3 = 0.5$ $days^{-1}$. This additional change alters only α_3^{th} (fourth column of **Table 5**), but the corresponding basic offspring number is $Q_0 = 81.710$, slightly higher than Q_0^1. The partial contributions of all eggs compartments to the overall Q_0 are given in **Table 6**.

The contribution of the first stage of quiescence eggs in all cases, as shown in **Table 6**, does not change due to change occurring in ε_2 and ε_3. With the new values $\varepsilon_2 = 0.001$ and $\varepsilon_3 = 0.5$ ($days^{-1}$), the contribution of the third quiescence eggs compartment increased in almost 10 times, and became the highest contributor, displacing the first stage. The basic offspring number corresponding to the simplified model is given by the first row of **Table 6** (see Appendix).

Summarizing, assuming that α_i, μ_i and σ_i do not change, when the values of ε_2 and ε_3 ($days^{-1}$) in **Table 3** (0.0277 and 0.0181) are changed to 0.001 and 0.5, respectively, then the quiescence eggs increase the fitness of mosquito population. Notice that the values of ε_1 and ε_4 do not matter in this issue.

Up to now the model was discussed considering constant values for the model parameters. But, the effect of

Table 5. Calculation of the critical values α_2^{*}, $\alpha_2^{\#}$, α_3^{th}, ε_2^{*}, $\varepsilon_2^{\#}$ and ε_3^{th}, where "dnc" stands for value that does not change with respect to the contiguous column. The critical values in column labelled as **Table 3** corresponds to values of model parameters given in **Table 3**. In columns labelled as **Table 3** (ε_2) and **Table 3** (ε_2, ε_3) correspond to critical values calculated by changing only the value(s) of parameter(s) between parenthesis.

Critical	Table 3	Table 3 (ε_2)	Table 3 (ε_2, ε_3)
α_2^{*} ($days^{-1}$)	0.0144	0.00052	dnc
$\alpha_2^{\#}$ ($days^{-1}$)	−0.102	−0.0037	dnc
α_3^{th} ($days^{-1}$)	−0.01	0.00144	0:0396
ε_2^{*} ($days^{-1}$)	0.0175	dnc	dnc
$\varepsilon_2^{\#}$ ($days^{-1}$)	−0.00247	dnc	dnc
ε_3^{th} ($days^{-1}$)	−0.0597	0.420	dnc

Table 6. The basic reproduction number Q_0 calculated using the values given in **Table 3** and **Table 4**. The basic reproduction number corresponding to a unique eggs compartment is $Q_0^1 = 81.158$.

Values	Stage 1	Stage 2	Stage 3	Stage 4	Q_0
Table 3	31.21	18.49	4.946	0.1502	54.787
Table 3 (ε_2)	31.21	2.433	18.05	0.5481	52.230
Table 3 (ε_2, ε_3)	31.21	2.433	48.02	0.0529	81.710

quiescence eggs in the size of mosquito population becomes important in tropical (wet and dry seasons) and temperate (rigorous winter seasons) regions.

The experiments carried out by Silva and Silva [5] showed that eggs of *A. aegypti* presented more productivity index after being stored for 4 months. This period encompasses the unfavorable seasons (dry or/and cold). After this period, in the beginning of favorable seasons, mosquito population can be settled quickly at higher infestation levels. **Table 7** shows the partial contributions of quiescence eggs to overall basic offspring number. Two seasons (summer, 28°C, and winter, 16°C) and two extreme abiotic conditions, the favorable (high) and unfavorable (low), according to equal $(i = 1, \cdots, 4)$ hatchable rates $\varepsilon_i = 5.0$ and $\varepsilon_i = 0.001$ (days^{-1}), respectively. The values of eclosion and mortality rates μ_i and σ_i are maintained fixed in all seasons, because the experiments in [5] were carried out for a unique temperature (28°C).

In a favorable abiotic conditions (high ε_i), the partial contribution of first stage of quiescence eggs is almost the overall offspring number. However, in hostile abiotic conditions (low ε_i), the quiescence stages 2, 3 and 4, in this order, contribute more than first quiescence stage to overall offspring number. This behavior has important influence in seasonality of abiotic conditions. For instance, in the end of favorable seasons, more eggs are transferred to quiescence stages than to hatchable states, due to decreasing in the hatchable rates ε_i (for instance, the row labelled "summer (low)" of **Table 7**, $Q_0 = 8.076$). After the passage of unfavorable season ("winter (low)" of **Table 7**, $Q_0 = 0.530$), eggs are allowed to hatch in the beginning of next favorable season ("winter (high)" of **Table 7**, $Q_0 = 5.223$), remembering that these eggs have been stored for around 4 months. However, these quiescence eggs are highly proficuous in originating larvae (high productivity index of hatching). During this transition of seasons, these quiescence eggs contribute mainly to recolonize the region quickly. Sinceafter, the population of mosquitoes is maintained at the infestation level due to the increasing of hatchable rates ε_i to the previous values ("summer (high)" of **Table 7**, $Q_0 = 79.57$). Notice that the variation of 5×10^3 times in ε_i resulted only in a variation of 10 times in Q_0.

5. Conclusions

A mathematical model encompassing four quiescence stages was analyzed. From the model, it was concluded that under certain conditions, the quiescence eggs can improve the fitness of *A. aegypti* population.

The capacity of the *A. aegypti* eggs being stored during hostile abiotic factors and, then, hatching to larvae in favorable season with increased fitness, is essential to sustain *A. aegypti* population to face seasonality. When the quiescence eggs having approximately 120 days are allowed to hatch, these eggs presented the most producible capacity to originate larvae [5]. This period of 4 months corresponds to approximately the worst abiotic conditions to *A. aegypti* to survive. Hence, the quiescence of eggs of 4 months joined to the higher capacity of hatching seems to be an important strategy to *A. aegypti* population to persist in seasonally varying environment.

Another aspect is regarded to dengue transmission, due to the possibility of the eggs infected with dengue virus sustaining dengue epidemics [12]. For this reason, it is important to analyze dengue transmission modelling taking into account the infected and non-infected quiescence eggs. One of the possible applications of this kind of modelling is the assessment of biological control by intracellular bacterium *Wolbachia* [13].

Quantitative analyses, such as the dynamical trajectories, are left to further work. For instance, the dynamical trajectories of the system of Equations (1) are obtained numerically considering the initial conditions, at $t = 0$, given by

Table 7. The basic offspring number Q_0 calculated using the values given in **Table 3** and **Table 4**, varying only the transition rates ε_i for two seasons: Summer (28°C) and winter (16°C). Two values are used for $i = 1, \cdots, 4$ (days^{-1}): $\varepsilon_i = 5.0$ (high) and $\varepsilon_i = 0.001$ (low). The basic reproduction number corresponding to a unique eggs compartment is $Q_0^1 = 5.327$ for winter season (for summer, the values is that provided in **Table 6**).

Seasons	Stage 1	Stage 2	Stage 3	Stage 4	Q_0
Summer (high)	78.04	1.531	6.4×10^{-3}	7.1×10^{-7}	79.57
Summer (low)	0.404	3.933	2.412	1.328	8.076
Winter (high)	5.122	0.101	4.2×10^{-4}	4.6×10^{-8}	5.223
Winter (low)	0.027	0.258	0.153	0.087	0.530

$$\left(\left[\left(E_i^s\left(0\right)=0, E_i\left(0\right)=0 \right), i=1,\cdots,4 \right], A\left(0\right)=0, M\left(0\right)=1 \right)$$

which corresponds to the introduction of one mosquito in a previously uninfested region. In other words, the equilibrium point before the introduction of infectious case is given by P^0. Depending on the value of the basic offspring number, the mosquito population goes to extinction (P^0, when $Q_0 < 1$), or colonizes successfully (P^*, when $Q_0 > 1$).

Conflict of Interests

The author(s) declare(s) that there is no conflict of interests regarding the publication of this article.

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Appendix

Simplified Model

The model described by system of Equations (1) can be simplified joining the quiescence and hatchable stages. For instance, calling $E_i' = E_i^s + E_i$, then (for $i = 1$, $\alpha_{i-1} E_{i-1}^s = f \phi M$)

$$\frac{\mathrm{d}}{\mathrm{d}t} E_i' = \alpha_{i-1} E_{i-1}^s - \alpha_i E_i^s - (\mu_i + \sigma_i) E_i$$

is approximated as

$$\frac{\mathrm{d}}{\mathrm{d}t} E_i' = \alpha_{i-1} E_{i-1}' - (\mu_i + \sigma_i + \alpha_i) E_i',$$

for $i = 1, \cdots, 4$. This simplification allows the system to eliminate four equations. The simplified system is

$$\begin{cases} \dfrac{\mathrm{d}}{\mathrm{d}t} E_1 = f \phi M - (\mu_1 + \sigma_1 + \alpha_1) E_1 \\[2mm] \dfrac{\mathrm{d}}{\mathrm{d}t} E_2 = \alpha_1 E_1 - (\mu_2 + \sigma_2 + \alpha_2) E_2 \\[2mm] \dfrac{\mathrm{d}}{\mathrm{d}t} E_3 = \alpha_2 E_2 - (\mu_3 + \sigma_3 + \alpha_3) E_3 \\[2mm] \dfrac{\mathrm{d}}{\mathrm{d}t} E_4 = \alpha_3 E_3 - (\mu_4 + \sigma_4) E_4 \\[2mm] \dfrac{\mathrm{d}}{\mathrm{d}t} A = (\sigma_1 E_1 + \sigma_2 E_2 + \sigma_3 E_3 + \sigma_4 E_4) \left(1 - \dfrac{A}{k}\right) - (\mu_a + \sigma_a) A \\[2mm] \dfrac{\mathrm{d}}{\mathrm{d}t} M = \sigma_a A - \mu_f M, \end{cases}$$

where the prime was dropped out.

Defining the average period of time that eggs stay at stage i (d_i) as

$$d_i = \frac{1}{\mu_i + \sigma_i + \alpha_i},$$

with $\alpha_4 = 0$, and the probabilities of eggs at stage i going to next stage $i + 1$ (a_i) or to hatch at stage i (c_i), and probability of surviving aquatic phase (c_a) as

$$\begin{cases} a_i = \dfrac{\alpha_i}{\mu_i + \sigma_i + \alpha_i} = \alpha_i d_i \\[3mm] c_i = \dfrac{\sigma_i}{\mu_i + \sigma_i + \alpha_i} \\[3mm] c_a = \dfrac{\sigma_a}{\mu_a + \sigma_a}, \end{cases}$$

for $i = 1, \cdots, 4$, two equilibrium points are given.

The first equilibrium is the absence of mosquito population, the trivial equilibrium P^0, given by

$$P^0 = \left(\overline{E}_1 = 0, \overline{E}_2 = 0, \overline{E}_3 = 0, \overline{E}_4 = 0, \overline{A} = 0, \overline{M} = 0\right)$$

The non-trivial equilibrium P^* is given by

$$P^* = \left(\overline{E}_1 = E_1^*, \overline{E}_2 = E_2^*, \overline{E}_3 = E_3^*, \overline{E}_4 = E_4^*, \overline{A} = A^*, \overline{M} = M^*\right)$$

where the coordinates written in terms of the previously defined parameters are

$$
\begin{cases}
E_1^* = d_1 f \phi M^* \\
E_2^* = d_2 a_1 f \phi M^* \\
E_3^* = d_3 a_2 a_1 f \phi M^* \\
E_4^* = d_4 a_3 a_2 a_1 f \phi M^* \\
E_4^* = a_3 a_2 a_1 f \phi M^* \\
A^* = \dfrac{\mu_f}{\sigma_a} M^*,
\end{cases}
$$

and the number of adult mosquitoes M^* is

$$
M^* = \frac{\sigma_a}{\mu_f} k \left(1 - \frac{1}{Q_0}\right).
$$

The basic offspring number Q_0 is defined by

$$
Q_0 = q_0 c_a \frac{f \phi}{\mu_f}, \tag{16}
$$

with q_0 being given by

$$
q_0 = c_1 + a_1 c_2 + a_2 a_1 c_3 + a_3 a_2 a_1 c_4,
$$

which is the overall production of larvae by all compartments of eggs. Clearly, the non-trivial equilibrium point is biologically feasible if $Q_0 > 1$.

Letting $\alpha_1 = 0$, the basic offspring number Q_0^1 without quiescence stages is equal to Equation (7), which can be obtained by letting $\alpha_1 = 0$ in Equation (16). The difference between Q_0 and Q_0^1 is

$$
Q_0 - Q_0^1 = \delta_1 \frac{\alpha_1 \mu_1}{\theta_2} c_a \frac{f \phi}{\mu_f},
$$

where $\theta_2 > 0$ is given by

$$
\theta_2 = \left(\mu_1 + \sigma_1 + \alpha_1\right)\left(\mu_2 + \sigma_2 + \alpha_2\right)\left(\mu_3 + \sigma_3 + \alpha_3\right)\left(\mu_4 + \sigma_4\right)\left(\mu_1 + \sigma_1\right),
$$

and δ_1 is given by

$$
\delta_1 = -\mu_4 \left(p_1 - p_4\right)\left(\alpha_2 + \alpha_2^*\right)\alpha_3 - \mu_3 \left(\mu_4 + \sigma_4\right)\left(p_1 - p_3\right)\left(\alpha_2 + \alpha_2^{\#}\right),
$$

where

$$
\begin{cases}
\alpha_2^* = \dfrac{\mu_2 \left(\mu_4 + \sigma_4\right)\left(p_1 - p_2\right)}{\mu_4 \left(p_1 - p_4\right)} \\[2ex]
\alpha_2^{\#} = \dfrac{\mu_2 \left(\mu_3 + \sigma_3\right)\left(p_1 - p_2\right)}{\mu_3 \left(p_1 - p_3\right)} \\[2ex]
\alpha_3^{th} = -\dfrac{\mu_3 \left(\mu_4 + \sigma_4\right)\left(p_1 - p_3\right)\left(\alpha_2 + \alpha_2^{\#}\right)}{\mu_4 \left(p_1 - p_4\right)\left(\alpha_2 + \alpha_2^*\right)},
\end{cases}
$$

with

$$
\frac{1}{\alpha_2^*} - \frac{1}{\alpha_2^{\#}} = \frac{\alpha_2^{\#} - \alpha_2^*}{\alpha_2^* \alpha_2^{\#}} = \frac{\mu_3 \mu_4 \left(\mu_1 + \sigma_1\right)\left(p_3 - p_4\right)}{\mu_1 \mu_2 \left(\mu_3 + \sigma_3\right)\left(\mu_4 + \sigma_4\right)\left(p_1 - p_2\right)}.
$$

Notice that α_2^* and $\alpha_2^\#$ are the critical values given by Equation (9) dropping out the factor $\varepsilon_2/(\mu_2 + \sigma_2)$, while for α_3^{th}, the absent factor is $\varepsilon_3/(\mu_3 + \sigma_3)$. For this reason, in **Table 3**, the values for ε_i, $i = 1, \cdots, 4$, were set $\varepsilon_i = \mu_i + \sigma_i$. Using values given in **Table 3** and **Table 4**, from the second column of **Table 5**, the inequality $Q_0^1 > Q_0$ is always true. Remember that $Q_0^1 = 81.158$ and $Q_0 = 54.787$.

Conversely to the general model, the simplified version of the model does not allow the change in the critical values α_2^*, $\alpha_2^\#$ and α_3^{th} in order to obtain situations where $Q_0 > Q_0^1$ (see Equations (11), (12), (13) and (14), corresponding to cases **B**, **C** and **D** in main text).

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