ARTICLE IN PRESS YJDEQ:8062

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J. Differential Equations ••• (••••) •••–•••

Journal of Differential Equations

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Stage-structured models of intra- and inter-specific competition within age classes

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Received 6 January 2015; revised 1 July 2015

Abstract

In some species, larvae and adults experience competition in completely different ways. Simple stage-structured models without larval competition usually yield a single delay equation for the adults. Using an age structured system incorporating competition among both larvae and adults, we derive a system of distributed delay equations for the numbers of larvae and adults. The system is neither cooperative nor reducible to a single equation for either variable. Positivity, boundedness and uniform strong persistence are established. Linear stability analysis of equilibria is difficult due to the strong coupling, but results are proved for small delays using monotone systems theory and exponential ordering. For small delay we prove a theorem on generic convergence to equilibria, which does not directly follow from standard theory but can be proved indirectly using comparison arguments. Finally, we consider an extension to two-strain competition and prove theorems on the linear stability of the boundary equilibria.
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MSC: 34K12; 34K20; 34K25; 92D25

Keywords: Competition; Stage structure; Delay; Monotone system; Exponential ordering

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http://dx.doi.org/10.1016/j.jde.2015.09.048
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Please cite this article in press as: J. Fang et al., Stage-structured models of intra- and inter-specific competition within age classes, J. Differential Equations (2015), http://dx.doi.org/10.1016/j.jde.2015.09.048

1. Introduction

In species that have distinct life stages, the juvenile and adult individuals of the species often have very different characteristics. This is particularly true in the case of insect and amphibian species that generally have a larval stage and undergo metamorphosis. Larvae often have a completely different diet from the adults, are often adapted to a different (often aquatic) environment, and have completely different dispersal characteristics. Adult insects can disperse great distances while their larvae are often confined and relatively immobile. On the other hand, with some marine species such as barnacles it is the larvae that move while adults do not. These differences have implications for the study of competition and highlight the importance of paying careful attention to competition among larvae as well as among the adults of a species.

It is known that competition among mosquito larvae occurs in confined environments and there have been studies of its effects on adult body size and adult longevity (e.g. Reiskind and Lounibos [18]). This is important because competition among mosquito larvae can be significant in the transmission of diseases such as dengue fever, yellow fever, chikungunya and malaria. Larval competition can affect traits such as adult longevity which has a major impact on malaria transmission due to the relatively long developmental stage of the malaria parasite in the adult mosquito. Larval competition may also alter susceptibility of adult mosquitoes to dengue infection (Alto et al. [3]). Armistead et al. [4] describe interspecific competition between the larvae of two mosquito species in the USA, *Aedes albopictus* and *Aedes japonicus*, suggesting that *Ae. albopictus* larvae have a competitive advantage over those of *Ae. japonicus*. Gilpin [9] discusses larval competition as a growth-regulating mechanism in *Drosophila*. Schade and Vamosi [21] and Messina [16] describe the effects of competition among the larvae of seed beetles. Prado et al. [17] present evidence of intraspecific competition among the larvae of pit-trapping antlions in Brazil. Blanchard et al. [5] describe competition between the larvae of the American slipper limpet *Crepidula fornicata* and the Japanese oyster *Crassostrea gigas*, and report results which suggest that limpet larvae compete with oyster larvae by depleting phytoplankton concentrations. In the context of invasive species, Smith [25] has examined the competitive effects of the larvae of two widely introduced anurans, the cane toad and the Cuban treefrog, on the growth and development of the larvae of native anurans.

In this paper we assume that an individual larva competes with all other larvae but not with any adults, and similarly that adults compete only with other adults. Thus, competition is solely within age classes and does not occur between individuals at different life stages. These assumptions should be realistic for some insect and amphibian species that undergo metamorphoses, since in such species the larvae and adults often have a different diet and do not compete for food, and moreover larvae and adults are often adapted to different environments. In amphibians it is often the case that the larvae live in an aquatic environment and the adults in a terrestrial one, as is usually the case for the urodeles, a carnivorous order that includes salamanders (Wells [26]). On the other hand, in beetles of the genus *helichus* the larvae are terrestrial and the adults are aquatic, living mostly in running water (Clifford [6]). Some beetles, for example the *elmidae* (riffle beetles), are actually aquatic as both larvae and adults, leading to the possibility of competition between all individuals. For such species the modelling in this paper may not be so realistic.

Using the well known McKendrick von-Forster equation as a starting point, we propose a simple single species age-structured model with two age classes (larvae and adults) that incorporates intra-specific competition within those classes based on the assumptions described in the previous paragraph. Using the technique of integration along characteristics, the model is reduced to

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a system of two delay differential equations for the numbers $I(t)$ and $M(t)$ of immature (larval) and mature (adult) individuals at time t. The system involves both discrete and distributed time delay terms since the maturation rate at time t depends on the birth rate at the time $t-\tau$, where τ is the larval developmental time, and also because at each stage of its development a larva competes with all other larvae present, which leads to a distributed delay term. Unusually in stage-structured population models of this type, there is no decoupling in the system and it is not possible to reduce the model equations to a single equation for the number of adults. After establishing basic but important properties of the model, we prove population persistence (in the strong uniform sense) under a natural condition. Then the problem of the linear stability of equilibria is treated, which is surprisingly difficult. The structure of the model equations, the absence of certain monotonicity properties and the inability to decouple leads to characteristic equations that do not immediately lend themselves to commonly applied theorems that, in other simpler systems, might make it possible to restrict attention to real roots (such as the results in Chapter 5 of Smith [22]). However, under some restriction on the delay, it is possible to treat the linear stability problem with the aid of the concept of exponential ordering. A central result of this paper is a result on generic convergence to equilibria under certain conditions including smallness of the delay. Again, this result does not follow immediately from known theorems but it can be established with the aid of a comparison argument. Generic convergence to equilibria, and information on the local stability of equilibria, can make it possible to make statements about the global stability of a positive equilibrium if it is further known that only one such equilibrium exists. Uniqueness or otherwise of positive equilibria is itself dependent on the model parameters, coefficient functions and the function that describes how the egg-laying rate depends on the number of adults, and we investigate this dependence. Finally, we propose an extension of the model to the case of competition between two strains of a species. Here, again, competition is only within age classes but larvae of a particular strain compete both among themselves and with those of the other strain, and similarly for adults. With the aid of the results established for the single species case, we are able to completely determine the local stability of the boundary equilibria in terms of verifiable inequalities, leading to insights into which strain may win the competition and the effect on this of both larval and adult competition.

Systems with both discrete and distributed delays are common in the neural networks literature (Liu et al. [15], Ruan and Filfil [20]) and in fuzzy systems theory (Yoneyama [27]), though the distributed delays in these contexts tend to assume other forms.

2. Single species model

2.1. Model derivation

Suppose the population can be divided into immature and mature individuals defined respectively as those of age less than some threshold age τ (the maturation age) and those of age greater than τ. Within each age group, all individuals have the same birth and death rates, which may be density-dependent. Let $u(t,a)$ be the population density of age a at time t, then the numbers $I(t)$ and $M(t)$ of immature and mature individuals, respectively, are given by

$$I(t)=\int_0^\tau u(t,a)\,da \quad \text{and} \quad M(t)=\int_\tau^\infty u(t,a)\,da. \tag{1}$$

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In this section we derive alternative formulations of a model to be solved for these variables $I(t)$ and $M(t)$. One of these models consists of a pair of differential equations with distributed delay (system (4)). The other consists of a pair of integral equations (system (5), (6)). In fact, as we shall see, it can sometimes work to our advantage to couple one of the differential equations of (4) with the integral equation variant of the other differential equation.

According to the McKendrick von-Foerster equation for an age-structured population, which is usually considered as a starting point for describing an age structured population (see, e.g., [7,10] and the references therein), we have

$$\begin{aligned} \frac{\partial u(t,a)}{\partial t} + \frac{\partial u(t,a)}{\partial a} &= -d_I u(t,a) - u(t,a) f(I(t)), \qquad a < \tau \\ \frac{\partial u(t,a)}{\partial t} + \frac{\partial u(t,a)}{\partial a} &= -d_M u(t,a) - u(t,a) g(M(t)), \qquad a \geq \tau \end{aligned} \tag{2}$$

where d_I and d_M are the density-independent death rates for immature and adult individuals, and the functions $f(\cdot)$ and $g(\cdot)$ represent intraspecific competition between individuals of the same age group, which each depend on the total population size of the respective group. Integrating each equation of (2) over the age interval to which it relates, we obtain the following equations for $I(t)$ and $M(t)$:

$$\begin{aligned} \frac{dI(t)}{dt} &= -d_I I(t) - I(t) f(I(t)) + u(t,0) - u(t,\tau), \\ \frac{dM(t)}{dt} &= -d_M M(t) - M(t) g(M(t)) + u(t,\tau) - u(t,\infty). \end{aligned}$$

The term $u(t,0)$ represents the birth rate of the population and therefore we assume that $u(t,0) = b(M(t))$, a function of the mature population size $M(t)$. The density of age ∞ is assumed to be zero, that is, $u(t,\infty) = 0$. To close the system, we calculate $u(t,\tau)$ in terms of $u(t-\tau,0) = b(M(t-\tau))$ which is achieved by the technique of integration along characteristics with the aid of the variable $V^s(t) = u(t, t-s)$. By direct calculations, we arrive at

$$\frac{d}{dt} V^s(t) = -(d_I + f(I(t))) V^s(t)$$

for $t - s \leq \tau$, with $V^s(s) = u(s,0) = b(M(s))$. It follows that

$$V^s(t) = V^s(s) \exp\left[-\int_s^t (d_I + f(I(\xi)))\, d\xi \right] = b(M(s)) \exp\left[-d_I(t-s) - \int_s^t f(I(\xi))\, d\xi \right].$$

Setting $s = t - \tau$, we have, for $t \geq \tau$,

$$u(t,\tau) = V^{t-\tau}(t) = b(M(t-\tau)) e^{-d_I \tau - \int_{t-\tau}^t f(I(\xi))\, d\xi} = b(M(t-\tau)) e^{-d_I \tau - \int_0^\tau f(I(t-\tau+\xi))\, d\xi}. \tag{3}$$

Therefore, the age structured model (2) can be reduced into the following system of differential equations with distributed delay:

$$\frac{dI(t)}{dt} = -d_I I(t) - I(t) f(I(t)) + b(M(t)) - b(M(t-\tau)) \exp\left[-d_I \tau - \int_0^\tau f(I(t-\tau+\xi))\, d\xi\right],$$

$$\frac{dM(t)}{dt} = -d_M M(t) - M(t) g(M(t)) + b(M(t-\tau)) \exp\left[-d_I \tau - \int_0^\tau f(I(t-\tau+\xi))\, d\xi\right]. \tag{4}$$

The functions $b(\cdot)$, $f(\cdot)$ and $g(\cdot)$ are all nonnegative, nondecreasing and vanish at zero. All terms are easily interpreted. The maturation rate, which features as the last term in each equation, contains three factors: (i) $b(M(t-\tau))$, the egg laying rate at time $t-\tau$; (ii) $e^{-d_I \tau}$, the probability of surviving natural death and (iii) $\exp(-\int_0^\tau f(I(t-\tau+\xi))\, d\xi)$, the survival probability due to intra-specific competition which incorporates competitive pressure experienced by an immature individual at all stages of development. This last term brings new features to the model. The key feature of the model described by (4) is that the equation for the adult population size $M(t)$ cannot be decoupled from the system, which makes system (4) more challenging than most previously studied stage-structured models described by delay-differential equations; see for example the models in [11,1,2,19,14]. System (4) can, however, be cast into an integral equation form. It is easily checked, by differentiation, that

$$I(t) = \int_{t-\tau}^{t} b(M(\xi)) \exp\left(\int_{\xi}^{t} (-d_I - f(I(\eta)))\, d\eta\right) d\xi \tag{5}$$

is the integral equation formulation of the $I(t)$ equation of (4). For ages $a > \tau$, solving the second equation of (2) by integration along characteristics, we find that

$$u(t,a) = u(\tau + t - a, \tau) \exp\left(-\int_{\tau}^{a} (d_M + g(M(\eta + t - a)))\, d\eta\right)$$

for $a > \tau$ and $t \geq a$. We then calculate $u(\tau + t - a, \tau)$ using (3), to find that

$$u(t,a) = b(M(t-a)) e^{-d_I \tau} \exp\left(-\int_0^\tau f(I(t-a+\xi))\, d\xi\right) \times \exp\left(-\int_{\tau}^{a} (d_M + g(M(\eta + t - a)))\, d\eta\right)$$

for $a > \tau$ and $t \geq a$. For adult ages $a > \tau$, but at times $t < a$, we need an alternative expression for $u(t,a)$, since in this case the characteristic lines pass through the a axis. In this case the

solution depends on the initial age distribution $u(0,a) = u_0(a)$, where $u_0(a) \geq 0$ is prescribed. The outcome is that

$$u(t,a) = u_0(a-t)\exp\left(-\int_0^t (d_M + g(M(\eta)))\,d\eta\right)$$

for $a > \tau$ and $t < a$. The total adult population $M(t)$ is then calculated from the integral in (1):

$$\begin{aligned} M(t) = &\int_\tau^t b(M(t-a))e^{-d_I\tau}\exp\left(-\int_0^\tau f(I(t-a+\xi))\,d\xi\right) \\ &\times \exp\left(-\int_\tau^a (d_M + g(M(\eta+t-a)))\,d\eta\right)da \\ &+ \int_t^\infty u_0(a-t)\exp\left(-\int_0^t (d_M + g(M(\eta)))\,d\eta\right)da \end{aligned} \tag{6}$$

for $t \geq \tau$.

2.2. Positivity and boundedness of solutions

From the basic theory of delay differential equations (e.g., Hale and Verduyn Lunel [12]), we know that system (4) with the initial conditions

$$I(\theta) = \phi_1(\theta) \text{ and } M(\theta) = \phi_2(\theta),\ \theta \in [-\tau, 0]$$

has a unique solution $(I(t,\phi), M(t,\phi))$ which is defined for all positive time provided that all solutions are bounded. To analyse model (4), we first make the following biologically reasonable assumptions:

1. The birth rate function $b(M)$ is a nonnegative and increasing function for all $M \geq 0$, and $b(0) = 0$;
2. the density-dependent death rate function $f(I)$ is positive and increasing for $I > 0$ while $g(M)$ is nonnegative and nondecreasing for all $M \geq 0$; moreover, $f(0) = 0$ and $g(0) = 0$;
3. there exists an increasing function $\overline{B}$ such that $b(M) \leq \overline{B}(M)$, and the function $\overline{B}$ satisfies one of the following:
   (a) $\overline{B}$ is strictly sublinear, that is, for any $\alpha \in (0,1)$, $M > 0$, $\overline{B}(\alpha M) > \alpha\overline{B}(M)$; or
   (b) $\overline{B}$ is sublinear, that is, for any $\alpha \in (0,1)$, $M \geq 0$, $\overline{B}(\alpha M) \geq \alpha\overline{B}(M)$ and $g(M)$ is strictly increasing.

Since system (4) describes populations, it is important to establish positivity and boundedness of its solutions, and we do so in the following theorem.

Theorem 2.1. *Suppose assumptions (1)–(3) above are satisfied and that $I(t) \geq 0$ and $M(t) \geq 0$ for all $t \in [-\tau, 0]$, and also $M(0) > 0$. Then the solution $(I(t), M(t))$ of system (4) exists for all $t \geq 0$ and satisfies $M(t) > 0$ and $I(t) > 0$ for all $t > 0$. Moreover, every solution is eventually bounded, that is, $\limsup_{t\to\infty} M(t) \leq K$ and $\limsup_{t\to\infty} I(t) \leq K$ for some constant K.*

Proof. We first establish positivity of solutions. It follows from [22, Theorem 5.2.1] that $M(t) \geq 0$ in its maximal interval of existence. Suppose $M(\tilde{t}) = 0$ for some values of $\tilde{t}$. By continuity of solutions, any such values of $\tilde{t}$ must be greater than zero and $\dot{M}(\tilde{t}) \leq 0$. Let $t_0 = \inf\{\tilde{t} : \tilde{t} > 0,\ M(\tilde{t}) = 0\}$, then $\dot{M}(\tilde{t}) > 0$ from the second equation of (4), a contradiction. Therefore, no such t_0 exists and $M(t) > 0$ for all $t \geq 0$. Knowing this, we find from the integral equation (5) that $I(t) > 0$ for all $t > 0$.

Next, we show that solutions remain bounded. From the second equation of (4), we have

$$\frac{dM(t)}{dt} \leq \overline{B}(M(t-\tau)) - d_M M(t) - M(t)g(M(t)).$$

Moreover, according to Theorem 3.2 of [29], the equation

$$\frac{du(t)}{dt} = \overline{B}(u(t-\tau)) - d_M u(t) - u(t)g(u(t)) \tag{7}$$

admits a globally asymptotically stable equilibrium which attracts all positive solutions. Therefore, any solution of equation (7) is bounded. Since $\overline{B}(M)$ is an increasing function, the comparison principle (see for example [22, Theorem 5.1.1]) holds and implies that $M(t) \leq u(t)$ with $u(\theta) = M(\theta)$ for $\theta \in [-\tau, 0]$. Therefore, we have boundedness of $M(t)$, which implies that $I(t)$ is also bounded since $I(t) \leq \int_{t-\tau}^{t} b(M(\xi))\, d\xi$.

A byproduct of the boundedness of solutions is the global existence of solutions, that is, the solution of system (4) with initial data $(I(\theta), M(\theta))$, $\theta \in [-\tau, 0]$, $(I(t), M(t))$ exists for all $t \geq 0$. □

2.3. Persistence

Intra-specific competition goes away as populations go to zero. At low densities, one adult, with a life expectancy of $1/d_M$, produces $b'(0)$ eggs per unit time, and these hatch and mature to the adult stage with probability $e^{-d_I \tau}$. The product of these three terms gives the average number of adults produced by one adult over its life span. This product, the basic reproduction number $\mathcal{R}_0$, is given by

$$\mathcal{R}_0 = \frac{b'(0)e^{-d_I \tau}}{d_M}.$$

We prove the following result on persistence of the species.

Theorem 2.2. *Suppose the hypotheses of Theorem 2.1 hold and, in addition, that $b(M) \leq b'(0)M$ for all $M \geq 0$. Then:*

- *if $\mathcal{R}_0 < 1$, every solution $(I(t), M(t))$ of system (4) goes to $(0, 0)$;*

- *if $\mathcal{R}_0 > 1$, there exists $\eta > 0$, which is independent of the initial conditions, such that*

$$\liminf_{t\to\infty} I(t) > \eta \text{ and } \liminf_{t\to\infty} M(t) > \eta.$$

Proof. From the second equation of (4),

$$\frac{dM(t)}{dt} \le b'(0)e^{-d_I\tau}M(t-\tau) - d_M M(t).$$

When $\mathcal{R}_0 < 1$, the zero equilibrium of the equation

$$\frac{du(t)}{dt} = b'(0)e^{-d_I\tau}u(t-\tau) - d_M u(t)$$

is globally asymptotically stable, that is, $\lim_{t\to\infty} u(t) = 0$. The comparison principle (see, for example, [22, Theorem 5.1.1]) implies that $M(t) \le u(t)$ for any solution of system (4) with $M(\theta) = u(\theta)$ for $\theta \in [-\tau, 0]$. Therefore, $\lim_{t\to\infty} M(t) = 0$. Since $I(t) \le \int_{t-\tau}^{t} b(M(\xi))\,d\xi$, we have $\lim_{t\to\infty} I(t) = 0$ also.

Next we establish population persistence in the case $\mathcal{R}_0 > 1$. Let

$$\mathcal{M} := C([-\tau, 0], \mathbb{R}^2_+), \quad \mathcal{M}_0 := \{\phi \in \mathcal{M} : \phi_i(0) > 0,\ i = 1, 2\} \quad \text{and} \quad \partial\mathcal{M}_0 := \mathcal{M}\backslash\mathcal{M}_0.$$

Clearly, $\mathcal{M}_0$ is an open set relative to $\mathcal{M}$. Define the solution semiflow $\Phi(t)$ by

$$\Phi(t)\phi(\theta) = (I(t+\theta), M(t+\theta)),$$

where $(I(t), M(t))$ is the solution of system (4) with initial data $(I(\theta), M(\theta)) = \phi(\theta)$ for all $\theta \in [-\tau, 0]$. It then follows from Theorem 2.1 that $\Phi(t)$ is point dissipative and $\Phi(t)\mathcal{M}_0 \subset \mathcal{M}_0$. Let $\omega(\phi)$ be the omega limit set of the orbit

$$\gamma^+(\phi) := \{\Phi(t)\phi : \forall t \ge 0\}$$

and define

$$\mathcal{M}_\partial := \{\phi \in \partial\mathcal{M}_0 : \Phi(t)\phi \in \partial\mathcal{M}_0, \forall t \ge 0\}.$$

Then the proof of Theorem 2.1 implies that

$$\mathcal{M}_\partial = \{\phi \in \partial\mathcal{M}_0 : \phi_2 = 0\}.$$

Hence,

$$\omega(\phi) = \{(0, 0)\}, \quad \forall \phi \in \mathcal{M}_\partial.$$

For the function $b(\cdot)$, there exist positive constants k and η such that $b(M) \ge (b'(0) - k\eta)M$ for all $M \in [0, \eta]$. Since $\mathcal{R}_0 > 1$, we can choose η small enough such that

$$\frac{(b'(0) - k\eta)e^{-d_I\tau}e^{-\tau f(b(\eta)\tau)}}{d_M + g(\eta)} > 1. \tag{8}$$

Next, we establish the following weak persistence for $\mathcal{R}_0 > 1$.

Claim: For all solutions $(I(t), M(t))$ with $M(\theta) \not\equiv 0$ on $[-\tau, 0]$, we have

$$\limsup_{t\to\infty} M(t) \geq \eta.$$

Suppose the claim is false. Then there is a solution with

$$\limsup_{t\to\infty} M(t) < \eta$$

and, since the inequality is strict, there exists T such that $M(t) < \eta$ for all $t > T$. From the integral equation for $I(t)$ (equation (5)), $I(t) < b(\eta)\tau$ for all $t > T + \tau$ and it follows that

$$\begin{aligned}\frac{dM(t)}{dt} &\geq b(M(t-\tau))e^{-d_I\tau}e^{-\tau f(b(\eta)\tau)} - (d_M + g(\eta))M(t)\\ &\geq (b'(0) - k\eta)e^{-d_I\tau}e^{-\tau f(b(\eta)\tau)}M(t-\tau) - (d_M + g(\eta))M(t).\end{aligned}$$

Since (8) holds, the nonzero solutions of the equation

$$\frac{du(t)}{dt} = (b'(0) - k\eta)e^{-d_I\tau}e^{-\tau f(b(\eta)\tau)}u(t-\tau) - (d_M + g(\eta))u(t)$$

will grow without bound and, by the comparison principle, the same is true for $M(t)$. This contradicts boundedness of solutions and, therefore, the claim holds.

The above claim shows that the element $(0, 0) \in \mathcal{M}$ is a uniform weak repeller for $\mathcal{M}_0$ in the sense that

$$\limsup_{t\to\infty} \|\Phi(t)\phi - (0,0)\| \geq \eta \text{ for all } \phi \in \mathcal{M}_0,$$

with the maximum norm $\|\cdot\|$. Define a continuous function $p : \mathcal{M} \to \mathbb{R}_+$ by

$$p(\phi) = \min(\phi_1(0), \phi_2(0)), \quad \forall \phi = (\phi_1, \phi_2) \in \mathcal{M}.$$

Thus, p is a generalised distance function for the semiflow $\Phi(t)$ (see Definition 1.3.1 in [28]). It then follows from Theorem 1.3.2 of [28] that there exists $\epsilon > 0$ such that $\min\{p(\psi) : \psi \in \omega(\phi)\} > \epsilon$ for any $\phi(\theta) \not\equiv 0$ on $[-\tau, 0]$. Hence,

$$\liminf_{t\to\infty} I(t) \geq \epsilon \text{ and } \liminf_{t\to\infty} M(t) \geq \epsilon$$

uniformly for all solutions with $M(0) > 0$. □

2.4. Linear stability of equilibria

Introduction of competition among immature individuals, as modelled in (2), may have the effect of increasing the number of positive equilibria in the model. Either the differential form of the model, or the variant system of integral equations, yield that any equilibrium (I^*, M^*) satisfies

$$M^*(d_M + g(M^*)) = b(M^*)\exp\{-\tau(d_I + f(I^*))\},$$
$$I^*(d_I + f(I^*)) = b(M^*)\Big(1 - \exp\{-\tau(d_I + f(I^*))\}\Big). \tag{9}$$

Letting (I^*, M^*) denote any equilibrium, we investigate its linear stability. This can be achieved by linearising at the equilibrium one of system (4), the variant system (5), (6), or a system comprised of the differential form of one equation and the integral form of the other. The characteristic equations obtained in each case look very different, but their equivalence can be confirmed through tedious calculations. The approach that lends itself best to further analytic study is through linearising the first equation of (4) and the integral equation (5). Setting $M = M^* + \tilde{M}$, $I = I^* + \tilde{I}$, these linearised equations assume the form

$$\tilde{M}'(t) = -[d_M + g(M^*) + M^* g'(M^*)]\tilde{M}(t) + e^{-\tau(d_I + f(I^*))}\left[b'(M^*)\tilde{M}(t-\tau) - b(M^*)f'(I^*)\int_0^\tau \tilde{I}(t-\tau+\xi)\,d\xi\right] \tag{10}$$

and

$$\tilde{I}(t) = b'(M^*)\int_0^\tau e^{-\xi(d_I + f(I^*))}\tilde{M}(t-\xi)\,d\xi - b(M^*)f'(I^*)\int_0^\tau e^{-\xi(d_I + f(I^*))}\int_{t-\xi}^t \tilde{I}(\eta)\,d\eta\,d\xi. \tag{11}$$

Solutions of the linearised system of the form $(\tilde{I}(t), \tilde{M}(t)) = (c_1, c_2)\exp(\lambda t)$ exist whenever λ satisfies a characteristic equation that can be cast into the form

$$\lambda + d_M + g(M^*) + M^* g'(M^*) = b'(M^*)\exp\left\{-\tau(\lambda + d_I + f(I^*))\right\} - \frac{b(M^*)b'(M^*)f'(I^*)\tau^2 e^{-\tau(d_I + f(I^*))}k(\lambda\tau)k(\tau(\lambda + d_I + f(I^*)))}{1 + b(M^*)f'(I^*)\tau\left\{k(\tau(d_I + f(I^*))) - k(\tau(\lambda + d_I + f(I^*)))\right\}/\lambda} \tag{12}$$

where

$$k(x) = \frac{1 - e^{-x}}{x} \tag{13}$$

which satisfies $k(x) > 0$, $k'(x) < 0$ and $k''(x) > 0$ for all $x \in \mathbb{R}$. The properties of the right hand side of (12) as a function of λ are important and it turns out to be convenient to express the characteristic equation in the form

$$\lambda + d_M + g(M^*) + M^* g'(M^*) = e^{-\tau(d_I + f(I^*))}b'(M^*)H(\lambda\tau, c, A) \tag{14}$$

where

$$H(x, c, A) = e^{-x} - \frac{Ak(x)k(x+c)}{1 + A\left\{k(c) - k(x+c)\right\}/x} \tag{15}$$

and

$$c = \tau(d_I + f(I^*)), \quad A = b(M^*)f'(I^*)\tau^2. \tag{16}$$

In the subsequent analysis, we always assume that $b(M^*) > 0$, $b'(M^*) > 0$ and $f'(I^*) > 0$. We prove under certain further conditions that the dominant root (the root of greatest real part) of the characteristic equation (12) is a real number, so that only the real roots of the characteristic equation need to be considered. This is proved using Proposition 3.2 in Smith and Thieme [23]. That result is concerned with the linear stability of an equilibrium x_0 of a scalar delay equation of the form

$$x'(t) = f(x_t) \tag{17}$$

where f is a functional in $C([-\tau, 0], \mathbb{R})$ and $x_t(s) = x(t+s)$, $s \in [-\tau, 0]$. Let K_μ be the cone in $C([-\tau, 0], \mathbb{R})$ defined by

$$K_\mu = \{\phi \in C \ : \ \phi \geq 0 \text{ and } \phi(s)e^{\mu s} \text{ is nondecreasing on } [-\tau, 0]\}$$

and let $\leq_\mu$ be the partial ordering on $C([-\tau, 0], \mathbb{R})$ induced by K_μ, that is

$$\phi \leq_\mu \psi \Longleftrightarrow \phi \leq \psi \text{ and } (\psi(s) - \phi(s))e^{\mu s} \text{ is nondecreasing on } [-\tau, 0]. \tag{18}$$

Let $df(\hat{x}_0)$ denote the linearisation of f at the equilibrium x_0, where $\hat{x}_0$ is the function in $C([-\tau, 0], \mathbb{R})$ which is identically equal to $x_0 \in \mathbb{R}$. By Proposition 3.2 in [23], if there exists $\mu \geq 0$ such that

$$df(\hat{x}_0)(\phi) + \mu\phi(0) \geq 0 \quad \text{for all} \quad \phi \in C([-\tau, 0], \mathbb{R}) \quad \text{such that} \quad \phi \geq_\mu 0, \tag{19}$$

then the stability of x_0 can be determined by examining only the real roots of the characteristic equation of the linearisation of (17) at x_0. The results in [23] are actually for scalar equations, but our system can be interpreted as scalar if we take the view that we are solving the integral equation (11) for $\tilde{I}(t)$ as a functional of $\tilde{M}_t$, where $\tilde{M}_t(s) = \tilde{M}(t+s)$, $s \leq 0$, and inserting the solution into (10) which thereby becomes a scalar equation for $\tilde{M}(t)$. In fact (11) can be solved explicitly using the Laplace transform technique. We assume that $\tilde{I} \equiv 0$ for $t < 0$. Under these circumstances the following property holds:

$$\mathcal{L}\left\{\int_{t-\xi}^{t} \tilde{I}(\eta)\,d\eta\right\} = \frac{1}{s}(1 - e^{-\xi s})\mathcal{L}\{\tilde{I}(t)\} \tag{20}$$

for $\xi > 0$, where $\mathcal{L}$ denotes the Laplace transform and s is the transform variable. Applying the Laplace transform to (11) in the form

$$\tilde{I}(t) = K(t) - b(M^*)f'(I^*)\int_0^\tau e^{-\xi(d_I + f(I^*))}\int_{t-\xi}^{t} \tilde{I}(\eta)\,d\eta\,d\xi, \tag{21}$$

and using property (20) and the Laplace convolution theorem, gives

$$\tilde{I}(t) = \int_0^t \varrho(t-\bar{t})K(\bar{t})\,d\bar{t} \tag{22}$$

where

$$\varrho(t) = \mathcal{L}^{-1}\left\{\frac{1}{1+b(M^*)f'(I^*)\tau\left\{k(\tau(d_I+f(I^*)))-k(\tau(s+d_I+f(I^*)))\right\}/s}\right\} \tag{23}$$

or, alternatively,

$$\varrho(t) = \mathcal{L}^{-1}\left\{\frac{1}{1+b(M^*)f'(I^*)\displaystyle\int_0^\tau e^{-\xi(d_I+f(I^*))}\left(\frac{1-e^{-\xi s}}{s}\right)d\xi}\right\}. \tag{24}$$

The properties of $\varrho(t)$, a delicate function, need to be carefully understood and are stated in the following result.

Proposition 2.1. *Assume that $b(M^*) > 0$, $b'(M^*) > 0$ and $f'(I^*) > 0$. Then the function $\varrho(t)$ defined by (23) or (24) behaves as a Dirac delta function at $t = 0$ and drops instantaneously from $\varrho(0) = \infty$ to a finite (negative) value such that*

$$\lim_{t\to 0+}\varrho(t) = -b(M^*)f'(I^*)\left(\frac{1-e^{-\tau(d_I+f(I^*))}}{d_I+f(I^*)}\right). \tag{25}$$

On the interval $t \in (0,\infty)$, $\varrho(t)$ converges to zero in an oscillatory manner.

Proof. Note that $\varrho(t)$ is independent of $K(t)$. Information about $\varrho(t)$ can therefore be gained from particular choices of $K(t)$. In particular, we find that $\varrho(t)$ is the solution of (21) in the particular case when $K(t) = \delta(t)$, the Dirac delta function. Thus, $\varrho(t)$ satisfies $\varrho \equiv 0$ for $t < 0$ and

$$\varrho(t) = \delta(t) - b(M^*)f'(I^*)\int_0^\tau e^{-\xi(d_I+f(I^*))}\int_{t-\xi}^t \varrho(\eta)\,d\eta\,d\xi \tag{26}$$

for $t \geq 0$. Owing to the behaviour at $t = 0$, the limit in (25) does not follow from the initial value formula for the Laplace transform. However, it can be deduced from (26) with care, as follows. The inner integral may include zero in its interval $[t-\xi, t]$. On the interval $(0, t]$, $\varrho(\eta)$ is finite and its integral over such an interval tends to zero as $t \to 0$ and can be ignored in the evaluation of the limit $\lim_{t\to 0+}\varrho(t)$. So, only values of ξ greater than t are important and the outer integral is effectively over the interval $\xi \in [t,\tau]$. Also $\varrho(\eta) = 0$ for $\eta < 0$. So the inner integral approaches $\int_{0-}^{0+}\varrho(\eta)\,d\eta = \int_{0-}^{0+}\delta(\eta)\,d\eta = 1$ as $t \to 0$. In the end, as $t \to 0$, we end up with (25).

The fact that $\varrho(t)$ is oscillatory follows directly from (26). The role played by the delta function is transitory; for times $t > \tau$ it plays no further role and can be ignored. The two remaining terms, which involve $\varrho(t)$, have opposite sign. It is easily seen that on any time interval of length at least τ, $\varrho(t)$ cannot remain positive, nor remain negative, because in either case (26) produces a contradiction. To check that $\lim_{t\to\infty}\varrho(t) = 0$ we will show that all the poles of $\mathcal{L}\{\varrho(t)\}$ (i.e. all the zeros of the denominator in (24)) satisfy $\operatorname{Re} s < 0$. Then, if we compute $\varrho(t)$ using (24), the inversion formula for Laplace transforms and Cauchy's residue theorem, we shall find $\varrho(t)$ in the form of a sum of the residues at those poles and those residues will be decaying exponentials if the poles all satisfy $\operatorname{Re} s < 0$.

For $t > \tau$, by differentiating (26) we find that $\varrho(t)$ also satisfies

$$\varrho'(t) = -b(M^*)f'(I^*)\left(\frac{1-e^{-\tau(d_I+f(I^*))}}{d_I+f(I^*)}\right)\varrho(t) + b(M^*)f'(I^*)\int_0^\tau e^{-\xi(d_I+f(I^*))}\varrho(t-\xi)\,d\xi. \tag{27}$$

The ansatz $\varrho(t) = e^{st}$ yields a characteristic equation for (27) which has $s = 0$ as one of its roots, and no other real roots. Dividing that characteristic equation by s yields the characteristic equation satisfied by the poles of $\mathcal{L}\{\varrho(t)\}$, namely

$$1 + b(M^*)f'(I^*)\int_0^\tau e^{-\xi(d_I+f(I^*))}\left(\frac{1-e^{-\xi s}}{s}\right)d\xi = 0. \tag{28}$$

The two characteristic equations have the same roots except for the fact that $s = 0$ does not satisfy (28). This distinction is crucial because (27), with its delay term having a positive coefficient, lends itself to the application of Theorem 5.5.1 on page 92 of Smith [22], from which we conclude that the dominant root of the characteristic equation associated with (27) is a real number. But we know that the only real root of that characteristic equation is $s = 0$. Therefore, any other root satisfies $\operatorname{Re} s < 0$ and we deduce that this is the case for *all* the roots of (28) since that equation lacks the zero root. Thus, all the poles of $\mathcal{L}\{\varrho(t)\}$ satisfy $\operatorname{Re} s < 0$ and so $\lim_{t\to\infty}\varrho(t) = 0$. □

We are now in a position to prove the following.

Proposition 2.2. *If $b(M^*) > 0$, $b'(M^*) > 0$, $f'(I^*) > 0$ and if τ is small enough so that there exists $\mu \geq 0$ such that*

$$\mu - (d_M + g(M^*) + M^*g'(M^*)) \geq e^{-\tau(d_I+f(I^*))}b(M^*)b'(M^*)f'(I^*)\left(\frac{1-e^{-\tau(d_I+f(I^*)-\mu)}}{d_I+f(I^*)-\mu}\right)\left(\frac{e^{\mu\tau}-1}{\mu}\right)\int_0^\infty \varrho^+(r)e^{\mu r}\,dr, \tag{29}$$

where $\varrho^+(t) = \max(\varrho(t), 0)$ and $\varrho(t)$ is defined by (23) or (24), then the dominant root of the characteristic equation (12) is a real number.

Proof. We need to check condition (19) as it applies to our problem. First we satisfy ourselves that it is possible to choose $\mu > 0$ satisfying (29). At a first glance this appears to be clear, since we could pick any μ such that the left hand side of (29) is positive, and then (for that particular μ) simply pick τ sufficiently small such that (29) holds, which appears to work on the basis of the apparent behaviour of the right hand side of (29) as $\tau \to 0$. However, $\varrho(t)$, and hence also $\varrho^+(t)$, depend on τ and it is not immediately clear that $\int_0^\infty \varrho^+(r)e^{\mu r}\,dr < \infty$. However, we know from Proposition 2.1 that $\lim_{t\to\infty}\varrho(t) = 0$. Moreover, since the convergence is exponential, it suffices to drop the superscript on ϱ here and assure ourselves of the finiteness of the integral $\int_0^\infty \varrho(r)e^{\mu r}\,dr$. This integral is finite if the exponential decay of $\varrho(r)$ to zero is fast enough to overcome the exponentially growing term $e^{\mu r}$ in the integrand. For a μ chosen as described above, pick any $c > \mu$. Then, the decay of $\varrho(r)$ to zero will be sufficiently fast if $\operatorname{Re} s < -c$ for all roots s of the characteristic equation (28). We claim that this is the case if τ is chosen sufficiently small such that

$$\frac{b(M^*)f'(I^*)}{c}\left[\frac{1-e^{-\tau(d_I+f(I^*)-c)}}{d_I+f(I^*)-c} - \frac{1-e^{-\tau(d_I+f(I^*))}}{d_I+f(I^*)}\right] < 1. \tag{30}$$

The square bracketed quantity in (30) is positive because $c > 0$ and $k(x)$, defined in (13), is decreasing. Let s be a root of (28). Assuming (30) we claim, for a contradiction, that $\operatorname{Re} s \geq -c$. From (28), this root satisfies

$$\begin{aligned}
1 &\leq b(M^*)f'(I^*)\int_0^\tau e^{-\xi(d_I+f(I^*))}\left|\frac{1-e^{-\xi s}}{s}\right| d\xi \\
&= b(M^*)f'(I^*)\int_0^\tau e^{-\xi(d_I+f(I^*))}\left|\int_0^\xi e^{-\eta s}\,d\eta\right| d\xi \\
&\leq b(M^*)f'(I^*)\int_0^\tau e^{-\xi(d_I+f(I^*))}\int_0^\xi e^{-\eta \operatorname{Re} s}\,d\eta\,d\xi \\
&\leq b(M^*)f'(I^*)\int_0^\tau e^{-\xi(d_I+f(I^*))}\int_0^\xi e^{c\eta}\,d\eta\,d\xi \\
&= \frac{b(M^*)f'(I^*)}{c}\left[\frac{1-e^{-\tau(d_I+f(I^*)-c)}}{d_I+f(I^*)-c} - \frac{1-e^{-\tau(d_I+f(I^*))}}{d_I+f(I^*)}\right]
\end{aligned}$$

which contradicts (30). Thus, for τ sufficiently small, μ can be chosen to satisfy (29).

In (19) we take $\phi(s) = \tilde{M}_t(s)$, and so $\phi(0) = \tilde{M}(t)$. Basically $df(\hat{x}_0)(\phi) + \mu\phi(0)$ is the right hand side of (10) with the addition of $\mu\tilde{M}(t)$, and with $\tilde{I}(t)$ given by (22) and $K(t)$ chosen as in (11), so that

$$\tilde{I}(t) = b'(M^*)\int_0^t \varrho(t-\bar{t})\int_0^\tau e^{-\xi(d_I+f(I^*))}\tilde{M}(\bar{t}-\xi)\,d\xi\,d\bar{t}.$$

Even though $\tilde{M}$ is a perturbation from a steady state value, and therefore need not be positive, we only need to check (19) for $\tilde{M} \geq_\mu 0$ which, by (18), includes the requirement that $\tilde{M} \geq 0$. For $\tilde{M} \geq 0$,

$$\tilde{I}(t) \leq b'(M^*) \int_0^t \varrho^+(t-\bar{t}) \int_0^\tau e^{-\xi(d_I+f(I^*))} \tilde{M}(\bar{t}-\xi)\, d\xi\, d\bar{t}$$

and therefore

$$\begin{aligned} -\int_0^\tau \tilde{I}(t-\tau+\xi)\, d\xi &= -\int_{t-\tau}^t \tilde{I}(\eta)\, d\eta \\ &\geq -b'(M^*) \int_{t-\tau}^t \int_0^\eta \varrho^+(\eta-\bar{t}) \int_0^\tau e^{-\xi(d_I+f(I^*))} \tilde{M}(\bar{t}-\xi)\, d\xi\, d\bar{t}\, d\eta. \end{aligned}$$

Since we check (19) for $\tilde{M} \geq_\mu 0$, from (18) we have that $\tilde{M}(s)e^{\mu s}$ is nondecreasing on $[-\tau, 0]$ so that

$$\tilde{M}(\bar{t}-\xi)e^{\mu(\bar{t}-\xi)} \leq \tilde{M}(\bar{t})e^{\mu\bar{t}}$$

and therefore

$$-\int_0^\tau \tilde{I}(t-\tau+\xi)\, d\xi \geq -b'(M^*) \int_{t-\tau}^t \int_0^\eta \varrho^+(\eta-\bar{t})\tilde{M}(\bar{t}) \left(\frac{1-e^{-\tau(d_I+f(I^*)-\mu)}}{d_I+f(I^*)-\mu} \right) d\bar{t}\, d\eta.$$

Since $\bar{t} \leq \eta$ we may now use $\tilde{M}(\bar{t})e^{\mu\bar{t}} \leq \tilde{M}(\eta)e^{\mu\eta}$ to obtain

$$-\int_0^\tau \tilde{I}(t-\tau+\xi)\, d\xi \geq -b'(M^*) \left(\frac{1-e^{-\tau(d_I+f(I^*)-\mu)}}{d_I+f(I^*)-\mu} \right) \int_{t-\tau}^t \tilde{M}(\eta) \int_0^\eta \varrho^+(\eta-\bar{t})e^{\mu(\eta-\bar{t})} d\bar{t}\, d\eta.$$

Since $\eta \leq t$ we have $\tilde{M}(\eta)e^{\mu\eta} \leq \tilde{M}(t)e^{\mu t}$ and therefore, after some simplification,

$$\begin{aligned} -\int_0^\tau \tilde{I}(t-\tau+\xi)\, d\xi &\geq -b'(M^*) \left(\frac{1-e^{-\tau(d_I+f(I^*)-\mu)}}{d_I+f(I^*)-\mu} \right) \tilde{M}(t) \int_{t-\tau}^t \int_0^\eta \varrho^+(\eta-\bar{t})e^{\mu(t-\bar{t})}\, d\bar{t}\, d\eta \\ &= -b'(M^*) \left(\frac{1-e^{-\tau(d_I+f(I^*)-\mu)}}{d_I+f(I^*)-\mu} \right) \tilde{M}(t) \int_0^\tau \int_0^{t-\bar{\eta}} \varrho^+(t-\bar{t}-\bar{\eta})e^{\mu(t-\bar{t})}\, d\bar{t}\, d\bar{\eta} \\ &= -b'(M^*) \left(\frac{1-e^{-\tau(d_I+f(I^*)-\mu)}}{d_I+f(I^*)-\mu} \right) \tilde{M}(t) \int_0^\tau e^{\mu\bar{\eta}} \int_0^{t-\bar{\eta}} \varrho^+(r)\, e^{\mu r}\, dr\, d\bar{\eta} \end{aligned}$$

$$\geq -b'(M^*)\left(\frac{1-e^{-\tau(d_I+f(I^*)-\mu)}}{d_I+f(I^*)-\mu}\right)\tilde{M}(t)\int_0^\tau e^{\mu\bar{\eta}}\int_0^\infty \varrho^+(r)\,e^{\mu r}\,dr\,d\bar{\eta}$$

$$= -b'(M^*)\left(\frac{1-e^{-\tau(d_I+f(I^*)-\mu)}}{d_I+f(I^*)-\mu}\right)\tilde{M}(t)\left(\frac{e^{\mu\tau}-1}{\mu}\right)\int_0^\infty \varrho^+(r)\,e^{\mu r}\,dr.$$

Using this and the fact that $\tilde{M}(t-\tau)\geq 0$ (which follows from $\tilde{M}\geq_\mu 0$), we now check (19) using the right hand side of (10) as follows:

$$\begin{aligned}
&df(\hat{x}_0)(\phi)+\mu\phi(0)\\
&=-[d_M+g(M^*)+M^*g'(M^*)]\tilde{M}(t)+\mu\tilde{M}(t)\\
&+e^{-\tau(d_I+f(I^*))}\left[b'(M^*)\tilde{M}(t-\tau)-b(M^*)f'(I^*)\int_0^\tau \tilde{I}(t-\tau+\xi)\,d\xi\right]\\
&\geq -[d_M+g(M^*)+M^*g'(M^*)]\tilde{M}(t)+\mu\tilde{M}(t)\\
&-e^{-\tau(d_I+f(I^*))}b(M^*)b'(M^*)f'(I^*)\left(\frac{1-e^{-\tau(d_I+f(I^*)-\mu)}}{d_I+f(I^*)-\mu}\right)\tilde{M}(t)\left(\frac{e^{\mu\tau}-1}{\mu}\right)\int_0^\infty \varrho^+(r)\,e^{\mu r}\,dr
\end{aligned}$$

which is non-negative for $\tilde{M}\geq 0$, by (29). □

The next result is concerned with obtaining a good bound, valid for $x\geq 0$, for the function $H(x,c,A)$ defined in (15). This function need not be monotone in x.

Proposition 2.3. *For $x,c,A\geq 0$,*

$$H(x,c,A)\leq \max\left\{0,\ 1-\frac{Ak(c)}{1+A/2}\right\} \tag{31}$$

with $k(x)$ given by (13).

Proof. First note that, for some θ between c and $x+c$, $k(c)-k(x+c)=-xk'(\theta)\leq -xk'(0)=\frac{1}{2}x$ since $k''(x)>0$ and $k'(0)=-\frac{1}{2}$. Hence

$$H(x,c,A)\leq e^{-x}-\frac{Ak(x)k(x+c)}{1+A/2}:=\overline{H}(x,c,A).$$

Next, we prove that $\overline{H}(x,c,A)\leq \max(0,\ \overline{H}(0,c,A))$, even though $\overline{H}(x,c,A)$ is not necessarily monotone in x. Note that $\overline{H}(\infty,c,A)=0$. We claim that at any stationary point of the function $x\to\overline{H}(x,c,A)$, we must have $\overline{H}<0$. Routine computation shows that, at a value x with $\partial\overline{H}/\partial x=0$,

$$\overline{H}(x,c,A)=-\frac{A}{1+A/2}\Big(k(x)k'(x+c)+k'(x)k(x+c)+k(x)k(x+c)\Big). \tag{32}$$

The function $k(x)$ defined by (13) can be expressed as

$$k(x) = \int_0^1 e^{-tx}\,dt$$

and therefore

$$k(x)k'(x+c) + k'(x)k(x+c) + k(x)k(x+c) = \int_0^1\int_0^1 e^{-tx-s(x+c)}(1-t-s)\,dt\,ds := F(x,c).$$

Now $F(0,0) = 0$ and, since $x, c \geq 0$,

$$\begin{aligned}\frac{\partial F}{\partial c} &= -\int_0^1\int_0^1 s\,e^{-tx-s(x+c)}(1-t-s)\,dt\,ds \\ &\geq -\int_0^1\int_0^1 s(1-t-s)\,dt\,ds = \frac{1}{12}\end{aligned}$$

so $F(x,c)$ increases with c for each fixed $x \geq 0$ and therefore, for $x \geq 0$,

$$\begin{aligned}F(x,c) \geq F(x,0) &= \int_0^1\int_0^1 e^{-(t+s)x}(1-t-s)\,dt\,ds \\ &= \frac{x-2+4e^{-x}-(x+2)e^{-2x}}{x^3}.\end{aligned}$$

Finally, we show that the numerator of this expression is non-negative. Letting $\varphi(x) = x - 2 + 4e^{-x} - (x+2)e^{-2x}$, we have $\varphi(0) = 0$, $\varphi'(0) = 0$ and $\varphi''(x) = 4e^{-2x}(e^x - 1 - x) \geq 0$ for all $x \geq 0$. Hence $\varphi(x) \geq 0$ for all $x \geq 0$, and so $F(x,c) \geq 0$ for all $x, c \geq 0$. It follows from (32) that $\overline{H} < 0$ at any stationary point of the function $x \to \overline{H}(x,c,A)$, as claimed. From this, it follows that, for any $c, A \geq 0$, the function $x \to \overline{H}(x,c,A)$ is either negative for all $x \geq 0$ or attains its maximum at $x = 0$. Therefore $H(x,c,A) \leq \max(0, \overline{H}(0,c,A))$ and the estimate (31) follows. □

We present our main linear stability result as follows.

Theorem 2.3. *Let $(I^*, M^*) \neq (0,0)$ be any non-trivial equilibrium of system (4), so that I^* and M^* satisfy (9). Assume that the hypotheses of Proposition 2.2 hold and that*

$$e^{-\tau(d_I + f(I^*))}b'(M^*)\max\left\{0,\ 1 - \frac{b(M^*)f'(I^*)\tau^2 k(c)}{1 + b(M^*)f'(I^*)\tau^2/2}\right\} < d_M + g(M^*) + M^* g'(M^*) \tag{33}$$

with $k(x)$ given by (13) and c in (16). Then (I^*, M^*) is locally asymptotically stable.

Proof. Working with the characteristic equation in its alternative form (14), we know from Proposition 2.2 that only its real roots need to be considered. Using the bound in Proposition 2.3, with the value of A given in (16), any real root $\lambda \geq 0$ of the characteristic equation must satisfy

$$\begin{aligned} d_M + g(M^*) + M^* g'(M^*) &\leq \lambda + d_M + g(M^*) + M^* g'(M^*) \\ &= e^{-\tau(d_I + f(I^*))} b'(M^*) H(\lambda\tau, c, A) \\ &\leq e^{-\tau(d_I + f(I^*))} b'(M^*) \max\left\{0,\ 1 - \frac{Ak(c)}{1 + A/2}\right\}. \end{aligned}$$

Since A is given in (16), it follows that if (33) holds then in fact no real roots with $\lambda \geq 0$ can exist. The stability assertion follows. □

2.5. Generic convergence to equilibria

Note that, when $\tau = 0$, system (4) reduces to a scalar ordinary differential equation and every bounded solution converges to an equilibrium. The folklore in the theory of delay differential equations says that small delays are harmless and can be ignored (see, e.g., [22]). In this section, among other things, we verify this folklore in the sense that the generic convergence to equilibria remains valid for system (4) when τ is sufficiently small.

The theory in Smith and Thieme [24] is often appropriate for establishing results on generic convergence. However, the monotonicity condition assumed in [24] is not satisfied for system (4) because the recruitment term for the mature population, namely

$$b(M(t-\tau)) \exp\left[-d_I \tau - \int_0^\tau f(I(t-\tau+\xi))\, d\xi\right],$$

is decreasing in the immature population, and the recruitment term for the immature population:

$$b(M(t)) - b(M(t-\tau)) \exp\left[-d_I \tau - \int_0^\tau f(I(t-\tau+\xi))\, d\xi\right]$$

is not nondecreasing in the mature population. Thus, a quasi-positive matrix used to construct an exponential ordering may not exist.

Our approach is to combine comparison arguments and the persistence of linear stability/instability of equilibria when the time delay is small. More precisely, we first employ the implicit function theorem to show that small delay does not alter the local stability or instability of equilibria. Then we sandwich the equation for the mature population between two auxiliary equations which fit the framework of monotone semiflows established in [22] when the delay is small. These two auxiliary equations become indistinguishable in the limit when the delay tends to zero. Such a property enables us to use the persistence of local asymptotic stability of equilibria to establish the generic convergence to equilibria when the delay is small.

2.5.1. Equilibria

To study the persistence of global dynamics when the delay τ is small, we first introduce a set of sufficient conditions under which the number, location and stability of equilibria do not change too much. We use E^τ, $\tau \geq 0$, to denote the set of all non-negative equilibria of system (4). Note that E^0 is the set of such equilibria for the model without delay, which reduces to a one-dimensional undelayed ODE for the variable M only. Equilibria in the absence of delay take the form $(I, M) = (0, M^0) \in E^0$ and, at such an equilibrium, there is just one (real) eigenvalue, denoted λ^0 in Lemma 2.2 below. Once delay is present, there are always infinitely many eigenvalues associated with an equilibrium and stability is then determined by the *dominant* eigenvalue.

Lemma 2.1. *Assume that $b, g \in C^1(\mathbb{R}, \mathbb{R}^+)$ satisfy*

$$\liminf_{x\to\infty} |b(x) - (d_M + g(x))x| > 0 \tag{34}$$

and

$$b'(M^0) - d_M - g'(M^0)M^0 - g(M^0) \neq 0, \quad \forall q^0 := (0, M^0) \in E^0. \tag{35}$$

Then the following two statements are valid:

(i) *E^0 consists of finitely many elements;*
(ii) *there exist $\tau_0 > 0$ and $\epsilon_0 > 0$ such that*

$$E^\tau \subset \bigcup_{q^0 \in E^0} \mathcal{N}_{\epsilon_0}(q^0)$$

and the set $\mathcal{N}_{\epsilon_0}(q^0) \cap E^\tau, \forall q^0 \in E^0, \tau \in [0, \tau_0]$, is a singleton $\{q^\tau\}$, where $\mathcal{N}_{\epsilon_0}(q^0)$ is the ball in $\mathbb{R}^2$ centred at q^0 with radius ϵ_0. Furthermore, q^τ is continuous in $\tau \in [0, \tau_0]$.

Proof. Assumption (34) ensures that E^0 is bounded and assumption (35) ensures that E^0 does not have an accumulation point. Therefore, the first statement of the theorem holds.

From the implicit function theorem, one can see from assumption (35) that in a neighbourhood of each $q^0 \in E^0$, there is a unique equilibrium $q^\tau \in E^\tau$ when τ is small. Assumption (34) excludes the possibility of a bifurcation of equilibria from infinity as τ increases from 0 to a positive value. This, together with assumption (35), implies that each q^τ is isolated in E^τ and that E^τ is uniformly bounded for τ sufficiently small. □

2.5.2. Persistence of linear stability

Lemma 2.2. *Assume that the conditions in Lemma 2.1 hold. Let λ^0 be the eigenvalue at the equilibrium $q^0 \in E^0$. Then, for small positive τ, there is a continuous function λ^τ of τ such that λ^τ is the dominant eigenvalue at the equilibrium $q^\tau \in E^\tau$, where $q^\tau := (I^\tau, M^\tau) \to q^0$ as $\tau \to 0$. An associated eigenfunction is given by $(\gamma, 1)e^{\lambda^\tau \theta}$ with*

$$\gamma = \gamma(\tau, \lambda^\tau) := \frac{b'(M^\tau) \int_0^\tau e^{-\xi(\lambda^\tau + d_I + f(I^\tau))}\, d\xi}{1 + b(M^\tau) f'(I^\tau) \int_0^\tau e^{-\xi(d_I + f(I^\tau))} \int_{-\xi}^0 e^{\lambda^\tau \theta}\, d\theta\, d\xi}.$$

Proof. For convenience, we rewrite the characteristic equation (14) as the following system, with $\lambda = c_1 + ic_2$:

$$\begin{cases} 0 = c_1 + d_M + g(M^\tau) + M^\tau g'(M^\tau) - b'(M^\tau)e^{-\tau(d_I + f(I^\tau))}\mathrm{Re}\{H(\lambda\tau, c^\tau, A^\tau)\} := G_1(\lambda, \tau), \\ 0 = c_2 - b'(M^\tau)e^{-\tau(d_I + f(I^\tau))}\mathrm{Im}\{H(\lambda\tau, c^\tau, A^\tau)\} := G_2(\lambda, \tau). \end{cases} \tag{36}$$

Since $\partial G_1(\lambda^0, 0)/\partial c_1 = 1$, applying the implicit function theorem to the first equation of (36), with λ being real, we obtain the existence of a real eigenvalue λ^τ which is the unique real eigenvalue near λ^0 when τ is sufficiently small. Since

$$\begin{pmatrix} \dfrac{\partial G_1}{\partial c_1}(\lambda^0, 0) & \dfrac{\partial G_1}{\partial c_2}(\lambda^0, 0) \\ \dfrac{\partial G_2}{\partial c_1}(\lambda^0, 0) & \dfrac{\partial G_2}{\partial c_2}(\lambda^0, 0) \end{pmatrix} = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix},$$

we may apply the implicit function theorem to (36) with λ complex to conclude that, for sufficiently small τ, the real eigenvalue λ^τ near λ^0 is unique not only in $\mathbb{R}$ but also in $\mathbb{C}$.

From relation (11) it is clear that $(\gamma, 1)e^{\lambda^\tau\theta}$ is an associated eigenfunction of λ^τ. Moreover, γ is well defined when τ is small and $\gamma \to 0$ as $\tau \to 0$.

Let $\lambda = \mu^\tau$ be an eigenvalue at the equilibrium q^τ such that

$$\mathrm{Re}\,\mu^\tau \geq \lambda^\tau.$$

We show that, in fact, $\lambda^\tau = \mu^\tau$ when τ is sufficiently small. From (36),

$$|\mu^\tau| \leq C_0 + C_1|H(\mu^\tau\tau, c^\tau, A^\tau)|$$

where C_0 and C_1 are two constants independent of small τ. Next we show that μ^τ is uniformly bounded in small τ. Indeed, note that

$$H(\mu^\tau\tau, c^\tau, A^\tau) = e^{-\mu^\tau\tau} - \gamma(\tau, \mu^\tau)\frac{b(M^\tau)f'(I^\tau)}{b'(M^\tau)}\int_0^\tau e^{\mu^\tau(-\tau+\xi)}\,d\xi$$

and

$$\begin{aligned} |\gamma(\tau, \mu^\tau)| &\leq \frac{|b'(M^\tau)|\int_0^\tau |e^{-\xi(\mu^\tau + d_I + f(I^\tau))}|\,d\xi}{1 - b(M^\tau)|f'(I^\tau)|\int_0^\tau e^{-\xi(d_I + f(I^\tau))}\int_{-\xi}^0 |e^{\mu^\tau\theta}|\,d\theta\,d\xi} \\ &\leq \frac{|b'(M^\tau)|\int_0^\tau e^{-\xi(\mathrm{Re}\,\mu^\tau + d_I + f(I^\tau))}\,d\xi}{1 - b(M^\tau)|f'(I^\tau)|\int_0^\tau e^{-\xi(d_I + f(I^\tau))}\int_{-\xi}^0 e^{\mathrm{Re}\,\mu^\tau\theta}\,d\theta\,d\xi} \\ &\leq \frac{|b'(M^\tau)|\int_0^\tau e^{-\xi(\lambda^\tau + d_I + f(I^\tau))}\,d\xi}{1 - b(M^\tau)|f'(I^\tau)|\int_0^\tau\int_{-\xi}^0 e^{\lambda^\tau\theta}\,d\theta\,d\xi} \\ &:= C_2(\tau), \end{aligned}$$

where $C_2(\tau)$ is uniformly bounded in small τ. It then follows that

$$\begin{aligned}|H(\mu^\tau\tau, c^\tau, A^\tau)| &\le |e^{-\mu^\tau\tau}| + \left|\gamma(\tau,\mu^\tau)\frac{b(M^\tau)f'(I^\tau)}{b'(M^\tau)}\int_0^\tau e^{\mu^\tau(-\tau+\xi)}\,d\xi\right| \\ &\le e^{-\lambda^\tau\tau} + C_2(\tau)\left|\frac{b(M^\tau)f'(I^\tau)}{b'(M^\tau)}\right|\int_0^\tau e^{\lambda^\tau(-\tau+\xi)}\,d\xi \\ &:= C_3(\tau),\end{aligned}$$

where $C_3(\tau)$ is uniformly bounded in small τ. Hence,

$$|\mu^\tau| \le C_0 + C_1C_3(\tau)$$

and therefore $|\mu^\tau|$ is bounded in small τ.

Now we are ready to show that $\lambda^\tau = \mu^\tau$ when τ is small. As $\tau \to 0$, the boundedness implies that μ^τ has a convergent subsequence. Denote the limit by μ^0. Then μ^0 is an eigenvalue at q^0, and hence, $\mu^0 = \lambda^0$. By the uniqueness of the eigenvalue guaranteed by the implicit function theorem, $\lambda^\tau = \mu^\tau$ when τ is small. □

Notation. Let $\mathbb{R}_+ := [0, +\infty)$ and define $A, B : \mathbb{R} \to \mathbb{R}$ by

$$A(s) = d_I + f(s), \quad B(s) = d_M + g(s).$$

Obviously, both A and B are nondecreasing. For $s > 0$, define $X^s = C([-s, 0], \mathbb{R})$. We equip X^s with the topology induced by the maximum norm $\|\cdot\|$. Let $X^s_+ = C([-s, 0], \mathbb{R}_+)$. For any $\phi, \psi \in X$, we write $\phi \ge \psi$ provided that $\phi - \psi \in X^s_+$. For any $\phi, \psi \in X$, we write $\phi > \psi$ provided that $\phi \ge \psi$ but $\phi \not\equiv \psi$. For any $\phi, \psi \in X$, we write $\phi > \psi$ provided that $\phi - \psi \in \operatorname{Int} X^s_+$.

Using the above notation, we may rewrite (5) in the form $I(t) = h(I_t, M_t)$, where $h : X^\tau \times X^\tau \to \mathbb{R}$ is defined by

$$h(\phi_1, \phi_2) = \int_{-\tau}^{0} b(\phi_2(\xi))e^{-\int_\xi^0 A(\phi_1(\eta))\,d\eta}\,d\xi.$$

Note that relation (5) between the mature and immature populations holds at time t if and only if, during the period $[t - \tau, t]$, there is no artificial introduction of immature individuals. Therefore, model (4) is meaningful for $t > 0$ if and only if the initial functions defined in the time interval $[-\tau, 0]$ belong to the set

$$Y^\tau_+ = \left\{\phi = (\phi_1, \phi_2) : \phi_2 \in X^\tau_+,\ \phi_1(\theta) = \int_{-\tau}^{\theta} b(\phi_2(\xi))e^{-\int_\xi^\theta A(\phi_1(\eta))\,d\eta}\,d\xi\right\}.$$

Clearly, Y^τ_+ is much smaller than $X^\tau_+ \times X^\tau_+$ because ϕ_1 is uniquely determined by ϕ_2. We use Z^r_+ to denote the set of all functions $\phi = (\phi_1, \phi_2) : [-r, 0] \to \mathbb{R}^2_+$ having the following three properties:

(i) there exists at most one discontinuous point $s \in (-r, -\tau]$;
(ii) $\phi|_{[-r,s]} = 0$;
(iii) $\phi_1(\theta) = h((\phi_1)_\theta, (\phi_2)_\theta), \theta \in [s, 0]$.

Then, Y_+^τ can be naturally extended to be a subset of Z_+^r by choosing $s = -\tau$. We use U_+^r to denote the second component of such an extended set, that is,

$$U_+^r = \{\phi : [-r, 0] \to \mathbb{R}_+ : \phi|_{[-r,-\tau)} \equiv 0,\ \phi|_{[-\tau,0]} \in X_+^\tau\}.$$

In what follows, we are interested in the global dynamics of solutions of (4) with initial functions in Y_+^τ.

2.5.3. Two auxiliary equations

The recruitment term for the mature population at time $t > 0$ can be written as $R(I_t, M_t)$, where $R : Z_+^r \to \mathbb{R}$ is defined by

$$R(\phi_1, \phi_2) = b(\phi_2(-\tau)) \exp\left\{\int_{-\tau}^{0} -A(h((\phi_1)_\xi, (\phi_2)_\xi))\, d\xi\right\}.$$

If $f(s)$ is nondecreasing in s, then $h(\phi_1, \phi_2)$ is nonincreasing in ϕ_1 and $R(\phi_1, \phi_2)$ is nondecreasing in ϕ_1. Therefore, the recruitment term can be controlled in the following way:

$$b(\phi_2(-\tau))e^{-A(0)\tau} \geq R(\phi_1, \phi_2) \geq b(\phi_2(-\tau)) \exp\left\{\int_{-\tau}^{0} -A(h(0, (\phi_2)_\xi))\, d\xi\right\}. \tag{37}$$

Also, when $\tau \to 0$, the immature population vanishes and the above three quantities all tend to $b(\phi_2(0))$. Inequality (37) enables us to treat the equation for the mature population only.

We use relation (37) to construct two auxiliary equations which admit the comparison principle under certain conditions. One of these is

$$\begin{cases} v'(t) = -B(v(t))v(t) + b(v(t-\tau))e^{-A(0)\tau}, \\ v_0 = \phi \in X_+^\tau, \end{cases} \tag{38}$$

and the other is

$$\begin{cases} w'(t) = -B(w(t))w(t) + b(w(t-\tau)) \exp\left\{-\int_{-\tau}^{0} A(h(0, w_{t+\xi}))\, d\xi\right\}, \\ w_0 = \phi \in U_+^r. \end{cases} \tag{39}$$

Assume that b is bounded by a nondecreasing function b_1 with $\lim_{s\to\infty} b_1(s)/s = 0$. Then one may show that there exists $K_0 > 0$ such that, for any $K \geq K_0$, $[0, K]$ is positively invariant for both (38) and (39), and any solution eventually enters $[0, K]$. Define

$$b_{\max} = \max_{s\in[0,K_0+1]} b(s), \quad b'_{\max} = \max_{s\in[0,K_0+1]} b'(s), \quad b'_{\min} = \min_{s\in[0,K_0+1]} b'(s),$$
$$A'_{\max} = \max_{s\in[0,K_0+1]} A'(s).$$

Let $L_1 \geq A(0)$ be a Lipschitz constant for the function $s \to sB(s)$, $s \in [0, K_0 + 1]$. Define

$$\tau_1 := \sup_{\mu > L_1} \frac{1}{\mu - A(0)} \ln \frac{\mu - L_1}{\max\{0^+, -b'_{\min}\}} \tag{40}$$

and

$$\tau_2 := \sup_{\mu > L_1} \frac{1}{2\mu} \ln \frac{\mu - L_1}{\max\{0^+, -b'_{\min}\} + b_{\max} b'_{\max} A'_{\max} \mu^{-2}}, \tag{41}$$

where 0^+ is understood as the limit to 0 from the right. The above simple expression for τ_2 has the advantage of being explicit but the most important requirement is for a number $\mu > 0$ such that the curly bracketed term in (43) is positive. This may in practice be the case over a larger interval of τ than $[0, \tau_2]$ with τ_2 given by (41). In fact, if we vary $b'_{\min}$ and $A'_{\max}$, we find that $\tau_2 \to \infty$ as $\max\{0, -b'_{\min}\} \to 0$ and $A'_{\max} \to 0$. Similarly, $\tau_1 \to \infty$ as $\max\{0, -b'_{\min}\} \to 0$. In particular, when $A'_{\max} = 0$, that is, $f \equiv 0$, the model (4) is uncoupled and the two auxiliary equations reduce to the second component of the decoupled model.

We have the following results on generic convergence for the two auxiliary equations.

Lemma 2.3.

(i) *For $\phi \in X^\tau_+$, if $\tau \leq \tau_1$, then either $v(t; \phi)$ converges to some equilibrium or there is a strictly decreasing sequence ϕ_n converging to ϕ such that $v(t; \phi_n)$ converges to the same equilibrium for all n.*

(ii) *For $\phi \in U^r_+$, if $\tau \leq \tau_2$, then either $w(t; \phi)$ converges to some equilibrium or there is a strictly increasing sequence ϕ_n converging to ϕ such that $w(t; \phi_n)$ converges to the same equilibrium for all n.*

Proof. We only prove (ii). The proof for (i) is similar and will be briefly commented on at the end. Fix $\phi \in U^r_+$. There exists $t_1 > r$ such that

$$w_t \in X^r_+, \quad \|w_t\| \leq K_0, \quad t \geq t_1.$$

We use an argument similar to that in [22, Proposition 1.2, Ch. 6] to verify that the solution semiflow $\{w_t(t_1; \cdot)\}_{t \geq 0}$ on $[0, K_0 + 1]$ is strongly order preserving provided that $\tau \leq \tau_2$, with τ_2 defined in (41). In the notation introduced at (17) and thereafter, we write (39) in the form $w'(t) = \breve{f}(w_t)$ with

$$\breve{f}(w_t) = -B(w(t))w(t) + R(0, w_t)$$

and we work with the exponential ordering $\leq_\mu$ defined in (18). The application of the idea in [22, Proposition 1.2, Ch. 6] requires that we check the existence of a $\mu > 0$ such that, whenever $\phi \leq_\mu \psi$,

$$\mu(\psi(0) - \phi(0)) + \breve{f}(\psi) - \breve{f}(\phi) \geq 0.$$

Now take ϕ and ψ such that $\phi \leq_\mu \psi$. Then

$$
\begin{aligned}
&\mu(\psi(0)-\phi(0))+\breve{f}(\psi)-\breve{f}(\phi)\\
&=\mu(\psi(0)-\phi(0))+b(\psi(-\tau))\exp\left\{-\int_{-\tau}^{0}A\left(\int_{-\tau}^{0}b(\psi(\xi+\eta))e^{d_I\eta}\,d\eta\right)d\xi\right\}\\
&\quad-b(\phi(-\tau))\exp\left\{-\int_{-\tau}^{0}A\left(\int_{-\tau}^{0}b(\phi(\xi+\eta))e^{d_I\eta}\,d\eta\right)d\xi\right\}\\
&-\big(B(\psi(0))\psi(0)-B(\phi(0))\phi(0)\big).
\end{aligned}
$$

From (18), $\phi\le\psi$ and so, by the Lipschitz property,

$$
\begin{aligned}
B(\psi(0))\psi(0)-B(\phi(0))\phi(0)&\le|B(\psi(0))\psi(0)-B(\phi(0))\phi(0)|\le L_1|\psi(0)-\phi(0)|\\
&=L_1(\psi(0)-\phi(0))
\end{aligned}
$$

giving a bound on the last term. The difference of the two terms involving exponentials can be written as

$$
\begin{aligned}
&b(\psi(-\tau))\left[\exp\left\{-\int_{-\tau}^{0}A\left(\int_{-\tau}^{0}b(\psi(\xi+\eta))e^{d_I\eta}\,d\eta\right)d\xi\right\}\right.\\
&\left.-\exp\left\{-\int_{-\tau}^{0}A\left(\int_{-\tau}^{0}b(\phi(\xi+\eta))e^{d_I\eta}\,d\eta\right)d\xi\right\}\right]\\
&+\big[b(\psi(-\tau))-b(\phi(-\tau))\big]\exp\left\{-\int_{-\tau}^{0}A\left(\int_{-\tau}^{0}b(\phi(\xi+\eta))e^{d_I\eta}\,d\eta\right)d\xi\right\}
\end{aligned}
\tag{42}
$$

and estimated as follows. By the mean value theorem, with c some unknown intermediate value, and using the second property of (18), the last term in (42) can be bounded in absolute value as follows:

$$
\begin{aligned}
&\big[b(\psi(-\tau))-b(\phi(-\tau))\big]\exp\left\{-\int_{-\tau}^{0}A\left(\int_{-\tau}^{0}b(\phi(\xi+\eta))e^{d_I\eta}\,d\eta\right)d\xi\right\}\\
&=b'(c)[\psi(-\tau)-\phi(-\tau)]\exp\left\{-\int_{-\tau}^{0}A\left(\int_{-\tau}^{0}b(\phi(\xi+\eta))e^{d_I\eta}\,d\eta\right)d\xi\right\}\\
&\ge\min\{0,b'_{\min}\}[\psi(-\tau)-\phi(-\tau)]e^{-A(0)\tau}\\
&\ge\min\{0,b'_{\min}\}[\psi(0)-\phi(0)]e^{(\mu-A(0))\tau}.
\end{aligned}
$$

By the mean value theorem applied to the function $x \to e^{-x}$, the first term in (42) can be written in the form

$$-e^{-\theta} b(\psi(-\tau)) \int_{-\tau}^{0} \left\{ A\left(\int_{-\tau}^{0} b(\psi(\xi+\eta)) e^{d_I \eta}\, d\eta \right) - A\left(\int_{-\tau}^{0} b(\phi(\xi+\eta)) e^{d_I \eta}\, d\eta \right) \right\} d\xi$$

for an unknown (positive) θ. Next we apply the mean value theorem to the integrand, and then to the difference $b(\psi(\xi+\eta)) - b(\phi(\xi+\eta))$ that arises, giving

$$-e^{-\theta} b(\psi(-\tau)) \int_{-\tau}^{0} A'(a(\xi)) \int_{-\tau}^{0} b'(\zeta(\xi,\eta))(\psi(\xi+\eta) - \phi(\xi+\eta)) e^{d_I \eta}\, d\eta\, d\xi$$

for some unknown positive functions $a(\xi)$ and $\zeta(\xi,\eta)$. Since $\xi+\eta \le 0$, by the second property in (18), $\psi(\xi+\eta) - \phi(\xi+\eta) \le (\psi(0) - \phi(0)) e^{-\mu(\xi+\eta)}$. Using also that $e^{d_I \eta} \le 1$, the first term in (42) can be bounded below by

$$-b_{\max} A'_{\max} b'_{\max} (\psi(0) - \phi(0)) \int_{-\tau}^{0} \int_{-\tau}^{0} e^{-\mu(\xi+\eta)} d\eta\, d\xi,$$

i.e. by $-b_{\max} A'_{\max} b'_{\max} (\psi(0) - \phi(0))(e^{\mu\tau} - 1)^2/\mu^2$. Putting all these estimates together,

$$\begin{aligned} &\mu(\psi(0) - \phi(0)) + \breve{f}(\psi) - \breve{f}(\phi) \\ &\ge \left\{ \mu - L_1 + \min\{0, b'_{\min}\} e^{(\mu - A(0))\tau} - b_{\max} A'_{\max} b'_{\max} (e^{\mu\tau} - 1)^2/\mu^2 \right\} (\psi(0) - \phi(0)) \end{aligned} \tag{43}$$

and we need to find a $\mu > 0$ for which the curly bracketed coefficient is non-negative. It suffices to find a $\mu > 0$ such that

$$\mu - L_1 + \min\{0, b'_{\min}\} e^{2\mu\tau} - b_{\max} A'_{\max} b'_{\max} \frac{e^{2\mu\tau}}{\mu^2} \ge 0 \tag{44}$$

holds, since the latter requirement is stronger. A number $\mu > 0$ satisfying (44) exists if $\tau \le \tau_2$, where τ_2 is defined by (41).

The proof for case (i) is similar, but simpler. In this case we can show, with

$$\breve{f}(v) = -B(v(0))v(0) + b(v(-\tau)) e^{-A(0)\tau},$$

that

$$\mu(\psi(0) - \phi(0)) + \breve{f}(\psi) - \breve{f}(\phi) \ge \left\{ \mu - L_1 + \min\{0, b'_{\min}\} e^{(\mu - A(0))\tau} \right\} (\psi(0) - \phi(0))$$

and a suitable μ can be found if $\tau \le \tau_1$, with τ_1 defined by (40).

Note that $w_{t_1}(\theta, \phi)$ can be approximated from below and above in $[0, K_0 + 1]$. The proof is then complete, by [22, Proposition 4.4, Ch. 1]. □

2.5.4. Comparison principle

Let $v(t;\phi), t>0$ be the solution of (38) with $v_0=\phi\in X_+^\tau$, $w(t;\psi)$ be the solution of (39) with $w_0=\psi\in U_+^\tau$, and $(I(t;\varphi), M(t;\varphi))$ be the solution of model (4) with $(I_0, M_0)=\varphi:=(\varphi_1,\varphi_2)\in X_+^\tau\times X_+^\tau$.

Lemma 2.4. *Let $K>K_0$ be fixed. Then there exists $\tau_3=\tau_3(K)>0$ such that for $\tau\le\tau_3$, $v(t;\phi)\ge M(t;\varphi)\ge w(t;\psi), t>0$ provided that*

$$K\ge\phi(\theta)\ge\varphi_2(\theta)\ge\psi(\theta),\quad \theta\in[-\tau,0].$$

Proof. The proof is similar to that of [22, Theorem 1.1, Ch. 6]. We omit the details. □

2.5.5. Generic convergence to equilibria when the delay is small

Let E^τ, $\tau\ge 0$, be the equilibria set of (4). For $\epsilon>0$, define the set

$$E_\epsilon^0:=\bigcup_{q^0\in E^0}\mathcal{N}_\epsilon(q^0),$$

where $\mathcal{N}_\epsilon(q^0)\subset\mathbb{R}^2$ is the ball centred at q^0 with radius ϵ. For $K\ge K_0$, define the set

$$Q_K^\tau:=\left\{\phi_2:\ \phi=(\phi_1,\phi_2)\in Y_+^\tau \text{ with } \|\phi_2\|\le K \text{ and } \lim_{t\to\infty}(I(t;\phi),M(t;\phi))\in E^\tau\right\}.$$

Theorem 2.4. *Assume that the conditions in Lemma 2.1 are satisfied. Then, for $K\ge K_0$, there exists $\tau_4=\tau_4(K)>0$ such that Q_K^τ is dense in $[0,K]_{X_+^\tau}$ when $\tau\le\tau_4$.*

Proof. Define the set

$$P:=\{x\in\mathbb{R}_+:\ (0,x)\in E^0 \text{ is unstable}\}$$

and

$$S=\{\phi=(\phi_1,\phi_2)\in Y_+^\tau:\phi_2(0)\notin P\}.$$

Clearly, S is dense in Y_+^τ. We divide the proof into two steps.

Step 1. Show that for $\epsilon>0$ and $\phi\in S$, there exist $q^0\in E^0$, τ_5 and $t_2>0$ such that

$$(I(t;\phi),M(t,\phi))\in\mathcal{N}_\epsilon(q^0),\quad \tau\in[0,\tau_5],\quad t\ge t_2.$$

Indeed, assume, without loss of generality, that $\phi_2>0$. Otherwise, $M(t;\phi)\equiv 0$. We use $\tilde\phi_2\in U_+^r$ to denote the natural extension of ϕ_2. Then there exist $\psi_n^{\tau,+}\in X_+^\tau$ and $\psi_n^{\tau,-}\in U_+^r$ such that

$$\psi_n^{\tau,-}<\psi_{n+1}^{\tau,-}<\cdots<\tilde\phi_2$$

and

$$\phi_2<\cdots<\psi_{n+1}^{\tau,+}<\psi_n^{\tau,+},\quad n\ge 1.$$

By [22, Proposition 4.4, Ch.1], we see that when $\tau \le \min\{\tau_1, \tau_2, \tau_5\}$ there exists an equilibrium v^τ of (38) such that either

$$\lim_{t\to\infty} v(t, \phi_2) = v^\tau$$

or

$$\lim_{t\to\infty} v(t; \psi_n^{\tau,+}) = v^\tau, \quad \forall n \ge 1.$$

Similarly, there exists an equilibrium w^τ of (39) such that either

$$\lim_{t\to\infty} w(t, \tilde{\phi}_2) = w^\tau$$

or

$$\lim_{t\to\infty} w(t; \psi_n^{\tau,-}) = w^\tau, \quad \forall n \ge 1.$$

By the comparison principle, we have

$$w^\tau \le \liminf_{t\to\infty} M(t) \le \limsup_{t\to\infty} M(t) \le v^\tau.$$

Next, we show that $|w^\tau - v^\tau| \to 0$ as $\tau \to 0$. We argue by contradiction assuming that, up to a subsequence, $\lim_{\tau\to 0} w^\tau = w^0 \ne v^0 = \lim_{\tau\to 0} v^\tau$. Note that, when $\tau \to 0$, the functions $w(t, \phi_2)$, $w(t; \psi_n^{\tau,-})$, $v(t, \phi_2)$ and $v(t; \psi_n^{\tau,+})$ converge (up to a subsequence) uniformly in $t \ge 0$ to $z_1(t)$, $z_{2,n}(t)$, $z_3(t)$ and $z_{4,n}(t)$ which are all solutions of

$$z'(t) = -B(z(t))z(t) + b(z(t))$$

with initial values $\phi_2(0)$, $\lim_{\tau\to 0} \phi_n^{\tau,-}(0)$, $\phi_2(0)$ and $\lim_{\tau\to 0} \phi_n^{\tau,+}(0)$, respectively. Since

$$\lim_{n\to\infty} \lim_{\tau\to 0} \phi_n^{\tau,\pm}(0) = \phi_2(0) \notin P,$$

solutions $z_1(t)$, $z_{2,n}(t)$, $z_3(t)$ and $z_{4,n}(t)$ converge to the same equilibrium z^* as $t \to \infty$ for large n. This contradicts $w^0 \ne v^0$. Thus, the first step is complete.

Step 2. We show that the unique equilibrium q^τ in $\mathcal{N}_\epsilon(q^0)$ found in Step 1 is linearly asymptotically stable and

$$\lim_{t\to\infty} (I(t; \phi), M(t, \phi)) = q^\tau.$$

Indeed, from Step 1 we know that q^0 must be linearly stable. Let $\lambda^\tau < 0$ be the dominant eigenvalue at the equilibrium q^τ. Since $\lim_{\tau\to 0} \lambda^\tau = \lambda^0$, we may define a negative number

$$\lambda^{\max} = \max_{\tau\le\tau_4}\{\lambda^\tau\}.$$

We rewrite (4) as an abstract ODE of the form

$$y'(t) = Ly(t) + H(y(t)),$$

where $y(t) = (I_t, M_t) - q^\tau$, L is the linear part and H is the higher order term. For $\epsilon > 0$, there exists $\delta > 0$ such that

$$\|H(y(t))\| \le \epsilon \|y(t)\| \quad \text{when} \quad \|y(t)\| \le \delta.$$

Then we can choose τ and δ small enough such that

$$\|y(t)\| \le \|y(0)\| e^{\lambda^{\max} t} + \int_0^t e^{\lambda^{\max}(t-s)} \frac{-\lambda^{\max}}{2} |y(s)|\, ds.$$

By Gronwall's inequality, $\|y(t)\|_X \le \|y(0)\|_X e^{\frac{1}{2}\lambda^{\max} t} \to 0$ as $t \to \infty$. □

Theorem 2.5. *Assume that the conditions in Lemma 2.1 are satisfied. If E^0 consists of no more than two elements, then there exists $\tau_6 > 0$ such that all solutions of (4) starting from Y_+^τ are convergent to the unique stable equilibrium when $\tau \le \tau_6$, where τ_6 is independent of the initial functions.*

Proof. If E^0 consists of no more than two elements, then there exists a unique linearly stable equilibrium in E^τ when τ is small. At the same time, if $M(t) \not\equiv 0$, then $M(t) > 0$ for all large time for any τ.

Now we repeat the arguments in the proof of Theorem 2.4 but with the initial time being taken as a large number t_3 such that $M(t_3) > 0$ and the solution (I_t, M_t) lies in a small neighbourhood of the global attractor for all time $t \ge t_3$. The rest of the proof is the same as that of Theorem 2.4. □

Remark 2.1. The global convergence result established in Theorem 2.5 is also valid for (4) with initial functions in $X_+^\tau \times X_+^\tau$.

2.6. *Uniqueness of positive equilibria and global stability*

One by-product of the threshold dynamics result (Theorem 2.2) is the existence of at least one positive equilibrium when $\mathcal{R}_0 > 1$. In what follows, we show that under certain conditions there is just one positive equilibrium.

Proposition 2.4. *Assume that*

(i) *the birth rate function b is increasing and subhomogeneous (sublinear), that is $b(\alpha x) \ge \alpha b(x)$ for any $\alpha \in [0, 1]$ and $x \ge 0$;*
(ii) *the nonnegative functions f, g are nondecreasing.*

Then, the positive equilibrium (if it exists) is unique.

Proof. If (I, M) is an equilibrium for system (4), then it satisfies

$$d_I I + f(I) I = b(M) - b(M) e^{-d_I \tau - f(I)\tau},$$
$$d_M M + M g(M) = b(M) e^{-d_I \tau - f(I)\tau}.$$

If there are two positive equilibria, say (I_1, M_1) and (I_2, M_2), then it is easy to see that $I_1 \neq I_2$ and $M_1 \neq M_2$. Without loss of generality, we assume $M_1 < M_2$ and, therefore, there is $\alpha \in (0, 1)$ such that $M_1 = \alpha M_2$. Since the function b is subhomogeneous, we have

$$b(\alpha M_2) \geq \alpha b(M_2).$$

Therefore,

$$\begin{aligned} e^{-d_I\tau - f(I_1)\tau} &= \frac{d_M M_1 + M_1 g(M_1)}{b(M_1)} = \frac{\alpha[d_M M_2 + M_2 g(\alpha M_2)]}{b(\alpha M_2)} \\ &\leq \frac{\alpha[d_M M_2 + M_2 g(\alpha M_2)]}{\alpha b(M_2)} \leq \frac{\alpha[d_M M_2 + M_2 g(M_2)]}{\alpha b(M_2)} \\ &= e^{-d_I\tau - f(I_2)\tau}, \end{aligned}$$

from which we see that $I_1 > I_2$, since f is nondecreasing and $I_1 \neq I_2$. Define

$$h(x) = \frac{d_I x + f(x)x}{1 - e^{-d_I\tau - f(x)\tau}} = \frac{A(x)x}{1 - e^{-A(x)\tau}}$$

with $A(x) = d_I + f(x)$, as in Section 2.5. Then, $A'(x) \geq 0$ for all $x > 0$ and

$$h'(x) = \frac{(A(x) + xA'(x))(1 - e^{-A(x)\tau}) - A(x)xA'(x)\tau e^{-A(x)\tau}}{(1 - e^{-A(x)\tau})^2}.$$

We estimate the numerator of $h'(x)$ as follows:

$$\begin{aligned} &(A(x) + xA'(x))(1 - e^{-A(x)\tau}) - A(x)xA'(x)\tau e^{-A(x)\tau} \\ &> (A(x) + xA'(x))(1 - e^{-A(x)\tau}) - (A(x) + xA'(x))A(x)\tau e^{-A(x)\tau} \\ &= (A(x) + xA'(x))(1 - e^{-A(x)\tau} - A(x)\tau e^{-A(x)\tau}) \geq 0 \end{aligned}$$

since $1 - e^{-A(x)\tau} - A(x)\tau e^{-A(x)\tau} \geq 0$ for all τ. Therefore, $h(x)$ is an increasing function and

$$b(M_1) = h(I_1) > h(I_2) = b(M_2),$$

a contradiction. Hence, we must have $I_1 = I_2$ and $M_1 = M_2$. □

Combining the previous proposition with the persistence (Theorem 2.2), local stability (Theorem 2.3) and generic convergence results (Theorem 2.4), we have the global stability of the positive equilibrium when the delay τ is small.

Theorem 2.6. *Assume that*

(i) *the birth rate function b is increasing and strictly subhomogeneous (sublinear), that is $b(\alpha x) > \alpha b(x)$ for any $\alpha \in (0, 1)$ and $x > 0$;*
(ii) *the nonnegative functions f, g are nondecreasing.*

Then, if $\mathcal{R}_0 > 1$, system (4) admits a positive equilibrium which is globally asymptotically stable to all nontrivial solutions.

3. Two-strain competition

In this section we consider competition between two strains $u(t,a)$ and $v(t,a)$. The variables

$$I_u(t) = \int_0^\tau u(t,a)\,da, \quad I_v(t) = \int_0^\tau v(t,a)\,da,$$
$$M_u(t) = \int_\tau^\infty u(t,a)\,da, \quad M_v(t) = \int_\tau^\infty v(t,a)\,da \tag{45}$$

stand for the total numbers at time t of larvae (I) and adults (M) of each of the strains u and v. The following equations describe competition at the immature stage and are therefore for ages $a \in (0,\tau)$:

$$\begin{aligned}\frac{\partial u(t,a)}{\partial t} + \frac{\partial u(t,a)}{\partial a} &= -d_{Iu}u(t,a) - u(t,a)f_{uu}(I_u(t)) - u(t,a)f_{uv}(I_v(t)),\\ \frac{\partial v(t,a)}{\partial t} + \frac{\partial v(t,a)}{\partial a} &= -d_{Iv}v(t,a) - v(t,a)f_{vv}(I_v(t)) - v(t,a)f_{vu}(I_u(t)).\end{aligned} \tag{46}$$

For competition at the mature stage, i.e. for ages $a > \tau$:

$$\begin{aligned}\frac{\partial u(t,a)}{\partial t} + \frac{\partial u(t,a)}{\partial a} &= -d_{Mu}u(t,a) - u(t,a)g_{uu}(M_u(t)) - u(t,a)g_{uv}(M_v(t)),\\ \frac{\partial v(t,a)}{\partial t} + \frac{\partial v(t,a)}{\partial a} &= -d_{Mv}v(t,a) - v(t,a)g_{vv}(M_v(t)) - v(t,a)g_{vu}(M_u(t)).\end{aligned} \tag{47}$$

The functions $f_{uu}(\cdot)$, $f_{uv}(\cdot)$, $f_{vu}(\cdot)$, $f_{vv}(\cdot)$ in (46) all increase with respect to their single variable. Intra-specific competition among the larvae of strain u is described by $f_{uu}(\cdot)$, while $f_{uv}(\cdot)$ describes the competitive effect of the larvae of strain v on the larvae of strain u. Similar interpretations can be given to $f_{vu}(\cdot)$ and $f_{vv}(\cdot)$. Similar assumptions and similar interpretations apply to the g functions in (47) which describe intra- and interspecific competition among the adults of the two strains. From (45), (46) and (47),

$$\begin{aligned}\frac{dI_u(t)}{dt} &= u(t,0) - u(t,\tau) - [d_{Iu} + f_{uu}(I_u(t)) + f_{uv}(I_v(t))]I_u(t),\\ \frac{dI_v(t)}{dt} &= v(t,0) - v(t,\tau) - [d_{Iv} + f_{vv}(I_v(t)) + f_{vu}(I_u(t))]I_v(t),\\ \frac{dM_u(t)}{dt} &= u(t,\tau) - [d_{Mu} + g_{uu}(M_u(t)) + g_{uv}(M_v(t))]M_u(t),\\ \frac{dM_v(t)}{dt} &= v(t,\tau) - [d_{Mv} + g_{vv}(M_v(t)) + g_{vu}(M_u(t))]M_v(t).\end{aligned} \tag{48}$$

The terms $u(t,0)$ and $v(t,0)$ are the birth rates for strains u and v and we assume

$$u(t,0) = b_u(M_u(t), M_v(t)), \quad v(t,0) = b_v(M_u(t), M_v(t)),$$

and that b_u and b_v satisfy

$$b_u(0, M_v) = 0 \quad \text{and} \quad b_v(M_u, 0) = 0 \tag{49}$$

where b_u and b_v are functions representing the egg laying rates for strains u and v. The egg laying rate for strain u must be zero if no adults of that strain are present, hence the assumption $b_u(0, M_v) = 0$ and similarly for strain v. We allow the egg laying rate b_u for strain u to depend not only on the number of adults $M_u(t)$ of that strain, but also on the number of adults $M_v(t)$ of the other strain. Dependence on both $M_u(t)$ and $M_v(t)$ is likely if the adults of two strains compete for a common limited food resource, since a significant increase in the number of adults of one strain will make it more difficult for the adults of the other strain to find enough food, and this in turn will affect their egg-laying rate. A particular case would be to have b_u depending only on $M_u(t)$, and b_v depending only on $M_v(t)$, which would probably be reasonable if the two strains consume different food resources or share a resource available in abundance. Note that both intra- and interspecific competition among adults is also modelled by terms in the right hand sides of (47). The terms $u(t,\tau)$ and $v(t,\tau)$ are the maturation rates for the two strains, and these can be computed using the equations of system (46) using integration along characteristics as explained in Section 2. The outcome is that, for ages $a \le \tau$,

$$\begin{aligned}
u(t,a) &= b_u(M_u(t-a), M_v(t-a)) \\
&\quad \times \exp\left(-\int_0^a \{d_{Iu} + f_{uu}(I_u(\eta+t-a)) + f_{uv}(I_v(\eta+t-a))\}\,d\eta\right), \\
v(t,a) &= b_v(M_u(t-a), M_v(t-a)) \\
&\quad \times \exp\left(-\int_0^a \{d_{Iu} + f_{vv}(I_v(\eta+t-a)) + f_{vu}(I_u(\eta+t-a))\}\,d\eta\right),
\end{aligned}$$

from which we calculate $u(t,\tau)$ and $v(t,\tau)$. Equations (48) become

$$\begin{aligned}
\frac{dI_u(t)}{dt} &= b_u(M_u(t), M_v(t)) - b_u(M_u(t-\tau), M_v(t-\tau)) \\
&\quad \times \exp\left(-\int_0^\tau \{d_{Iu} + f_{uu}(I_u(\eta+t-\tau)) + f_{uv}(I_v(\eta+t-\tau))\}\,d\eta\right) \\
&\quad - [d_{Iu} + f_{uu}(I_u(t)) + f_{uv}(I_v(t))]I_u(t), \\
\frac{dI_v(t)}{dt} &= b_v(M_u(t), M_v(t)) - b_v(M_u(t-\tau), M_v(t-\tau)) \\
&\quad \times \exp\left(-\int_0^\tau \{d_{Iu} + f_{vv}(I_v(\eta+t-\tau)) + f_{vu}(I_u(\eta+t-\tau))\}\,d\eta\right)
\end{aligned} \tag{50}$$

$$- [d_{Iv} + f_{vv}(I_v(t)) + f_{vu}(I_u(t))]I_v(t), \tag{51}$$

$$\frac{dM_u(t)}{dt} = b_u(M_u(t-\tau), M_v(t-\tau)) \times \exp\left(-\int_0^\tau \{d_{Iu} + f_{uu}(I_u(\eta+t-\tau)) + f_{uv}(I_v(\eta+t-\tau))\}\,d\eta\right) - [d_{Mu} + g_{uu}(M_u(t)) + g_{uv}(M_v(t))]M_u(t), \tag{52}$$

$$\frac{dM_v(t)}{dt} = b_v(M_u(t-\tau), M_v(t-\tau)) \times \exp\left(-\int_0^\tau \{d_{Iu} + f_{vv}(I_v(\eta+t-\tau)) + f_{vu}(I_u(\eta+t-\tau))\}\,d\eta\right) - [d_{Mv} + g_{vv}(M_v(t)) + g_{vu}(M_u(t))]M_v(t). \tag{53}$$

Assumption (49) implies that if either strain is absent the above model reduces to the form of model (4) for the remaining strain.

We are interested in the stability of the boundary equilibria of model (50)–(53), i.e. those equilibria in which one strain is absent. This enables us to make predictions about the roles of larval vs. adult competition in determining the outcome of the competition between the two strains. In an equilibrium in which the v strain is absent, the I and M components of the u strain, denoted I_u^* and M_u^*, satisfy

$$\begin{aligned} M_u^*(d_{Mu} + g_{uu}(M_u^*)) &= b_u(M_u^*, 0)\exp\{-\tau(d_{Iu} + f_{uu}(I_u^*))\}, \\ I_u^*(d_{Iu} + f_{uu}(I_u^*)) &= b_u(M_u^*, 0)\Big(1 - \exp\{-\tau(d_{Iu} + f_{uu}(I_u^*))\}\Big). \end{aligned} \tag{54}$$

On setting $I_u = I_u^* + \tilde{I}_u$, $M_u = M_u^* + \tilde{M}_u$, $I_v = \tilde{I}_v$ and $M_v = \tilde{M}_v$, with $\sim$ denoting a small perturbation, we find that the linearisation of system (50)–(53) about the steady state with $I_u = I_u^*$, $M_u = M_u^*$ and $I_v = M_v = 0$ is as follows, where the subscript $*$ denotes evaluation at $(M_u^*, 0)$:

$$\begin{aligned} \frac{d\tilde{I}_u(t)}{dt} = {} & \tilde{M}_u(t)\left[\frac{\partial b_u}{\partial M_u}\right]_* + \tilde{M}_v(t)\left[\frac{\partial b_u}{\partial M_v}\right]_* \\ & - \exp\{-\tau(d_{Iu} + f_{uu}(I_u^*))\}\left[\tilde{M}_u(t-\tau)\left[\frac{\partial b_u}{\partial M_u}\right]_* + \tilde{M}_v(t-\tau)\left[\frac{\partial b_u}{\partial M_v}\right]_*\right. \\ & \left. - b_u(M_u^*, 0)\int_0^\tau \Big\{f'_{uu}(I_u^*)\tilde{I}_u(\eta+t-\tau) + f'_{uv}(0)\tilde{I}_v(\eta+t-\tau)\Big\}\,d\eta\right] \\ & - \Big(d_{Iu} + f_{uu}(I_u^*) + I_u^* f'_{uu}(I_u^*)\Big)\tilde{I}_u(t) - I_u^* f'_{uv}(0)\tilde{I}_v(t), \end{aligned} \tag{55}$$

$$\frac{d\tilde{I}_v(t)}{dt} = \left[\frac{\partial b_v}{\partial M_v}\right]_* \tilde{M}_v(t) - e^{-\tau(d_{Iu}+f_{vu}(I_u^*))}\left[\frac{\partial b_v}{\partial M_v}\right]_* \tilde{M}_v(t-\tau) - (d_{Iv} + f_{vu}(I_u^*))\tilde{I}_v(t), \tag{56}$$

$$\frac{d\tilde{M}_u(t)}{dt} = \exp\{-\tau(d_{Iu} + f_{uu}(I_u^*))\}\left[\tilde{M}_u(t-\tau)\left[\frac{\partial b_u}{\partial M_u}\right]_* + \tilde{M}_v(t-\tau)\left[\frac{\partial b_u}{\partial M_v}\right]_*\right.$$
$$\left. - b_u(M_u^*, 0)\int_0^\tau \left\{f'_{uu}(I_u^*)\tilde{I}_u(\eta + t - \tau) + f'_{uv}(0)\tilde{I}_v(\eta + t - \tau)\right\} d\eta\right]$$
$$- \left(d_{Mu} + g_{uu}(M_u^*) + M_u^* g'_{uu}(M_u^*)\right)\tilde{M}_u(t) - M_u^* g'_{uv}(0)\tilde{M}_v(t), \tag{57}$$

$$\frac{d\tilde{M}_v(t)}{dt} = e^{-\tau(d_{Iu} + f_{vu}(I_u^*))}\left[\frac{\partial b_v}{\partial M_v}\right]_* \tilde{M}_v(t-\tau) - (d_{Mv} + g_{vu}(M_u^*))\tilde{M}_v(t), \tag{58}$$

where in various places we have used assumption (49), which implies in particular that $b_v(M_u^*, 0) = [\partial b_v/\partial M_u]_{(M_u^*,0)} = 0$. We may now prove the following theorem concerning the local stability of any equilibrium in which the v strain is absent. Inequality (60) ensures the stability of such an equilibrium to perturbations in which the v strain remains absent. The addition of inequality (59) ensures that the equilibrium remains stable to perturbations involving small introductions of the v strain.

Theorem 3.1. *Let $(I_u^*, 0, M_u^*, 0)$ be an equilibrium of (50)–(53) with $I_u^* > 0$ and $M_u^* > 0$ satisfying (54). Suppose the birth functions b_u and b_v satisfy (49) and that the functions f_{ij} and g_{ij}, for $i, j \in \{u, v\}$, are all strictly increasing, differentiable and all satisfy $f_{ij}(0) = g_{ij}(0) = 0$. Suppose also that $[\partial b_u/\partial M_u]_{(M_u^*,0)} > 0$ and that*

$$e^{-\tau(d_{Iu} + f_{vu}(I_u^*))}\left|\left[\frac{\partial b_v}{\partial M_v}\right]_{(M_u^*,0)}\right| < d_{Mv} + g_{vu}(M_u^*) \tag{59}$$

and

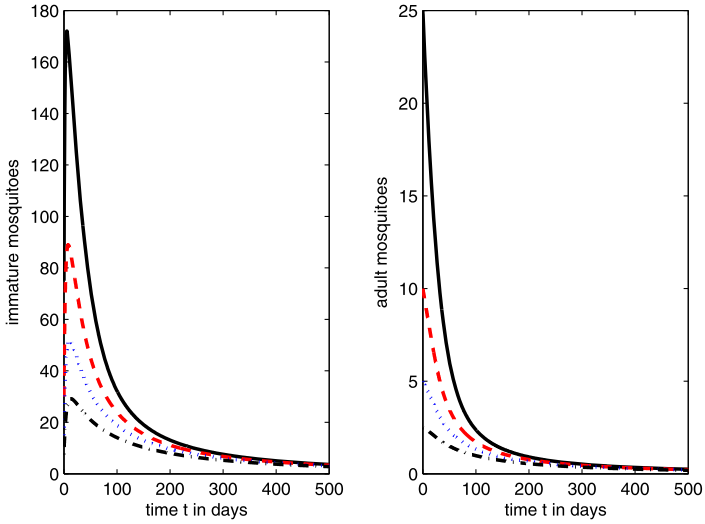
$$e^{-\tau(d_{Iu} + f_{uu}(I_u^*))}\left[\frac{\partial b_u}{\partial M_u}\right]_{(M_u^*,0)} \max\left\{0,\ 1 - \frac{b_u(M_u^*, 0) f'_{uu}(I_u^*)\tau^2 k(c_u)}{1 + b_u(M_u^*, 0) f'_{uu}(I_u^*)\tau^2/2}\right\}$$
$$< d_{Mu} + g_{uu}(M_u^*) + M_u^* g'_{uu}(M_u^*) \tag{60}$$

with $k(x)$ given by (13) and $c_u = \tau(d_{Iu} + f_{uu}(I_u^*))$. Then the equilibrium $(I_u^*, 0, M_u^*, 0)$ is locally asymptotically stable as a solution of (50)–(53).

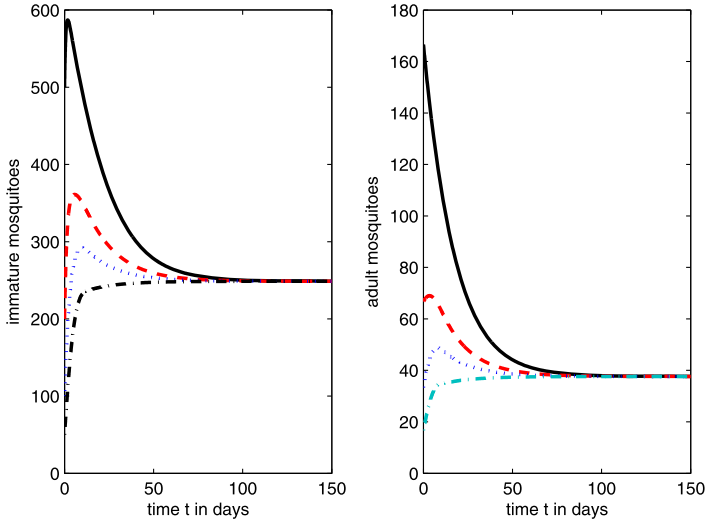
Proof. Inequality (59) and Theorem 3.2.1 in Kuang [13] imply that the solution $\tilde{M}_v(t)$ of (58) satisfies $\tilde{M}_v(t) \to 0$ as $t \to \infty$. It then follows from (56) that $\tilde{I}_v(t) \to 0$. It is then sufficient to prove that $(\tilde{I}_u(t), \tilde{M}_u(t)) \to (0, 0)$ in the case when $\tilde{I}_v(t) = \tilde{M}_v(t) = 0$. But in this case the linearised analysis reduces to the corresponding analysis for the single species model presented in Section 2; see in particular Theorem 2.3. Inequality (60) is just inequality (33) of Theorem 2.3, adapted to the notation of system (50)–(53). □

4. Simulations

We present the results of some numerical simulations of system (4), using mosquito growth as a case study. It is generally accepted that mosquito populations are regulated by density-dependent factors, particularly in the larval stage of development when there is additional



(a) $\tau = 23.5$ days.



(b) $\tau = 10$ days.

Fig. 1. Solutions of (4) for various initial values and two values of τ. In (a) the numbers of immature and adult mosquitoes tend to zero; in (b) they tend to positive equilibrium values.

density-dependent mortality [4]. We assume that intra-specific competition increases the death rate for both immature and adult mosquitoes, and therefore we made the following choices for the functions f and g in (2) and (4):

$$f(x) = \mu_I x \quad \text{and} \quad g(x) = \mu_M x \tag{61}$$

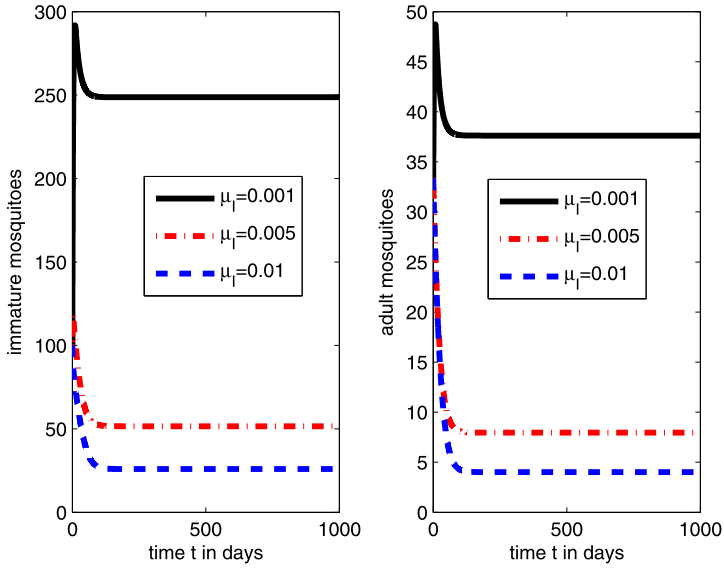


Fig. 2. Solutions of (4) for various values of the parameter μ_I, introduced in (61), which measures the density-dependent contribution to per-capita larval mortality. For the chosen parameter values, $\mathcal{R}_0 = 13.53$ independently of μ_I.

where $\mu_I = 0.01$ per larva, and $\mu_M = 0.001$ per adult, per day. The density-independent contributions to the per-capita larval and adult mortality rates were taken as $d_I = 0.2$ and $d_M = 0.03$ per day. The female mosquito birth rate was taken as $b(M(t)) = bM(t)$, with $b = 3$ per day. These parameters are consistent with those suggested in [8]. The maturation delay τ is sensitive to the local weather conditions, and tends to decrease as temperature increases [8].

If, due to a temperature drop, the maturation delay increases from $\tau = 10$ to $\tau = 23.5$, then the basic reproduction number drops from 13.53 to 0.91. Simulations for both scenarios support the hypothesis that if $\mathcal{R}_0 > 1$ all non-trivial non-negative solutions of system (4) approach the positive equilibrium (see Figs. 1(b) and 2), while if $\mathcal{R}_0 < 1$ solutions approach zero (see Fig. 1(a)). Other simulations not included here suggest that the global stability of the non-zero equilibrium holds, for the parameter values just mentioned, for any other τ such that $\mathcal{R}_0 > 1$. Moreover, increasing the parameter μ_I, which was introduced in (61) and measures the density-dependent contribution to per-capita larval mortality, significantly decreases the equilibrium numbers of both larval and adult mosquitoes (see Fig. 2). However, $\mathcal{R}_0$ is independent of μ_I and $\mathcal{R}_0 > 1$ for the chosen values of the other parameters. Therefore, for those parameter values, the mosquito population persists for arbitrarily large μ_I.

Acknowledgments

S.G. would like to thank the Leverhulme Trust for its support, under Research Fellowship No. RF-2014-512. J.F. is supported in part by the National Natural Science Foundation of China (No. 11371111) and the Fundamental Research Funds for the Central Universities of China (AUGA5710050313). Y.L. is supported in part by NSFC (11301442) and RGC (PolyU 253004/14P). We thank the referee for the comments.

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Please cite this article in press as: J. Fang et al., Stage-structured models of intra- and inter-specific competition within age classes, J. Differential Equations (2015), http://dx.doi.org/10.1016/j.jde.2015.09.048