

Modelling parasitism and predation of mosquitoes by water mites

Lourdes Esteva · Gerardo Rivas ·
Hyun Mo Yang

Received: 1 September 2005 / Revised: 1 July 2006 /
Published online: 8 August 2006
© Springer-Verlag 2006

Abstract Parasitism and predation are two ecological interactions that can occur simultaneously between two species. This is the case of Culicidae (Insecta: Diptera) and water mites (Acari: Hydrachnidia). The larva mites are parasites of aquatic and semiaquatic insects, and deutonymphs and adults are predators of insect larvae and eggs. Since several families of water mites are associated with mosquitoes there is an interest in the potential use of these mites as biological control agents. The aim of this paper is to use mathematical modelling and analysis to assess the impact of predation and parasitism in the mosquito population. We propose a system of ordinary differential equations to model the interactions among the larval and adult stages of mosquitoes and water mites. The model exhibits three equilibria: the first equilibrium point corresponds to the state where the two species are absent, the second one to the state where only mosquitoes are present (water mites need insects to complete their life cycle), and the third one is the coexistence equilibrium. We analyze conditions for the asymptotic stability of equilibria, supported by analytical and numerical methods. We discuss the different scenarios that appear when we change the parasitism and predation parameters. High rates of parasitism and moderate predation can drive two species to a stable coexistence.

L. Esteva (✉) · G. Rivas
Facultad de Ciencias, UNAM 04510, México, D.F. Mexico
e-mail: lesteva@lya.fciencias.unam.mx

G. Rivas
e-mail: grl@fciencias.unam.mx

H. M. Yang
Departamento de Matemática Aplicada UNICAMP – IMECC Caixa Postal 6065,
CEP: 13081-970, Campinas, Brazil
e-mail: hyunyang@ime.unicamp.br

Keywords Parasitism · Predation · Mosquitoes · Water mites · Coexistence equilibrium · Population dynamics

1 Introduction

In the natural aquatic communities there are groups of arthropods that have diverse ecological interactions with other insects during their history life. This is the case of water mites whose basic life cycle consists of eggs, prelarva, larva, three nymphal stages, and adult stage [17]. Larvae need to parasitize aquatic or semiaquatic insects to become nymph, and hence to complete their life cycle. On the other hand, nymphae and adult mites feed on eggs and insect larvae [3, 18]. Thus, there are two major phases in the population dynamics of the water mites and insects: parasitism and predation.

Water mites are parasites and predaceous of different kind of insects, particularly mosquitoes. Experimental and field studies regarding the influence of water mites on their host have been made over the last years [9–11, 16, 17]. This research activity has partially resulted from an increased interest in the use of water mites as a biological control of species of mosquitoes transmissors of diseases.

Although considerable advances in the knowledge of the parasitic and predator associations of water mites with mosquitoes have been made, yet the information is fragmentary. There have been several descriptive studies of community structure and estimation of some demographic parameters [1, 10, 18, 19], but quantitative investigations of the population dynamics of water mites interacting with mosquitoes are needed. The aim of this paper is to model the impact of parasitic and predation relations on the population dynamics of both species. For this end we formulate a mathematical model for the interactions among the larval and adult stages of mosquitoes and water mites. Since the maturation time of each involved stages is different, we consider more adequate a continuous approach consisting of a 6-dimensional system of differential equations. We discuss the different scenarios that appear when we change the parasitism and predation parameters.

Predator-prey and host-parasitoid interactions have been studied extensively. Predator-prey models have been applied to the analysis of communities, and biological control of insects [4, 7, 12]. The host-parasite models have been used on the biological control of insects [8], to compare the strategies of nematodes in different types of habits of their hosts [14], among other applications. On the other hand, experimental works jointly with mathematical models have been contributed to the analysis of the inference of the immune response by helminth endoparasites [2], or to determinate the mechanisms that cause the stability into host-parasitoid interaction of pest insects of citrus [12].

The structure of the present work is as follows. In the first section we formulate the model. Analysis of the model and numerical results are presented in Sects. 3, 4, and 5. Discussion follows in Sect. 6.

2 The model

The mosquito population is divided in two phases: the immature stages (larvae and pupae) denoted by P , and the adult stage. The immature mosquito population becomes adult at a per capita rate α . In the presence of water mites, the adult population is divided in healthy mosquitoes M , and parasitized mosquitoes W . The per capita mortality rates of P , M , and W are denoted by μ_P , μ_M and μ_W , respectively. Since parasitism could increase mortality of mosquitoes, we assume $\mu_M \leq \mu_W$.

The net oviposition rate per female mosquito is proportional to their density, but it is also regulated by a carrying capacity effect depending on the occupation of the available breeding sites. We assume that the per capita oviposition rate of healthy and parasitized mosquitoes are given by $\phi_M \left(1 - \frac{P}{C_M}\right)$ and $\phi_W \left(1 - \frac{P}{C_M}\right)$ respectively, where C_M is the carrying capacity related to the amount of available nutrients and space, and ϕ_M and ϕ_W are the intrinsic oviposition rate of both populations. According to biological observations parasitism reduces the birth capacity of mosquitoes, thus we assume that $\phi_W \leq \phi_M$.

In this model, a crude Lotka-Volterra form of predation is assumed with mosquito larvae being consumed by adult mites at a rate proportional to their density, k_2P , per predator.

For the water mites population we will consider the life stages according to parasitism or predation of mosquitoes: prelarval water mites, L_1 , that search for adult mosquitoes; larval water mites, L_2 , that parasitize adult mosquitoes; and the predatory water mites, A , consisting of deutonymphs and adults that predate mosquito larvae.

The per capita mortality rates of L_1 , L_2 , and A are given by μ_{L_1} , μ_{L_2} , and μ_A , respectively. In the absence of mosquitoes, the per capita oviposition rate of water mites is given by $\phi_A \left(1 - \frac{L}{C_A}\right)$, where C_A is the carrying capacity and ϕ_A , the intrinsic oviposition rate. Following [12], we assume that the mosquito consumption is directly related to the fecundity of water mites. Then, the per capita oviposition rate of adult water mites is incremented by a term $qk_2P/C_M \left(1 - \frac{L}{C_A}\right)$, where q denotes the increasing of the egg load under the consumption of C_M mosquito larvae.

As explained in Sect. 1, water mites need to parasitize mosquitoes to complete their life cycle. We assume that water mites search independently and randomly and their searching efficiency is constant. Then, following [13] the rate of parasitism of mosquitoes by water mites is given by $M(1 - e^{-aL_1})$, where a is the searching efficiency of water mites. However, in order to simplify the model we will approximate the expression above by aML_1 . Thus, flow from the prelarval stage L_1 to the larval stage L_2 is given by k_1ML_1 , where $k_1 = ab$, and $1/b$ is the average searching time. Larvae L_2 become adult at per capita rate σ .

According to the assumptions above the model is given by

$$\begin{aligned}
 P' &= \phi_M \left(1 - \frac{P}{C_M}\right) M + \phi_W \left(1 - \frac{P}{C_M}\right) W - (\alpha + \mu_P)P - k_2PA \\
 M' &= \alpha P - k_1ML_1 - \mu_MM \\
 W' &= k_1ML_1 - \mu_WW \\
 L'_1 &= (\phi_A + qk_2P/C_M) \left(1 - \frac{L_1}{C_A}\right) A - \mu_{L_1}L_1 - k_1ML_1 \\
 L'_2 &= k_1ML_1 - (\sigma + \mu_{L_2})L_2 \\
 A' &= \sigma L_2 - \mu_AA.
 \end{aligned}
 \tag{1}$$

All parameters of the model are non-negative. It can be shown that solutions starting in the region

$$\Omega = \{(P, M, W, L_1, L_2, A) \in \mathbb{R}_+^6 : 0 \leq P \leq C_M, 0 \leq L_1 \leq C_A\}$$

remain there for all $t \geq 0$. Therefore, Ω is positively invariant under system (1), and it is sufficient to consider solutions in this region where the usual existence, uniqueness and continuation results hold for the system.

3 Boundary equilibrium points

From system (1) at equilibrium we immediately identify the following equilibria which are at the boundary of Ω :

$$P_0 = (0, 0, 0, 0, 0, 0), \quad P_M = (P^*, M^*, 0, 0, 0, 0),$$

where

$$P^* = \left(1 - \frac{1}{R_M}\right) C_M \tag{2}$$

$$M^* = \frac{\alpha}{\mu_M} P^* \tag{3}$$

and

$$R_M = \frac{\phi_M \alpha}{\mu_M (\alpha + \mu_P)}. \tag{4}$$

Thus, P_0 is the equilibrium where both species are absent and P_M , the state where only mosquitoes are present. Note that if the mosquito population is zero then water mites can not complete their life cycle and therefore they will not be able to survive.

From the expression for P^* it follows that P_M will be feasible if and only if $R_M > 1$. The parameter R_M is the *basic offspring number* of mosquitoes, that is, the average number of mosquitoes produced by a single mosquito during

its survival time. This can be seen as follows: since $\frac{1}{\alpha + \mu_P}$ is the average time of survival of an immature mosquito and $\frac{1}{\alpha}$ is the average time of its permanence as such, then $\frac{\alpha}{\alpha + \mu_P}$ is the probability that an egg will succeed to become an adult mosquito. On the other hand, $\frac{\phi_M}{\mu_M}$ is the average number of eggs oviposited by one mosquito. Thus, the product of the last two quantities, which is equal to R_M , is the average number of mosquitoes produced by a single mosquito. Then, P_M will be feasible if and only if the basic offspring number is larger than one.

The stability properties of P_0 are given by the eigenvalues of the derivative of system (1) evaluated in this point which is given by

$$DF(P_0) = \begin{bmatrix} -(\alpha + \mu_P) & \phi_M & \phi_W & 0 & 0 & 0 \\ \alpha & -\mu_M & 0 & 0 & 0 & 0 \\ 0 & 0 & -\mu_W & 0 & 0 & 0 \\ 0 & 0 & 0 & -\mu_{L_1} & 0 & \phi_A \\ 0 & 0 & 0 & 0 & -\sigma - \mu_{L_2} & 0 \\ 0 & 0 & 0 & 0 & \sigma & -\mu_A \end{bmatrix}. \tag{5}$$

Solving $\text{Det}(\lambda I - DF(P_0)) = 0$ we find that the eigenvalues of $DF(P_0)$ are $-\mu_A, -\mu_{L_1}, -\mu_W, -(\sigma + \mu_{L_2})$, and the roots of the polynomial

$$p_1(\lambda) = \lambda^2 + (\alpha + \mu_P + \mu_M)\lambda + (\alpha + \mu_P)\mu_M(1 - R_M).$$

The roots of p_1 have negative real part if and only if its coefficients are positive, and it is clear that this is equivalent to the condition $R_M < 1$. Then, the trivial equilibrium P_0 is locally asymptotically stable if $R_M < 1$ and a saddle point if $R_M > 1$.

To prove global stability of P_0 in Ω when $R_M \leq 1$ we use the Lyapunov function $V_1 : \Omega \rightarrow R$ given by

$$V_1 = \alpha P + (\alpha + \mu_P)(M + W). \tag{6}$$

The orbital derivative of V_1 is given by

$$\dot{V}_1 = -(\alpha + \mu_P) \left[\mu_M(1 - R_M(1 - P/C)) + \mu_W(1 - rR_M(1 - P/C)) + \frac{\alpha k_2 AP}{\alpha + \mu_P} \right], \tag{7}$$

where $r = \frac{\phi_W \mu_M}{\phi_M \mu_W} \leq 1$ by hypothesis. If $R_M \leq 1$ then $\dot{V}_1 \leq 0$, system (1) shows that the maximal invariant set contained in $\dot{V}_1 = 0$ is P_0 which is locally asymptotically stable. Therefore, it follows from La-Salle Lyapunov Theorem [6] that P_0 is globally asymptotically stable in Ω .

When $R_M > 1$ the equilibrium P_M is feasible, and its stability is determined by the matrix $DF(P_M)$. After some calculations we find that the eigenvalues of

$DF(P_M)$ are $-\mu_W$ and the roots of the polynomials

$$p_2(\lambda) = \lambda^2 + \left(\frac{\phi_M}{C_M} M^* + \alpha + \mu_P + \mu_M \right) \lambda + \mu_M(\alpha + \mu_P)(R_M - 1),$$

$$p_3(\lambda) = \lambda^3 + a_1\lambda^2 + a_2\lambda + a_3,$$

where

$$\begin{aligned} a_1 &= k_1M^* + \mu_{L_1} + \mu_A + \sigma + \mu_{L_2} \\ a_2 &= (\sigma + \mu_{L_2})(k_1M^* + \mu_{L_1} + \mu_A) + \mu_A(k_1M^* + \mu_{L_1}) \\ a_3 &= \mu_A(k_1M^* + \mu_{L_1})(\sigma + \mu_{L_2}) - \left(\phi_A + qk_2 \frac{P^*}{C_M} \right) \sigma k_1M^*. \end{aligned}$$

Since $R_M > 1$, the coefficients of the polynomial p_2 are positive which in turn implies that its roots have negative real part.

By the Routh-Hurwitz criteria, the polynomial p_3 has roots with negative real part if and only if $a_i > 0, i = 1, \dots, 3$, and $a_1a_2 > a_3$. The coefficients a_1 and a_2 are positive, and the last condition is straightforward. Therefore, the stability of P_M is given by the sign of a_3 , which is positive if and only if

$$R_A \equiv \frac{(\phi_A + qk_2P^*/C_M)k_1M^*\sigma}{\mu_A(k_1M^* + \mu_{L_1})(\sigma + \mu_{L_2})} < 1. \tag{8}$$

Global stability of P_M can be proven for the special case $\phi_A + qk_2 \leq \mu_A$ via de Lyapunov function defined in Ω as

$$V_2 = L_1 + L_2 + A. \tag{9}$$

The orbital derivative of V_2 is given by

$$\dot{V}_2 = [(\phi_A + qk_2P/C_M)(1 - L_1/C_A) - \mu_A]A - \mu_{L_1}L_1 - \mu_{L_2}L_2. \tag{10}$$

Since P/C_M , and L/C_A are less or equal than one, $\dot{V}_2 \leq 0$. Then, all solutions starting in Ω approach the maximal invariant set contained in $\dot{V}_2 = 0$ [6]. It can be seen readily that this set is the projection of Ω on the plane $W = L_1 = L_2 = A = 0$. Here Eq. 1 become the following two dimensional system in P and M :

$$\begin{aligned} P' &= \phi_M \left(1 - \frac{P}{C_M} \right) M - (\alpha + \mu_P)P \\ M' &= \alpha P - \mu_M M. \end{aligned}$$

Applying Bendixon criteria [20] it can be seen that this system does not have periodic orbits, and since P_M is locally asymptotically stable, all trajectories with

initial conditions $P(0)$ and $M(0)$ different from zero approach this equilibrium. Therefore P_M is globally asymptotically stable in Ω minus the subspace $P = M = 0$.

The parameter R_A defined in (8) can be interpreted as the average number of eggs oviposited by a single mite that survives to the adult stage when the number of larvae and adult mosquitoes are at the equilibria P^* and M^* , respectively. Then, assuming that the mosquito population is at the equilibrium P_M^* , the condition $R_A < 1$ says that if the average number of adult water mites resulting from a single mite is less than one, only the mosquito population can survive.

Inequality (8) can be reformulated in terms of R_M, k_1 and k_2 as

$$k_2 < \frac{\mu_A(\sigma + \mu_{L_2})R_M}{q\sigma(R_M - 1)} \left(1 - s + \frac{\mu_{L_1}\mu_M R_M}{\alpha C_M(R_M - 1)k_1} \right), \tag{11}$$

where $s = \frac{\phi_A\sigma}{\mu_A(\sigma + \mu_{L_2})}$.

This implies that P_M is stable in the region of the parameter space k_1k_2 below the hyperbola given by the right hand side of (11) which has asymptote $\bar{k}_1 = \frac{\mu_A(\sigma + \mu_{L_2})R_M}{q\sigma(R_M - 1)}(1 - s)$. Note that this asymptote is positive for $s < 1$, and negative for $s > 1$.

4 Coexistence equilibria

In terms of L_1 and P , the coordinates M, W, L_2 , and A of the non trivial equilibrium points of system (1) are given by

$$\begin{aligned} M &= \frac{\alpha}{k_1L_1 + \mu_M}P \\ W &= \frac{k_1\alpha}{\mu_W(k_1L_1 + \mu_M)}PL \\ L_2 &= \frac{k_1\alpha}{(\sigma + \mu_{L_2})(k_1L_1 + \mu_M)}PL \\ A &= \frac{\sigma k_1\alpha}{\mu_A(\sigma + \mu_{L_2})(k_1L_1 + \mu_M)}PL. \end{aligned} \tag{12}$$

Those equilibria have biological meaning for $0 < L_1 < C_A$ and $0 < P < C_M$. Substituting (12) in the first and third equations of (1) and solving for L_1 , we obtain after some manipulations that the solutions (P, L_1) are the intersections of the two curves $L_1 = f(P), L_1 = g(P)$ given by

$$\begin{aligned} f(P) &= \frac{\mu_M(R_M - 1 - R_MP/C_M)}{k_1[1 - rR_M + rR_MP/C_M + \alpha sk_2P/\phi_A(\alpha + \mu_P)]}, \\ g(P) &= \frac{C_A[\alpha k_1P(\phi_A(s - 1) + sqk_2P/C_M) - \phi_A\mu_{L_1}\mu_M]}{k_1[\alpha sP(\phi_A + qk_2P/C_M) + C_A\phi_A\mu_{L_1}]}, \end{aligned} \tag{13}$$

where $r = \frac{\phi_W\mu_M}{\mu_W\phi_M} \leq 1$.

If $R_M \leq 1$ then $f(P) \leq 0$ for $P \geq 0$, therefore $R_M > 1$ is a necessary condition for positive solutions of (13), and in the following we assume this.

Notice that $f(P) \leq 0$ for $P \geq P^*$, where P^* is given by (2). If $rR_M < 1$, the denominator in the expression for $f(P)$ is positive for all $P \geq 0$. In this case $f(0) = \frac{\mu_M(R_M-1)}{1-rR_M} > 0$, and $f(P)$ is a decreasing function for $P \geq 0$. If $rR_M \geq 1$, $\lim_{P \rightarrow 0^+} f(P) < 0$, and the denominator of $f(P)$ has a root $P_f \in [0, P^*)$. Furthermore, $\lim_{P \rightarrow P_f^-} f(P) = -\infty$, $\lim_{P \rightarrow P_f^+} f(P) = \infty$, and $f(P)$ is a positive decreasing function for $P_f < P < P^*$.

On the other hand, it is easy to verify that $g(P)$ has a positive root P_g , and $g(P) < 0$ for $0 \leq P < P_g$. Furthermore, $g(P)$ is positive and increasing for $P_g \leq P$, and $\lim_{P \rightarrow \infty} g(P) = C_A$.

From the above analysis we conclude that $f(P)$ and $g(P)$ have a unique intersection $0 < L_1 < C_A$ if and only if $P_g < P^*$, which implies $g(P^*) > 0$. The last inequality is equivalent to

$$R_A = \frac{(\phi_A + qk_2P^*/C_M)k_1M^*\sigma}{\mu_A(k_1M^* + \mu_{L_1})(\sigma + \mu_{L_2})} > 1. \tag{14}$$

Figures 2a and b show the intersection of $f(P)$ and $g(P)$ when $r = 0.028$ and $r = 0.1$, respectively. In both figures $\mu_A = 0.01 \text{ day}^{-1}$, $\mu_{L_1} = \mu_{L_2} = 0.02 \text{ day}^{-1}$, $k_1 = 0.001 \text{ day}^{-1}$, $k_2 = 0.005 \text{ day}^{-1}$, $q = 0.001$, $R_M = 30$ and $C_M = 1,000$ which implies $P^* = 967$ and $R_A = 60$.

We summarize the above results in the following theorem.

Theorem 1 *System (1) has a unique coexistence equilibrium P_{MA} given by the solution of Eqs. 12 and 13 if and only if $R_M > 1$ and $R_A > 1$.*

Then, if the average number of adult water mites resulting from a single mite is bigger than one, the coexistence equilibrium is feasible, and the equilibrium point P_M is unstable. In the parameter space k_1k_2 the region of existence of P_{MA} corresponds the points (k_1, k_2) above the hyperbola given by Eq. 11 (Fig. 1).

Writing inequality (14) in the equivalent form

$$k_1 > \frac{\mu_{L_1}}{M^* \left(\frac{(\phi_A + qk_2P^*/C_M)\sigma}{\mu_A(\sigma + \mu_{L_2})} - 1 \right)} = k_1^*, \tag{15}$$

we obtain a lower bound k_1^* of the rate of parasitism necessary for coexistence of both species in terms of their demographic parameters and the rate k_2 of predation.

The parameter $R_W = rR_M$ represents the number of adult mosquitoes produced by a parasitized mosquito. When r decreases it is expected that the number of larvae \bar{P} (and consequently adult mosquitoes $\bar{M} + \bar{W}$) decreases as it can be seen in Fig. 2. However, in the same figures it is observed that the impact of the reduction of r on the prelarvae water mites \bar{L}_1 is very small.

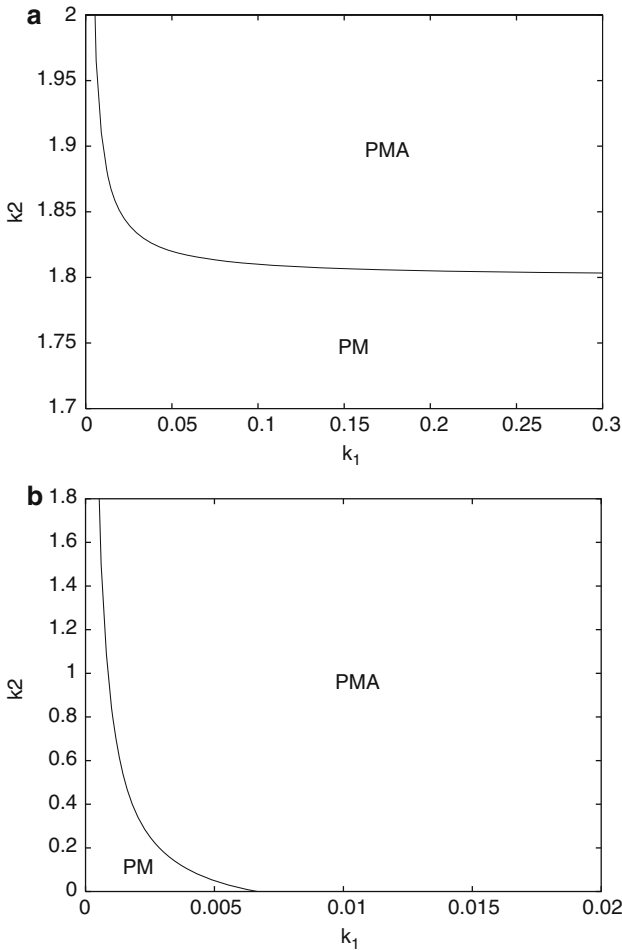


Fig. 1 Regions of existence and stability of the equilibria P_M and P_{MA} in the parameter space k_1 and k_2 for different values of ϕ_A . **a** $\phi_A = 0.01 \text{ day}^{-1}$, **b** $\phi_A = 0.02 \text{ day}^{-1}$. The values of the other parameters are given in Table 1

The equilibrium P_{MA} could not be found explicitly and its local stability is very difficult to determine since we must show that the eigenvalues of the 6×6 Jacobian matrix at P_{MA} have negative real part. Nevertheless, the numerical simulations suggest that this equilibrium is stable (see next section).

5 Numerical results

In this section we present some numerical results for model (1). In particular, we are interested in the impact of predation and parasitism on the different populations of mosquitoes and water mites. For this, we will vary the parameters

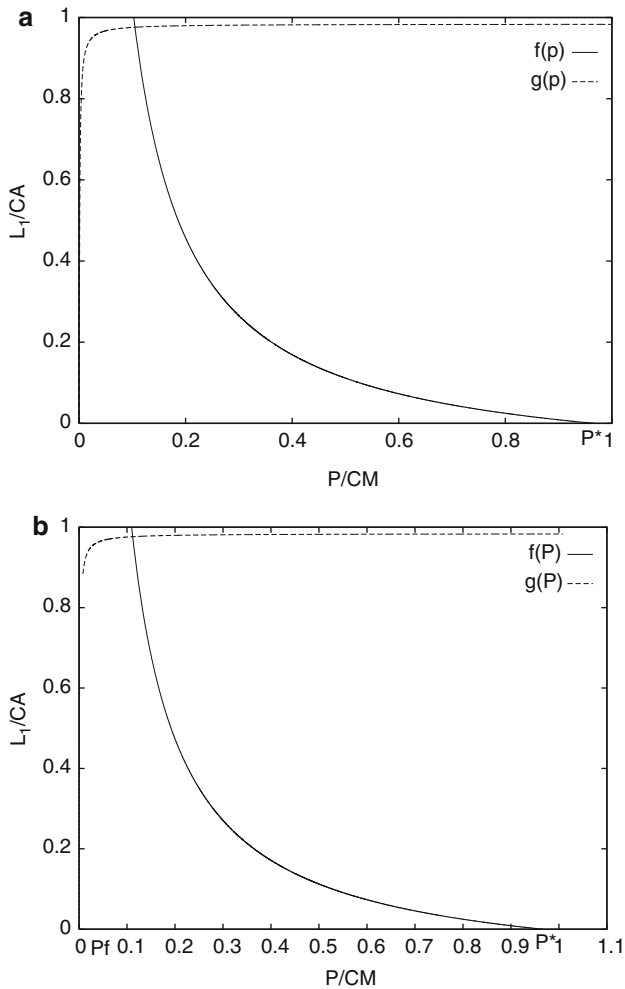


Fig. 2 Coexistence equilibrium P_{MA} given by the intersection of the normalized graphs of $f(P)$ and $g(P)$ in the space $(P/C_M, L_1/C_A)$. **(a)** $\mu_W = 0.7 \text{ day}^{-1}$, **(b)** $\mu_W = 0.2 \text{ day}^{-1}$. The values of the other parameters are $\phi_M = 5 \text{ day}^{-1}$, $\phi_W = 1 \text{ day}^{-1}$, $\phi_A = 0.75 \text{ day}^{-1}$, $\mu_M = 0.1 \text{ day}^{-1}$, $\mu_{L_1} = \mu_{L_2} = 0.02 \text{ day}^{-1}$, $\mu_A = 0.01 \text{ day}^{-1}$, $k_1 = 0.001 \text{ day}^{-1}$, $k_2 = 0.005 \text{ day}^{-1}$, $q = 0.001$, $C_M = 1000$, and $C_A = 100$. In the graphs, P_f and P^* are the zeros of the numerator and denominator of $f(P)$ (see Eq. 13)

k_1, k_2 in the numerical simulations. In all cases the conditions for the coexistence equilibrium P_{MA} are satisfied.

The vital parameters of mosquitoes and water mites are given in Table 1, and except for μ_W , they are in agreement with values reported in the literature for *Aedes aegypti* mosquitoes (e.g. [5]) and for different kind of water mites [18]. We assume that the carrying capacity of mosquitoes and water mites are the same $C_M = C_A = 100$, μ_W is two times the natural mortality μ_M and $q = 0.0005$.

Table 1 Parameter values for model (1)

ϕ_M	ϕ_A	μ_P	μ_M	μ_W	μ_{L_1}	μ_{L_2}	μ_A	α	σ	q	C_M	C_A
10	0.75	0.05	0.07	0.14	0.02	0.02	0.016	0.05	0.1	0.005	100	100

Units are days⁻¹ except for q , C_A and C_M

In Fig. 3 we show the temporal courses of the population sizes of P , M , W , L_1 and A , respectively, when the value of the parasitism rate k_1 is equal to 0.001, 0.01, 0.1 and 0.9. When we increase k_1 it is observed that the mosquito larvae population P remains almost constant (Fig. 3a), but the population size of healthy adult mosquitoes M initially decreases drastically and then stabilizes to values that approach zero as k_1 increases (Fig. 3b). On the other hand, the parasitized mosquitoes W first increase and then decrease to an equilibrium as it is shown in Fig. 3c.

Both populations of prelarva and adult mites approach the equilibrium values monotonically (Figs. 3d, e) for all values of k_1 . However, we notice that the variation of the prelarva population with respect to k_1 is very small, which could be due to the fact that parasitic loads are limited by factors related to searching time in the aquatic environment, and the specific place where they are allocated on the host. The great increasing of the adult water mites is produced by the combination of the entrance of larvae and the gaining due to parasitism of mosquitoes.

In Fig. 4 we increase the values of the predation rate k_2 from 0 to 0.9. We notice that for k_2 sufficiently big ($k_2 > 0.5$) the population sizes of P , M and W decrease drastically, and present damped oscillations around the equilibrium (Figs. 4a–c). Water mites populations also decrease and have oscillations toward the equilibrium, but the decrease observed in the prelarva population L_1 is less severe (Figs. 4d, e). The observed fluctuations result from predation of adult water mites on mosquitoes as in the classic predator-prey model. However, the great decrease of the water mite adults is due to the fact that larva water mites can not become adults due to the reduction of mosquitoes by predation. Since larva water mites are not predators of early stages of mosquitoes their population size is not strongly affected.

We also carried out numerical simulation for different oviposition rates of parasitized mosquitoes. We take values of ϕ_W that range from 0 to 7.5. In all cases we did not find great differences in the sizes of the populations.

6 Discussion

Most of the studies in population dynamics of mites have been done on species that are important for humans, as it is the case of ticks of cattle, mites predators of other plague mites of different cultures, and ectoparasitic mites of bees like *Varroa jacobsoni*. For water mites and their interaction with insects, these studies are scarce, being limited mainly to the determination of some demographic

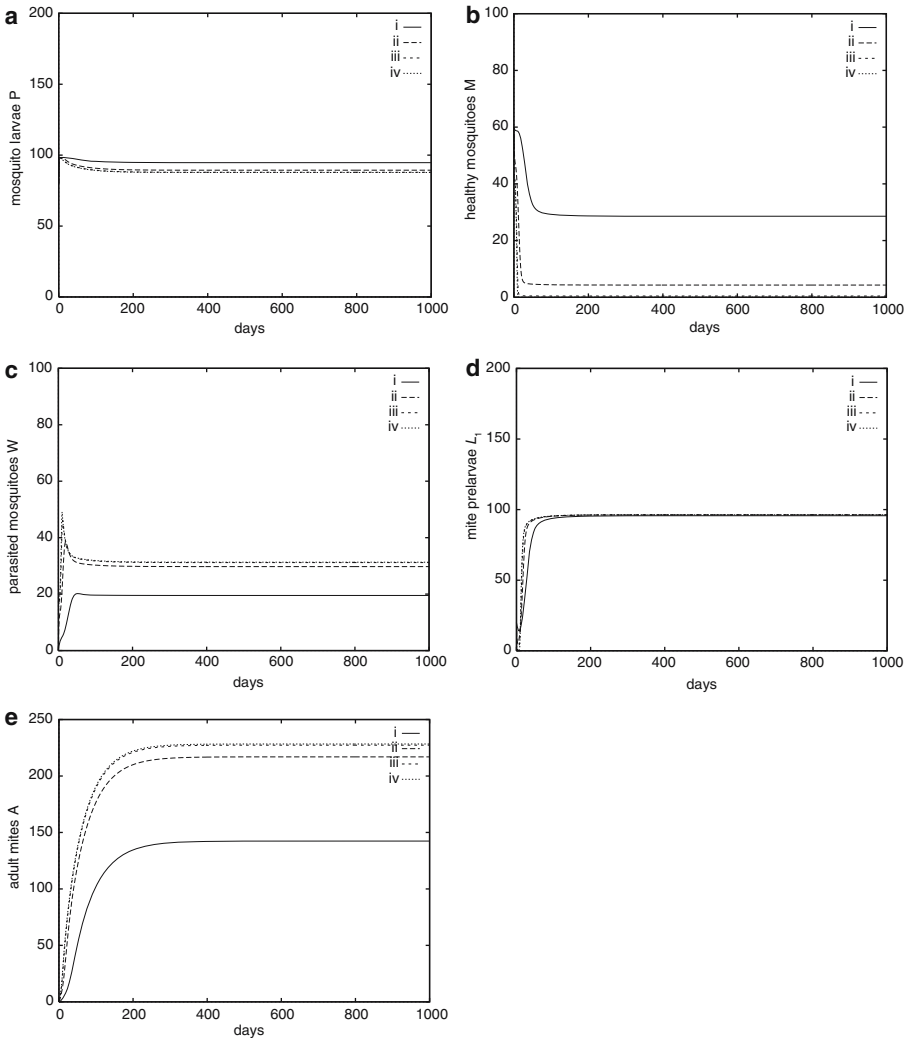


Fig. 3 Numerical simulations of system (1) for the parasitism rate k_1 equal to *i* 0.001 day⁻¹, *ii* 0.01 day⁻¹, *iii* 0.1 day⁻¹ and *iv* 0.9 day⁻¹. The values of the other parameters are given in Table 1. The initial conditions are $P = 80$, $M = 60$, $L_1 = 20$ and $A = L_2 = W = 0$

parameters. For example, there is evidence that parasitism of water mites on Culicidae affects the metabolism of females of this species with consequent reduction of their birth rate [11], however, there are no quantitative results and only a few field and experimental observations show that the damage on the mosquitoes population is not so strong to bring the mosquitoes to extinction.

On the other hand, there is a predator-prey relationship between water mites and Culicidae since the larvae of this species are part of the potential food for deutonymphs and adults of the water mites. Thus population dynamics of the

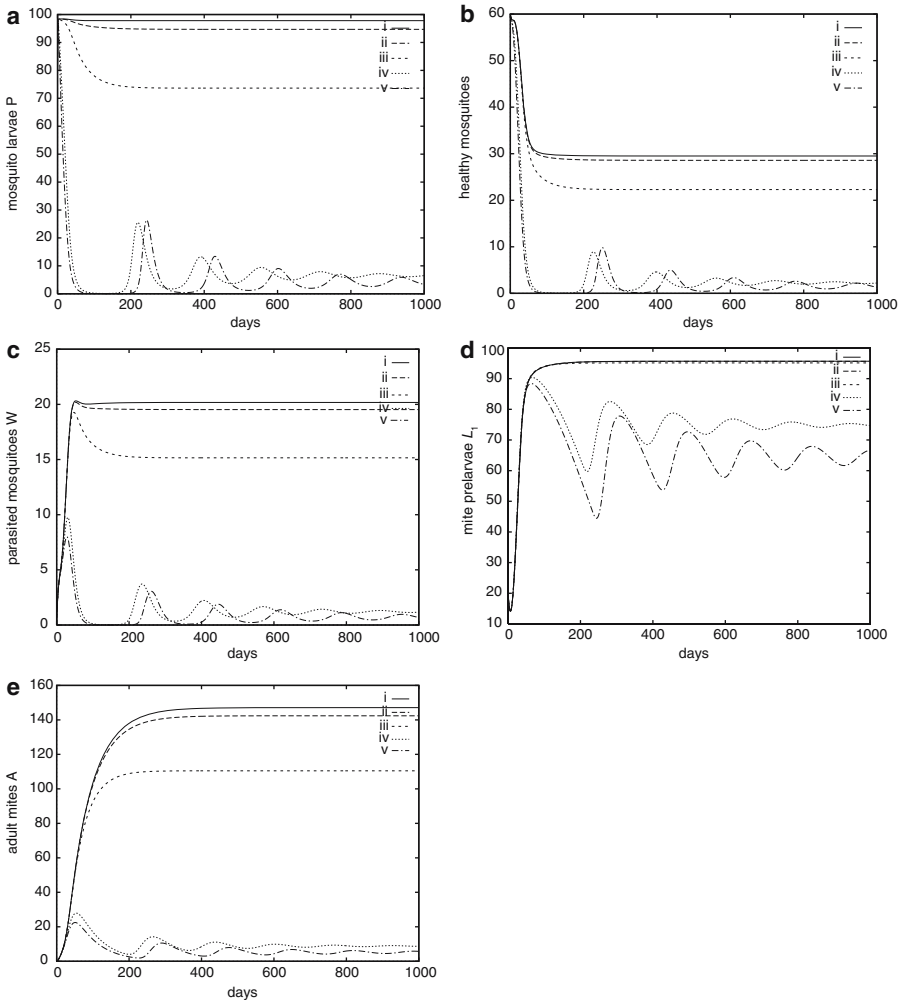


Fig. 4 Numerical simulations of system (1) for the predation rate k_2 equal to *i* 0.0 day^{-1} , *ii* 0.001 day^{-1} , *iii* 0.01 day^{-1} , *iv* 0.5 day^{-1} and *v* 0.9 day^{-1} . The values of the other parameters are given in Table 1. The initial conditions are $P = 80, M = 60, L_1 = 20$ and $A = L_2 = W = 0$

water mites has a substantive dependency respect to the mosquitoes. Yet, the measurements of how the predation by water mites affect the dynamics of mosquito populations are insufficient.

The degree of temporal co-occurrence between mite larval and potential mosquito host species in part explain the host preferences, but host species could also differ in their susceptibility to parasitism when given equivalent exposure to larval water mites [16].

Population dynamics of predators and prey, as well as of parasites and host need additional information on population parameters. These can be obtained

by sampling in the field and by experiments in the laboratory. It is clear that the aquatic environment restricts possibilities for sampling and experimentation on water mites. Nevertheless, the small size and short duration of the history life of this population could allow a suitable design of experiments and sampling adequate for the estimation of the parameters needed in population dynamics models.

In this paper we propose and analyze a simple mathematical model for the parasitism and predation relations between water mites and mosquitoes. These ecological interactions are modeled by the mass action law. The model incorporates the larval and adult stages of the two population. We also include a class of parasitized mosquitoes which has a lower birth rate and higher mortality rate than healthy mosquitoes.

Under the biological assumptions given in Sect. 2 our model has three equilibrium points. One corresponds to the absence of the two populations, and the system evolves to that state if the basic offspring number of mosquito population $R_M \leq 1$. When $R_M > 1$ a second equilibrium P_M emerges where only mosquito population is present. The possible absence of water mites does not alter the population dynamics of Culicidae, but the absence of the mosquitoes is a limiting factor for water mites, since without mosquitoes they can not complete their life cycle. For this reason there is not an equilibrium where only water mites are present.

Stability analysis of P_M reveals that this equilibrium is stable when the average number of water mites resulting from a single water mite is less than one ($R_A < 1$). When the conditions of stability of P_M not longer hold, we found an interior equilibrium where two species coexist. The behavior of the populations can be interpreted in terms of the region of existence of equilibria with respect to $k_1 k_2$ given in Fig. 1. If the oviposition rate of water mites ϕ_A times the fraction of larvae that survive to the adult state is less than the mortality rate μ_A (or equivalent $s < 1$), the water mite population would not be able to survive for low predation rates k_2 , no matter the value of the parasitism rate k_1 and the initial state of the population. Moreover, high rates of predation will drive the system to coexistence of the two population even for low rates of parasitism (Fig. 1a). If $s > 1$, coexistence can be reached even in the absence of predation if parasitism is sufficiently high (Fig. 1b). In either cases we could conclude that the dynamics of mosquitoes and water mites populations are more sensitive to predation than to parasitism in the sense that for any value of k_1 , it is enough to increment k_2 sufficiently to enter to the coexistence region.

Predation could increase the fertility rate, then giving the opportunity to the water mite population to increase. If in the absence of mosquitoes the basic offspring of water mites is bigger than one, predation is not essential to their survival. This result is in agreement with the fact that mosquitoes are not the only food source of water mites (other sources can be microcrustaceans or other species of mites [18]).

In the numerical simulation shown in Sect. 5 we observe that moderate rates of predation and high rates of parasitism drive the total population sizes of water mites and mosquitoes to an equilibrium that is far from zero (see Fig. 3). On the

contrary, the populations of larval and adult mosquitoes as well as adult water mites tend to levels very close to zero as the predation rate increases (Fig. 4). Then, for high rates of predation, small fluctuations of the environment could drive both population to extinction. It seems that in terms of the population sizes of water mites and mosquitoes, parasitism is an ecological interaction more stable than predation.

Some biological studies suggest that water mites species could be a potential biological control of mosquitoes populations. In [16] it is mentioned that *Arrenurus* mite parasitism has a significant detrimental effect on certain *Aedes* species of mosquitoes that are common in Canada. Mite genera predators of mosquitoes that could be biological controls are *Limnesia* that consume large amounts of mosquito eggs and *Piona* that is a voracious predator of mosquito larva [15].

Several aspects of the biology of water mites must be considered to evaluate them as possible control agents of mosquitoes. The main consideration is the impact of an individual mite: how many prey a predator can consume, or the extent of detrimental effects of a parasite on its hosts. Other aspects include the water mites reproductive rate, dispersal efficiency, host or prey specificity, and distribution relative to mosquitoes.

In spite of the biological research on this subject, systematic studies about the extent of the impact of water mites on mosquito population that could be used as a basis for a control program are still scarce and fragmentary. We think that mathematical models jointly with experimental data could be a powerful tool to address important questions concerning the dynamical interactions of water mites and mosquitoes, and to assess the effectivity of biological control of mosquitoes using water mites.

Acknowledgements We want to express our gratitude to Johannes Müller for his valuable help. We also thank two anonymous referees for their careful reading that helped to improve this paper. L.E. and G.R. wants to acknowledge support from project No. IN218403, PAPIIT-UNAM.

References

1. Bader, C.: Some biological and ecological data on water mites, mainly some significant data on the life-duration. *Int. J. Acar.* **6**(3), 239–243 (1980)
2. Berding, C., Keymer, A.E., Murray, J.D., Slater, A.F.G.: The population dynamics of acquired immunity to helminth infection: experimental and natural transmission. *J. Theor. Biol.* **126**, 167–182 (1987)
3. Davids, C.: The influence of larval parasitism on life history strategies. in water mites (Acar: Hydrachnidia). *Arch. Hydrobiol.* **141**(1), 35–43 (1997)
4. Dixon, A.F.G.: *Insect Predator-Prey Dynamics*. Cambridge University Press, Cambridge (2000)
5. Gubler, D.J.: Dengue. In: Monath T.P. (ed.) *The Arbovirus: Epidemiology and Ecology*, vol. II, pp. 213–261. CRC Press, Florida (1986)
6. Hale, J.K.: *Ordinary Differential Equations*. Wiley, New York (1969)
7. Hassell, M.P.: Foraging strategies, population models, and biological control: a case of study. *J. Anim. Ecol.* **49**, 603–628 (1980)
8. Hassell, M.P., May, R.M.: Stability in insect host-parasite models. *J. Anim. Ecol.* **42**, 693–726 (1973)
9. Laird, M.: Some natural enemies of mosquitoes in the vicinity of Palmamal, New Britain. *Trans. R. Soc. N.Z.* **76**, 453–476 (1947)

10. Lanciani, C.A., Boyt, A. D.: The effect of a parasitic water mite, *Arrenurus pseudotenuicollis* (Acari: Hydrachnellae), on the survival and reproduction of the mosquito *Anopheles crucians* (Diptera: Culicidae). *J. Med. Entomol.* **14**, 10–15 (1977)
11. Mullen, G.: Acarine parasites of mosquitoes I. A critical review of all know records of mosquitoes parasitized by mites (Acarina: Hydrachnellae). *Proc. N.J. Mosq. Exterm. Assoc.* **61**, 90–94 (1975)
12. Murdoch, W., Briggs, Ch. J., Swarbrick, S.: Host suppression and stability in a parasitoid-host system: experimental demonstration. *Science* **309**, 610–613 (2005)
13. Nicholson, A.J., Bailey, V.A.: An outline of the dynamics of animal population. *Aust J. Zool.* **2**, 9–65 (1954)
14. Roberts, M.G.: A pocket guide to host-parasite models. *Parasitol. Today* **11**(5), 172–177 (1995)
15. Smith, B.P.: The potential of mites as biological control agents of mosquitoes. In: Hoy, M., Cunnigham, G., Knutson, L. (eds.) *Research needs for development of biological control of pest by mites*, pp. 79–85. *Agric. Exp. Stn. Univ. Calif., USA* (1983)
16. Smith, B.P., McIver, S.B.: Factors influencing host selection and successful parasitism of *Aedes* spp. mosquitoes by *Arrenurus* spp. mites. *Can J. Zool.* **62**, 1114–1120 (1984)
17. Smith, B.P.: Host-parasite interaction and impact of larval water mites on insects. *Ann. Rev. Entomol.* **33**, 487–507 (1988)
18. Smith, I.M., Cook, D.R.: Water mites. In: Thorp and Covich (eds.) *Freshwater invertebrates from North American*, pp. 470–492, *Academic, USA* (1991)
19. Stechmann, D.H.: Zum Wirtskreis synopsischer *Arrenurus*-Arten (Hydrachnellae, Acari) mit parasitischer Entwicklung an Nematocera (Diptera). *Z. Parasitkd.* **62**, 267–283 (1980)
20. Verhulst, F.: *Nonlinear Differential Equations and Dynamical Systems*. Springer, Berlin Heidelberg New York (1990)