DYNAMICS OF STAGE-STRUCTURED DISCRETE MOSQUITO POPULATION MODELS

Junliang Lu[a] and Jia Li[a]

Abstract We formulate discrete-time stage-structured models, based on systems of difference equations, for mosquito populations. We include the four distinct mosquito metamorphic stages, egg, pupa, larva, and adult, in the models. We derive a formula for the inherent net reproductive number, and investigate existence and stability of fixed points. We also show that the models, by means of numerical simulations, exhibit richer dynamics.

Keywords Mosquito population, stage structure, discrete model, stability, period-doubling bifurcation.

MSC(2000) 39A11, 92D15, 92D25, 92D30, 92D40.

1. Introduction

Mosquito-borne diseases, such as malaria, dengue fever, and West Nile, transmitted between humans by blood-feeding mosquitoes, have been big concerns for the public health in the United States and in the world.

Malaria is by far the world's most important tropical parasitic disease. It is the 5th cause of death from infectious diseases worldwide (after respiratory infections, HIV/AIDS, diarrheal diseases, and tuberculosis), and the 2nd leading cause of death from infectious diseases in Africa, after HIV/AIDS. It is a public health problem today in more than 109 countries and territories inhabited by some 3.3 billion people, and approximately half of the world's population is at risk of malaria, particularly those living in lower-income countries. There were 247 million cases of malaria in 2006, causing nearly one million deaths, mostly among African children, and 190 - 311 million clinical episodes, and 708,000 - 1,003,000 deaths in 2008. Malaria has been eradicated in the United States since the early 1950's. However, 63 outbreaks of locally transmitted mosquito-borne malaria have occurred between 1957 and 2009, and 1500 cases of malaria, on average, are reported every year in the United States [8, 37].

Dengue fever (DF) and dengue hemorrhagic fever (DHF) are second only to malaria in the number of people affected worldwide by mosquito-borne diseases. Globally, there are an estimated 50 to 100 million cases of DF and several hundred thousand cases of DHF per year. In 2007, 900,782 cases of DF and 26,413 cases of

Email adresses:ljlmath@gmail.com, jl0002@uah.edu(Junliang Lu);
        li@math.uah.edu (Jia Li)
[a]Department of Mathematical Sciences, University of Alabama in Huntsville,
Huntsville, AL 35806, USA

DHF reported in Americas. Outbreaks were reported in 11 countries. Between 100 to 200 suspected cases introduced into the U.S. each year by travelers [9].

The West Nile virus (WNV) was first detected in the Western Hemisphere in 1999 and has since rapidly spread across the North American continent into all 48 continental states, seven Canadian provinces, and throughout Mexico. Over 15,000 people in the U.S. have tested positive for WNV infection since 1999, including over 500 deaths. People of all ages can develop serious illness [30].

The life cycle of the mosquito-borne diseases is complicated. For example, malaria in humans is due to infection by one of four Plasmodium species and the infection begins when sporozoites are injected into the blood of a human host by a female mosquito of the genus Anopheles. The sporozoites migrate to the liver where they enter liver cells and develop schizonts, which give rise, via asexual reproduction, to the form which invades the blood cells, the merozoites. In the blood, some merozoites differentiate into sexual erythrocytic stages (gametocytes), and the gametocytes are ingested by a mosquito when it ingests human blood. Within the mosquito the gametocytes develop into microgametes and macrogametes (the male and female gametes) that fuse to form a zygote. This becomes a motile ookinete form which bores through the gut wall of the vector and forms an oocyst from which large numbers of sporozoites are released. These sporozoites then invade the salivary glands of the mosquito from which they are injected into a human host when the vector feeds. Such a life-cycle of the Plasmodium species causes the transmission of malaria between infected humans and mosquitoes [4, 6, 36].

No vaccines are available for these mosquito-borne diseases. An effective way to prevent the mosquito-borne diseases is to control mosquitoes, which has been one of the major intensive efforts in many years. To set any feasible optimal strategy in the control of mosquitoes, we need to have a better understanding of the population dynamics of mosquitoes. and hence to formulate appropriate mathematical mosquito models.

There are modeling works on mosquitoes in the literature in malaria transmission models. However, the metamorphic structure differences of mosquitoes has been ignored by assuming homogeneous mosquito populations in most of the disease modeling [4, 22, 26, 31–33, 38].

Mosquitoes undergo complete metamorphosis going through four distinct stages of development, egg, pupa, larva, and adult, during a lifetime. They are completely metamorphically as well as ecologically distinct. After drinking blood, adult females lay a raft of 40 to 400 tiny white eggs in standing water or very slow-moving water. Within a week, the eggs hatch into larvae (sometimes called wrigglers) that breathe air through tubes which they poke above the surface of the water. Larvae eat bits of floating organic matter and each other. Larvae molt four times as they grow; after the fourth molt, they are called pupae. Pupae (also called tumblers) also live near the surface of the water, breathing through two horn-like tubes (called siphons) on their back. Pupae do not eat. When the skin splits after a few days from a pupa, an adult emerges. The adult lives for only a few weeks and the full life-cycle of a mosquito takes about a month [5, 27, 28].

It is clear that, to have more realistic modeling of mosquitoes, we need to include the stage structure. In particular, the different stages have different responses to environment and regulating factors to the population [35]. Some mosquitoes modeling works have included mosquito stages [23], and the four mosquito stages are included in the malaria model in [34], the analysis for which nevertheless seems

mathematically untractable.

In this paper, we formulate stage-structured mosquitoes models based on different assumptions, where the four stages are explicitly included, in Section 2. We then calculate the inherent net reproductive number and determine the global stability for the trivial fixed (the origin) in Section 3. The existence, uniqueness, and stability of positive fixed points are investigated in Section 4. Numerical examples are given in Section 5 to demonstrate the rich dynamics of the stage-structured mosquito models. Brief discussions are given in Section 6.

2. The model formulation

Let $E(t), L(t), P(t)$ and $M(t)$ denote the numbers of eggs, larvae, pupae, and adults of mosquitoes, respectively, at time t. We then assume that the oviposition rate, denoted by b, and the survival probability of the eggs, denoted by s_0, are constants. While interspecific competition and predation are rather rare events and could be discounted as major causes of larval mortality, intraspecific competition could represent a major density dependent source for them, and hence the effect of crowding could be an important factor in the population dynamics of mosquitoes [14, 16, 34]. More specifically, considering the inhibitory effects of larvae density on the egg hatching, we assume the surviving-adjusted hatching rate, denoted by $s_e = s_e(L)$, to be a function of larvae L. Due to the intraspecific competition, the effect of crowding, and possible cannibalism that larvae may eat smaller larvae, we assume the surviving-adjusted pupation rate, denoted by $s_l = s_l(L)$, is a function of larvae L. Because the pupae do not eat, we assume the surviving-adjusted emergence rare from pupae to adults to be constant and denoted by s_p. The adults survival function is also assumed to be density-dependent, denoted by $s_m = s_m(M)$. Then we arrive at the following four-stage-structured model of for the mosquito population:

$$
\begin{aligned}
E(t+1) &= bs_0 M(t), \\
L(t+1) &= s_e(L(t))E(t), \\
P(t+1) &= s_l(L(t))L(t), \\
M(t+1) &= s_p P(t) + s_m(M(t))M(t).
\end{aligned}
\tag{2.1}
$$

Comparing the different lifespan for the four stages, we assume function $s_m(M)$ satisfies the following conditions (H1) [2].

$$
\begin{aligned}
&s_i(z) \in C^1[0, \infty), \quad s_i(0) := \alpha_i, \quad 0 < \alpha_i \le 1, \quad s_i'(z) \le 0, \quad (s_i(z)z)' > 0, \\
&\lim_{z \to \infty} s_i(z) = 0, \quad \lim_{z \to \infty} s_i(z)z := k_i, \quad 0 < k_i < \infty.
\end{aligned}
\tag{H1}
$$

The density-dependent functions $s_e(L)$ and $s_l(L)$ are assumed to satisfy either conditions (H1), or conditions (H2) given below.

$$
s_i(z) \in C^1[0, \infty), \quad s_i(0) := \alpha_i, \quad 0 < \alpha_i \le 1, \quad s_i'(z) \le 0, \quad \lim_{z \to \infty} s_i(z) = 0,
$$

$$
\exists\, k_i > 0, \quad (s_i(z)z)' \begin{cases} > 0, & z < k_i, \\ < 0, & z > k_i, \end{cases} \quad \lim_{z \to \infty} s_i(z)z = 0.
\tag{H2}
$$

Conditions (H1) assume that the surviving-adjusted hatching and pupation rates and the adult survival rate are all decreasing, but the total numbers of eggs, pupae,

and adults are increasing and saturating to fixed numbers, as the number of individuals increases. For example, these rates may have the Beverton-Holt form such that $s_i(z) = (\alpha_i k_i)/(k_i + \alpha_i z)$, [7]. On the other hand, conditions (H2) characterize the fact that while those rates are decreasing, as the number of individuals increases, the total numbers increase to certain levels, k_i, but then decrease as the number of individuals exceeds the threshold. The Ricker-type function $s_i(z) = \alpha_i e^{-z/k_i}$ has such properties.

Define $x(t) := (E(t), L(t), P(t), M(t))^T$. System (2.1) can be written as the following matrix form:

$$x(t+1) = A(x(t))x(t),\qquad(2.2)$$

where the projection matrix $A(x)$ is given by

$$A(x) = \begin{pmatrix} 0 & 0 & 0 & bs_0 \\ s_e(L) & 0 & 0 & 0 \\ 0 & s_l(L) & 0 & 0 \\ 0 & 0 & s_p & s_m(M) \end{pmatrix}.$$

Let $A = (a_{ij}) \in \mathbb{R}^{n \times m}$ and $B = (b_{ij}) \in \mathbb{R}^{n \times m}$. We say that $A \leq B$ if and only if $a_{ij} \leq b_{ij}$ for all $i = 1, \cdots, n$, and $j = 1, \cdots, m$. Hence, from assumption (H1) or (H2), we have $A(x) \geq A(y)$, for any $x \leq y$.

Furthermore, it is easy to see that system (2.1) or (2.2) is point dissipative [17, 20]. In fact, under assumption (H1) or (H2), it follows that

$$M(t+1) = s_p P(t) + s_m(M(t))M(t) = s_p s_e(L(t))L(t) + s_m(M(t))M(t)$$
$$\leq s_p \bar{k}_e + k_m := \omega_4,$$

for all $t \geq 0$. Then, it follows from system (2.1) that

$$E(t+1) \leq bs_0(s_p \bar{k}_e + k_m) := \omega_1,$$
$$L(t+1) \leq s_e(0)bs_0(s_p \bar{k}_e + k_m) := \omega_2,$$
$$P(t+1) \leq \bar{k}_l,$$

for all $t \geq 0$, where $\bar{k}_i = k_i$ if (H1) is assumed, or $\bar{k}_i = s_i(k_i)k_i$, if (H2) is assumed. We summarize the basic properties of the system as follows.

Theorem 2.1. *System* (2.1) *or* (2.2) *is point dissipative. Define set* Ω *by*

$$\Omega := \{x(t) = (E, L, P, M) \in \mathbb{R}_+^4 : 0 \leq E \leq \omega_1, 0 \leq L \leq \omega_2, 0 \leq P \leq \bar{k}_l, 0 \leq M \leq \omega_4\}.$$
$$(2.3)$$

Then Ω *is positively invariant under the flows of system* (2.2) *and is attracting to all solutions of* (2.2) *if conditions* (H1) *or* (H2) *hold.*

3. The inherent net reproductive number and dynamics of the trivial fixed point

System (2.2) has the trivial fixed point, $E_0 := (0, 0, 0, 0)^T$, and its linearization at the trivial fixed point is an age-structured linear Leslie population model. As is well-known, one of the important characterizations for a linear Leslie matrix model is the inherent net reproductive number which is the expected number of offspring per

mosquito over the course of its lifetime, and the inherent net reproductive number also determines the asymptotic dynamics of the linear system [10,12,13]. Using the techniques in [1,3,13], we find the inherent net reproductive number, r_0, for system (2.2) as follows.

Define the fertility and the transition matrices, respectively, as

$$F = \begin{pmatrix} 0 & 0 & 0 & bs_0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix}, \quad T = \begin{pmatrix} 0 & 0 & 0 & 0 \\ \alpha_1 & 0 & 0 & 0 \\ 0 & \alpha_2 & 0 & 0 \\ 0 & 0 & \alpha_3 & \alpha_4 \end{pmatrix}.$$

Then the inherent projection matrix of the nonlinear system (2.2) is

$$A(0) = \begin{pmatrix} 0 & 0 & 0 & bs_0 \\ \alpha_1 & 0 & 0 & 0 \\ 0 & \alpha_2 & 0 & 0 \\ 0 & 0 & \alpha_3 & \alpha_4 \end{pmatrix} = F + T,$$

and thus, the inherent net reproductive number is the positive, simple, and strictly dominant eigenvalue of $F(I-T)^{-1}$, denoted by r_0. Simple calculation show that

$$r_0 = \frac{bs_0 \alpha_1 \alpha_2 \alpha_3}{1 - \alpha_4} = \frac{bs_0 s_e(0) s_l(0) s_p}{1 - s_m(0)}.$$

We then determine the stability of the trivial fixed point.

Since $x(t) \geq 0$ for all $x \geq 0$, it follows from (2.2) and conditions (H1) that

$$x(1) = A(x(0))x(0) \leq A(0)x(0),$$

and

$$x(2) = A(x(1))x(1) \leq A(0)x(1) \leq A^2(0)x(0).$$

Continuing in this manner, we have

$$x(t) \leq A^t(0)x(0).$$

Note that $A(0)$ is non-negative, irreducible, and primitive. Then $A(0)$ has a positive, simple, and strictly dominant eigenvalue, which is the inherent net reproductive number, r_0. If $r_0 < 1$, then it follows, [18], that

$$\lim_{t \to \infty} A^t(0) = 0.$$

If $r_0 > 1$, $A(0)$ has a positive strictly dominant eigenvalue greater than one. That is, the linearization of system (2.2) at the trivial fixed point has a positive eigenvalue greater than one, which implies the instability of the trivial fixed point. Therefore, we arrive at the following stability result for the trivial fixed point.

Theorem 3.1. *The trivial fixed point of system* (2.2), $E_0 = (0,0,0,0)$, *is globally asymptotically stable if the inherent net reproductive number $r_0 < 1$, and is unstable if $r_0 > 1$.*

4. The positive fixed point

System (2.2) may have positive fixed points. We first determine its existence and uniqueness, and then find conditions that ensure the stability of the positive fixed point.

4.1. Existence of the positive fixed point

Let $E_1 = (E, L, P, M)$ be a positive fixed point. Then its components satisfy the following system

$$E = bs_0 M, \tag{4.1a}$$

$$L = s_e(L)E, \tag{4.1b}$$

$$P = s_l(L)L, \tag{4.1c}$$

$$M = s_p P + s_m(M)M. \tag{4.1d}$$

It follows from (4.1b) that

$$\frac{L}{s_e(L)} = E = bs_0 M. \tag{4.2}$$

Define $F(L) = L/s_e(L)$. Then

$$F'(L) = \frac{1}{s_e(L)} - \frac{Ls_e'(L)}{s_e^2(L)} > 0.$$

Note that $F(0) = 0$ and $\lim_{L \to \infty} F(L) = \infty$ under assumption (H1) or (H2). Then there exists a unique positive solution, $L(M)$, to equation (4.2). We also note that, as a function of M,

$$L'(M) = bs_0 s_e(L(M)) + s_e'(L(M))L'(M)bs_0 M. \tag{4.3}$$

Solving (4.3) for $L'(M)$, we have

$$L'(M) = \frac{bs_0 s_e(L(M))}{1 - bs_0 M s_e'(L(M))} > 0. \tag{4.4}$$

That is, L is a monotone increasing function of M.

Substituting this solution $L(M)$ into (4.1c) and then into (4.1d), we obtain

$$M = s_p s_l(L(M))s_e(L(M))bs_0 M + s_m(M)M. \tag{4.5}$$

To solve for a positive solution $M > 0$ to equation (4.5), we define function

$$H(M) := bs_0 s_p s_l(L(M))s_e(L(M)) + s_m(M) - 1. \tag{4.6}$$

Then system (2.2) has a positive fixed point if and only if there exists a positive root of $H(M) = 0$.

Since

$$H'(M) = bs_0 s_p \left(s_l'(L(M))s_e(L(M)) + s_l(L(M))s_e'(L(M)) \right) L'(M) + s_m'(M), \tag{4.7}$$

it follows from (H1), or (H2), and (4.4) that $H'(M) < 0$; that is, $H(M)$ is a monotone decreasing function with respect to M.

Since $\lim_{M\to\infty} H(M) = -1$ from assumption (H1) or (H2), then $H(M) = 0$ has a unique positive root if and only if $H(0) > 0$, which is equivalent to

$$r_0 = \frac{bs_0 s_p s_l(0) s_e(0)}{1 - s_m(0)} > 1.$$

In summary, we obtain the following existence result.

Theorem 4.1. *System (2.2) has a unique positive fixed point if and only if the inherent next reproductive number $r_0 > 1$.*

4.1.1. The stability of the positive fixed point

Suppose $r_0 > 1$ and that E_1 is the unique positive fixed point. The Jacobian of system (2.2) at E_1 has the form of

$$J = \begin{pmatrix} 0 & 0 & 0 & bs_0 \\ s_e(L) & s'_e(L)E & 0 & 0 \\ 0 & (s_l(L)L)' & 0 & 0 \\ 0 & 0 & s_p & (s_m(M)M)' \end{pmatrix}.$$

Then the characteristic polynomial of J is given by

$$f(\lambda) = \lambda^4 + a_1\lambda^3 + a_2\lambda^2 + a_4,$$

where

$$a_1 = -\left(s'_e(L)E + (s_m(M)M)'\right) = -(s'_e(L)bs_0 M + s_m(M) + s'_m(M)M),$$
$$a_2 = s'_e(L)E \left(s_m(M)M\right)' = s'_e(L)bs_0 M(s_m(M) + s'_m(M)M),$$
$$a_4 = -bs_0 s_p s_e(L) \left(s_l(L)L\right)' = -bs_0 s_p s_e(L)(s_l(L) + s'_l(L)L).$$

Define

$$b_1 = -a_4 a_1, \quad b_2 = a_2 - a_4 a_2, \quad b_3 = a_1, \quad b_4 = 1 - a_4^2,$$

and

$$c_2 = b_4 b_2 - b_1 b_3, \quad c_3 = b_4 b_3 - b_1 b_2, \quad c_4 = b_4^2 - b_1^2 = (b_4 - b_1)(b_4 + b_1).$$

It follows from the Jury stability criterion [21, 29] that the roots of the characteristic polynomial $f(\lambda)$ all have magnitudes less than one if

$$f(1) > 0, \quad f(-1) > 0, \quad |a_4| < 1, \quad |b_4| > |b_1|, \quad |c_4| > |c_2|.$$

We focus on the case where conditions (H1) are satisfied, and have the following local stability results for the positive fixed point.

Theorem 4.2. *Assume the density-dependent functions s_i, $i = e, l, m$, all satisfy conditions (H1). The unique positive fixed point, E_1, is locally asymptotically stable if either condition*

$$s'_e(L)bs_0 M + (s_m(M)M)' > 0 \tag{H3}$$

holds, or condition

$$0 < -s'_e(L)bs_0M - (s_m(M)M)' < s_m(M) - bs_0s_ps_es'_l(L)L + s'_e(L)bs_0M(s_m(M)M)'$$
(H4)

is satisfied, where E, L, P, and M are the components of the positive fixed point E_1.

Proof. Since

$$f(\pm 1) = 1 \pm a_1 + a_2 + a_4,$$
$$f(1) - f(-1) = 2a_1.$$
(4.8)

Assume condition (H3) holds. Then $a_1 < 0$, and

$$
\begin{aligned}
f(1) &= 1 + a_1 + a_2 + a_4 \\
&= 1 - (s'_e(L)bs_0M + s_m(M) + s'_m(M)M) + s'_e(L)bs_0M(s_m(M) + s'_m(M)M) \\
&\quad - bs_0s_ps_e(L)(s_l(L) + s'_l(L)L) \\
&= s'_e(L)bs_0M(s'_m(M)M - bs_0s_ps_e(L)s_l(L)) - s'_m(M)M - bs_0s_ps_e(L)s'_l(L)L \\
&> 0.
\end{aligned}
$$

Furthermore, it follows from (4.8) that $f(-1) > 0$.

Notice that, at the positive fixed point from (4.6),

$$1 = s_m(M) + bs_0s_ps_e(L)s_l(L) > bs_0s_ps_e(L)s_l(L) > |a_4|.$$

Then

$$|b_4| - |b_1| = 1 - a_4^2 - |a_4||a_1| > |a_4|\left(1 - |a_4| - |a_1|\right).$$
(4.9)

If assumption (H3) holds, then

$$
\begin{aligned}
1 - |a_4| - |a_1| &= 1 - bs_0s_ps_e(L)(s_l(L) + s'_l(L)L) - s'_e(L)bs_0M - s_m(M) - s'_m(M)M \\
&= -bs_0s_ps_e(L)s'_l(L)L - s'_e(L)bs_0M - s'_m(M)M > 0,
\end{aligned}
$$

and hence $|b_4| > |b_1|$.

Suppose $|b_4| > |b_1|$. Then $c_4 > 0$, and it follows from $a_2 < 0$ and $-1 < a_4 < 0$ that

$$
\begin{aligned}
c_2 &= b_4b_2 - b_1b_3 = (1 - a_4^2)(a_2 - a_4a_2) + a_4a_1^2 \\
&= (1 - a_4^2)(1 - a_4)a_2 + a_1^2a_4 < 0.
\end{aligned}
$$

Then

$$
\begin{aligned}
|c_4| - |c_2| &= c_4 + c_2 = b_4^2 - b_1^2 + b_2b_4 - b_1b_3 \\
&= b_4(b_2 + b_4) - b_1(b_1 + b_3) \\
&= (1 - a_4^2)\left(1 - a_4^2 + a_2(1 - a_4)\right) + a_4a_1^2(1 - a_4) \\
&= (1 - a_4)\left((1 - a_4^2)(1 + a_4 + a_2) + a_1^2a_4\right).
\end{aligned}
$$

Suppose (H3) holds and hence $f(1) > 0$. Then $-a_1 > 0$ and it follows, in addition from $-1 < a_4 < 0$, that $|c_4| - |c_2| > 0$, if $1 - a_4^2 - a_1a_4 > 0$. However,

$$
\begin{aligned}
1 - a_4^2 - a_1a_4 &= 1 - a_4(a_4 + a_1) = 1 - a_4(f(1) - 1 - a_2) \\
&= 1 + a_4 - a_4f(1) + a_2a_4 > 0.
\end{aligned}
$$

Hence $|c_4| - |c_2| > 0$.

Therefore, if (H3) holds, the positive fixed point is locally asymptotically stable. We next assume

$$s'_e(L)bs_0M + (s_m(M)M)' < 0.$$

Then $a_1 > 0$, and $f(1) > 0$ provided $f(-1) > 0$. It follows from $f(-1) = 1 - a_1 + a_2 + a_4$ that if $0 < a_1 < 1 + a_2 + a_4$, that is, if (H4) holds, then $f(-1) > 0$.

Suppose assumption (H4) holds. Then $a_1 > 0$ and it follows from (4.9) that

$$|b_4| - |b_1| = 1 - a_4^2 - |a_4||a_1| = 1 - a_4(a_4 + a_1) = 1 - a_4f(1) + a_4 + a_4a_2 > 0.$$

Moreover, since

$$|c_4| - |c_2| = (1 - a_4)((1 - a_4^2)f(-1) + (1 - a_4^2)a_1 + a_1^2a_4)$$
$$= (1 - a_4)((1 - a_4^2)f(-1) + a_1(1 - a_4^2 + a_1a_4)),$$

$|c_4| - |c_2| > 0$, if $1 - a_4^2 + a_1a_4 > 0$. It is easy to see that

$$1- a_4^2 + a_1a_4 = 1 - a_4(a_4 - a_1)$$
$$= 1 - a_4(a_4 - a_1 + 1 + a_2 - 1 - a_2)$$
$$= 1 - a_4f(-1) + a_4 + a_2a_4 > 0.$$

Hence $|c_4| > |c_2|$. Therefore, positive fixed E_1 is locally asymptotically stable. The proof is complete. □

The dynamics of system (2.2) are richer and more complex if s_e and s_l satisfy conditions (H2). We give local stability results for the positive fixed point in the following theorem.

Theorem 4.3. *Let $s_m(M)$ satisfy conditions* (H1), *and $s_e(L)$ and $s_l(L)$ both satisfy conditions* (H2). *Then we have the following stability results.*

1. *Assume $(s_l(L)L)' > 0$. Then E_1 is locally asymptotically stable if conditions* (H3) *or* (H4) *are satisfied.*

2. *Assume $(s_l(L)L)' < 0$ and $(s_m(M)M)' < -s'_e(L)bs_0M$. Then E_1 is locally asymptotically stable if*

$$-s'_e(L)bs_0M - (s_m(M)M)' < 1 + bs_0s_ps_e(L)s_l(L) + bs_0s_ps_e(L)s'_l(L)L$$
$$+ s'_e(L)bs_0M(s_m(M)M)'.$$
(H5)

3. *Assume $(s_l(L)L)' < 0$ and $-s'_e(L)bs_0M < (s_m(M)M)'$. Then E_1 is locally asymptotically stable if*

$$-bs_0s_ps_e(L)s'_l(L)L < 2bs_0s_ps_e(L)s_l(L) - s'_e(L)bs_0M - s'_m(M)M. \quad \text{(H6)}$$

Here E, L, P, and M are the components of the positive fixed point E_1.

The proof, with tedious algebra, is similar to that of Theorem 4.2, and is omitted.

4.2. Uniform persistence

We have shown that if $r_0 > 1$, the trivial fixed point is unstable and there exists a unique positive fixed point. Moreover, employing the technique shown in $[1, 2]$, we can show that if $r_0 > 1$, system (2.2) is uniformly persistent; that is, there exists a positive number $\rho \in \mathbb{R}_+^4$, such that for every solution, $x(t)$, of (2.2) with $x(0) > 0$, $\liminf_{t \to \infty} x(t) \geq \rho > 0$. This is equivalent to say that the trivial fixed point is a uniform repeller $[15, 19]$.

Let $G := A(x(t))x(t)$ be the map from $\mathbb{R}_+^4$ to $\mathbb{R}_+^4$ and let D be the boundary of Ω defined in (2.3). Then it follows from Theorem 2.1 that $G^t(\Omega \setminus D) \subset \Omega \setminus D$, where $G^t(x)$ denotes the tth iteration of x under G, and hence there exists a global attract X in Ω [18].

For $r_0 > 1$, the trivial fixed point is unstable. Let $M := \{(0, 0, 0, 0)\} \subset X$. Then M is a compact subset of Ω and $\Omega \setminus M$ is positively invariant. Set M is also isolated in X.

Since $A(0)$ is nonnegative and irreducible, it has a dominant positive eigenvalue, $r > 1$, which has a corresponding positive left eigenvector, $\eta > 0$, such that

$$\eta^T A(0) = r\eta^T.$$

Let $1 < r^* < r$. Then

$$\eta^T A(0) > r^* \eta^T.$$

We define a vector norm $\|\cdot\|$ such that $\|x\| := \eta^T x$. Clearly this norm is equivalent to the $2-$ norm, $\|x\|_2 = (\sum x_i)^{1/2}$. Since $A(x)$ is continuous, there exists $\rho > 0$, such that

$$\eta^T A(x) > r^* \eta^T, \tag{4.10}$$

for all $x \in N_\rho(0) := \{x \in \mathbb{R}_+^4, \|x\| \leq \rho\}$.

Let $x(t)$ be a solution of system (2.2). If $x(t) \in N_\rho(0)$, then it follows from (4.10) that

$$p^T x(t+1) = \eta^T A(x(t))x(t) > r^* \eta^T x(t),$$

that is, $\|x(t+1)\| > r^*\|x(t)\| > \|x(t)\|$, for all $x(t) \in N_\rho(0)$. Hence $\liminf_{t \to \infty} x(t) \geq \rho$, which implies that the trivial fixed point is a uniform repeller and then system (2.2) is uniformly persistent. In summary, we have the following result.

Theorem 4.4. *The trivial fixed point is a uniform repeller and system* (2.2) *is uniformly persistence if* $r_0 > 1$.

5. Numerical examples

We provide simple numerical examples to demonstrate the dynamics of system (2.2) as follows.

Example 5.1. In this example, we assume s_e, s_l, and s_m all have the Beverton-Holt form such that $s_i(z) = \frac{\alpha_i k_i}{k_i + \alpha_i z}$, $i = e, l, m$, and use the following parameters

$$\begin{array}{cccc} s_0 = 0.6, & \alpha_e = 0.5, & \alpha_l = 0.4, & \alpha_m = 0.7, \\ k_e = 500, & k_l = 200, & k_m = 1000, & s_p = 0.5. \end{array}$$

If $b = 4.5$, the inherent net reproductive number $r_0 = 0.9 < 1$. Trivial fixed point E_0 is globally stable and the mosquito population goes extinct. If $b = 8$, the inherent

net reproductive number $r_0 = 1.6 > 1$. The trivial fixed point becomes unstable and there exists a positive fixed point, $E_1 = (313.8399, 137.9042, 43.2367, 65.3841)$, which is asymptotically stable. Both cases are shown in Figure 1.
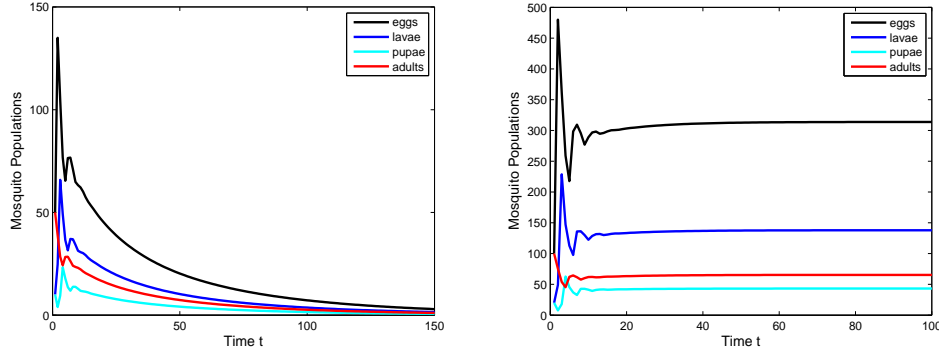

Figure 1. The function forms and parameters are given in Example 5.1. As $b = 4.5$, the inherent net reproductive number $r_0 = 0.9 < 1$. E_0 is globally asymptotically stable. Solutions approach E_0 as $t \to \infty$, shown in the left figure. As $b = 8$, the inherent net reproductive number $r_0 = 1.6 > 1$. E_0 is unstable and $E_1 = (313.8399, 137.9042, 43.2367, 65.3841)$ is asymptotically stable. Solutions approach E_1, as $t \to \infty$, shown in the right figure.

Example 5.2. We assume, in this example, that $s_m(M)$ still has the Beverton-Holt form such that $s_m(z) = \frac{\alpha_m k_m}{k_m + \alpha_m z}$, but $s_i(L)$, $i = e, l$, have the Ricker-type nonlinearity such that $s_i(L) = \alpha_i e^{-L/k_i}$, $i = e, l$. We use the following set of parameters

$$s_0 = 0.6, \quad \alpha_e = 0.3, \quad \alpha_l = 0.8, \quad \alpha_m = 0.01,$$
$$k_e = 500, \quad k_l = 200, \quad k_m = 1000, \quad s_p = 0.8.$$

If $b = 13$, the inherent net reproductive number $r_0 = 0.9455 < 1$. Trivial fixed point E_0 is globally stable and the mosquito population goes extinct. As $b = 16$, the inherent net reproductive number $r_0 = 1.1636 > 1$. The trivial fixed point becomes unstable and there exists a positive fixed point $E_1 = (75, 3596, 21.6499, 15.5429, 7.8500)$ which is asymptotically stable. Both cases are shown in Figure 2.

Example 5.3. Population models with the Ricker-type nonlinearity have richer and more complex dynamics [11, 24, 25]. We assume, in this example, the same structure as that given in Example (5.2), that is, $s_m(z) = \frac{\alpha_m k_m}{k_m + \alpha_m z}$, and $s_i(L) = \alpha_i e^{-L/k_i}$, $i = e, l$. We use the following set of parameters

$$s_0 = 0.8, \quad \alpha_e = 0.8, \quad \alpha_l = 0.8, \quad \alpha_m = 0.2,$$
$$k_e = 300, \quad k_l = 350, \quad k_m = 500, \quad s_p = 0.8,$$

and let b vary, but keep all $r_0 > 1$. The period-doubling bifurcation appears as expected.
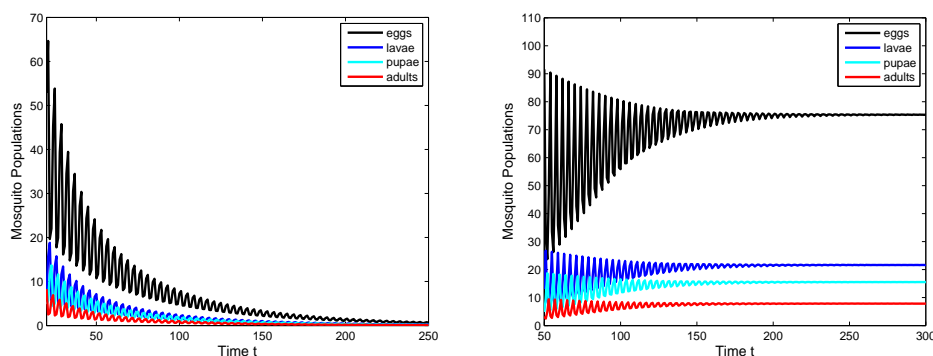
Figure 2.   The function forms and parameters are given in Example 5.2. As $b = 13$, the inherent net reproductive number $r_0 = 0.9455 < 1$. E_0 is globally asymptotically stable. Solutions approach E_0 as $t \to \infty$, shown in the left figure. As $b = 16$, the inherent net reproductive number $r_0 = 1.1636 > 1$. E_0 is unstable and $E_1 = (75, 3596, 21.6499, 15.5429, 7.8500)$ is asymptotically stable. Solutions approach E_1, as $t \to \infty$, shown in the right figure.

If $b = 5$, the inherent net reproductive number $r_0 = 2.56$. There exists a unique positive fixed point, E_1, which is asymptotically stable. If $b = 15$, we have $r_0 = 7.68$. A stable 2-cycle appears. As $b = 21.5$, we have $r_0 = 11.008$. A cycle with a large period exists. At $b = 70$, we have $r_0 = 35.84$. The system exhibits chaotic behavior. All are shown, with only larvae for clearer views, in Figure 3 .

6. Concluding remarks

Mosquito-borne diseases have been big concerns for the public health in the United States and in the world. An effective way to prevent these diseases is to control mosquitoes. To set any feasible optimal strategy in the control of mosquitoes, we need to have a better understanding of the population dynamics of mosquitoes.

Mosquitoes undergo complete metamorphosis going through four distinct stages of development, and these different stages have different responses to environment and different regulating factors to the population. To build a theoretical framework and a fundamental analytic basis for further studies, we formulated discrete-time models for mosquitoes, including the four distinct stages. We assumed density-dependent vital rates with either the Beverton-Holt form or the Ricker-type form. We derived the formula for the net inherent net reproductive number, r_0, and determined the global stability of the trivial fixed point as $r_0 < 1$. We further showed that if $r_0 > 1$, the trivial fixed point becomes unstable, and there exists a unique positive fixed point. We also established conditions for the stability of the positive fixed point.

While we are only able to show the local stability of the positive fixed point for the models with the Beverton-Holt form survival functions, the stability seems global. The models with the Ricker-type nonlinearity, nevertheless, have much more complex dynamics. Using numerical examples, we demonstrated that the period-doubling bifurcation occurs. Further investigation is needed, particularly as we
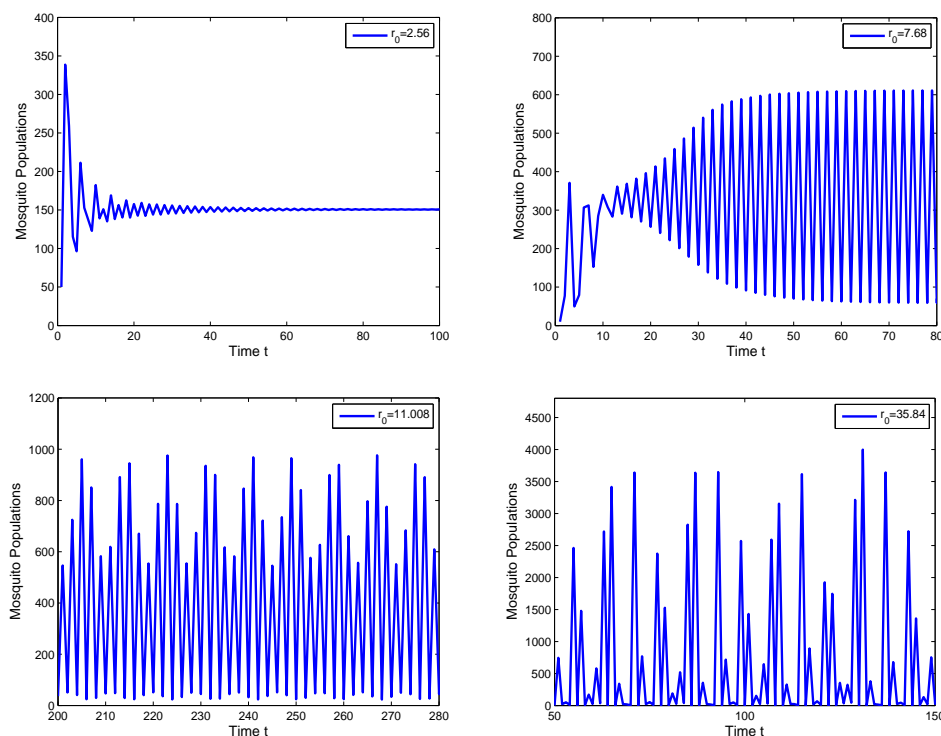
Figure 3. The function forms and parameters are given in Example 5.3. As $b = 5$, $r_0 = 2.56$. Positive fixed point E_1 is asymptotically stable, as shown in the upper left figure. At $b = 15$, $r_0 = 7.68$, and a stable 2-cycle appears, as shown in the upper right figure. If $b = 21.5$, $r_0 = 11.008$, and a cycle with a large period exists, as shown in the lower left figure. At $b = 70$, $r_0 = 35.84$, and the system exhibits chaotic behavior, as shown in the lower right figure. All populations shown in the figures are only larvae for clearer views.

incorporate the mosquitoes into disease transmission models, and is planned in our future research.

References

[1] A. S. Ackleh and R. A. Chiquet, *The global dynamics of a discrete juvenile-adult model with continuous and seasonal reproduction,* J. Biol. Dyn., 3(2009), 101-115.

[2] A. S. Ackleh and P. De Leenheer, *Discrete three-stage population model:persistence and global stability results,* J. Biol. Dyn., 2(2008), 415-427.

[3] L. J. S. Allen and P.van den Driessche, *The basic reproduction number in some discrete-time epidemic models,* J. Diff. Eqn. Appl., 14(2008), 1127-1147.

[4] R. M. Anderson and R. M. May, *Infectious Diseases of Humans, Dynamics and Control,* Oxford Univ. Press, Oxford, 1991.

[5] N. Becker, *Mosquitoes and Their Control,* Kluwer Academic/Plenum, New York, 2003.

[6] T. Bradley, *Malaria and drug resistance, MBChB Special Study Module Project*

Report, Department of Microbiology and Immunology, University of Leicester, `http://www-micro.msb.le.ac.uk/224/Bradley/Bradley.html`, 1996.

[7] H. Caswell, *Matrix Population Models,* (2nd ed.), Sinauer, Sunderland, 2001.

[8] CDC, *Malaria Fact Sheet, 2010,* `http://www.cdc.gov/malaria/about/facts.html`, 2010.

[9] CDC, *Dengue Fact Sheet, 2010,* `http://www.cdc.gov/Dengue/faqFacts/fact.html`.

[10] J. M. Cushing, *Nonlinear matrix models and population dynamics,* Nat. Res. Mod., 2 (1988), 539-580.

[11] J. M. Cushing, *An Introduction to Structrued Population Dynamics,* SIAM, Philadelphia, 1998.

[12] J. M. Cushing, *On the relationship between r and R_0 and its role in the bifurcation of stable equilibria of Darwinian matrix models,* J. Biol. Dyn., published online (2010).

[13] J. M. Cushing and Z.Yicang, *The net reporductive value and stability in matrix population models,* Nat. Res. Mod., 8(1994), 297-333.

[14] C. Dye, *Intraspecific competition amongst larval aedes aegypti: Food exploitation or chemical interference. Ecol. Ento.,* 7(1982), 39-46.

[15] A. Fonda, *Uniformly persistent semidynamical systems,* Proceed. of Amer. Math. Soc., 104(1988), 111-116.

[16] R. M. Gleiser, J. Urrutia, and D. E. Gorla, *Effects of crowding on populations of aedes albifasciatus larvae under laboratory conditions,* Ento. Exper. Appl., 95(2000), 135-140.

[17] J. K. Hale, *Discrete dissipative processes, In: Ordinary and Partial Differential Equations,* Lec. Notes in Math., W. N. Everitt and B. D. Sleeman (eds), 564(1976), 207-224.

[18] J. K. Hale and P. Waltman, *Persistence in infinite-dimensional systems,* SIAM, J. Math. Anal., 20(1989), 388-395.

[19] J. Hofbauer and J. W. H. So, *Uniform persistence and reprllors for maps,* Proceed. of Amer. Math. Soc., 107(1989), 1137-1142.

[20] N. Levinson, *Transformation theory of nonlinear differential equations of the second order,* Ann. Math., 4(1944), 723-737.

[21] E. R. Lewis, *Network Models in Population Biology,* Springer, New York, 1977.

[22] Jia Li, *A malaria model with partial immunity in humans,* Math. Bio. Eng., 5(2008), 789-801.

[23] Jia Li, *Simple stage-structured models for wild and transgenic mosquito populations,* J. Diff. Eqns. Appl., 17(2009), 327-347.

[24] Jia Li, *Malaria model with stage-structured mosquitoes,* Math. Bio. Eng., (2011), in press.

[25] Jia Li, Baojun Song, and Xiaohong Wang, *An extended Ricker population model with Allee effects,* J. Diff. Eqns. Appl., 13(2007), 309-321.

[26] G. MacDonald, *The Epidemiology and Control of Malaria,* Oxford Univ. Press, London, 1957.

[27] Mosquito Life Cycle, `http://www.co.westchester.ny.us/health/WNVmosquito-life-cycle.htm`.

[28] Mosquito Life Cycle Printout, http://www.enchantedlearning.com/subjects/insects/mosquito/life cycle.shtml.

[29] J. D. Murray, *Mathematical Biology I. An Introduction (3rd ed.),* Springer, New York, 2002.

[30] NBII, *West Nile Virus,*http://westnilevirus.nbii.gov, 2010.

[31] G. A. Ngwa, *Modelling the dynamics of endemic malaria in growing populations,* Dis. Conti. Dyn. Sys. Series B, 4(2004), 1172-1204.

[32] G. A. Ngwa, *On the population dynamics of the malaria vector,* Bull. Math. Biol., 68(2006), 2161-2189.

[33] G. A. Ngwa and W. S. Shu, *A mathematical model for endemic malaria with variable human and mosquito populations,* Math. Comp. Modelling, 32(2000), 747-763.

[34] M. Otero, H. G. Solari, and N. Schweigmann, *A stochastic population dynamics model for Aedes aegypti: formulation and application to a city with temperate climate,* Bull. Math. Biol., 68(2006), 1945-1974.

[35] D. Ruiz, G. Poveda, I. D. Velez, M. L. Quinones, G. L. Rua, L. E. Velasquesz, and J. S. Zuluaga, *Modelling entomological-climatic interactions of Plasmodium falciparum malaria transmission in two Colombian endemic-regions: contributions to a National Malaria Early Warning System,* Malaria Journal, 5(2006), 66.

[36] W. H. Wernsdorfer, *The importance of malaria in the world, in: Malaria, Vol. 1, Epidemiology, Chemotherapy, Morphology, and Metabolism,* J. P. Kreier (ed.), Academic Press, New York, 1980.

[37] World Health Organization, World Malaria Report 2010, http://www.who.int/malaria/world_malaria_report_2010/en.

[38] H. M. Yang, *Malaria transmission model for different levels of acquired immunity and temperature-dependent parameters (vector),* Rev Saude Publica, 34(2000), 223-231.