# A NEW MODEL WITH DELAY
# FOR MOSQUITO POPULATION DYNAMICS

Hui Wan

Jiangsu Key Laboratory for NSLSCS
School of Mathematical Science
Nanjing Normal University, Nanjing, 210023, China

Huaiping Zhu

LAboratory of Mathematical Parallel Systems (LAMPS)
Centre for Disease Modeling
Department of Mathematics and Statistics
York University, Toronto, Ontario, M3J 1P3, Canada

(Communicated by Jia Li)

Abstract. In this paper, we formulate a new model with maturation delay for mosquito population incorporating the impact of blood meal resource for mosquito reproduction. Our results suggest that except for the usual crowded effect for adult mosquitoes, the impact of blood meal resource in a given region determines the mosquito abundance, it is also important for the population dynamics of mosquito which may induce Hopf bifurcation. The existence of a stable periodic solution is proved both analytically and numerically. The new model for mosquito also suggests that the resources for mosquito reproduction should not be ignored or mixed with the impact of blood meal resources for mosquito survival and both impacts should be considered in the model of mosquito population. The impact of maturation delay is also analyzed.

1. **Introduction.** Mosquito life goes through four stages: egg, larva, pupa, and adult. Each of these stages can be easily recognized by their special appearance. The duration of the whole cycle, from egg laying to an adult mosquito eclosion, varies between 7 and 20 days, depending on the ambient temperature of the swamp and the mosquito species involved [12].

The feeding habits of mosquitoes are quite unique in that only the adult females bite human and animals in order to take blood meals, and the male mosquitoes feed only on plant juices. Female mosquitoes feed on man, domestic animals, such as cattle, horses, goats, etc; all species of birds including chickens and ducks; all types of wild animals including deer, rabbits; and they also feed on snakes, lizards, frogs, and toads. Female mosquitoes will not lay viable eggs without blood meals.

Therefore, the abundance of mosquito in a region in closely related to the blood meal resources available in the region ([16]).

Most male mosquitoes live about a week while females can live up to a month. The life span of an adult mosquito usually depends on several factors: temperature, humidity, sex of the mosquito and season of the year [28].

A lot of mosquito-borne diseases, such as malaria, dengue and West Nile virus, are transmitted by mosquitoes. Understanding the population dynamics of mosquitoes is fundamental to the study of the epidemiology of these diseases for the purpose of optimal control and prevention. Studies on the population structure of mosquitoes have important implications for the prediction and assessment of the effects of many vector control strategies. Since only the adult female mosquitoes are responsible for transmitting diseases, therefore in general, models focus only on describing the dynamics of adult female mosquitoes. There have been extensive dynamical modeling studies of the mosquito population (See [4, 5, 7, 8, 9, 10, 11, 19, 21] etc.) and there are variety of single-species models which may be used to model the mosquito population (See [1, 3, 6, 17, 22, 25] etc.). Ruan ([23]) gives an extensive survey on models with delay of discrete and distributed types for mosquito population or single species population.

One can see that all of these models mentioned above do not distinguish the essential blood meal resource for eggs laying from the resource for adult mosquito survival. It is our aim to formulate a new model for mosquito population dynamics which incorporate the impact of the necessary resource not only for mosquito survival but also for mosquito reproduction.

This paper is organized as follows. In Section 2, we provide the derivation of a new model for the population of adult female mosquitoes, considering the effect of limited resource for the reproduction and development of mosquito population. We analyze the dynamics of this model in Section 3, including the existence of equilibria, stability, and Hopf bifurcation. Finally, we present some numerical simulations and comment on our findings in Section 4.

2. **Derivation of the new model.** Let $M(t)$ be the population size of female mosquitoes at time $t$ ($t \geq 0$). We start with the Logistic equation and rewrite it as

$$\frac{dM(t)}{dt} = rM(t) - dM(t) - \kappa M(t)^2, \tag{1}$$

where $r$, $d$ ($r > d$) and $\kappa$ denote per capita birth rate, per capita death rate and intraspecific competition rate respectively.

The right hand side of (1) consists of three parts: new birth, natural death and population decreases due to the intraspecific competition for survival. Considering the aquatic stages for the development of eggs into adult mosquitoes. If we denote the maturation time as $\tau$, and if on average, each female mosquito produce $r$ number of eggs, then $rM(t - \tau)$ number of mosquito will emerge. Female Mosquitoes need blood meals to lay viable eggs, hence the availability of blood meals is crucial for mosquito reproduction. It's natural to adopt a Ricker function

$$rM(t)e^{-\alpha M(t)}$$

to reflect the restriction of the blood meal resource for reproduction of eggs. Note that different from the model in [6] for which the Ricker function is used to model the impact of the whole environmental resources, here we use Ricker function to model the impact of the blood meal resource on the reproduction of mosquito eggs. This

function is nonlinear and reaches its maximum at $M(t) = 1/\alpha$, hence the reciprocal of $\alpha$ represents the size of female mosquito population at which the maximum number of mosquito eggs can be laid. Therefore, it is reasonable to use $1/\alpha$ to measure the maximum blood meal resource of a given region that the maximum eggs reproductivity can be reached. A sufficient small $\alpha > 0$ means the region has enough resource of blood meals for female mosquitoes to reproduce.

Assuming $\mu$ is the natural death rate of mosquitoes during the preadult stages, thus, according to the derivation in [18], the term $e^{-\mu\tau}$ denotes the survival rate during these stages. Thus the population growth model for adult female mosquitoes can be written as

$$\frac{dM(t)}{dt} = re^{-\alpha M(t-\tau)}M(t-\tau)e^{-\mu\tau} - dM(t) - \kappa M(t)^2. \tag{2}$$

Note that model (2) is reduced to the Logistic equation (1) when $\tau = 0$, $\alpha = 0$; (2) becomes a special case of model in [6] when $\kappa = 0$, i.e. the intraspecific competition is ignored; and (2) is simplified to a exponential growth model when $\tau$, $\alpha$ and $\kappa$ are zero simultaneously. In the following, we consider the model (2) with $r > d > 0$, $\mu > 0$, $\tau \geq 0$ $\alpha \geq 0$, $\kappa \geq 0$, and $\alpha^2 + \kappa^2 \neq 0$.

For model (2), we first have the following result.

**Proposition 1.** *Let $X := C([-\tau, 0], \mathbb{R}_+ \setminus \{0\})$. Then for any given $\phi(\theta) \in X$, there is a unique solution of (2) satisfying $M(\theta) = \phi(\theta)$, $\theta \in [-\tau, 0]$, and the solution remains positive and bounded.*

*Proof.* By the method in [2], one can show that for each $\phi(\theta) \in X$, there is a unique solution of (2) through $\phi(\theta)$. Denote this solution by $M(\phi, t)$ ($M(t)$ for short). If $t_0 > 0$ is the first time that $M(t_0)$ becomes zero, then $dM(t_0)/dt \geq 0$ by (2), which is impossible, therefore $M(t)$ remains positive for all $t \geq 0$.

We next show that $M(t)$ is bounded. Let $M_1 = (r-d)/\kappa$ and let $M_2 = \max_{\theta \in [-\tau, 0]} \phi(\theta)$. If we denote $\overline{M} = \max(M_1, M_2)$, then we claim that $M(t) \leq \overline{M}$. Note that $M(t) \leq M_2 \leq \overline{M}$ for $t \in [-\tau, 0]$. If $t_1 > 0$ is the first time at which $M(t_1) = \overline{M}$. Then

$$\begin{aligned}\frac{dM(t_1)}{dt} &= re^{-\alpha M(t_1-\tau)}M(t_1-\tau)e^{-\mu\tau} - dM(t_1) - \kappa M(t_1)^2 \\ &< (r - d - \kappa\overline{M})\overline{M} \leq (r - d - \kappa M_1)\overline{M} = 0.\end{aligned}$$

This implies that when $M(t)$ reaches $\overline{M}$, it will be decreasing. Therefore, $M(t) \leq \overline{M}$ for $t > 0$. $\square$

By Proposition 1, model (2) is mathematically well-defined and biologically reasonable.

## 3. Dynamical analysis.

3.1. **Existence of equilibria.** For the existence of equilibria, it is not difficult to verify that there exists a threshold value for the delay $\tau$, defined as

$$\tau_e := \frac{1}{\mu} \ln\left(\frac{r}{d}\right),$$

such that if $\tau \geq \tau_e$, then Eq. (2) admits only the trivial equilibrium $M(t) = 0$, and if $0 \leq \tau < \tau_e$, then Eq. (2) admits two equilibria, one is $M(t) = 0$ and the other is

a positive equilibrium at $M(t) = M^*(\tau)$, where $M^*(\tau)$ is the positive real root of the equation

$$re^{-\mu\tau}e^{-\alpha M} = d + \kappa M. \tag{3}$$

Note that when exists $(0 \le \tau < \tau_e)$, $M^*(\tau)$ is strictly monotone decreasing with respect to $\alpha$ and $\kappa$.

3.2. **Stability of the trivial equilibrium.** Linearizing Eq. (2) about $M(t) = 0$ yields

$$\frac{dM(t)}{dt} = re^{-\mu\tau}M(t - \tau) - dM(t). \tag{4}$$

Since $M(t) = 0$ is a single nonnegative equilibrium in the space $X$ defined in Proposition (1) for $\tau > \tau_e$, according to the well-known Hayes theorem [2] and Theorem 2.3.1 of [24], we have the following theorem:

**Theorem 3.1.** *If $\tau > \tau_e$, $M(t) = 0$ is globally asymptotically stable with respect to nonnegative initial data. If $0 \le \tau < \tau_e$, $M(t) = 0$ is unstable.*

3.3. **Linear stability of $M^*(\tau)$ and Hopf bifurcation.** Let $y(t) = M(t) - M^*(\tau)$. Linearizing (2) about $M^*(\tau)$ yields

$$\frac{dy(t)}{dt} = P(M^*(\tau))y(t - \tau) - Q(M^*(\tau))y(t), \tag{5}$$

where

$$P(M) = (d + \kappa M)(1 - \alpha M),$$
$$Q(M) = d + 2\kappa M.$$

Then, the characteristic equation of (5) becomes

$$P(M^*(\tau))e^{-\lambda\tau} = Q(M^*(\tau)) + \lambda. \tag{6}$$

Note that

$$P(M^*(\tau)) - Q(M^*(\tau)) = -\alpha\kappa M^{*2}(\tau) - (\kappa + \alpha d)M^*(\tau) < 0 \tag{7}$$

for $\tau \in [0, \tau_e)$, it is easy to prove that $M^*(\tau)$ is locally asymptotically stable when $\tau = 0$. Then, in the following we just need to prove the cases when $\tau \in (0, \tau_e)$.

Since the left part and the right part of (6) are strictly monotone decreasing and strictly monotone increasing with respect to $\lambda$ respectively, it follows from (7) that 0 or any positive real number can not be the root of (6).

We now look for purely imaginary roots of (6). Let $\lambda = \omega i$ ($\omega > 0$) be a root of (6). Considering the real and imaginary parts of (6), we have

$$P(M^*(\tau))\cos(\omega\tau) = Q(M^*(\tau)), \quad P(M^*(\tau))\sin(\omega\tau) = -\omega. \tag{8}$$

Equivalently,

$$\cos(\omega\tau) = \frac{Q(M^*(\tau))}{P(M^*(\tau))}, \quad \sin(\omega\tau) = -\frac{\omega}{P(M^*(\tau))}. \tag{9}$$

Squaring and adding both sides of (9) yields

$$\omega = \sqrt{P(M^*(\tau))^2 - Q(M^*(\tau))^2}. \tag{10}$$

Note that $Q(M^*(\tau)) > 0$, it follows from (7) and (10) that if (6) has a pair of purely imaginary roots we must have $P(M^*(\tau)) + Q(M^*(\tau)) < 0$ and $P(M^*(\tau)) < 0$. Hence, from (9) we have $\cos(\omega\tau) < 0$ and $\sin(\omega\tau) > 0$. Therefore, $\omega\tau \in ((4k - 3)\pi/2, (2k - 1)\pi)$ for some positive integer $k$.

Let $G(M) = P(M) + Q(M)$. Then,

$$G(M) = -\alpha\kappa M^2 + (3\kappa - \alpha d)M + 2d. \tag{11}$$

Note that $G(M)$ is a parabola which is concave down with $G(0) = 2d > 0$. We consider two cases $G(M^*(0)) \geq 0$ (Fig. 1) and $G(M^*(0)) < 0$ (Fig. 2).

If $G(M^*(0)) \geq 0$, one can easily get that, $G(M^*(\tau)) > \min(2d, G(M^*(0))) \geq 0$ for $\tau \in (0, \tau_e)$ (See Fig.1), which implies that $P(M^*(\tau))^2 < Q(M^*(\tau))^2$, therefore from (10) that (6) does not have purely imaginary roots. Therefore, the assertion that all the roots of (6) have negative real parts when $\tau \in (0, \tau_e)$ follows from the fact that $M^*(\tau)$ is locally asymptotically stable when $\tau = 0$.

Now we consider the case $G(M^*(0)) < 0$. Note that if we regard $M^*(\tau)$ as a function of $\tau$ determined by (3), we have

$$\frac{dM^*(\tau)}{d\tau} = -\frac{\mu(d + \kappa M^*)}{\kappa + \alpha(d + \kappa M^*)}, \tag{12}$$

which is negative, therefore $M^*(\tau)$ is a strictly decreasing function of $\tau$. Hence $M^*(\tau) < M^*(0)$, $\tau \in (0, \tau_e)$ and it follows from the Intermediate Value Theorem that there exists a unique $\tau_h \in (0, \tau_e)$ such that $G(M^*(\tau_h)) = 0$, and $G(M^*(\tau)) > 0$ for $\tau \in (\tau_h, \tau_e)$ while $G(M^*(\tau)) < 0$ for $\tau \in (0, \tau_h)$ (See Fig.2). When $\tau \in [\tau_h, \tau_e)$, then $G(M^*(\tau)) \geq 0$ which implies that $P(M^*(\tau))^2 \leq Q(M^*(\tau))^2$ and purely imaginary root of (6) does not exist. Therefore, any root of (6) will not cross the imaginary axes and the stability of $M^*$ will not change.
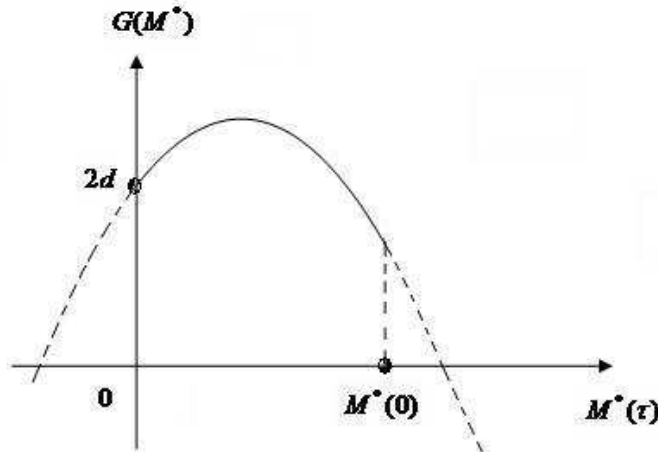


FIGURE 1.   Case $G(M^*(0)) \geq 0$. For $\tau \in (0, \tau_e)$, $G(M^*(\tau)) > 0$.

Therefore, according to the above argument, we have proved the following theorem.

**Theorem 3.2.** *Consider the model* (2) *with* $G(M)$ *defined in* (11).

1. *If* $G(M^*(0)) \geq 0$, *then the positive equilibrium* $M^*(\tau)$ *is locally asymptotically stable for* $\tau \in [0, \tau_e)$.
2. *If* $G(M^*(0)) < 0$, *then there exists a unique* $\tau_h \in (0, \tau_e)$ *satisfying* $G(M^*(\tau_h))$ $= 0$. *Furthermore,* $M^*(\tau)$ *is locally asymptotically stable when* $\tau = 0$ *and the stability of* $M^*(\tau)$ *will not change when* $\tau \in [\tau_h, \tau_e)$.
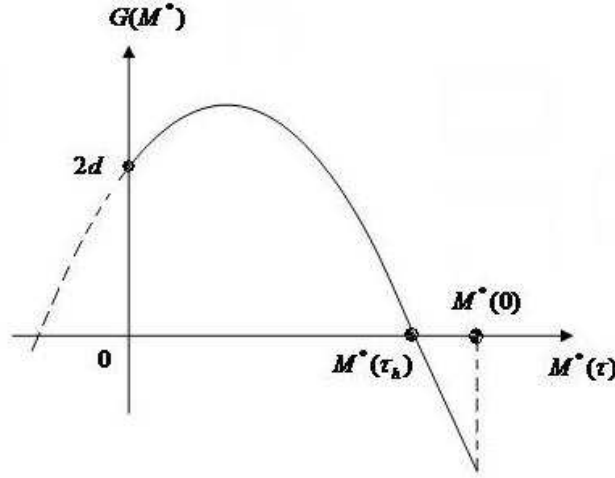
FIGURE 2. Case $G(M^*(0)) < 0$. There exists a $\tau_h \in (0, \tau_e)$ such that $G(M^*(\tau_h)) = 0$ and $G(M^*(\tau)) < 0$ for $\tau \in (0, \tau_h)$.

By Theorem 3.2, if Hopf bifurcation occurs, there holds $G(M^*(0)) < 0$. We now study the Hopf bifurcation using $\alpha$ and $\kappa$ as parameters .

First note that if $\alpha = 0$ and $\kappa > 0$, from (3), we can get that $M^*(0) = \frac{r-d}{\kappa}$. Then $G(M^*(0)) = 3r - d > 0$ for $r > d$. Therefore, Hopf bifurcation will not occur.

If $\alpha > 0$ and $\kappa = 0$, we have $G(M^*(0)) = d\left(2 - \ln\left(\frac{r}{d}\right)\right)$. Hence, $G(M^*(0)) < 0$ leads to $r > de^2$ which is independent of $\alpha$.

Now we consider the case $\alpha > 0$ and $\kappa > 0$. It is not difficult to see that $G(M^*(0)) = 0$ is equivalent to

$$\begin{cases} G(M^*(0)) = 0, \\ re^{-\alpha M^*(0)} = d + \kappa M^*(0). \end{cases} \tag{13}$$

Solving (13) yields

$$M^*(0) = \frac{d\left(1 - LambertW\left(\frac{de^3}{r}\right)\right)}{LambertW\left(\frac{de^3}{r}\right)\kappa}, \tag{14}$$

$$\alpha = \frac{LambertW\left(\frac{de^3}{r}\right)\left(3 - LambertW\left(\frac{de^3}{r}\right)\right)}{d\left(1 - LambertW\left(\frac{de^3}{r}\right)\right)}\kappa, \tag{15}$$

where $LambertW\left(\frac{de^3}{r}\right)$, a Lambert W function ([27]), is the solution of the equation $xe^x = \frac{de^3}{r}$. Since $r > d$, then $LambertW\left(\frac{de^3}{r}\right) < 3$. Besides,

$$M^*(0) > 0 \Leftrightarrow LambertW\left(\frac{de^3}{r}\right) < 1 \Leftrightarrow r > de^2.$$

Therefore, if and only if $r > de^2$, there exists $\kappa, \alpha > 0$ such that $G(M^*(0)) = 0$. The half line defined by (15) with $\kappa > 0$ separates the first quadrant of the $(\kappa, \alpha)$-plane into two parts, and $G(M^*(0)) > 0$ holds for the area below the line while for the area above the line, $G(M^*(0)) < 0$ (See Fig.3).

Let

$$D_1 = \{(\kappa, \alpha) : \kappa \geq 0, \alpha \geq 0, \kappa^2 + \alpha^2 \neq 0, \alpha < \xi\kappa\},$$

$$D_2 = \{(\kappa, \alpha) : \kappa \geq 0, \alpha \geq 0, \kappa^2 + \alpha^2 \neq 0, \alpha > \xi\kappa\},$$

where

$$\xi = \frac{LambertW\left(\frac{de^3}{r}\right)\left(3 - LambertW\left(\frac{de^3}{r}\right)\right)}{d\left(1 - LambertW\left(\frac{de^3}{r}\right)\right)}.$$

According to the above analysis, we have the following theorem:

**Theorem 3.3.**     *1. If $r \leq de^2$, $G(M^*(0)) \geq 0$ for all $(\kappa, \alpha) \in \{(\kappa, \alpha) : \kappa \geq 0, \alpha \geq 0, \kappa^2 + \alpha^2 \neq 0\}$.*
*2. If $r > de^2$, $G(M^*(0)) = 0$ for the points on the line $\alpha = \xi\kappa(\kappa > 0)$ and this straight line separates the first quadrant of the $(\kappa, \alpha)$-plane into two parts $D_1$ and $D_2$. $G(M^*(0)) > 0$ for $(\kappa, \alpha) \in D_1$ and $G(M^*(0)) < 0$ for $(\kappa, \alpha) \in D_2$.*
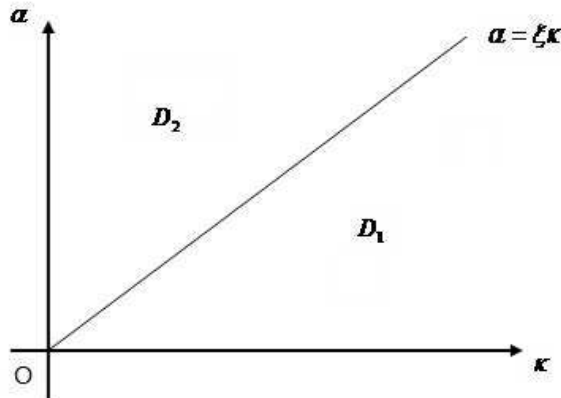


FIGURE 3. When $r > de^2$, the line $\alpha = \xi\kappa$ separates the first quadrant of the $(\kappa, \alpha)$-plane into two parts. For the $D_2$ part and the positive part of the $\alpha$-axis, the condition $G(M^*(0)) < 0$ holds which is a necessary condition for the Hopf bifurcation.

In the rest of this section, we study the case $G(M^*(0)) < 0$ and $\tau \in (0, \tau_h)$.

Note that when $G(M^*(\tau)) < 0$ and $\tau \in (0, \tau_h)$, $P(M^*(\tau)) < -Q(M^*(\tau)) < 0$, therefore, $P(M^*(\tau))^2 > Q(M^*(\tau))^2$. Our idea is to determine the sufficient condition for Hopf bifurcation.

It follows from (10) that in order to find $\omega > 0$ such that $\omega i$ is a purely imaginary root of (6), it is equivalent to find a root of the coupled system

$$\begin{cases} \cos(\tau\sqrt{P(M^*(\tau))^2 - Q(M^*(\tau))^2}) = \dfrac{Q(M^*(\tau))}{P(M^*(\tau))} \\ \sin(\tau\sqrt{P(M^*(\tau))^2 - Q(M^*(\tau))^2}) = -\dfrac{\sqrt{P(M^*(\tau))^2 - Q(M^*(\tau))^2}}{P(M^*(\tau))}, \end{cases} \quad (16)$$

for $\tau \in (0, \tau_h)$.

Let $k$ be a positive integer. We define $x = \gamma_k(\tau)$ to be the unique solution of the following equation

$$\cos(x) = \frac{Q(M^*(\tau))}{P(M^*(\tau))}, \quad x \in \left( \frac{4k-3}{2}\pi, (2k-1)\pi \right]. \tag{17}$$

Thus,

$$\gamma_k(\tau) = \arccos \frac{Q(M^*(\tau))}{P(M^*(\tau))} + 2(k-1)\pi. \tag{18}$$

Obviously, for fixed $k$, $x = \gamma_k(\tau)$ is continuous on $[0, \tau_h]$ and differentiable on $[0, \tau_h)$, with

$$\gamma_k(0) = \arccos \frac{Q(M^*(0))}{P(M^*(0))} + 2(k-1)\pi$$

and

$$\gamma_k(\tau_h) = (2k-1)\pi.$$

Moreover, using the fact that $P(M^*) < -Q(M^*) < 0$, $dM^*/d\tau < 0$ and

$$Q(M^*)\frac{dP(M^*)}{d\tau} - P(M^*)\frac{dQ(M^*)}{d\tau} = -(2\alpha\kappa^2 M^{*2} + 2\alpha d\kappa M^* + \alpha d^2 + d\kappa)\frac{dM^*}{d\tau},$$

we have

$$\frac{d\gamma_k(\tau)}{d\tau} = \frac{1}{\sqrt{P(M^*)^2 - Q(M^*)^2}} \left( \frac{dQ(M^*)}{d\tau} - \frac{Q(M^*)}{P(M^*)} \frac{dP(M^*)}{d\tau} \right) > 0 \tag{19}$$

for all $\tau \in [0, \tau_h)$. Hence $\gamma_k(\tau)$ is strictly increasing.

Consider the function $f(\tau) = \tau\omega(\tau) = \tau\sqrt{P(M^*(\tau))^2 - Q(M^*(\tau))^2}$, $\tau \in [0, \tau_h]$. First note that $f(\tau)$ is always nonnegative and is continuous on $[0, \tau_h]$ and differentiable on $[0, \tau_h)$, with $f(0) = f(\tau_h) = 0$. Moreover,

$$\frac{df(\tau)}{d\tau} = \frac{P(M^*)^2 - Q(M^*)^2 + \tau P(M^*)\frac{dP(M^*)}{d\tau} - \tau Q(M^*)\frac{dQ(M^*)}{d\tau}}{\sqrt{P(M^*)^2 - Q(M^*)^2}} \tag{20}$$

For the positive solutions of (16), we have the following lemma.

**Lemma 3.4.** *Let $\tilde{\tau}$ be the biggest $\tau \in (0, \tau_h)$ such that $f(\tilde{\tau}) = f_{\max}$ where $f_{\max}$ is the maximum for $\tau \in [0, \tau_h]$ and $N > 0$ be the smallest integer such that*

$$f_{\max} \leq (2N-1)\pi.$$

*Then the following hold:*

*(i) $\tau = \tau^*$ is a solution of (16) if and only if there exists an integer $0 < k \leq N$ such that the curves of $\gamma_k(\tau)$ and $f(\tau)$ intersect at $\tau = \tau^*$;*

*(ii) If $\gamma_N(\tilde{\tau}) < f(\tilde{\tau})$, then there are at least $2N$ solutions of (16) in the interval $(0, \tau_h)$.*

*(iii) If $\gamma_N(\tilde{\tau}) > f(\tilde{\tau})$, then there are at least $2(N-1)$ solutions of (16) in the interval $(0, \tau_h)$.*

*Proof.* (i) Note that $\tau = \tau^* > 0$ is a solution of (16) if and only if

$$\begin{cases} x = \gamma_k(\tau) \\ x = f(\tau) \\ x \in \left( \dfrac{4k-3}{2}\pi, (2k-1)\pi \right) \end{cases} \tag{21}$$

for some integer $k > 0$, which means $\gamma_k(\tau)$ and $f(\tau)$ intersect at $\tau^*$. Since $f(\tau) \leq f_{\max} \leq (2N - 1)\pi$, any $\gamma_i(\tau)$ with $i \geq N + 1$ cannot intersect the function $f(\tau)$. Hence $k \leq N$ and (i) is proved.

(ii) If $\gamma_i(\tilde{\tau}) < f(\tilde{\tau})$, then there are at least $2N$ intersection points of the functions $\gamma_i(\tau)$ and $f(\tau)$, $1 \leq i \leq N$, with at least $N$ points on each side of $\tau = \tilde{\tau}$, since each $\gamma_i(\tau)$ is always strictly increasing on $[0, \tau_h)$ with $\gamma_i(\tau_h) = (2k - 1)\pi$ and $f(\tau)$ is always nonnegative and is continuous on $[0, \tau_h]$ and differentiable on $[0, \tau_h)$, with $f(0) = f(\tau_h) = 0$. Then, the assertion (ii) follows from (i).

(iii) This case is similar to (ii), we omit it here. $\qquad\square$

Before giving a sufficient condition for a Hopf bifurcation for model (2), we also need to prove the following lemma about the transversality condition.

**Lemma 3.5.** *Let $\lambda = \lambda(\tau)$ be a root of the characteristic equation (6), with $\lambda(\tau^*) = i\omega$, $\omega > 0$ for some $\tau^* > 0$. Then*

$$Sign\left(\frac{dRe(\lambda(\tau^*))}{d\tau}\right) = Sign\left(\frac{df(\tau^*)}{d\tau} - \frac{d\gamma_i(\tau^*)}{d\tau}\right) \tag{22}$$

*for some integer $i \geq 1$, where $Sign(x)$ is the sign function.*

*Proof.* Differentiating both sides of (6) with respect to $\tau$ yields

$$\left(\frac{dP(M^*)}{d\tau} - \lambda P(M^*) - \tau P(M^*)\frac{d\lambda}{d\tau}\right)e^{-\lambda\tau} = \frac{dQ(M^*)}{d\tau} + \frac{d\lambda}{d\tau}. \tag{23}$$

Solving for $d\lambda/d\tau$ in the above equation gives

$$\frac{d\lambda}{d\tau} = \frac{\frac{dP(M^*)}{d\tau}e^{-\lambda\tau} - \lambda P(M^*)e^{-\lambda\tau} - \frac{dQ(M^*)}{d\tau}}{1 + \tau P(M^*)e^{-\lambda\tau}}. \tag{24}$$

By (6), $P(M^*)e^{-\lambda\tau} = Q(M^*) + \lambda$. Substituting this into the above expression. It follows that

$$\frac{d\lambda}{d\tau} = \frac{\left(\frac{dP(M^*)}{d\tau}\frac{1}{P(M^*)} - \lambda\right)(\lambda + Q(M^*)) - \frac{dQ(M^*)}{d\tau}}{1 + \tau(\lambda + Q(M^*))}. \tag{25}$$

When $\tau = \tau^*$ and $\lambda = i\omega(\tau^*)$, then, from (10) and (25) we have

$$\frac{dRe(\lambda(\tau^*))}{d\tau}$$

$$= Re\left(\frac{\left(\frac{dP(M^*)}{d\tau}\frac{1}{P(M^*)} - i\omega\right)(i\omega + Q(M^*)) - \frac{dQ(M^*)}{d\tau}}{1 + \tau(i\omega + Q(M^*))}\right)$$

$$= \frac{\frac{dP(M^*)}{d\tau}\left(\frac{Q(M^*)}{P(M^*)} + \tau P(M^*)\right) - \frac{dQ(M^*)}{d\tau}(1 + \tau Q(M^*)) + P(M^*)^2 - Q(M^*)^2}{(1 + \tau Q(M^*))^2 + (\omega\tau)^2}.$$

On the other hand, according to (19) and (20),

$$\frac{df(\tau^*)}{d\tau} - \frac{d\gamma_i(\tau^*)}{d\tau}$$

$$= \frac{\frac{dP(M^*)}{d\tau}\left(\frac{Q(M^*)}{P(M^*)} + \tau P(M^*)\right) - \frac{dQ(M^*)}{d\tau}(1 + \tau Q(M^*)) + P(M^*)^2 - Q(M^*)^2}{\sqrt{P(M^*)^2 - Q(M^*)^2}}.$$

Obviously,

$$Sign\left(\frac{dRe(\lambda(\tau^*))}{d\tau}\right) = Sign\left(\frac{df(\tau^*)}{d\tau} - \frac{d\gamma_i(\tau^*)}{d\tau}\right)$$

for some integer $i \geq 1$.                                                                         □

Now, with Lemma (3.4) and Lemma (3.5), we can give a sufficient condition for the existence of Hopf bifurcation for model (2).

**Theorem 3.6.** *Let $\tau^*$ be a solution of* (16). *Then there exists a unique integer $k \geq 1$ such that $f(\tau^*) = \gamma_k(\tau^*)$. If*

$$\frac{df(\tau^*)}{d\tau} \neq \frac{d\gamma_k(\tau^*)}{d\tau},$$

*then there is a Hopf bifurcation at $\tau = \tau^*$ of small amplitude periodic solutions bifurcating from the equilibrium $M^*$. When $\tau$ is sufficiently close to $\tau^*$, the periods of these periodic solutions lie in the interval $(2\tau^*/(2k-1), 4\tau^*/(4k-3))$.*

*Proof.* If $\tau^*$ is a solution of (16), then characteristic equation (6) has a purely imaginary root, $i\omega$, $\omega = \sqrt{P(M^*(\tau))^2 - Q(M^*(\tau))^2}$, for $\tau = \tau^*$. Moreover, since $\gamma_i(\tau) \neq \gamma_j(\tau)$ for $i \neq j$, by Lemma (3.4), there exists a unique integer $k$ such that $f(\tau^*) = \gamma_k(\tau^*)$. Besides, if $df(\tau^*)/d\tau \neq d\gamma_k(\tau^*)/d\tau$, from Lemma (3.5),

$$\left.\frac{dRe(\lambda(\tau))}{d\tau}\right|_{\tau=\tau^*} \neq 0,$$

where $\lambda = \lambda(\tau)$ is a root of (6) with $\lambda(\tau^*) = i\omega$, which implies that the transversality condition satisfied. Since

$$\frac{2\pi}{\omega} = \frac{2\pi\tau^*}{f(\tau^*)} = \frac{2\pi\tau^*}{\gamma_k(\tau^*)}$$

and $\gamma_k(\tau^*) \in ((4k-3)\pi/2, (2k-1)\pi)$, therefore,

$$\frac{2\tau^*}{2k-1} < \frac{2\pi}{\omega} < \frac{4\tau^*}{4k-3}.$$

By the Hopf bifurcation theorem for delay differential equations ([15]), there is a Hopf bifurcation of small amplitude periodic solutions at $\tau = \tau^*$ with periods in the interval

$$\left(\frac{2\tau^*}{2k-1}, \frac{4\tau^*}{4k-3}\right).$$

□

**Remark 1.** It is interesting to note that the transversality condition is satisfied if and only if the curves $f(\tau)$ and $\gamma_k(\tau)$ cross transversally. Thus this formula gives a way to check the transversality condition geometrically.

**Remark 2.** From (7), (12) and (11), it is not difficult to prove that $\omega$ is monotone decreasing with respect to $\tau$. Then, the period of the periodic solution bifurcating from $M^*(\tau^*)$ via Hopf bifurcation is increasing with respect to $\tau$.

4. **Discussion and numerical simulations.** Considering the importance of the impacts of the limited resource directly related to mosquito reproduction (like blood meals, swamps, etc.) without which female mosquitoes may survive but they may not be able to lay viable eggs, we separated the resource into two types, one is for adult mosquitoes to survive (the crowding effect) and the other is for female mosquitoes to reproduce. Accordingly, we formulate a new model with maturation delay for female mosquitoes to incorporate the impacts of limited resource not only on mosquito survival but also on mosquito reproduction. Comparing to other models available we surveyed in section 1, limited resource for mosquito reproduction, which can determine the abundance of mosquito population in a region, plays an important role in the population dynamics of mosquitoes.
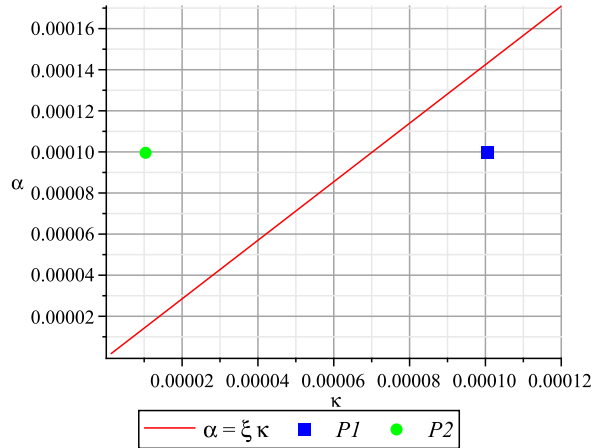


FIGURE 4. Bifurcation diagram in the $(\kappa, \alpha)$-plane when $r > de^2$, the values of other parameters are $r = 42$, $\mu = 0.28$, $d = 1/21$.

It is not difficult to see that, if the impact of blood meal resource in a given region is ignored, then $\alpha$ is 0 in model (2), which implies that the given region has enough resource of blood meals for female mosquitoes and the birth rate is a linear function which is the same as the model in [1]. Then, there will be no sustained oscillations in model (2) since $G(M^*(\tau)) > 0$ for all nonnegative $\tau$. While for $\alpha > 0$, the birth rate function becomes nonlinear, the positive equilibrium $M^*(\tau)$ will decrease with respect to $\alpha$ and there may be periodic solutions obtained via Hopf bifurcation when $G(M^*(0)) < 0$. Therefore, we can assert that the effect of sufficient amount of blood meal resource for female mosquitoes is crucial to the abundance of mosquito population.

If we do not consider the intraspecific competition for adult mosquito survival, i.e. $\kappa$ is zero, model (2) becomes a special case of the model in [6]. Comparing the results of the two models, the nonlinear birth rate function brings Hopf bifurcation for both models. But, according to our result, the positive equilibrium will decrease with respect to the intraspecific competition rate $\kappa$ when it is positive.

In order to demonstrate the theoretical results established in this paper and estimate the effect of maturation delay, we present some numerical simulations.
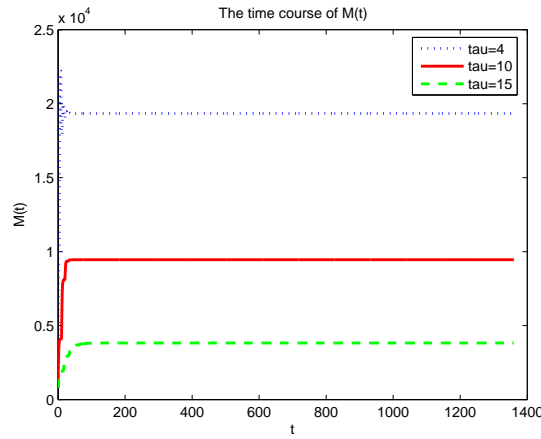
FIGURE 5. Solutions of $M(t)$ with different $\tau$ in the case $G(M^*(0))$ $\geq 0$. The values of parameters are $r = 42$, $\alpha = 0.0001$, $\mu = 0.28$, $d = 1/21$, $\kappa = 0.0001$. Note that $G(M^*(0)) = 0.7279 > 0$, $\tau_e$ $= 24.2221$ and for different $\tau$, $M(t)$ all converge to a stable positive equilibrium with respect to time $t$ (days).
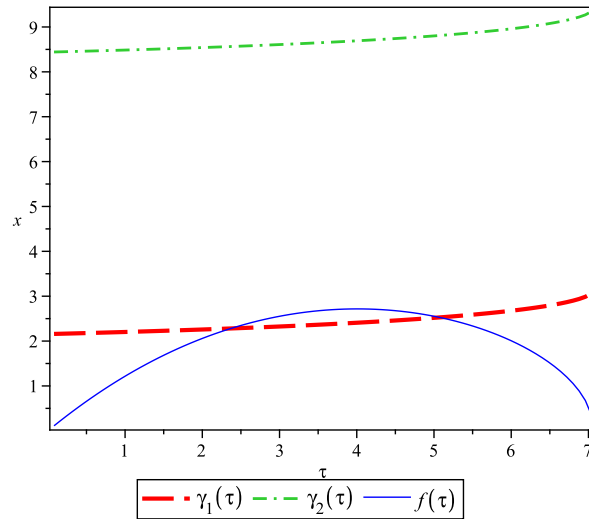


FIGURE 6. Intersections of $f(\tau)$ and $\gamma_k(\tau)$. $\kappa = 0.00001$ and the values of other parameters are the same as those listed in Fig.5 except for $\tau$. Note that $G(M^*(0)) = -0.7596 < 0$, $\tau_e = 24.2221$, $\tau_h = 7.0684$ and there are two $\tau^*$ where $f(\tau)$ intersects with $\gamma_k(\tau)$ transversally.

The time unit in the simulation is day. From [26], we assume that the maximum per capita birth rate is $r = 42$. $\alpha$, the reciprocal of which reflects the maximum blood meal resource in a given region, is assumed to be 0.0001 ([13, 14]). The
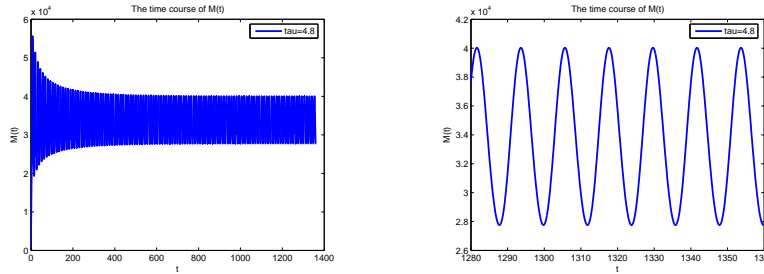
(a) The time $t$ varies from 0 to 1360 days.

(b) The time $t$ varies from 1280 to 1360 days.

FIGURE 7. The time courses of $M(t)$ when $G(M^*(0)) < 0$ and $\tau = 4.8$. The values of parameters are the same as those listed in Fig.6 except for $\tau$. Note that a stable periodic solution of Model (2) exists.
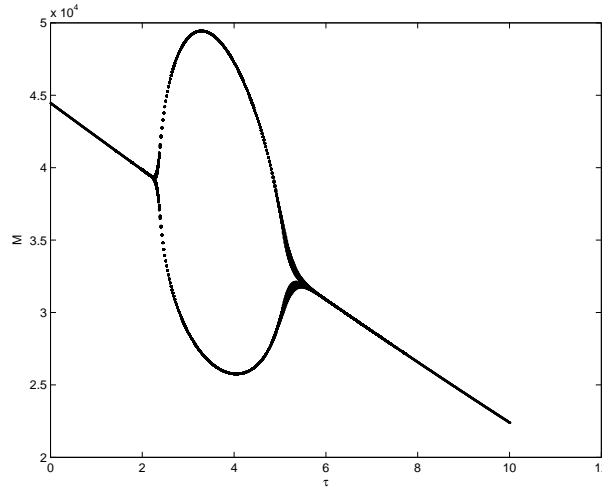


FIGURE 8. Bifurcation diagram when $G(M^*(0)) < 0$. The values of parameters are the same as those listed in Fig.6 except for $\tau$. A stable limit cycle bifurcates from the positive equilibrium near $\tau = 2.5$ and disappears near $\tau = 5$.

lifespan of adult female mosquitoes, according to [28], is assumed to be three weeks, then $d = 1/21$. Note that $r > de^2$. The death rate during the preadult stages is assumed to be 0.28 [20]. We keep the rate of intraspecific competition for survival $\kappa$ as a parameter (See Fig.4).

For $P_1$ ($\kappa = 0.0001$, $\alpha = 0.0001$) in Fig.4, by calculation using Matlab, $G(M^*(0))$ $= 1.0775 > 0$, $\tau_e = 24.2221$. From Fig.5, one can see that for three different values of $\tau$ smaller than $\tau_e$, $M(t)$ all converges to a stable positive equilibrium. Besides, with the decreasing of $\tau$, the value of positive equilibrium is increasing. This implies
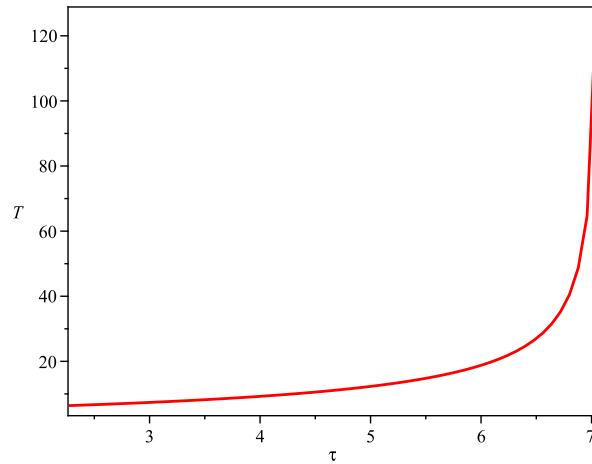
FIGURE 9. The graph of the period $T$ of the periodic solution. The values of parameters are the same as those listed in Fig.7 except for $\tau$. Note that $T$ is a monotone increasing function of $\tau$.
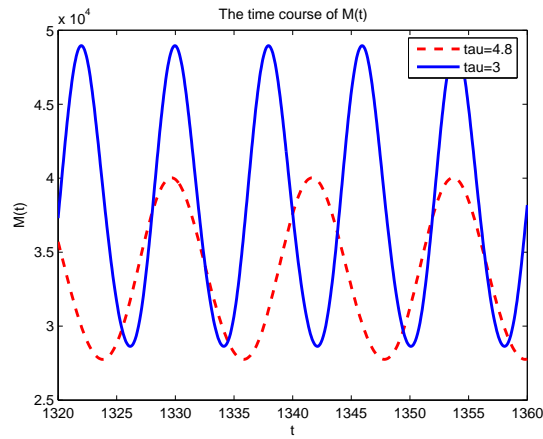


FIGURE 10. The time course of $M(t)$. The values of parameters are the same as those listed in Fig.7 except for $\tau$. Note that the bigger the value of $\tau$ is, the bigger the period of the periodic solution is.

that in the case of warmer temperature, the maturation time delay is getting shorter which will induce the increase of the number of mosquitoes in a region.

For $P_2$ ($\kappa = 0.00001$, $\alpha = 0.0001$) in Fig.4, by calculation using Matlab, $G(M^*(0)) = -0.1830 < 0$, $\tau_e = 24.2221$ and $\tau_h = 7.0684$. According to the graph depicted in Fig.6, there are two $\tau^*$ where $f(\tau)$ intersects with $\gamma_k(\tau)$ transversally. By Theorem 3.6, Hopf bifurcation occurs twice at the two intersections. Especially, near the smaller $\tau^*$, $M^*$ is local stable when $\tau < \tau^*$, while the stability will change when $\tau$

increases through $\tau^*$ and a stable periodic solution bifurcates from $M^*$ (See Fig.7 and Fig.8).

It is also interesting to note that any small amplitude periodic solution obtained via Hopf bifurcation has period less than $4\tau^*$. Moreover, the period is increasing with respect to $\tau$ (See Fig.9 and Fig.10). As described in Remark 2, our result is consistent with this observation.

As a final note we would like to point out that although the model we formulate in this paper is for the population dynamics of mosquitoes, it should be also applicable to other insects or species whose life cycles contain nonnegligible maturation delay and depends on specific resource for the reproduction of eggs and for the survival of adults.

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*E-mail address*: wanh2046@163.com
*E-mail address*: huaiping@mathstat.yorku.ca