

CULLING STRUCTURED HOSTS TO ERADICATE VECTOR-BORNE DISEASES

XINLI HU

Department of Applied Mathematics, Xi'an Jiaotong University, Xi'an, 710049 China

YANSHENG LIU

Department of Mathematics, Shandong Normal University, Jinan, 250014, P. R. China

JIANHONG WU

Center for Disease Modeling, York University, Toronto, Ontario, M3J 1P3 Canada

ABSTRACT. A compartmental model is developed, in the form of a nonautonomous system of delay differential equations subject to impulses at specific times, for mosquito-born disease control involving larvicides and insecticide sprays. Sufficient conditions in terms of the frequencies and rates of larvicides and insecticide sprays are derived, and numerical simulations are provided to illustrate the sharpness of these disease eradication conditions.

1. Introduction. Culling has been a common method for pest control and ecosystem management. In particular, culling has been used widely to control vector-borne diseases in the hope that culling the vector at carefully chosen times may intervene the disease transmission cycle and reduce the infection. A specific example is the larvicides and insecticide sprays as techniques in the war against mosquitoes, the vector for many mosquito-born diseases including West Nile virus (WNV) and Dengue fever.

Simons and Gourley [6] developed a time-dependent, stage-structured, single species population model to address the situation where the adults are subject to culling or trapping, which occurs at certain times. Their model takes the form of a nonautonomous scalar delay differential equation where time dependence arises due to the specific sequence of times when culling takes place. This model was extended by Gourley, Liu and Wu [2] to consider the West Nile virus management-motivated problems when immature mosquitoes are controlled by larviciding, and such an extension leads to a system of delay differential equations with impulses. The work [2] discussed the feasibility and effectiveness of either larvicides or insecticide sprays but not both. However, existing WNV control strategies normally involve a

2000 *Mathematics Subject Classification.* Primary: 34K45, 34K25; Secondary: 92D30, 34K60.

Key words and phrases. Culling, West Nile virus, structured population, disease eradication, delay.

This research was partially supported by NNSF of P. R. China (10871120), China Scholarship Council and the Science & Technology Development Funds of Shandong Education Committee(J08LI10)(YL), by Natural Sciences and Engineering Research Council of Canada and Mathematics for Information Technology and Complex Systems (JW), and by the Canada-China Disease Thematic Program sponsored via Network of Centers of Excellence and International Development Research Center (XH, YL JW). The corresponding author is Yansheng Liu.

combination of reducing the mosquito population at both the immature and mature levels. Therefore, in this paper we formulate a model that deals with the disease transmission dynamics when the vector (mosquito) is subject to culling at both the immature and mature levels, but possibly with different frequencies and rates. This model thus permits us to analyze the complementary impact of larvicides and insecticide sprays for an effective disease control program.

The model is formulated in Section 2. A brief discussion about the nonnegative property of model solutions is given and then disease eradication conditions are derived in Section 3, and are illustrated numerically in Section 4. Section 4 also contains some comments.

2. Model derivation.

2.1. Single-species population with culling. We consider a single-species population, with its density at age a and time t denoted by $u(t, a)$. We assume the maturation time is a constant $\tau > 0$ and use $b : R \rightarrow R$ to denote the function representing the birth rate. Therefore, $u(t, a)$ with $a < \tau$ is the density of immatures while $u(t, a)$ with $a > \tau$ corresponds to the density of matures. We also assume that both the immature and adult individuals are subject to culling: the immatures are culled at times

$$0 < t_1 < t_2 < t_3 < \cdots < t_j < \cdots, \quad \text{and } t_j \rightarrow \infty \text{ as } j \rightarrow \infty \quad (2.1)$$

at the rate $b_j \in [0, 1]$ (note that b_j is the culling rate while function b is the birth rate), while the adults are culled at times

$$0 < s_1 < s_2 < s_3 < \cdots < s_j < \cdots, \quad \text{and } s_j \rightarrow \infty \text{ as } j \rightarrow \infty \quad (2.2)$$

at the rates $c_j \in [0, 1]$.

Then we have, for the immature population, that

$$\frac{\partial u}{\partial t} + \frac{\partial u}{\partial a} = -\mu(a)u - \sum_{j=1}^{\infty} b_j(a)u(t_j^-, a)\delta(t - t_j), \quad 0 < a < \tau, \quad (2.3)$$

where δ is the usual delta function, $\mu(a)$ is the natural death rate for immatures, and the boundary condition is given by

$$u(t, 0) = b(u_m(t)), \quad u_m(t) = \int_{\tau}^{\infty} u(t, a)da. \quad (2.4)$$

We can integrate (2.3) from t_j^- to t_j^+ to obtain

$$u(t_j^+, a) = (1 - b_j(a))u(t_j^-, a). \quad (2.5)$$

We also have, for the mature population, that

$$\frac{\partial u}{\partial t} + \frac{\partial u}{\partial a} = -\mu_m u - \sum_{j=1}^{\infty} c_j u(s_j^-, a)\delta(t - s_j), \quad a > \tau, \quad (2.6)$$

where μ_m is the intrinsic death rate of the mature population. Therefore, using $u(t, \infty) = 0$, we obtain

$$\begin{aligned} \frac{du_m(t)}{dt} &= \int_{\tau}^{\infty} \left(-\frac{\partial u}{\partial a} - \mu_m u(t, a) - \sum_{j=1}^{\infty} c_j u(s_j^-, a)\delta(t - s_j) \right) da \\ &= u(t, \tau) - \mu_m u_m(t) - \sum_{j=1}^{\infty} c_j u_m(s_j^-)\delta(t - s_j). \end{aligned} \quad (2.7)$$

The maturation rate can be derived from (2.3)-(2.4) (see (2.15) in [2]) as, for $t \geq \tau$,

$$u(t, \tau) = u(t - \tau, 0) \exp\left(-\int_0^\tau \mu(s) ds\right) \prod_{j=k(t)}^{i(t)} (1 - b_j(\tau - (t - t_j))), \quad (2.8)$$

or

$$u(t, \tau) = b(u_m(t - \tau)) \exp\left(-\int_0^\tau \mu(s) ds\right) \prod_{j=k(t)}^{i(t)} (1 - b_j(\tau - (t - t_j))), \quad (2.9)$$

where

$$i(t) = \max\{i : t_i \leq t\}, \quad k(t) = \min\{i : t_i > t - \tau\}.$$

In summary, we get the following delay differential equation for the mature population $u_m(t)$:

$$\frac{du_m(t)}{dt} = S(t)b(u_m(t - \tau)) \exp\left(-\int_0^\tau \mu(s) ds\right) - \mu_m u_m(t) - \sum_{j=1}^\infty c_j u_m(s_j^-) \delta(t - s_j), \quad (2.10)$$

where

$$S(t) = \prod_{j=k(t)}^{i(t)} (1 - b_j(\tau - (t - t_j))). \quad (2.11)$$

2.2. West Nile virus control via mosquito culling. West Nile virus belongs to a family of viruses called Flaviviridae. It is spread by mosquitoes that have fed on the blood of infected birds. People, horses, and most other mammals are not known to develop infectious-level viremias very often, and thus are probably dead-end or incidental hosts.

To formulate a mathematical model for the West Nile virus dynamics between mosquitoes and birds when mosquitoes (including immature and mature) are culled, we consider three state variables $M_S(t)$, $M_I(t)$, and $B_I(t)$ for the total numbers of susceptible adult mosquitoes, infected adult mosquitoes, and infected birds, respectively.

Continuing the notation from last section, we use $u(t, a)$ to denote the density of immature mosquitoes at age a and assume the maturation length is a constant $\tau > 0$. We also assume that mosquitos at the immature stage are subject to culling at times t_j described in (2.1), and that both susceptible and infected mosquitoes may lay eggs but the virus is not passed on to their offsprings. The birth rate $u(t, 0)$ of mosquitoes is therefore assumed to be a function of the total number of adult mosquitoes $M_S(t) + M_I(t)$, so that

$$u(t, 0) = b(M_S(t) + M_I(t)),$$

where $b(\cdot)$ is the birth rate function. We further assume there is no vertical transmission between mosquitoes, so the uninfected mosquitoes population is increased via the maturation rate $u(t, \tau)$. It is diminished by infection, which may be acquired when uninfected mosquitoes feed from the blood of infected birds, by natural death at a rate d_S , and by culling at the times s_j as described in (2.2). Thus, susceptible adult mosquitoes satisfy an equation of the form

$$\frac{dM_S(t)}{dt} = u(t, \tau) - \gamma M_S B_I - d_S M_S - \sum_{j=1}^\infty c_j M_S(s_j^-) \delta(t - s_j), \quad (2.12)$$

where γ is the contact rate between uninfected mosquitoes and infected birds: γ equals the multiplication of the biting rate of mosquitoes and the transmission possibility between uninfected mosquitoes and infected birds.

Using the same argument leading to (2.9), we obtain

$$\begin{aligned} u(t, \tau) &= u(t - \tau, 0)S(t)\exp\left(-\int_0^\tau \mu(s)ds\right) \\ &= b(M_S(t - \tau) + M_I(t - \tau))S(t)\exp\left(-\int_0^\tau \mu(s)ds\right), \end{aligned}$$

with $S(t)$ given by (2.11). Thus, the equation for the susceptible mosquitoes is

$$\begin{aligned} \frac{dM_S(t)}{dt} &= b(M_S(t - \tau) + M_I(t - \tau))S(t)\exp\left(-\int_0^\tau \mu(s)ds\right) - \gamma M_S B_I - d_S M_S \\ &\quad - \sum_{j=1}^{\infty} c_j M_S(s_j^-) \delta(t - s_j). \end{aligned} \tag{2.13}$$

The infected mosquito population is generated via the infection of uninfected mosquitoes by infected birds and diminished by natural death at a rate d_I and culling at the times s_j . Thus,

$$\frac{dM_I(t)}{dt} = \gamma M_S B_I - d_I M_I - \sum_{j=1}^{\infty} c_j M_I(s_j^-) \delta(t - s_j). \tag{2.14}$$

Note that the above formulation is based on the assumption that the uninfected mosquitoes and infected mosquitoes are equally mixed, so that at each cull the proportions of each class removed are the same.

We assume the total number of birds in an area is some constant $N_B > 0$. Birds are divided into two classes: uninfected birds B_S and infected B_I , so that $B_S = N_B - B_I$. Then the change rate of infected birds is increased through infection of uninfected birds when they are bitten by infected mosquitoes and reduced by the natural death and disease-induced death (at a rate d_B). Thus,

$$\frac{dB_I(t)}{dt} = \beta(N_B - B_I)M_I - d_B B_I, \tag{2.15}$$

while β is the contact rate between infected mosquitoes and uninfected birds (β equals the multiplication of the biting rate of mosquitoes and the transmission possibility between infected mosquitoes and uninfected birds). Thus $\beta(N_B - B_I)M_I$ is the rate at which susceptible birds become infected birds, assumed to be given by the law of mass action.

3. Dynamics and disease eradication criteria. Now we consider the dynamics of the impulsive nonautonomous system constituting of (2.13)-(2.15) for $t > 0$, where $S(t)$ is given by (2.11). The system is solved [4] subject to the following initial data:

$$\begin{aligned} M_S(\theta) &= M_S^0(\theta), & \theta &\in [-\tau, 0], \\ M_I(\theta) &= M_I^0(\theta), & \theta &\in [-\tau, 0], \\ B_I(\theta) &= B_I^0 \in [0, N_B], \end{aligned} \tag{3.1}$$

where $M_S^0(\theta)$, $M_I^0(\theta)$ and B_I^0 are prescribed, and these initial functions (values) are assumed to be continuous and nonnegative. Throughout the remaining part of this

paper, we always assume that the birth function $b(\cdot)$ satisfies $b(0) = 0$ and $b(M) > 0$ for all $M > 0$.

By integrating (2.13) and (2.14) from s_j^- to s_j^+ , the following alternative version of model (2.13)-(2.15), when $t \geq \tau$, is obtained:

$$\left\{ \begin{array}{l} \frac{dB_I(t)}{dt} = \beta(N_B - B_I)M_I - d_B B_I; \\ \frac{dM_S(t)}{dt} = b(M_S(t - \tau) + M_I(t - \tau))S(t)\exp\left(-\int_0^\tau \mu(s)ds\right) \\ \qquad \qquad \qquad -\gamma M_S B_I - d_S M_S; \\ M_S(s_j^+) = (1 - c_j)M_S(s_j^-); \\ \frac{dM_I(t)}{dt} = \gamma M_S B_I - d_I M_I; \\ M_I(s_j^+) = (1 - c_j)M_I(s_j^-). \end{array} \right. \tag{3.2}$$

We first state as in [2] the following proposition on non-negativity of solutions.

Proposition 3.1 *The solution of system (3.2) subject to (3.1) satisfies*

$$M_S(t) \geq 0, \quad M_I(t) \geq 0, \quad B_I(t) \in [0, N_B] \quad \text{for } t \in (0, +\infty).$$

Proof. Similarly to the argument of [[2], Proposition 3.1], we can show that $B_I(t) \leq N_B$ for all $t > 0$. Now we show $M_S(t) \geq 0$ for all $t > 0$. This will be finished by the method of steps.

If $\tau < s_1$, as in [2], we know

$$M_S(t) \geq M_S^0(0)\exp\left(-\int_0^t (\gamma B_I(\xi) + d_S)d\xi\right), \tag{3.3}$$

and so $M_S(t) \geq 0$ for all $t \in (0, \tau]$.

If there are some positive integer k such that $s_1 < s_2 < \dots < s_k \leq \tau < s_{k+1}$, then (3.3) holds and so $M_S(t) \geq 0$ for all $t \in (0, s_1]$. Notice that $M_S(s_1^+) = (1 - c_1)M_S(s_1^-)$. Therefore,

$$M_S(t) \geq M_S(s_1^+)\exp\left(-\int_{s_1}^t (\gamma B_I(\xi) + d_S)d\xi\right),$$

and so $M_S(t) \geq 0$ for all $t \in (s_1, s_2]$. Repeating this analysis shows that $M_S(t) \geq 0$ for all $t \in (0, \tau]$.

The above argument can be continued to prove that $M_S(t) \geq 0$ for all $t \in (\tau, 2\tau], (2\tau, 3\tau], \dots$, and so it holds for all $t > 0$.

Now we are in position to show that $M_I(t) \geq 0$ and $B_I(t) \geq 0$ for $t > 0$. As in [2], the variable $(M_I(t), B_I(t))$ can be interpreted as satisfying a monotone dynamical system [7] in $[0, s_1]$, which means $M_I(t) \geq 0$ and $B_I(t) \geq 0$ for $t \in [0, s_1]$. Notice that $M_S(s_1^+) = (1 - c_1)M_S(s_1^-) = (1 - c_1)M_S(s_1) \geq 0$ and $B_I(s_1^+) = B_I(s_1) \geq 0$. One can again obtain that $(M_I(t), B_I(t))$ satisfies a monotone dynamical system in $[s_1, s_2]$, and so on so forth. We eventually obtain $M_I(t) \geq 0$ and $B_I(t) \geq 0$ for all $t > 0$. □

For convenience, we introduce

$$\begin{aligned} S^\infty &= \limsup_{t \rightarrow \infty} S(t), \\ b'_{max} &= \sup_{m \geq 0} b'(m), b_{max} = \sup_{m \geq 0} b(m). \end{aligned}$$

Furthermore, we write

$$\begin{aligned} d &=: \min(d_I, d_S), \quad \alpha(\varepsilon) =: (S^\infty + \varepsilon)b'_{max} \exp\left(-\int_0^\tau \mu(s) ds\right), \\ c_{inf} &=: \inf_{j \geq 1} c_j, \quad \delta_{inf} = \inf_{j \geq 1} (s_{j+1} - s_j), \quad \delta_{sup} = \sup_{j \geq 1} (s_{j+1} - s_j). \end{aligned} \quad (3.4)$$

We assume in the remaining part of this paper, $\delta_{sup} < \infty$.

Theorem 3.1. *Suppose one of the following conditions holds:*

(C1) $d > \alpha(0)$;

(C2) $d \leq \alpha(0)$, $c_{inf} \in (0, 1)$, $0 < \delta_{inf} < \delta_{sup} \leq \tau$, and

$$(1 - c_{inf}) + \frac{\alpha(0)}{d} (1 - \exp(-d\delta_{sup})) < 1.$$

(C3) $d \leq \alpha(0)$, $c_{inf} \in (0, 1)$, $\delta_{sup} > \tau$, and

$$\left[1 + \frac{\alpha(0)}{d} (1 - \exp(-d\delta_{sup}))\right]^{n_1 - 1} \cdot \left[(1 - c_{inf}) + \frac{\alpha(0)}{d} (1 - \exp(-d\delta_{sup}))\right] < 1,$$

where n_1 is a positive integer satisfying $n_1\tau \geq \delta_{sup} > (n_1 - 1)\tau$.

Then for any solution of (3.1)-(3.2), we have $B_I(t) \rightarrow 0$ and $M_I(t) \rightarrow 0$ as $t \rightarrow +\infty$.

Proof. Denote the total number of adult mosquitoes by $M_T(t) = M_S(t) + M_I(t)$. Notice by Proposition 3.1 that

$$\begin{cases} \frac{dM_T(t)}{dt} \leq b(M_T(t - \tau))S(t) \exp\left(-\int_0^\tau \mu(s) ds\right) - dM_T(t); \\ M_T(s_j^+) = (1 - c_j)M_T(s_j^-). \end{cases} \quad (3.5)$$

Suppose now that condition (C1) holds. Let $\varepsilon > 0$ be sufficiently small that

$$d > \alpha(\varepsilon). \quad (3.6)$$

Therefore, there exists $T_1 > 0$ sufficiently large that

$$M_T(t) \leq \hat{M}_T(t), \quad t \geq T_1, \quad (3.7)$$

where $\hat{M}_T(t)$ satisfies

$$\frac{d\hat{M}_T(t)}{dt} = \alpha(\varepsilon)\hat{M}_T(t - \tau) - d\hat{M}_T(t). \quad (3.8)$$

Combining this with (3.6) and the well known results (see [3]), by virtue of (3.7), we know $M_T(t) \rightarrow 0$ as $t \rightarrow +\infty$. Hence also $M_I(t) \rightarrow 0$, and this enables us to conclude from (3.2) that $B_I(t) \rightarrow 0$ as $t \rightarrow +\infty$.

Next assume condition (C2) is satisfied. Then there exists $\varepsilon > 0$ such that

$$(1 - c_{inf}) + \frac{\alpha(\varepsilon)}{d} (1 - \exp(-d\delta_{sup})) < 1. \quad (3.9)$$

Similarly as above, there exists $T_1 > 0$ such that (3.7) and (3.8) hold. Consider equation (3.8) subject to

$$\hat{M}_T(s_j^+) = (1 - c_j)\hat{M}_T(s_j^-). \quad (3.10)$$

Under condition (C2), there exists a positive number n satisfying $n\delta_{inf} \geq \tau > (n-1)\delta_{inf}$. Without loss of generality, suppose $s_1 \geq T_1$ and let $M_1 =: \sup_{t \in [s_n - \tau, s_n]} \hat{M}_T(t)$.

Then from (3.8) it follows that

$$\frac{d\hat{M}_T(t)}{dt} \leq M_1\alpha(\varepsilon) - d\hat{M}_T(t), \quad t \in (s_n, s_{n+1}]. \quad (3.11)$$

Multiplying (3.14) by $\exp(d(t - s_n))$ and then integrating it from s_n to t , we obtain

$$\begin{aligned} \hat{M}_T(t) &\leq \hat{M}_T(s_n^+) \exp(-d(t - s_n)) + \frac{M_1\alpha(\varepsilon)}{d} (1 - \exp(-d(t - s_n))) \\ &\leq M_1 \left[(1 - c_n) + \frac{\alpha(\varepsilon)}{d} (1 - \exp(-d\delta_{sup})) \right] \\ &\leq M_1 \left[(1 - c_{inf}) + \frac{\alpha(\varepsilon)}{d} (1 - \exp(-d\delta_{sup})) \right] \\ &\leq M_1, \quad t \in (s_n, s_{n+1}], \end{aligned}$$

where (3.9) is used. This, together with $\delta_{sup} \leq \tau$ and (3.8), means that (3.11) also holds for $t \in (s_{n+1}, s_{n+2}]$. Analogously, it follows that

$$\begin{aligned} \hat{M}_T(t) &\leq \hat{M}_T(s_{n+1}^+) \exp(-d(t - s_{n+1})) + \frac{M_1\alpha(\varepsilon)}{d} (1 - \exp(-d(t - s_{n+1}))) \\ &\leq M_1 \left[(1 - c_{inf}) + \frac{\alpha(\varepsilon)}{d} (1 - \exp(-d\delta_{sup})) \right] \\ &\leq M_1, \quad t \in (s_{n+1}, s_{n+2}], \end{aligned}$$

and inductively,

$$\begin{aligned} \hat{M}_T(t) &\leq \hat{M}_T(s_{2n-1}^+) \exp(-d(t - s_{2n-1})) + \frac{M_1\alpha(\varepsilon)}{d} (1 - \exp(-d(t - s_{2n-1}))) \\ &\leq M_1 \left[(1 - c_{inf}) + \frac{\alpha(\varepsilon)}{d} (1 - \exp(-d\delta_{sup})) \right], \quad t \in (s_{2n-1}, s_{2n}]. \end{aligned}$$

Consequently,

$$\hat{M}_T(t) \leq M_1 \left[(1 - c_{inf}) + \frac{\alpha(\varepsilon)}{d} (1 - \exp(-d\delta_{sup})) \right], \quad t \in (s_n, s_{2n}]. \quad (3.12)$$

Notice that $s_{2n} - s_n \geq n\delta_{inf} \geq \tau$. This, together with (3.8) and (3.12), guarantees that

$$\frac{d\hat{M}_T(t)}{dt} \leq M_1\alpha(\varepsilon) \left[(1 - c_{inf}) + \frac{\alpha(\varepsilon)}{d} (1 - \exp(-d\delta_{sup})) \right] - d\hat{M}_T(t), \quad t \in (s_{2n}, s_{2n+1}].$$

Similarly, we can obtain that

$$\hat{M}_T(t) \leq M_1 \left[(1 - c_{inf}) + \frac{\alpha(\varepsilon)}{d} (1 - \exp(-d\delta_{sup})) \right]^2, \quad t \in (s_n, s_{2n}],$$

and inductively, for $k \geq 1$, that

$$\hat{M}_T(t) \leq M_1 \left[(1 - c_{inf}) + \frac{\alpha(\varepsilon)}{d} (1 - \exp(-d\delta_{sup})) \right]^k, \quad t \in (s_{kn}, s_{2kn}].$$

This implies $\hat{M}_T(t) \rightarrow 0$ as $t \rightarrow +\infty$. By virtue of (3.7), the claimed result follows under condition (C2).

Finally, we consider the case where (C3) is satisfied. Then there exists $\varepsilon > 0$ such that

$$\left[1 + \frac{\alpha(\varepsilon)}{d} (1 - \exp(-d\delta_{sup})) \right]^{n_1-1} \cdot \left[(1 - c_{inf}) + \frac{\alpha(\varepsilon)}{d} (1 - \exp(-d\delta_{sup})) \right] < 1.$$

Similarly as above, there exists $T_1 > 0$ such that (3.7) and (3.8) hold. We consider equation (3.8) subject to (3.10). Without loss of generality, we suppose $s_1 \geq T_1$ and let

$$M_{[s_1-\tau, s_1]} =: \sup_{t \in [s_1-\tau, s_1]} \hat{M}_T(t).$$

If $s_2 - s_1 \leq \tau$, then by (3.12) it follows that

$$\frac{d\hat{M}_T(t)}{dt} \leq M_{[s_1-\tau, s_1]} \alpha(\varepsilon) - d\hat{M}_T(t), \quad t \in (s_1, s_2]. \quad (3.13)$$

From this we can obtain

$$\hat{M}_T(t) \leq M_{[s_1-\tau, s_1]} \left[(1 - c_{inf}) + \frac{\alpha(\varepsilon)}{d} (1 - \exp(-d\delta_{sup})) \right], \quad t \in (s_1, s_2]. \quad (3.14)$$

If $s_2 - s_1 > \tau$, then (3.13) and (3.14) hold for $t \in (s_1, s_1 + \tau]$. In this case, let k_0 be the integer such that $(k_0 - 1)\tau < s_2 - s_1 \leq k_0\tau$. Then $k_0 \leq n_1$. From (3.8) and (3.14) it follows that

$$\frac{d\hat{M}_T(t)}{dt} \leq M_{[s_1-\tau, s_1]} \left[(1 - c_{inf}) + \frac{\alpha(\varepsilon)}{d} (1 - \exp(-d\delta_{sup})) \right] \alpha(\varepsilon) - d\hat{M}_T(t)$$

for $t \in (s_1 + \tau, s_1 + 2\tau]$. Multiplying this inequality by $\exp(d(t - s_1 - \tau))$ and then integrating from $s_1 + \tau$ to t yields

$$\begin{aligned} \hat{M}_T(t) &\leq \hat{M}_T(s_1 + \tau) \exp(-d(t - s_1 - \tau)) \\ &\quad + \frac{M_{[s_1-\tau, s_1]} \left[(1 - c_{inf}) + \frac{\alpha(\varepsilon)}{d} (1 - e^{-d\delta_{sup}}) \right] \alpha(\varepsilon)}{1 - e^{-(d(t - s_1 - \tau))}} \\ &\leq M_{[s_1-\tau, s_1]} \left[(1 - c_{inf}) + \frac{\alpha(\varepsilon)}{d} (1 - e^{-d\delta_{sup}}) \right] \left[1 + \frac{\alpha(\varepsilon)}{d} (1 - e^{-d\delta_{sup}}) \right] \end{aligned}$$

for $t \in (s_1 + \tau, s_1 + 2\tau]$.

Repeating this analysis yields that

$$\hat{M}_T(t) \leq M_{[s_1-\tau, s_1]} \left[(1 - c_{inf}) + \frac{\alpha(\varepsilon)}{d} (1 - e^{-d\delta_{sup}}) \right] \cdot \left[1 + \frac{\alpha(\varepsilon)}{d} (1 - e^{-d\delta_{sup}}) \right]^{k_0-1}$$

for $t \in (s_1 + (k_0 - 1)\tau, s_2]$. As $k_0 \leq n_1$, we have

$$\hat{M}_T(t) \leq M_{[s_1-\tau, s_1]} \left[(1 - c_{inf}) + \frac{\alpha(\varepsilon)}{d} (1 - e^{-d\delta_{sup}}) \right] \cdot \left[1 + \frac{\alpha(\varepsilon)}{d} (1 - e^{-d\delta_{sup}}) \right]^{n_1-1} \quad (3.15)$$

for $t \in (s_1, s_2]$. From (3.14) it is easy to see that (3.15) also holds when $s_2 - s_1 \leq \tau$.

Inductively, we obtain that

$$\hat{M}_T(t) \leq M_{[s_1-\tau, s_1]} \left\{ \left[(1 - c_{inf}) + \frac{\alpha(\varepsilon)}{d} (1 - e^{-d\delta_{sup}}) \right] \cdot \left[1 + \frac{\alpha(\varepsilon)}{d} (1 - e^{-d\delta_{sup}}) \right]^{n_1-1} \right\}^k$$

for $t \in (s_k, s_{k+1}]$ and for $k = 1, 2, 3, \dots$. This means $\hat{M}_T(t) \rightarrow 0$ as $t \rightarrow +\infty$. By virtue of (3.7), the result follows. \square

We now consider some special cases.

Theorem 3.2. *Assume $d \leq \alpha(0)$. In addition, assume one of the following conditions holds:*

(C4) $s_j = j\tau$, $j = 1, 2, \dots$; and there exists $\varepsilon > 0$ such that

$$\prod_{j=1}^{+\infty} \left[(1 - c_j) + \frac{\alpha(\varepsilon)}{d} (1 - \exp(-d\tau)) \right] = 0.$$

(C5) there exists some integer m such that $s_{j+1} = s_j + \frac{\tau}{m}$, $c_j \equiv c \in (0, 1)$, $j = 1, 2, \dots$, and one of the following conditions holds:

(C5₁) $(1 - c) + \frac{\alpha(0)}{d}(1 - \exp(-\frac{d\tau}{m})) < 1$;

(C5₂) $\rho(A) < 1$, where $\rho(A)$ is the spectral radius of the matrix A given below

$$\begin{pmatrix} q(0) & 0 & 0 & \dots & 0 & (1-c) \\ q(0)(1-c) & q(0) & 0 & \dots & 0 & (1-c)^2 \\ q(0)(1-c)^2 & q(0)(1-c) & q(0) & \dots & 0 & (1-c)^3 \\ \dots & \dots & \dots & \dots & \dots & \dots \\ q(0)(1-c)^{m-2} & q(0)(1-c)^{m-3} & q(0)(1-c)^{m-4} & \dots & q(0) & (1-c)^{m-1} \\ q(0)(1-c)^{m-1} & q(0)(1-c)^{m-2} & q(0)(1-c)^{m-3} & \dots & q(0)(1-c) & q(0) + (1-c)^m \end{pmatrix},$$

with $q(\varepsilon) := \frac{\alpha(\varepsilon)}{d}(1 - \exp(-d\frac{\tau}{m}))$, $\forall \varepsilon \geq 0$.

Then $B_I(t) \rightarrow 0$ and $M_I(t) \rightarrow 0$ as $t \rightarrow +\infty$, where $B_I(t)$ and $M_I(t)$ satisfy (3.1)-(3.2).

Proof. As in the proof of Theorem 3.1, there exists $T_1 > 0$ such that (3.7) and (3.8) hold. We still consider equation (3.8) subject to (3.10). Without loss of generality, suppose $s_1 \geq T_1$ and $M_1 =: \sup_{t \in [s_1 - \tau, s_1]} \hat{M}_T(t)$.

Consider the case where (C4) holds. From (3.8) it follows that

$$\frac{d\hat{M}_T(t)}{dt} \leq M_1\alpha(\varepsilon) - d\hat{M}_T(t), \quad t \in (s_1, s_2]. \tag{3.16}$$

Multiplying (3.16) by $\exp(d(t - s_1))$ and then integrating it from s_1 to t leads to

$$\begin{aligned} \hat{M}_T(t) &\leq \hat{M}_T(s_1^+) \exp(d(t - s_1)) + \frac{M_1\alpha(\varepsilon)}{d}(1 - \exp(-d(t - s_1))) \\ &\leq M_1 \left[(1 - c_1) + \frac{\alpha(\varepsilon)}{d}(1 - \exp(-d\tau)) \right], \quad t \in (s_1, s_2]. \end{aligned}$$

By induction, we can obtain that

$$\hat{M}_T(t) \leq M_1 \prod_{j=1}^k \left[(1 - c_j) + \frac{\alpha(\varepsilon)}{d}(1 - \exp(-d\tau)) \right]$$

for $t \in (s_k, s_{k+1}]$. From (C4) and (3.7), we conclude that $B_I(t) \rightarrow 0$ and $M_I(t) \rightarrow 0$ as $t \rightarrow +\infty$ in this case.

Next we suppose (C5₁) holds. Then there exists $\varepsilon > 0$ such that

$$\bar{c} := (1 - c) + \frac{\alpha(\varepsilon)}{d}(1 - \exp(-\frac{d\tau}{m})) < 1. \tag{3.17}$$

Using similar arguments as above, and noticing that $s_{j+1} = s_j + \frac{\tau}{m}$, $c_j \equiv c \in (0, 1)$, $j = 1, 2, \dots$, we have

$$\hat{M}_T(t) \leq M_1 \left[(1 - c) + \frac{\alpha(\varepsilon)}{d}(1 - \exp(-d\frac{\tau}{m})) \right], \quad t \in (s_1, s_2];$$

and

$$\hat{M}_T(t) \leq M_1 \left[(1 - c)^2 + \frac{\alpha(\varepsilon)}{d}(1 - \exp(-d\frac{\tau}{m}))((1 - c) + 1) \right], \quad t \in (s_2, s_3].$$

Inductively, we have

$$\begin{aligned} & \hat{M}_T(t) \\ & \leq M_1 \left[(1-c)^{m-1} + \frac{\alpha(\varepsilon)}{d} (1 - \exp(-d\frac{\tau}{m})) ((1-c)^{m-2} + (1-c)^{m-3} + \cdots + 1) \right] \\ & \leq M_1 \left[(1-c)^{m-1} + \frac{\alpha(\varepsilon)}{c \cdot d} (1 - \exp(-d\frac{\tau}{m})) \right], \quad t \in (s_{m-1}, s_m]. \end{aligned}$$

Let

$$M_2 =: M_1 \left[(1-c)^{m-1} + \frac{\alpha(\varepsilon)}{c \cdot d} (1 - \exp(-d\frac{\tau}{m})) \right].$$

Then $\hat{M}_T(t) \leq M_2$ for $t \in (s_1, s_m]$. Furthermore, we have

$$\hat{M}_T(t) \leq M_2 \left[(1-c) + \frac{\alpha(\varepsilon)}{d} (1 - \exp(-d\frac{\tau}{m})) \right] = M_2 \bar{c}, \quad t \in (s_m, s_{m+1}];$$

and

$$\begin{aligned} \hat{M}_T(t) & \leq M_2 \left[(1-c)^2 + \frac{\alpha(\varepsilon)}{d} (1 - \exp(-d\frac{\tau}{m})) ((1-c) + 1) \right] \\ & = M_2 [\bar{c} + (1-c)(\bar{c}-1)], \quad t \in (s_{m+1}, s_{m+2}]. \end{aligned}$$

Inductively, we have

$$\begin{aligned} & \hat{M}_T(t) \\ & \leq M_2 \left[(1-c)^m + \frac{\alpha(\varepsilon)}{d} (1 - \exp(-d\frac{\tau}{m})) ((1-c)^{m-1} + (1-c)^{m-2} + \cdots + 1) \right] \\ & = M_2 \left\{ \bar{c} + [(1-c)^{m-1} + (1-c)^{m-2} + \cdots + (1-c)](\bar{c}-1) \right\}, \quad t \in (s_{2m-1}, s_{2m}]. \end{aligned}$$

Since $\bar{c} < 1$, we have

$$\hat{M}_T(t) \leq M_2 \bar{c}, \quad t \in (s_m, s_{2m}].$$

Inductively, we have

$$\hat{M}_T(t) \leq M_2 \bar{c}^k, \quad t \in (s_{km}, s_{(k+1)m}].$$

From this, together with (3.17), it follows that $B_I(t) \rightarrow 0$ and $M_I(t) \rightarrow 0$ as $t \rightarrow +\infty$.

Finally, we suppose (C5₂) holds. Since $\rho(A) < 1$, there exists $\varepsilon > 0$ such that $\rho(A(\varepsilon)) < 1$, where $A(\varepsilon)$ is given by

$$\begin{pmatrix} q(\varepsilon) & 0 & 0 & \cdots & 0 & (1-c) \\ q(\varepsilon)(1-c) & q(\varepsilon) & 0 & \cdots & 0 & (1-c)^2 \\ q(\varepsilon)(1-c)^2 & q(\varepsilon)(1-c) & q(\varepsilon) & \cdots & 0 & (1-c)^3 \\ \cdots & \cdots & \cdots & \cdots & \cdots & \cdots \\ q(\varepsilon)(1-c)^{m-2} & q(\varepsilon)(1-c)^{m-3} & q(\varepsilon)(1-c)^{m-4} & \cdots & q(\varepsilon) & (1-c)^{m-1} \\ q(\varepsilon)(1-c)^{m-1} & q(\varepsilon)(1-c)^{m-2} & q(\varepsilon)(1-c)^{m-3} & \cdots & q(\varepsilon)(1-c) & q(\varepsilon) + (1-c)^m \end{pmatrix}$$

Let

$$M_{i,j} := \sup_{(s_{im+j-1}, s_{im+j})} \hat{M}_T(t), \quad i = 1, 2, \dots; \quad j = 1, 2, \dots, m.$$

From (3.8) we know

$$\frac{d\hat{M}_T(t)}{dt} \leq \alpha(\varepsilon)M_{1,1} - d \cdot \hat{M}_T(t), \quad t \in (s_{2m}, s_{2m+1}];$$

and

$$\frac{d\hat{M}_T(t)}{dt} \leq \alpha(\varepsilon)M_{1,2} - d \cdot \hat{M}_T(t), \quad t \in (s_{2m+1}, s_{2m+2}];$$

and so on so forth. Finally, we have

$$\frac{d\hat{M}_T(t)}{dt} \leq \alpha(\varepsilon)M_{1,m} - d \cdot \hat{M}_T(t), \quad t \in (s_{3m-1}, s_{3m}].$$

From these inequalities it follows that

$$\hat{M}_T(t) \leq x(s_{2m}^+) + M_{1,1}q(\varepsilon) \leq M_{1,m}(1 - c) + M_{1,1}q(\varepsilon), \quad t \in (s_{2m}, s_{2m+1}];$$

$$\hat{M}_T(t) \leq x(s_{2m+1}^+) + M_{1,2}q(\varepsilon) \leq M_{2,1}(1 - c) + q(\varepsilon)M_{1,2} \quad t \in (s_{2m+1}, s_{2m+2}];$$

and

$$\hat{M}_T(t) \leq x(s_{3m-1}^+) + M_{1,m}q(\varepsilon) \leq M_{2,m-1}(1 - c) + q(\varepsilon)M_{1,m}, \quad t \in (s_{3m-1}, s_{3m}].$$

Therefore,

$$\begin{aligned} M_{2,1} &\leq M_{1,m}(1 - c) + M_{1,1}q(\varepsilon); \\ M_{2,2} &\leq q(\varepsilon)(1 - c)M_{1,1} + q(\varepsilon)M_{1,2} + (1 - c)^2M_{1,m}; \\ M_{2,3} &\leq q(\varepsilon)(1 - c)^2M_{1,1} + q(\varepsilon)(1 - c)M_{1,2} + q(\varepsilon)M_{1,3} + (1 - c)^3M_{1,m}; \\ &\vdots \\ M_{2,j} &\leq q(\varepsilon)(1 - c)^{j-1}M_{1,1} + q(\varepsilon)(1 - c)^{j-2}M_{1,2} + \cdots \\ &\quad + q(\varepsilon)(1 - c)M_{1,j-1} + q(\varepsilon)M_{1,j} + (1 - c)^jM_{1,m}; \\ &\vdots \\ M_{2,m} &\leq q(\varepsilon)(1 - c)^{m-1}M_{1,1} + q(\varepsilon)(1 - c)^{m-2}M_{1,2} + \cdots \\ &\quad + q(\varepsilon)(1 - c)M_{1,m-1} + (q(\varepsilon) + (1 - c)^m)M_{1,m}. \end{aligned}$$

That is

$$\begin{pmatrix} M_{2,1} \\ M_{2,2} \\ M_{2,3} \\ \vdots \\ M_{2,m-1} \\ M_{2,m} \end{pmatrix} \leq A(\varepsilon) \begin{pmatrix} M_{1,1} \\ M_{1,2} \\ M_{1,3} \\ \vdots \\ M_{1,m-1} \\ M_{1,m} \end{pmatrix}.$$

By induction, we obtain that

$$\begin{pmatrix} M_{n+1,1} \\ M_{n+1,2} \\ M_{n+1,3} \\ \vdots \\ M_{n+1,m-1} \\ M_{n+1,m} \end{pmatrix} \leq A(\varepsilon) \begin{pmatrix} M_{n,1} \\ M_{n,2} \\ M_{n,3} \\ \vdots \\ M_{n,m-1} \\ M_{n,m} \end{pmatrix},$$

where $n \geq 1$ is positive integers.

Since $\rho(A(\varepsilon)) < 1$, we have $M_{n,j} \rightarrow 0$ as $n \rightarrow +\infty$, $j = 1, 2, \dots, m$. This shows $B_I(t) \rightarrow 0$ and $M_I(t) \rightarrow 0$ as $t \rightarrow +\infty$. The proof is complete. \square

Theorem 3.3. *Suppose one of the following conditions holds:*

(C6) $d_I d_B > \gamma \beta N_B M^{**}$, where

$$M^{**} = \frac{S^\infty b_{max} \exp\left(-\int_0^\tau \mu(s) ds\right) (1 - c_{inf} e^{-d})}{d};$$

(C7) $d_I d_B \leq \gamma \beta N_B M^{**}$, but

$$\begin{aligned} \sup_{j \geq 1} \left[(\lambda_2(1 - c_j) - \lambda_1) e^{\lambda_1 \delta_j} + (\lambda_2 + (c_j - 1)\lambda_1) e^{\lambda_2 \delta_j} + c_j d_I (e^{\lambda_2 \delta_j} - e^{\lambda_1 \delta_j}) \right. \\ \left. - (\lambda_2 - \lambda_1)(1 - c_j) e^{-(d_B + d_I) \delta_j} \right] < \lambda_2 - \lambda_1, \end{aligned} \quad (3.18)$$

where $\lambda_1 < 0$ and $\lambda_2 \geq 0$ satisfy

$$\lambda^2 + (d_B + d_M)\lambda + (d_B d_M - \gamma \beta N_B M^{**}) = 0. \quad (3.19)$$

Then $B_I(t) \rightarrow 0$ and $M_I(t) \rightarrow 0$ as $t \rightarrow +\infty$, where $B_I(t)$ and $M_I(t)$ satisfy (3.1)-(3.2).

Proof. Suppose condition (C6) holds. We now deduce some growth estimation in this case. Notice that for each $\varepsilon > 0$, there exists $T_1 > 0$ such that $S(t) \leq S^\infty + \varepsilon$ as $t \geq T_1$. Therefore,

$$\frac{dM_T(t)}{dt} \leq (S^\infty + \varepsilon) \exp\left(-\int_0^t \mu(s) ds\right) b_{max} - dM_T(t), \quad t \geq T_1.$$

This, together with $M_T(s_j^+) = (1 - c_j)M_T(s_j^-)$ and the fact that ε is arbitrary, guarantees that

$$\limsup_{t \rightarrow \infty} M_T(t) \leq \frac{S^\infty b_{max} \exp\left(-\int_0^t \mu(s) ds\right)}{d}.$$

On the other hand, notice that $d_I d_B > \gamma \beta N_B M^{**}$. By (C6), there exists $\varepsilon_0 > 0$ such that

$$d_I d_B > \gamma \beta N_B M_{\varepsilon_0}^{**}, \quad (3.20)$$

where

$$M_{\varepsilon_0}^{**} = \frac{(S^\infty + \varepsilon_0) b_{max} \exp\left(-\int_0^t \mu(s) ds\right) (1 - c_{inf} e^{-d})}{d}. \quad (3.21)$$

Also for such ε_0 , there exists $T_2 > 0$ such that

$$S(t) \leq S^\infty + \varepsilon_0 \quad \text{and} \quad M_T(t) \leq \frac{(S^\infty + \varepsilon_0) b_{max} \exp\left(-\int_0^t \mu(s) ds\right)}{d} \quad \text{as} \quad t \geq T_2.$$

So from (3.2) it follows that

$$\begin{cases} \frac{dM_T(t)}{dt} \leq (S^\infty + \varepsilon_0) \exp\left(-\int_0^t \mu(s) ds\right) b_{max} - dM_T(t), & t \geq T_2; \\ M_T(s_j^+) = (1 - c_j)M_T(s_j^-). \end{cases} \quad (3.22)$$

For $s_j > T_2$ and $t \in (s_j, s_{j+1}]$, from (3.22) we know

$$M_T(t) \leq M_T(s_j^+) e^{-d(t-s_j)} + \frac{(S^\infty + \varepsilon_0) b_{max} \exp\left(-\int_0^t \mu(s) ds\right)}{d} (1 - e^{-d(t-s_j)})$$

for $t \in (s_j, s_{j+1}]$. This, together with

$$M_T(s_j^+) = (1 - c_j)M_T(s_j^-) \leq (1 - c_j) \frac{(S^\infty + \varepsilon_0) b_{max} \exp\left(-\int_0^t \mu(s) ds\right)}{d},$$

guarantees that

$$\begin{aligned}
 M_T(t) &\leq \frac{(S^\infty + \varepsilon_0)b_{max}\exp\left(-\int_0^\tau \mu(s)ds\right)}{d} \left(1 - c_j e^{-d(t-s_j)}\right) \\
 &= \frac{(S^\infty + \varepsilon_0)b_{max}\exp\left(-\int_0^\tau \mu(s)ds\right)}{d} (1 - c_{inf} e^{-d\delta_{sup}}) \\
 &=: M_{\varepsilon_0}^{**}, \quad t \in (s_j, s_{j+1}]. \tag{3.23}
 \end{aligned}$$

From (3.23) and (3.7), we conclude that $M_I(t) \leq \bar{M}_I(t)$ and $B_I(t) \leq \bar{B}_I(t)$ for $t \geq T_2$, where \bar{M} and \bar{B} satisfy

$$\begin{cases} \frac{d\bar{B}_I(t)}{dt} = \beta N_B \bar{M}_I - d_B \bar{B}_I, & t \geq 0; \\ \frac{d\bar{M}_I(t)}{dt} = \gamma \bar{M}_{\varepsilon_0}^{**} B_I - d_I \bar{M}_I, & t \neq s_j; \\ \bar{M}_I(s_j^+) = (1 - c_j) \bar{M}_I(s_j^-). \end{cases} \tag{3.24}$$

Using a similar argument to that in [Theorem 3.5, [2]], we can show that (3.20) and (3.24) imply that $\bar{M}_I(t) \rightarrow 0$ and $\bar{B}_I(t) \rightarrow 0$ as $t \rightarrow +\infty$, and so $M_I(t) \rightarrow 0$ and $B_I(t) \rightarrow 0$ as $t \rightarrow +\infty$.

Finally we assume condition (C7) is satisfied. Choose ε sufficiently small so that (3.18) holds as well if we replace λ_1 and λ_2 with λ_1^ε and λ_2^ε respectively, where $\lambda_1^\varepsilon < 0$ and $\lambda_2^\varepsilon > 0$ satisfy

$$\lambda^2 + (d_B + d_M)\lambda + (d_B d_M - \gamma \beta N_B M_\varepsilon^{**}) = 0.$$

Notice here that this equation is changed from (3.19) by replacing M^{**} with M_ε^{**} , which is defined as in (3.21).

Using a procedure similar to that developed in the proof of [Theorem 3.6, [2]], we obtain the desired result. \square

4. Simulations and discussions. We now carry out some simulations to examine the effectiveness of different combinations of immature culling and adult culling strategies for the system (3.1)-(3.2). Notice that all information about immature culling is embodied in the function $S(t)$ defined by (2.11). The parameter values and interpretations to be used in the simulations are given in Table 1.

Table 1: Parameter values used for the simulations. The data are taken from references [1, 2, 5, 8].

Para.	Meaning	value
d_L	Per capita death rate of mosquito larva (per day)	0.1
τ	Maturation time of mosquito larva (days)	10
d_M	Per capita natural death rate of mosquito (per day)	0.05
d_B	Disease-induced death rate of infected bird (per day)	0.1
N_B	Total number of birds b	500
β	Transmission rate from infected mosquitos to susceptible birds	0.0144/ N_B
γ	Transmission rate from infected birds to susceptible mosquitos	0.0792/ N_B
b	Maximum per capita daily egg production rate	10
1/a	Size of mosquito population at which egg laying is maximized	2500
b_j	Fraction of larva removed at the cull at time t_j	variable
c_j	Fraction of adult mosquito removed at the cull at time s_j	variable
1/ Δt	larva culling frequency	variable
1/ Δs	adult culling frequency	variable

In the simulations we take the birth function of mosquitoes as $b(M) = bM e^{-aM}$. The initial conditions are assumed to be $M_S(t) = 5000, M_I(t) = 600, B_I(t) = 100$ for $t \in [-\tau, 0]$. In all simulations, the larva culls and adult culls are at equally

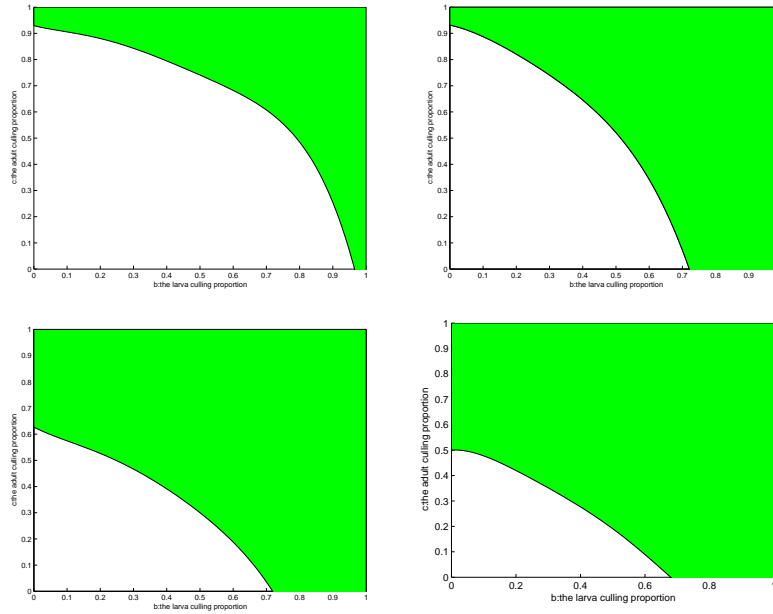
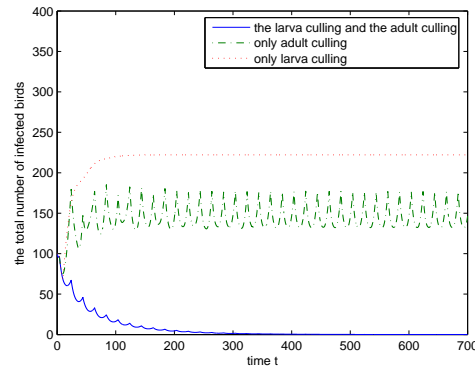


FIGURE 1. Minimal rates of culling and their relationship in order to eradicate the disease for different culling frequencies (cull the larval every Δt (days) and cull the adult every Δs) (days): (a). $\Delta t = 7, \Delta s = 14$; (b). $\Delta t = 3.5, \Delta s = 14$; (c). $\Delta t = 3.5, \Delta s = 7$; (d). $\Delta t = 3, \Delta s = 5$. All other parameters have values specified in Table 1.

spaced. The distance between two consecutive larva culls is denoted by Δt , so the larva cull times are given by $t_j = t_0 + j\Delta t, j = 1, 2, 3, \dots$ with $t_0 = 4$. The distance between two consecutive adult culls is denoted by Δs , and the adult cull times are thus given by $s_j = s_0 + j\Delta s, j = 1, 2, 3, \dots$ with $s_0 = 4$.

In Figure 1, in the space of (b^*, c^*) , where $b^* = b_j, c^* = c_j$ for all $j \geq 1$, the shaded area gives the region when the disease dies out. It shows that when the culling frequencies are low and when a single strategy of culling the immature or the adult mosquitos is implemented, the culling rate must be very large. The minimal culling rate to eliminate the disease by culling the adult mosquitos only is 0.92, 0.62, 0.5 when $\Delta s = 14, 7, 5$ respectively, while the minimal culling rate to eliminate the disease by culling the immature mosquitos only is 0.96, 0.72, 0.68 when $\Delta s = 7, 3.5, 3$ respectively. A combination of culling mosquitos at both the immature and adult stages requires much lower culling rates: with a combination such that $(\Delta t, \Delta s) = (3.5, 14)$, the rates $(b^*, c^*) = (0.5, 0.6)$ of culling will be sufficient.

Figure 2 shows a situation when a combination of larvicide and adulticide sprays eradicates the disease but neither larvicide nor adulticide can do so alone. Figure 3 shows that even if a combination of larvicide and adulticide cannot eradicate the disease, this strategy can substantially reduce the numbers of infected birds and infected mosquitos. Figure 4 illustrates a case where culling with low frequencies



has no effect on disease spread and oscillatory patterns of disease outbreak occurs. Figure 5 gives a comparison between condition ($C5_1$) (right) and the precise disease eradication (left, obtained through numerical simulation) for a wide range of culling frequencies. This indicates that our sufficient conditions are far from optimal.

In summary, our analysis and simulations show that a combination of larvicide and adulticide is much more effective than a single approach alone. A single approach of either larvicide or adulticide for West Nile virus eradication requires an extremely high culling rate that cannot be achieved in a real situation, but an optimal combination of both is feasible. Such a combination, even if it fails to eradicate the disease, can substantially reduce the numbers of infected birds and infected mosquitos.

Delay differential equations with impulses have been intensively investigated recently. Our study shows that such equations arise naturally from consideration of some human intervention strategies for disease control. However, we also show the great challenge to derive sharp disease eradication condition, in comparison with the case without impulses where disease eradication condition is normally associated with the the basic reproduction number for which there is a standard algorithm. Due to the hybrid nature of the model and the modeled biological reality, a sharp eradication condition must involve the estimation of growth/decay of the infection during the two consecutive culling times, that is described by a continuous flow, and the culling rates in a sequence of times which can be regarded as resetting the phase. Precise disease eradication conditions cannot be obtained without considering the iteration of curves (during the culling intervals). This proves to be a very difficult task, and the involvement of time delay due to the biological structure of mosquitos and the corresponding human intervention makes this much more challenging. Nevertheless, sufficient conditions derived here ensure the success of a combinational strategy of larvicide and adulticide, although their derivation from a sharp and necessary condition of disease eradication implies that more cost-effective strategies can be designed if further progress improving the sufficient conditions is achieved.

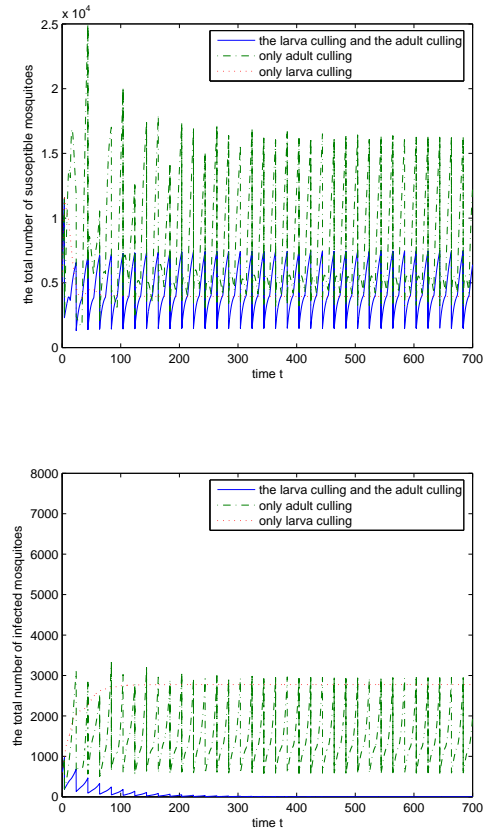
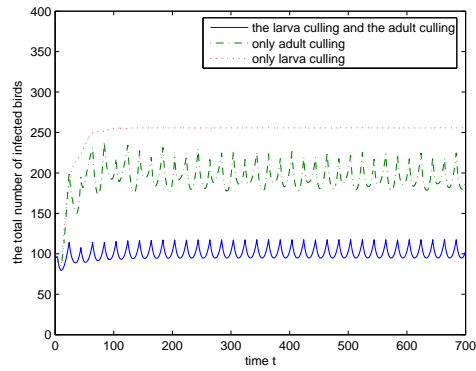


FIGURE 2. A combination of larvicide and adulticide sprays can eradicate the disease but neither larvicide nor adulticide can do so alone. Parameter values are $\Delta t = 10$, $\Delta s = 20$, $b_j = 0.80$, $c_j = 0.80$ and other parameters have the values shown in Table 1.



Acknowledgements. This work is honor of Professor Fred Brauer's 75th birthday and Professor Karl Hadeler's 70th birthday.

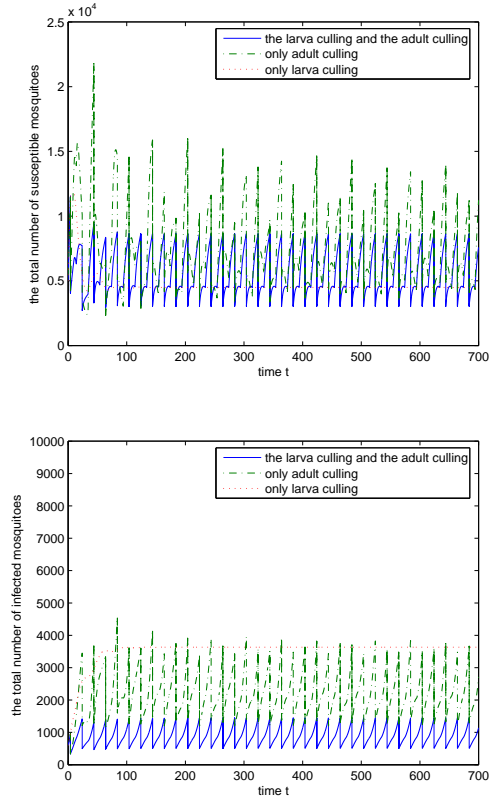
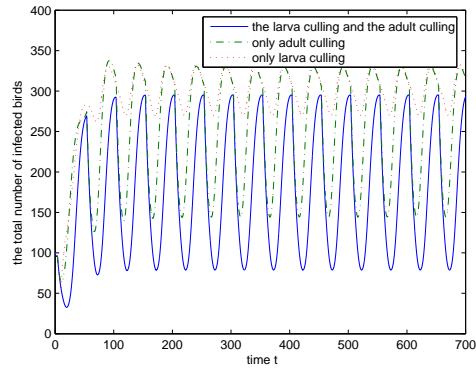


FIGURE 3. Even if a combination of larvicide and adulticide cannot eradicate the disease, this strategy can substantially reduce the numbers of infected birds and infected mosquitos. Parameter values are $\Delta t = 10, \Delta s = 20, b_j = 0.65, c_j = 0.65$ and other parameters have the values shown in Table 1.



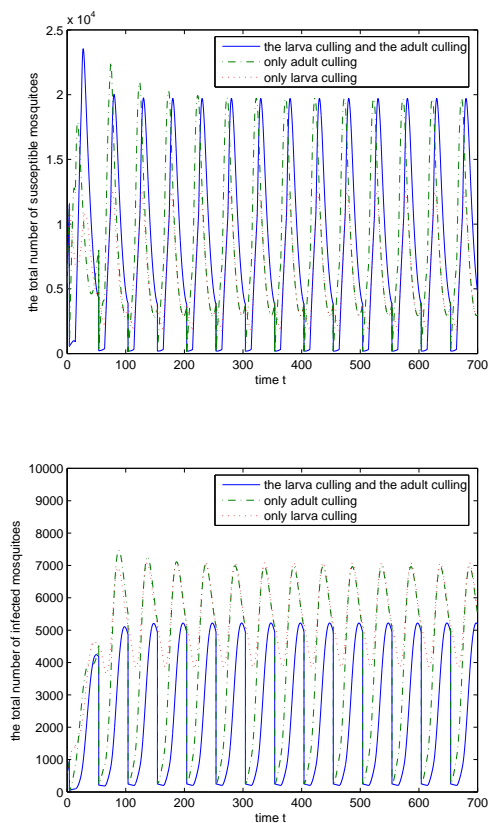


FIGURE 4. Culling with lower frequencies has little impact on disease spread, and disease outbreak seems to be recurrent. Parameter values are $\Delta t = 50$, $\Delta s = 50$, $b_j = 0.95$, $c_j = 0.95$ and other parameters have the values shown in Table 1.

REFERENCES

- [1] C. Bowman, A. B. Gumel, P. van den Driessche, J. Wu and H. Zhu, *A mathematical model for assessing control strategies against West Nile virus*, Bull. Math. Biol., **67** (2005), 1107–1133.
- [2] S. A. Gourley, R. Liu and J. Wu, *Eradicating vector-borne diseases via age-structured culling*, J. Math. Biol., **54** (2007), 309–335.
- [3] J. K. Hale, L. Verduyn and M. Sjoerd, “Introduction to Functional-Differential Equations,” Applied Mathematical Sciences, 99, Springer-Verlag, New York, 1993.
- [4] Y. Kuang, “Delay Differential Equations with Applications in Population Dynamics,” In: “Mathematics in Science and Engineering,” **191**, Academic Press, Inc., Boston, MA, 1993.
- [5] C. C. Lord and J. F. Day, *Simulation studies of St. Louis encephalitis and West Nile viruses: The impact of bird mortality*, Vector Borne Zoonotic Dis., **1** (2001), 317–329.
- [6] R. R. L. Simons and S. A. Gourley, *Extinction criteria in stage-structured population models with impulsive culling*, SIAM. J. Appl. Math., **66** (2006), 1853–1870 (electronic).
- [7] H. L. Smith, “Monotone Dynamical Systems. An Introduction to the Theory of Competitive and Cooperative Systems,” Mathematical Surveys and Monographs, 41, American Mathematical Society, Providence, RI, 1995.
- [8] M. J. Wonham, T. de-Camino-Beck and M. Lewis, *An epidemiological model for West Nile virus: Invasion analysis and control applications*, Proc. R. Soc. Lond. Ser. B, **271** (2004), 501–507.

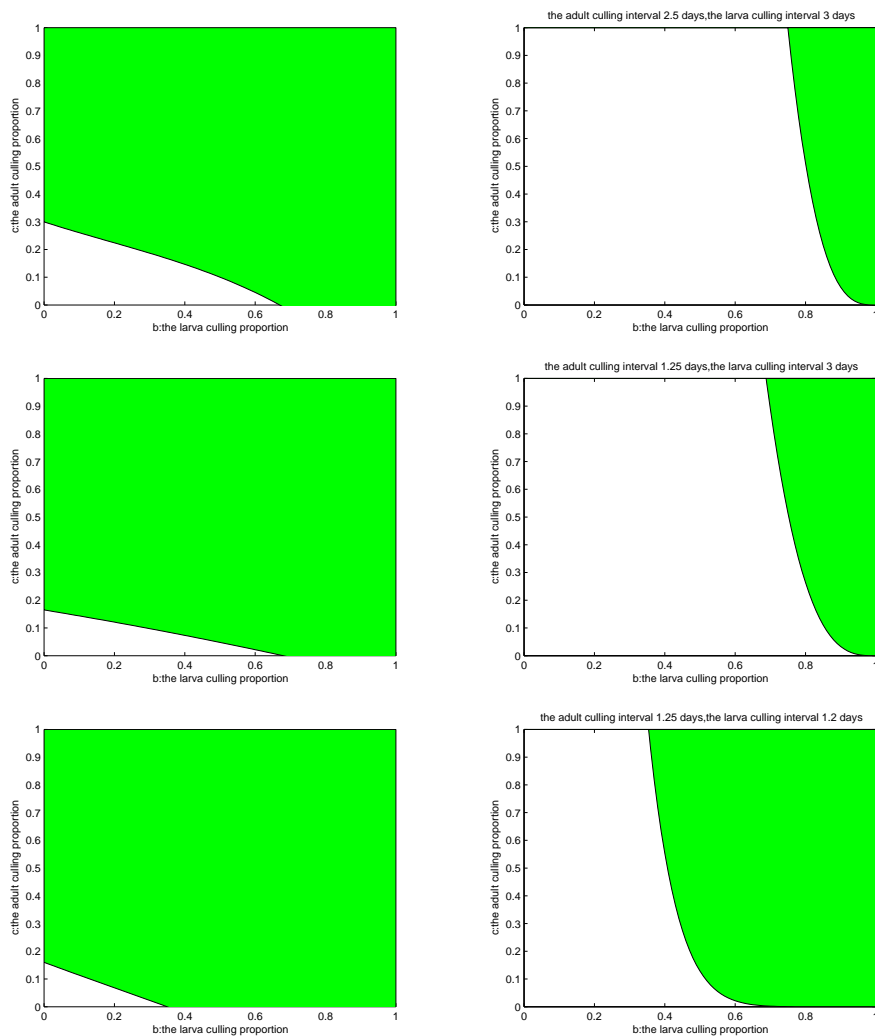


FIGURE 5. Comparison between condition $(C5_1)$ (right) and the precise disease eradication (left, obtained through numerical simulation) for a wide range of culling frequencies (cull the larval every Δt (days) and cull the adult every Δs (days)). This indicates that our sufficient conditions are far from optimal. Parameter values are (a). $\Delta t = 3, \Delta s = 2.5$; (b). $\Delta t = 3, \Delta s = 1.25$; (c). $\Delta t = 1.2, \Delta s = 1.25$, and other parameters have the values shown in Table 1.

Received February 5, 2007. Accepted September 19, 2008.

E-mail address: huxinli1975@yahoo.com.cn

E-mail address: yanshliu@gmail.com

E-mail address: wujh@mathstat.yorku.ca