Spatial dynamics of a model for the effect of variable ages at reproduction

Yijun Lou[1] & Yuxiang Zhang[2]

[1] Department of Applied Mathematics, Hong Kong Polytechnic University, Hong Kong SAR, P. R. China
[2] School of Mathematics, Tianjin University, Tianjin, P. R. China

E-mail: `yx.zhang@tju.edu.cn`

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Abstract. Some species may have totally different ages at successful reproduction (ages at maturity) in population growth. For example, *Ixodes* ticks, a vector species responsible for many tick-borne diseases, may suspend development and undergo diapause during maturation process, which naturally introduce distinct ages at reproduction. Although the age at reproduction is a key demographic trait that is probably under high selective pressure, it is highly variable and the effect of this variability on spatial establishment and invasion is not well understood. In this study, a spatial mechanistic model, in the form of reaction diffusion equations with nonlocal terms incorporating two different ages at reproduction, is formulated and mathematically analyzed from a dynamical system point of view. Specifically, the persistence of the species in a bounded domain indicated by the net reproduction number and the spreading property in an unbounded domain in terms of spreading speed and traveling waves are characterized. Numerical simulations are conducted to further illustrate the impact of ages at reproduction on the net reproduction number and the spreading speed of the species, in particular for various scenarios of fitness tradeoffs of the premature survival and early reproduction.

Keywords: Age at reproduction, reaction diffusion system, nonlocal delay, net reproduction number, traveling waves, spreading speed.

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1. Introduction

Individual heterogeneity is widely observed in natural populations, including age, sex, body mass, habitat use or habitat selection, prey selection and disease states [6, 7]. These variations between individuals play key roles in population dynamics, such as the species establishment and invasion. Quantifying the potential role of individual heterogeneity has been remaining an important objective in population ecology. The

age at which an organism starts to reproduce (i.e. age at recruitment or age at primiparity) is regarded as a very important demographic parameter defining the species population dynamics [6, 7, 11]. There are trade-offs between early reproduction and delayed maturation [11]. For example, organisms start to reproduce early may have a possibly increased probability of realizing reproduction. Intuitively, reproducing as early as possible may be a better strategy since the early recruitment not only increases the survival probability of the population at maturity, increases the number of offsprings of an individuals in individual's lifetime, but also decreases the generation time. However, early maturation requires high energy expenditure and leads to a fitness cost in the form of a higher death rate, and these individuals may suffer from the fitness cost such as reduced survival, future reproduction, or somatic growth.

As an important species in ecology and epidemiology, *Ixodes* ticks are the main vector to transmit various tick-borne pathogens, including Lyme disease, babesiosis, anaplasmosis and tick-borne encephalitis [14]. They may suspend host seeking, development or oviposition and undergo diapause for several months, caused by unfavorable environmental conditions, which naturally introduce distinct ages at reproduction [29]. From a theoretical point of view, there are several possible modeling frameworks to capture the population growth of diapausing species. One employs piecewise or seasonal parameter functions to distinguish the survival or the development rates between the normal growth and diapause periods [1, 13], based on this idea, a periodic dynamic model with piecewise or continuous parameters can be derived. Another idea is to carefully stratify the individuals into different classes with normal development delay to maturation or enlarged development delay due to diapause [29]. In this case, a model with two or more delays can be formulated [25, 29]. A further appropriate way to describe the paused larval development is introducing a state-dependent delay, which is used to describe the diapause triggered by strong intraspecific competition [3]. These modeling frameworks are carefully justified from biological arguments, while enrich the applications of mathematical tools on biological problems and motivate the developments of novel analytical tools.

Extending the modeling idea of [25, 28, 29] with the consideration of species movement in spatial habitats, we propose a reaction-diffusion model with two nonlocal delays for different developmental durations in the next section. Biologically, we assume that the advantage of early breeding may possibly be balanced by associated costs of depressed survival probability, which is driven by a limited amount of energy availability [6]. The dynamics of the model in a bounded domain will be analyzed in terms of the population persistence by using the net reproduction number as an index in section 3. Population invasion characterized by traveling wave solutions and spreading speed will be investigated for the model in an unbounded domain in section 4. Further numerical simulations will be performed to quantitatively study the tradeoff between normal maturation and delayed juvenile development in section 5 and the results will be discussed in the last section.

2. The model and assumptions on vital rates

Motivated by population growth with variable ages at reproduction for ticks, in particular the modeling idea in [25, 28, 29], we will formulate a hypothetical model to describe a single species with immature and mature stages living in a spatial habitat Ω with smooth boundary $\partial\Omega$. This mechanistic model will be simulated with parameters for *Ixodes scapularis* ticks. Adult ticks, $M(t,x) := M_1(t,x) + M_2(t,x)$ are classified into two classes $M_1(t,x)$ and $M_2(t,x)$ with different ages at maturation, τ_1 and τ_2, respectively. The proportions of eggs at birth that are supposed to have τ_1 and τ_2 development durations are p and $1-p$ respectively. Let $\rho_i(t,a,x)$, $i = 1,2$, represent the density of individuals of age a at time t and location x with the development period τ_i. Assume that all individuals are confined to the region $\Omega \subseteq \mathbb{R}^n$ for all times, and therefore the Neumann boundary condition is imposed on the boundary

$$\frac{\partial \rho_i(t,a,x)}{\partial n} = 0, \ \forall t > 0, \ x \in \partial\Omega, \ a > 0$$

where ∂n denotes the differentiation along the outward normal n to $\partial\Omega$. Following the standard argument for population dynamics with age structure and spatial diffusion, for type i individuals distinct with maturation delay τ_i, $i = 1, 2$, we have

$$\left(\frac{\partial}{\partial t} + \frac{\partial}{\partial a}\right)\rho_i(t,a,x) = D_i\Delta\rho_i(t,a,x) - d_i\rho_i(t,a,x), \qquad\qquad 0 < a \leq \tau_i,$$
$$\left(\frac{\partial}{\partial t} + \frac{\partial}{\partial a}\right)\rho_i(t,a,x) = D_M\Delta\rho_i(t,a,x) - (\mu + g(M(t,x)))\rho_i(t,a,x), a > \tau_i, \tag{1}$$

where Δ is the Laplace operator with respect to $x \in \Omega$; D_i, D_M are the diffusion coefficients; d_i is the death rate of immature individuals with maturation periods τ_i; μ is the density-independent death rate of adults while $g(\cdot)$ represents the density-dependent death rate. Then $M_i(t,x), i = 1,2$ can be characterized by

$$M_1(t,x) = \int_{\tau_1}^{\infty} \rho_1(t,a,x)da, \quad M_2(t,x) = \int_{\tau_2}^{\infty} \rho_2(t,a,x)da.$$

The egg reproduction rate at time t and location x is assumed to be a function $f(\cdot)$ of the total matured population density. Then the recruitment rates for two classes are

$$\rho_1(t,0,x) = pf(M(t,x)) \text{ and } \rho_2(t,0,x) = (1-p)f(M(t,x)).$$

As no individual can live forever, we assume $\rho_1(t,\infty,x) = \rho_2(t,\infty,x) = 0$.

Differentiating M_i with respect to t and using the growth law given in (1) for type i, $i = 1, 2$, we get

$$\frac{\partial M_i(t,x)}{\partial t} = D_M\Delta M_i(t,x) - (\mu + g(M(t,x)))M_i(t,x) + \rho_i(t,\tau_i,x). \tag{2} \boxed{\texttt{adult}}$$

To close the system, we need to express $\rho_i(t,\tau_i,x)$ by $M_i(t,x)$ explicitly. Note that $\rho_i(t,\tau_i,x)$ represents the newly matured individuals at time t with age τ_i, which is determined by the evolution process of $\rho_i(t-\tau_i,0,x)$ after τ_i units of time. It is clear that the evolution follows the growth law given in (1) for the immature population.

Let $v(r, a, x) = \rho_1(a + r, a, x)$, where $r \geq 0$. Then the integration along characteristics argument induces that

$$\frac{\partial v(r, a, x)}{\partial a} = \left[\frac{\partial \rho_1(t, a, x)}{\partial t} + \frac{\partial \rho_1(t, a, x)}{\partial a}\right]_{t=a+r} = D_1 \Delta v(r, a, x) - d_1 v(r, a, x), \tag{3}$$

$$v(r, 0, x) = \rho_1(r, 0, x) = pf(M(r, x)).$$

Regarding r as a parameter and solving equation (3), we get

$$v(r, a, x) = pe^{-d_1 a} \int_\Omega \Gamma(D_1 a, x, y) f(M_1(r, y)) dy, \tag{4} \boxed{\text{v}}$$

where Γ is the Green function associated with the Laplacian operator Δ and the homogeneous Neumann boundary condition. Letting $r = t - \tau_1$, $a = \tau_1$ in (4), we get

$$\rho_1(t, \tau_1, x) = pe^{-d_1 \tau_1} \int_\Omega \Gamma(D_1 \tau_1, x, y) f(M(t - \tau_1, y)) dy, \ t \geq \tau_1.$$

Similarly, we have

$$\rho_2(t, \tau_2, x) = (1 - p)e^{-d_2 \tau_2} \int_\Omega \Gamma(D_2 \tau_2, x, y) f(M(t - \tau_2, y)) dy, \ t \geq \tau_2.$$

Substituting $\rho_i(t, \tau_i, x)$ to (2), we get the following time-delayed reaction-diffusion equations when $t \geq \max\{\tau_1, \tau_2\}$:

$$\frac{\partial M_1(t, x)}{\partial t} = D_M \Delta M_1(t, x) - (\mu + g(M(t, x))) M_1(t, x)$$
$$+ pe^{-d_1 \tau_1} \int_\Omega \Gamma(D_1 \tau_1, x, y) f(M(t - \tau_1, y)) dy, \ t \geq \tau_1,$$

and

$$\frac{\partial M_2(t, x)}{\partial t} = D_M \Delta M_2(t, x) - (\mu + g(M(t, x))) M_2(t, x)$$
$$+ (1 - p)e^{-d_2 \tau_2} \int_\Omega \Gamma(D_2 \tau_2, x, y) f(M(t - \tau_2, y)) dy, \ t \geq \tau_2.$$

Adding the above two equations together, we arrive at a scalar equation for the total adult population density $M(t, x) = M_1(t, x) + M_2(t, x)$:

$$\frac{\partial M(t, x)}{\partial t} = D_M \Delta M(t, x) - (\mu + g(M(t, x))) M(t, x)$$
$$+ pe^{-d_1 \tau_1} \int_\Omega \Gamma(D_1 \tau_1, x, y) f(M(t - \tau_1, y)) dy \tag{5}\boxed{\text{total}}$$
$$+ (1 - p)e^{-d_2 \tau_2} \int_\Omega \Gamma(D_2 \tau_2, x, y) f(M(t - \tau_2, y)) dy, \ t > 0, \ x \in \Omega$$

$$\frac{\partial M}{\partial n} = 0, \ t > 0, \ x \in \partial\Omega,$$
$$M(t, x) = \phi(t, x), \ -\tau \leq t \leq 0, \ x \in \Omega,$$

where $\tau := \max\{\tau_1, \tau_2\}$ and the initial population distribution is ϕ.

Various unimodal birth functions have been validated in population growth model to account the psychological effect on the reproduction of populations. For example,

the Ricker type function $f(N) = bNe^{-aN}$, $a > 0$, $b > 0$, has been widely used in the well-studied Nicholson's blowflies equations. The Beverton-Holt type function $f(N) = \frac{bN}{1+aN^m}$, $m > 1$ is also commonly used for Mackey-Glass models. Thus, throughout this work, we assume functions f and g satisfy the following assumption:

(A1) $f, g \in C^1(\mathbb{R}_+, \mathbb{R}_+)$, $f(0) = g(0) = 0 \leq f'(0)$. $f(N) > 0$ and $g'(N) \geq 0$ for $N > 0$. Moreover, there exists $N^* > 0$ such that $f'(N) > 0$ for $0 < N < N^*$, and $f'(N) \leq 0$ for $N \geq N^*$.

Motivated by common properties of Ricker and Beverton-Holt type functions, we further assume the following condition:

(A2) $\frac{f(N)}{N}$ is nonincreasing for $N > 0$, and $g(N)$ is strictly increasing for $N > 0$.

It is obvious that $M_0 \equiv 0$ is always a solution of (5). Moreover, solving the equation

$$\mathcal{G}(N) := (pe^{-d_1\tau_1} + (1-p)e^{-d_2\tau_2})f(N) - [\mu + g(N)]N = 0, \qquad (6) \boxed{\texttt{positive eq}}$$

we can easily see that (A1) and (A2) imply the existence and uniqueness of a positive constant solution M^* for (5) provided

$$(pe^{-d_1\tau_1} + (1-p)e^{-d_2\tau_2})f'(0) > \mu. \qquad (7) \boxed{\texttt{inequality}}$$

Remark 2.1. *N^* can be ∞ in (A1), and all related results hold by a slight change in the proof. The assumptions (A1) and (A2) can be relaxed and related analytical results will be discussed in the discussion section (section 6).*

3. Population establishment in a bounded domain

⟨sec:bounded⟩ In this section, we assume the domain Ω is bounded, and investigate whether or not a population can successfully establish in the habitat, with the help of a biologically meaningful index, the net reproduction number. Let $\mathcal{X} := C(\bar{\Omega}, \mathbb{R})$ be the space of continuous functions from $\bar{\Omega}$ to $\mathbb{R}$ with the usual supremum norm $\|\cdot\|_{\mathcal{X}}$. Define $\mathcal{X}_+ = C(\bar{\Omega}, \mathbb{R}_+)$, then $(\mathcal{X}, \mathcal{X}_+)$ is an ordered Banach space. For any $\phi, \psi \in \mathcal{X}$, we write $\phi \geq \psi$ provided $\phi - \psi \in \mathcal{X}_+$, $\phi > \psi$ if $\phi - \psi \in \mathcal{X}_+ \setminus \{0\}$, and $\phi \gg \psi$ if $\phi - \psi \in int\mathcal{X}_+$. Let $\mathcal{C} := C([-\tau, 0], \mathcal{X})$. For any $\phi \in \mathcal{C}$, we define $\|\phi\| = \max_{\theta \in [-\tau,0]} \|\phi(\theta)\|_{\mathcal{X}}$. Then $\mathcal{C}$ is a Banach space with the positive cone $\mathcal{C}_+ := \{\phi \in \mathcal{C} : \phi(\theta) \in \mathcal{X}_+, \forall \theta \in [-\tau, 0]\}$. Let $\mathcal{D} := C([-\tau, 0], \mathbb{R})$. For any $\bar{\phi} \in \mathcal{D}$, we can regard $\bar{\phi}$ as an element in $\mathcal{C}$ by defining $\phi(\theta, x) = \bar{\phi}(\theta)$, $\forall (\theta, x) \in [-\tau, 0] \times \Omega$. Similarly, we regard any $a \in \mathbb{R}$ as a constant function in $\mathcal{X}$ or $\mathcal{C}$. For $b \in \mathbb{R}_+$, let $\mathcal{X}_b := \{\phi \in \mathcal{X}_+ : 0 \leq \phi(x) \leq b, x \in \bar{\Omega}\}$ and $\mathcal{C}_b := C([-\tau, 0], \mathcal{X}_b)$.

For any $\phi \in \mathcal{C}_+$, we define $F: \mathcal{C}_+ \to \mathcal{X}_+$ by

$$F(\phi)(x) = -g(\phi(0, x))\phi(0, x) + pe^{-d_1\tau_1}\int_\Omega \Gamma(D_1\tau_1, x, y)f(\phi(-\tau_1, y))dy$$

$$+ (1-p)e^{-d_2\tau_2}\int_\Omega \Gamma(D_2\tau_2, x, y)f(\phi(-\tau_2, y))dy.$$

Then (5) can be written as

$$\frac{\partial u(t, x)}{\partial t} = D_M \Delta u(t, x) - \mu u(t, x) + F(u_t)(x), \forall t > 0, x \in \Omega, \tag{8} \boxed{\texttt{abstract}}$$

where $u_t \in \mathcal{C}$ is defined by

$$u_t(\theta, x) = u(t + \theta, x), \forall (\theta, x) \in [-\tau, 0] \times \bar{\Omega}.$$

Let $T(t) : \mathcal{X} \to \mathcal{X}, t \geq 0$ be the semigroup associated with $D_M \Delta - \mu$ and the Neumann boundary condition. For any $\phi \in \mathcal{X}, t \geq 0$, we have

$$T(t)\phi(x) = e^{-\mu t} \int_\Omega \Gamma(D_M t, x, y)\phi(y)dy.$$

Then (8) can be written as the following integral equation:

$$u(t, x) = T(t)u(0, \cdot)(x) + \int_0^t T(t - s)F(u_s)(x)ds, \ \forall t > 0. \tag{9} \boxed{\texttt{integral}}$$

A solution $u(t, x)$ of (9) is said to be a mild solution of (8). For any $\phi \in \mathcal{C}_+$, it is easy to observe that

$$\phi(0, x) + hF(\phi)(x) \geq \phi(0, x)(1 - hg(\phi(0, x))) \geq 0,$$

provided $h \in \mathbb{R}_+$ small enough. Thus, we have

$$\lim_{h \to 0^+} \frac{1}{h} d(\phi(0, x) + hF(\phi), \mathcal{C}_+) = 0.$$

Then the general theory for abstract integral equations given in [18, Theorem 1] implies that for any $\phi \in \mathcal{C}_+$, (9) admits a unique nonnegative and non-continuable mild solution $u(t, x; \phi)$ on $[0, \sigma_\phi)$ with $u(\theta, x) = \phi(\theta, x)$ for any $(\theta, x) \in [-\tau, 0] \times \bar{\Omega}$. Moreover, $u(t, x; \phi)$ is a classic solution of (5) for $t > \tau$. Furthermore, we have the global existence of solutions as follows.

⟨leone⟩ **Lemma 3.1.** *Assume (A1) and (A2) hold. Let $u(t, x; \phi)$ be the solution of (5) with initial data $\phi \in \mathcal{C}_+$, then there exists $M^+ > 0$ such that $\limsup_{t \to \infty} u(t, x; \phi) \leq M^+$. Thus, $u(t, x; \phi)$ exists globally with $\sigma_\phi = \infty$.*

Proof. In order to investigate the boundedness of $u(t, x; \phi)$, we first consider an auxiliary equation that (5) can be compared with. Let

$$f^+(N) = \begin{cases} f(N), & 0 \leq N \leq N^*, \\ f(N^*), & N > N^*. \end{cases}$$

We know that $f^+(N) \geq f(N)$ for all $N \geq 0$, and $f^+(N) = f(N)$ for $N \in [0, N^*]$. Then (5) is dominated by

$$\frac{\partial u(t, x)}{\partial t} = D_M \Delta u(t, x) - \mu u(t, x) + F^+(u_t)(x), \forall t > 0, x \in \Omega, \tag{10} \boxed{\texttt{upp}}$$

where $F^+ : \mathcal{C}_+ \to \mathcal{X}_+$ is defined by

$$F^+(\phi)(x) = -g(\phi(0,x))\phi(0,x) + pe^{-d_1\tau_1} \int_\Omega \Gamma(D_1\tau_1, x, y)f^+(\phi(-\tau_1, y))dy$$

$$+ (1-p)e^{-d_2\tau_2} \int_\Omega \Gamma(D_2\tau_2, x, y)f^+(\phi(-\tau_2, y))dy.$$

It is obvious that f^+ is nondecreasing on $[0, \infty)$, which implies that F^+ is quasi-monotone on $\mathcal{C}_+$ in the sense that $F^+(\phi_1) \geq F^+(\phi_2)$ provided $\phi_1 \geq \phi_2$ with $\phi_1(0) = \phi_2(0)$. Moreover, solving

$$[\mu + g(N)]N = (pe^{-d_1\tau_1} + (1-p)e^{-d_2\tau_2})f^+(N),$$

we know that (10) admits a unique positive constant solution M^+ if (7) holds.

Let $u^+(t,x;\phi)$ be the solution of (10) with initial function $\phi \in \mathcal{C}_+$, and $\Phi_t^+ : \mathcal{C}_+ \to \mathcal{C}_+$ be the associated solution semiflow. Then it follows from [18, Proposition 1] that Φ_t^+ is monotone, and the comparison principle holds for the upper and lower solutions of (10). Moreover, by similar arguments as used in the proof of Theorem 3.4 later, we can verify that Φ_t^+ is strongly subhomogeneous in $\mathcal{C}_+$. Let $V = \mathcal{C}_+$ in [31, Theorem 2.3.4]. We know that either $\lim_{t\to\infty} u^+(t,x;\phi) = 0$ or the unique positive equilibrium M^+ is globally attractive in the sense that $\lim_{t\to\infty} u^+(t,x;\phi) = M^+$ for any $\phi \in \mathcal{C}_+\backslash\{0\}$ uniformly for $x \in \bar\Omega$. For any $\phi \in \mathcal{C}_+$, the comparison principle implies that $0 \leq u(t,x;\phi) \leq u^+(t,x;\phi)$ for all $t \geq 0$ and $x \in \bar\Omega$. Then the above threshold result implies that either $\lim_{t\to\infty} u(t,x;\phi) = 0$ or $\limsup_{t\to\infty} u(t,x;\phi) \leq M^+$. Thus, the solution of (5) is ultimately bounded and $\sigma_\phi = \infty$. $\qquad\square$

Let $\Phi_t : \mathcal{C}_+ \to \mathcal{C}_+$ be the solution semiflow of (5), that is

$$\Phi_t(\phi)(\theta,x) = u(t+\theta, x; \phi), \forall t \geq 0, \theta \in [-\tau, 0], x \in \bar\Omega.$$

From Lemma 3.1, we know that $u(t,x) \equiv M^+$ is an upper solution of (5). Denote

$$\mathcal{C}_{M^+} := \{\phi \in \mathcal{C}_+ : M^+ \geq \phi(\theta,x) \geq 0, \theta \in [-\tau, 0], x \in \bar\Omega\}.$$

Then the comparison principle implies that $\mathcal{C}_{M^+}$ is positively invariant for Φ_t. In what follows, without loss of generality, it is sufficient for us to study the long time dynamics of (5) on $\mathcal{C}_{M^+}$.

Linearizing (5) at $M_0 \equiv 0$, we get the following linear time-delayed differential equation:

$$\frac{\partial w(t,x)}{\partial t} = D_M \Delta w(t,x) - \mu w(t,x) + pe^{-d_1\tau_1} f'(0) \int_\Omega \Gamma(D_1\tau_1, x, y)w(t-\tau_1, y)dy$$

$$+ (1-p)e^{-d_2\tau_2} f'(0) \int_\Omega \Gamma(D_2\tau_2, x, y)w(t-\tau_2, y)dy, \quad t \geq 0, \ x \in \Omega$$

$$\frac{\partial w}{\partial n} = \quad 0, \quad t > 0, \ x \in \partial\Omega. \qquad\qquad (11)\boxed{\texttt{lineartotal}}$$

Letting $w(t, x) = e^{\lambda t} \psi(x)$ in (11), we get the following eigenvalue problem:

$$\lambda \psi(x) = D_M \Delta \psi(x) - \mu \psi(x) + pe^{-d_1 \tau_1} f'(0) \int_\Omega \Gamma(D_1 \tau_1, x, y) \psi(y) dy e^{-\lambda \tau_1}$$

$$+ (1-p)e^{-d_2 \tau_2} f'(0) \int_\Omega \Gamma(D_2 \tau_2, x, y) \psi(y) dy e^{-\lambda \tau_2}, \quad t \geq 0, \ x \in \Omega$$

$$\frac{\partial \psi}{\partial n} = \quad 0, \quad t > 0, \ x \in \partial \Omega. \qquad (12) \boxed{\texttt{eigen}}$$

In order to analyze the eigenvalues of (12), we first consider the following linear equation:

$$\frac{\partial w(t, x)}{\partial t} = D_M \Delta w(t, x) - \mu w(t, x) + pf'(0)e^{-d_1 \tau_1} \int_\Omega \Gamma(D_1 \tau_1, x, y) w(t, y) dy$$

$$+ (1-p)f'(0)e^{-d_2 \tau_2} \int_\Omega \Gamma(D_2 \tau_2, x, y) w(t, y) dy, \quad t \geq 0, \ x \in \Omega$$

$$\frac{\partial w}{\partial n} = \quad 0, \quad t > 0, \ x \in \partial \Omega,$$

and the corresponding eigenvalue problem:

$$\lambda \psi(x) = D_M \Delta \psi(x) - \mu \psi(x) + pe^{-d_1 \tau_1} f'(0) \int_\Omega \Gamma(D_1 \tau_1, x, y) \psi(y) dy$$

$$+ (1-p)e^{-d_2 \tau_2} f'(0) \int_\Omega \Gamma(D_2 \tau_2, x, y) \psi(y) dy, \quad t \geq 0, \ x \in \Omega$$

$$\frac{\partial \psi}{\partial n} = \quad 0, \quad t > 0, \ x \in \partial \Omega. \qquad (13) \boxed{\texttt{eig}}$$

Using similar arguments as in [23, Theorem 7.6.1], we know that (13) admits a principle eigenvalue λ_0 with a positive eigenfunction. Moreover, by [24, Theorem 2.2], we have the following observations.

⟨le2⟩ **Lemma 3.2.** *The problem* (12) *admits a principle eigenvalue* λ_τ *with a strongly positive eigenfunction, and for any* $\tau > 0$, λ_τ *has the same sign as* λ_0.

Now we define the next generation operator for (5), which measures how many individuals will be averagely reproduced by initial newborns in their whole lifetime, without the density-dependent regulations. Suppose we introduce the initial newborns at time $t = 0$ with distribution $\phi(x)$. After evolution, the distribution of matured individuals at time $t = \tau_1$ is given by

$$pe^{-d_1 \tau_1} \int_\Omega \Gamma(D_1 \tau_1, x, y) \phi(y) dy,$$

then at time $t > \tau_1$, the distribution of these adults after death and dispersal is given by

$$T(t - \tau_1)[pe^{-d_1 \tau_1} \int_\Omega \Gamma(D_1 \tau_1, \cdot, y) \phi(y) dy](x).$$

Note that each adult averagely produces $f'(0)$ newborns per unit time, then the total individuals produced by these adults are given by

$$\int_{\tau_1}^\infty f'(0)T(t - \tau_1)[pe^{-d_1 \tau_1} \int_\Omega \Gamma(D_1 \tau_1, \cdot, y) \phi(y) dy](x) dt$$

$$= \int_0^\infty T(t)[pe^{-d_1 \tau_1} f'(0) \int_\Omega \Gamma(D_1 \tau_1, \cdot, y) \phi(y) dy](x) dt$$

Similarly, the total individuals produced by those adults matured at time $t = \tau_2$ are given by

$$\int_{\tau_2}^{\infty} f'(0)T(t-\tau_2)[(1-p)e^{-d_2\tau_2}\int_{\Omega}\Gamma(D_2\tau_2,\cdot,y)\phi(y)dy](x)dt$$

$$= \int_0^{\infty} T(t)[(1-p)e^{-d_2\tau_2}f'(0)\int_{\Omega}\Gamma(D_2\tau_2,\cdot,y)\phi(y)dy](x)dt.$$

For any $\psi \in \mathcal{X}$, we define positive linear operators G_1 and G_2 by

$$G_1(\psi)(x) := pe^{-d_1\tau_1}f'(0)\int_{\Omega}\Gamma(D_1\tau_1,x,y)\psi(y)dy,$$

$$G_2(\psi)(x) := (1-p)e^{-d_2\tau_2}f'(0)\int_{\Omega}\Gamma(D_2\tau_2,x,y)\psi(y)dy.$$

Then the next generation operator is defined by $L : \mathcal{X}_+ \to \mathcal{X}_+$ as

$$L(\phi) = \int_0^{\infty} T(t)[G_1(\phi)+G_2(\phi)]dt.$$

and the net reproduction number is defined as the spectral radius of L, that is

$$R_0 = r(L).$$

For any $a \in \mathbb{R}$, let $\bar{a}(\theta) = a$, $\theta \in [-\tau, 0]$. We define

$$\bar{L}(a) := L(\bar{a}) = \int_0^{\infty} T(t)[G_1(\bar{a})+G_2(\bar{a})]dt.$$

Using similar arguments as used in Lemma 2.1 and Theorem 2.3 in [26], we have the following observation.

⟨le3⟩ **Lemma 3.3.** *Let λ_0 be given in Lemma 3.2, then $R_0 - 1$ has the same sign as λ_0. Moreover,*

$$R_0 = r(\bar{L}) = \frac{(pe^{-d_1\tau_1}+(1-p)e^{-d_2\tau_2})f'(0)}{\mu}.$$

Then we have the following observations for the dynamics of (5) on the positively invariant set $\mathcal{C}_{M+}$.

⟨threone⟩ **Theorem 3.4.** *Assume (A1) and (A2) hold. Let $u(t,x;\phi)$ be the solution of (5) with initial function $\phi \in \mathcal{C}_{M+}$. Then the following statements are valid:*

(i) *If $R_0 < 1$, then $\lim_{t\to\infty} u(t,x;\phi) = 0$ for any $\phi \in \mathcal{C}_{M+}$ uniformly for $x \in \bar{\Omega}$.*

(ii) *If $R_0 > 1$ and $M^+ \leq N^*$, then the unique positive equilibrium M^* is globally attractive in $\mathcal{C}_{M+}$. That is, $\lim_{t\to\infty} u(t,x;\phi) = M^*$ for all $\phi \in \mathcal{C}_{M+}\backslash\{0\}$ uniformly for $x \in \bar{\Omega}$.*

(iii) *If $R_0 > 1$ and $M^+ > N^*$, then there exists $M^- > 0$ such that*

$$M^- \leq \liminf_{t\to\infty} u(t,x;\phi) \leq \limsup_{t\to\infty} u(t,x;\phi) \leq M^+$$

for any $\phi \in \mathcal{C}_{M+}\backslash\{0\}$ uniformly for $x \in \bar{\Omega}$. Moreover, if f is nondecreasing in $[0, M^+]$, then $\lim_{t\to\infty} u(t,x;\phi) = M^*$.

Proof. From Lemmas 3.2 and 3.3, we know that $R_0 < 1$ is equivalent to $\lambda_\tau < 0$, and there exists a positive function $\psi_0(x) > 0$, $\forall x \in \bar{\Omega}$ such that $v(t, x) = e^{\lambda_\tau t}\phi_0(x)$ is a solution of (11). Then for any $\phi \in \mathcal{C}_{M^+}$, there exists a positive real number l such that $\phi(t, \cdot) \le lv(t, \cdot)$ for any $t \in [-\tau, 0]$. From (A2), it is easy to observe that $f(N) \le f'(0)N$ for any $N > 0$. Thus, the equation (5) is linearly controlled by (11). The comparison principle implies that $u(t, x; \phi) \le le^{\lambda_\tau t}\phi_0(x)$ for any $t > 0$ and $x \in \bar{\Omega}$. Taking the limit $t \to \infty$ and using the condition $\lambda_\tau < 0$, the statement (i) holds.

If $R_0 > 1$ and $M^+ \le N^*$, we have $M^* = M^+$ due to the uniqueness of the positive equilibrium, which implies that the solution semiflow Φ_t is monotone on $\mathcal{C}_{M^+}$. In order to prove statements (ii), we first prove *for any $\phi \in \mathcal{C}_{M^+}\backslash\{0\}$, $u(t, x; \phi) > 0$ for any $t \ge \tau$, $x \in \bar{\Omega}$*. By the monotonicity of Φ_t on $\mathcal{C}_{M^+}$, we know that $u(t, x; \phi) \ge 0$ for any $t > 0$ and $x \in \bar{\Omega}$. Moreover, it follows from (9) that

$$u(t, x) = T(t)u(0, \cdot)(x) + \int_0^t T(t - s)F(u_s)(x)ds,$$

$$\ge T(t)u(0, \cdot)(x) - \int_0^t T(t - s)g(u(s, x))u(s, x)ds,$$

$$\ge T(t)u(0, \cdot)(x) - G\int_0^t T(t - s)u(s, x)ds,$$

where $G := \max_{0 \le N \le M^+}\{g(N) + Ng'(N)\}$. From the comparison principle, we know that $u(t, x) \ge w(t, x)$, where $w(t, x)$ is the solution of the following equation:

$$w(t, x) = T(t)u(0, \cdot)(x) - G\int_0^t T(t - s)w(s, x)ds.$$

After a simple verification, we know that $w(t, x) = e^{-Gt}T(t)u(0, x) > 0$ provided $u(0, \cdot) > 0$. In the case of $u(0, \cdot) \equiv 0$, we claim there exists $t_0 \in [0, \tau]$ such that $u(t_0, \cdot) > 0$. Suppose, by contradiction, that $u(t, \cdot) \equiv 0$ for all $t \in [0, \tau]$. Then we have

$$\int_0^t T(t - s)F(u_s)(x)ds = 0, \forall t \in [0, \tau],$$

which implies that $f(u(s - \tau_1, y)) = f(u(s - \tau_2, y)) \equiv 0$, $\forall s \in [0, \tau]$, $y \in \bar{\Omega}$. It follows from (A1) that $u(s - \tau_1, y) = u(s - \tau_2, y) = 0$ for any $s \in [0, \tau]$, $y \in \bar{\Omega}$. Then $\phi \equiv 0$, a contradiction. Using t_0 as the new initial time, we get $u(t, x) > 0$ for all $t > t_0$. Consequently, we have $u(t, x; \phi) > 0$ for all $t \ge \tau$, $x \in \bar{\Omega}$. Moreover, we can verify that Φ_t, $t \ge \tau$ is strongly subhomogeneous in the sense that $\Phi_t(\alpha\phi) \gg \alpha\Phi_t(\phi)$ for any $\phi \gg 0$ in $\mathcal{C}_{M^+}$ and $\alpha \in (0, 1)$. From (A1) and (A2), it is easy to check that $F(\cdot)$ is strongly subhomogeneous in the sense that $F(\alpha\phi) \gg \alpha F(\phi)$, $\forall \alpha \in (0, 1)$, $\phi \gg 0$. Then we have

$$\alpha u(t, x; \phi) < T(t)[\alpha u(0, \cdot)](x) + \int_0^t T(t - s)F(\alpha u_s)(x)ds, \ \forall t > 0.$$

Thus, $\alpha u(t, x; \phi)$ is a lower solution of (9) with $\alpha u(\theta, x; \phi) = \alpha\phi(\theta, x)$ for $(\theta, x) \in [-\tau, 0] \times \bar{\Omega}$. Then the comparison principle implies that $u(t, x; \alpha\phi) \ge \alpha u(t, x; \phi) > 0$ for

all $(t, x) \in [\tau, \infty) \times \bar{\Omega}$. Since $F(\cdot)$ is monotone and strongly subhomogeneous on $\mathcal{C}_{M^+}$, we have

$$u(t, x; \alpha\phi) - \alpha u(t, x; \phi) \geq \int_0^t T(t - s)[F(\alpha u_s) - \alpha F(u_s)](x)dx,$$

$$\geq \int_0^t T(t - s)[\alpha g(u(s, x))u(s, x) - \alpha g(\alpha u(s, x)u(s, x))]ds > 0$$

for any $t \geq \tau$. Thus, $u(t, x; \alpha\phi) > \alpha u(t, x; \phi)$ for all $t \geq \tau$, $x \in \bar{\Omega}$. That is, Φ_t is strongly subhomogeneous for $t \geq \tau$. Then statement (ii) is a direct consequence of [31, Theorem 2.3.4].

In the case of $R_0 > 1$ and $M^+ > N^*$, we observe that $N^* < M^* \leq M^+$. Thus, the solution semiflow Φ_t is not monotone in $\mathcal{C}_{M^+}$, and the comparison principle does not hold anymore. From the property of f in (A1), we know that there exists a unique $N_* \in (0, N^*]$ such that $f(N_*) = f(M^+)$. Now we define $f^- : \mathbb{R}_+ \to \mathbb{R}_+$ by

$$f^-(N) = \begin{cases} f(N), & 0 \leq N \leq N_*, \\ f(M^+), & N > N_*. \end{cases}$$

Then f^- is nondecreasing in $\mathbb{R}_+$, and satisfies

$$f^-(N) \leq f(N) \leq f^+(N), \forall N \in [0, M^+],$$

and

$$f^-(N) = f(N) = f^+(N), \forall N \in [0, N_*].$$

Consider the auxiliary equation

$$\frac{\partial u(t, x)}{\partial t} = D_M \Delta u(t, x) - \mu u(t, x) + F^-(u_t)(x), \forall t > 0, x \in \Omega, \qquad (14) \boxed{\text{low}}$$

where $F^- : \mathcal{C}_+ \to \mathcal{X}_+$ defined by

$$F^-(\phi)(x) = -g(\phi(0, x))\phi(0, x) + pe^{-d_1\tau_1} \int_\Omega \Gamma(D_1\tau_1, x, y)f^-(\phi(-\tau_1, y))dy$$

$$+ (1 - p)e^{-d_2\tau_2} \int_\Omega \Gamma(D_2\tau_2, x, y)f^-(\phi(-\tau_2, y))dy.$$

For any $\phi \in \mathcal{C}_{M^+}$, denote $u^-(t, x; \phi)$ as the solution of (14) with $u^-(0, \cdot) = \phi$. Then we have

$$u^-(t, x; \phi) \leq u(t, x; \phi) \leq u^+(t, x; \phi), \forall t \geq 0, x \in \Omega. \qquad (15) \boxed{\text{compare}}$$

If $R_0 > 1$, it is easy to observe that (14) admits a unique positive constant solution $M^- \in (N_*, M^*)$. Using similar arguments as those in the proof of statement (ii), we know that M^- is globally attractive for (14). Then (15) implies that statement (iii) holds. Moreover, if f is nondecreasing in $[0, M^+]$, then we have $M^* = M^\pm$, which implies that $\lim_{t \to \infty} u(t, x; \phi) = M^*$. $\qquad \square$

⟨lem:I⟩ **Remark 3.1.** *As the tick-borne pathogen transmission risk can be measured by the density of nymphs (DON) in some sense [14], it is interesting to probe the dynamics of $I(t, x) = I_1(t, x) + I_2(t, x) = \int_0^{\tau_1} \rho_1(t, a, x)da + \int_0^{\tau_2} \rho_2(t, a, x)da$. By using the asymptotic system and theories of chain transitive sets [31], as discussed in [1], we can obtain that (i) If $R_0 < 1$, then $\lim_{t \to \infty} I(t, x; \phi) = 0$; (ii) If $R_0 > 1$ and $M^+ \leq N^*$, then there is $I^* = \frac{pf(M^*)(1-e^{-d_1\tau_1})}{d_1} + \frac{(1-p)f(M^*)(1-e^{-d_2\tau_2})}{d_2}$ such that $\lim_{t \to \infty} I(t, x; \phi) = I^*$; (iii) If $R_0 > 1$, $M^+ > N^*$ and f is nondecreasing in $[0, M^+]$, then $\lim_{t \to \infty} I(t, x; \phi) = I^*$.*

4. Spreading speed and traveling waves

⟨sec:unbounded⟩ In this section, we will investigate the system in a one-dimensional unbounded spatial domain $\Omega = \mathbb{R}$ under the assumptions (A1)-(A2) and (7) ($R_0 > 1$). We are interested in the pattern and speed of population spreading, which can be characterized by the traveling waves and asymptotic spreading speed, respectively.

Let $\mathbb{Y} = C(\mathbb{R}, \mathbb{R})$ be the set of all bounded and continuous functions from $\mathbb{R}$ to $\mathbb{R}$ equipped with compact open topology and the corresponding norm

$$\| u \|_{\mathbb{Y}} = \sum_{n=0}^{\infty} \frac{\max_{|x| \leq n} |u(x)|}{2^n}, \quad \forall u \in \mathbb{Y}.$$

For any $\phi, \psi \in \mathbb{Y}$, we can define $\phi \geq, >, \gg \psi$ with respect to the positive cone $\mathbb{Y}_+ = \{\phi \in \mathbb{Y} : \phi(x) \geq 0, \forall x \in \mathbb{R}\}$. Let $\mathbb{C} = C([-\tau, 0], \mathbb{Y})$, $\mathbb{C}_+ = C([-\tau, 0], \mathbb{Y}_+)$, $\mathbb{D} := C([-\tau, 0], \mathbb{R})$, and $\mathbb{D}_+ = C([-\tau, 0], \mathbb{R}_+)$. Then orders $\geq, >, \gg$ in $\mathcal{C}$ can be defined with the positive cone $\mathbb{C}_+$, and the norm is defined as $\|\phi\| = \max_{\theta \in [-\tau, 0]} \|\phi(\theta)\|_{\mathbb{Y}}, \forall \phi \in \mathbb{C}$. For any $a, b \in \mathbb{R}$ with $a \leq b$, we introduce $[a, b]_{\mathbb{C}} := \{\psi \in \mathbb{C} : b \geq \psi \geq a\}$. Clearly, any function in $\mathbb{D}$ can be regarded as an element in $\mathbb{C}$. Also, for any constant $a \in \mathbb{R}$, we can regard a as a constant function in $\mathbb{Y}, \mathbb{C}$, or $\mathbb{D}$.

Now we study the following delay differential equation for mature individuals:

$$\frac{\partial u(t, x)}{\partial t} = D_M \frac{\partial^2 u}{\partial x^2}(t, x) - \mu u(t, x) + F(u_t)(x), \forall t > 0, x \in \mathbb{R}, \tag{16}$$ `spr`

where

$$F(\phi)(x) = -g(\phi(0, x))\phi(0, x) + pe^{-d_1\tau_1} \int_{\mathbb{R}} \Gamma(D_1\tau_1, x - y)f(\phi(-\tau_1, y))dy$$

$$+ (1 - p)e^{-d_2\tau_2} \int_{\mathbb{R}} \Gamma(D_2\tau_2, x - y)f(\phi(-\tau_2, y))dy, \forall \phi \in \mathbb{C}_+,$$

and

$$\Gamma(t, z) = \frac{e^{\frac{-z^2}{4t}}}{\sqrt{4\pi t}}, \forall t > 0, z \in \mathbb{R}.$$

For any $\phi \in \mathbb{Y}_+$, define $\Upsilon(t) : \mathbb{Y}_+ \to \mathbb{Y}_+$ by

$$\Upsilon(t)\phi(x) = e^{-\mu t} \int_{\mathbb{R}} \frac{e^{\frac{-(x-y)^2}{4D_M t}}}{\sqrt{4\pi D_M t}} \phi(y)dy.$$

Then the corresponding integral equation of (16) is given by:

$$u(t,x) = \Upsilon(t)u(0,\cdot)(x) + \int_0^t \Upsilon(t-s)F(u_s)(x)ds, \ \forall t > 0, \ x \in \mathbb{R}. \qquad (17) \boxed{\texttt{sprintegral}}$$

Using similar arguments as those in the last section, we obtain that for any $\phi \in \mathbb{C}_+$, equation (17) admits a unique nonnegative mild solution $u(t,x;\phi)$ for $t \in [0,\infty)$, and $u(t,x;\phi)$ is a classic solution of (16) for $t > \tau$. Let Q_t be the solution semiflow of (16) in $\mathbb{C}_+$, that is

$$Q_t(\phi)(\theta,x) = u(t+\theta,x;\phi), \forall \phi \in \mathbb{C}_+, \theta \in [-\tau,0], x \in \mathbb{R}.$$

Denote

$$\mathbb{C}_{M^+} := \{\psi \in \mathbb{C} : M^+ \geq \psi(\theta,x) \geq 0, \theta \in [-\tau,0], x \in \mathbb{R}\}.$$

It is easy to observe that Q_t is positively invariant in $\mathbb{C}_{M^+}$. Let $\bar{Q}_t$ be the restriction of Q_t to $\mathbb{D}_{M^+}$, then $\bar{Q}_t$ is the solution semiflow of the following ordinary delay differential equation:

$$\frac{du(t)}{dt} = -\mu u(t) + \bar{F}(u_t), \forall t > 0, \qquad (18) \boxed{\texttt{sprode}}$$

where $\bar{F}$ is the restriction of F on $\mathbb{D}_{M^+}$, and defined by

$$\bar{F}(\phi) = -g(\phi(0))\phi(0) + pe^{-d_1\tau_1}f(\phi(-\tau_1)) + (1-p)e^{-d_2\tau_2}f(\phi(-\tau_2)).$$

Similar to the different scenarios in Theorem 3.4, we will discuss different cases, case I $(M^+ \leq N^*)$ and case II $(M^+ > N^*)$ in the following subsections.

4.1. Case I: $M^+ \leq N^*$

From Theorem 3.4 (ii), we know that if $R_0 > 1$ and $M^+ \leq N^*$, then $M^* = M^+$, and Q_t is order preserving in $\mathbb{C}_{M^+}$. Moreover, (18) admits only two constant equilibria 0 and M^+, and M^+ attracts any nonnegative solution of (18) in $\mathbb{D}_{M^+}$. For any $\phi \in \mathbb{C}_{M^+}$, we define the reflection operator $R(\phi)(\theta,x) := \phi(\theta,-x)$. For any $y \in \mathbb{R}$, we define the translation operator $T_y : \mathbb{C}_{M^+} \to \mathbb{C}_{M^+}$ by $T_y(\phi)(\theta,x) := \phi(\theta,x-y)$. Then we have the following observations for the solution semiflow Q_t in $\mathbb{C}_{M^+}$.

⟨monole⟩ **Lemma 4.1.** *Assume (A1), (A2), and $M^+ \leq N^*$. Then $Q_t : \mathbb{C}_{M^+} \to \mathbb{C}_{M^+}$ admits the following properties:*

(B1) $R[Q_t(\phi)] = Q_t[R(\phi)]$, $T_y[Q_t(\phi)] = Q_t[T_y(\phi)]$, $\forall y \in \mathbb{R}, \phi \in \mathbb{C}_{M^+}$;

(B2) Q_t *is continuous with respect to the compact open topology;*

(B3) Q_t *is order preserving in $\mathbb{C}_{M^+}$ in the sense that $Q_t(\phi) \geq Q_t(\psi)$ provided $\phi \geq \psi$ in $\mathbb{C}_{M^+}$;*

(B4) $\bar{Q}_t$ *admits only two fixed points 0 and M^+ in $\mathbb{D}_{M^+}$, and for any $\epsilon > 0$, there exists $\phi \in \mathbb{C}_{M^+}$ with $\| \phi \| < \epsilon$ such that $\bar{Q}_t(\phi) \gg \phi$;*

(B5) *One of the following two conditions holds:*

    (a) $Q_t[\mathbb{C}_{M^+}]$ *is precompact in $\mathbb{C}_{M^+}$;*

(b) *There exists a nonnegative number $\varsigma_t < \tau$ such that $Q_t[\phi] = \phi(\theta + \varsigma_t, x)$ for $-\tau \le \theta < -\varsigma_t$, and the operator*

$$S_t[\phi](\theta, x) := \begin{cases} \phi(0, x), & -\tau \le \theta < -\varsigma_t; \\ Q_t[\phi](\theta, x), & -\varsigma_t \le \theta \le 0, \end{cases}$$

is continuous on $\mathbb{C}_{M^+}$, and $S_t[\mathbb{C}_{M^+}]$ is precompact in $\mathbb{C}_{M^+}$.

(B6) *Q_t is subhomogenerous in the sense that $Q_t(\alpha\phi) \ge \alpha Q_t(\phi), \forall \alpha \in [0,1]$ and $\phi \in \mathbb{C}_{M^+}$.*

Proof. Since the coefficients of (16) are time and location independent, we can verify that both $u(t, -x)$ and $u(t, x - y), \forall y \in \mathbb{R}$, satisfy equation (16) if $u(t, x)$ is a solution of (16). Thus, the property (B1) holds. It follows from the continuity of solutions for initial values with respect to the compact open topology that (B2) holds. (B3) is a direct consequence of the comparison principle for the monotone delay differential system. It is obvious that $\bar{Q}_t$ admits only two fixed points 0 and M^+ in $\mathbb{C}_{M^+}$. Moreover, [23, Corollary 5.3.5] implies that $\bar{Q}_t$ is eventually strongly monotone. Then Dance-Hess connecting orbit lemma in [31] implies that $\bar{Q}_t$ admits a strongly monotone entire orbit connecting 0 and M^+. Thus (B4) holds. Using similar arguments as in [12, Section 5.1], we can verify that (B5)(a) becomes valid for $t \ge \tau$, and (B5)(b) holds with $\varsigma_t = t$ for $t \in (0, \tau)$. For any $\alpha \in [0, 1]$ and $\phi \in \mathbb{C}_{M^+}$, the subhomogeneity of F in $\mathbb{C}_{M^+}$ implies that

$$\alpha u(t, x; \phi) \le \Upsilon(t)\alpha u(0, \cdot)(x) + \int_0^t \Upsilon(t - s)F(\alpha u_s)(x)ds, \ \forall t > 0, \ x \in \mathbb{R}.$$

Thus, $\alpha u(t, x; \phi)$ is a lower solution of (16). Then the comparison principle implies that (B6) holds. $\square$

Based on Lemma 4.1, the general theory developed in [12] for monotone dynamical systems implies that there exists a positive number $c^* > 0$ such that c^* is the spreading speed of (16), and c^* is also the minimum wave speed for monotone traveling waves of (16) connecting 0 and M^*. We summarize the results as follows.

⟨spreading⟩ **Theorem 4.2.** *Assume (A1), (A2) and $R_0 > 1$ hold, and $M^+ \le N^*$. Let $u(t, x, \phi)$ be the unique solution of (16) with the initial data $\phi \in \mathbb{C}_{M^+}$. Then the following statements are valid:*

(i) *For any $c > c^*$, if $\phi \in \mathbb{C}_{M^+}$ has a compact support, then*

$$\lim_{t \to \infty, |x| \ge ct} u(t, x; \phi) = 0.$$

For any $c \in (0, c^*)$, $\lim_{t \to \infty, |x| \le ct} u(t, x; \phi) = M^*$ for any $\phi \in \mathbb{C}_{M^+} \setminus \{0\}$.

(ii) *For any $c \ge c^*$, (16) has a nondecreasing traveling wave solution $U(x + ct)$ such that $U(-\infty) = 0$ and $U(+\infty) = M^*$. Moreover, for any $c \in (0, c^*)$, (16) has no traveling wave $U(x + ct)$ connecting 0 to M^*.*

In order to characterize c^*, we consider the following linearization of (16) at $u \equiv 0$:

$$\frac{\partial u(t,x)}{\partial t} = D_M \frac{\partial^2 u}{\partial x^2} u(t,x) - \mu u(t,x) + pe^{-d_1\tau_1} f'(0) \int_{\mathbb{R}} \Gamma(D_1\tau_1, x-y) u(t-\tau_1, y) dy$$

$$+ (1-p)e^{-d_2\tau_2} f'(0) \int_{\mathbb{R}} \Gamma(D_2\tau_2, x-y) u(t-\tau_2, y) dy, \quad t \geq 0, \ x \in \mathbb{R}. \quad (19) \boxed{\texttt{linspr}}$$

Since $f'(0) > 0$ and $f(N) \leq f'(0)N$, $\forall N \geq 0$ in (A2), it follows that (16) satisfies the linear determinacy condition (F3) in [12, Section 5.1]. Let $u(t,x) = e^{\nu x} w(t)$, $\nu > 0$ be the solution of (19), we get the following equation:

$$\frac{dw(t)}{dt} = (D_M\nu^2 - \mu)w(t) + pe^{-d_1\tau_1}f'(0)\gamma_1(\nu)w(t-\tau_1)$$

$$+ (1-p)e^{-d_2\tau_2}f'(0)\gamma_2(\nu)w(t-\tau_2), \quad (20) \boxed{\texttt{eqnu}}$$

where

$$\gamma_1(\nu) := \int_{\mathbb{R}} \Gamma(D_1\tau_1, y)e^{\nu y} dy, \quad \gamma_2(\nu) := \int_{\mathbb{R}} \Gamma(D_2\tau_2, y)e^{\nu y} dy.$$

Note that Γ is the Green function with respect to the Laplacian operator Δ, then we calculate that

$$\gamma_1(\nu) = e^{D_1\tau_1\nu^2}, \quad \gamma_2(\nu) = e^{D_2\tau_2\nu^2}.$$

Clearly, (20) is cooperative and irreducible (see [23, Section 5.3]). Then its characteristic equation

$$\lambda = D_M\nu^2 - \mu + pe^{-d_1\tau_1}f'(0)\gamma_1(\nu)e^{-\lambda\tau_1} + (1-p)e^{-d_2\tau_2}f'(0)\gamma_2(\nu)e^{-\lambda\tau_2}$$

admits a principal eigenvalue $\lambda(\nu)$, which is real and greater than the real parts of all other roots. Since $\gamma_i(\nu) > 1$, $i = 1, 2$ and $R_0 > 1$, a proof by contradiction implies that $\lambda(\nu) > 0$ for all $\nu \geq 0$. Following the idea in [12], we introduce function

$$\Psi(\nu) := \frac{\lambda(\nu)}{\nu}, \quad \forall \nu > 0.$$

Then we have $\lim_{\nu \to 0^+} \Psi(\nu) = \lim_{\nu \to +\infty} \Psi(\nu) = +\infty$ due to $\lambda(\nu) > D_M\nu^2 - \mu$. From [12, Lemma 3.8], we know that $\Psi(\nu)$ attains its minimum at some $\nu^* \in (0, \infty)$, then [12, Theorem 3.10] implies that

$$c^* = \Psi(\nu^*) := \inf_{\nu > 0} \Psi(\nu).$$

Moreover, from the property of $\Psi(\nu)$, we know that (c^*, ν^*) is the unique point such that

$$c^* = \Psi(\nu^*) \text{ and } \frac{\partial \Psi(\nu)}{\partial \nu}\Big|_{\nu^*} = 0.$$

Let

$$P(c, \nu) := D_M\nu^2 - c\nu - \mu + pe^{-d_1\tau_1}f'(0)\gamma_1(\nu)e^{-\nu c\tau_1} + (1-p)e^{-d_2\tau_2}f'(0)\gamma_2(\nu)e^{-\nu c\tau_2}.$$

Then we have the following result on the spreading speed c^*:

⟨cstarle⟩ **Lemma 4.3.** *If $R_0 > 1$, then the following statements are valid:*

(i) *(c^*, ν^*) is uniquely determined by $P(c, \nu) = 0$ and $\frac{\partial P(c,\nu)}{\partial \nu} = 0$.*

(ii) If $c > c^*$, $P(c, \nu) = 0$ admits two positive real roots $\nu_1(c) < \nu^* < \nu_2(c)$ such that

$$P(c, \nu) < 0, \quad \forall \nu \in (\nu_1(c), \nu_2(c)), \quad P(c, \nu) > 0, \quad \forall \nu \in \mathbb{R} \setminus [\nu_1(c), \nu_2(c)].$$

(iii) If $c < c^*$, then $P(c, \nu) > 0$ for any $\nu \in \mathbb{R}_+$.

4.2. Case II: $M^+ > N^*$

In this scenario, (16) may not be monotone in $\mathbb{C}_{M^+}$, and thus the theories and methods for monotone dynamical systems, as used in the previous subsection, becomes invalid directly. In order to establish the existence of spreading speed and traveling waves, we employ the sandwich arguments for which two auxiliary equations are used to compare (16) with. For that purpose, we introduce two auxiliary equations:

$$\frac{\partial u(t, x)}{\partial t} = D_M \Delta u(t, x) - \mu u(t, x) + F^+(u_t)(x), \forall t > 0, x \in \mathbb{R}, \qquad (21) \boxed{\texttt{uppr}}$$

and

$$\frac{\partial u(t, x)}{\partial t} = D_M \Delta u(t, x) - \mu u(t, x) + F^-(u_t)(x), \forall t > 0, x \in \mathbb{R}, \qquad (22) \boxed{\texttt{lowr}}$$

where F^+ and F^- are defined as in Section 3. Using these two equations, the following result can be established.

⟨unspr⟩ **Theorem 4.4.** *Assume (A1), (A2) and $R_0 > 1$ hold, and $M^+ > N^*$. Then there exists the spreading speed c^* of (16) in the following sense:*

(i) For any $c > c^*$, if $\phi \in \mathbb{C}_{M^+}$ has a compact support, then

$$\lim_{t \to \infty, |x| \geq ct} u(t, x; \phi) = 0.$$

(ii) For any $c \in (0, c^*)$, if $\phi \in \mathbb{C}_{M^+} \setminus \{0\}$, then

$$M^- \leq \liminf_{t \to \infty, |x| \leq ct} u(t, x; \phi) \leq \limsup_{t \to \infty, |x| \leq ct} u(t, x; \phi) \leq M^+.$$

Moreover, if f is nondecreasing on $[0, M^+]$, then $\lim\limits_{t \to \infty, |x| \leq ct} u(t, x; \phi) = M^*$.

Proof. Let $u^+(t, x; \phi)$ and $u^-(t, x; \phi)$ be the solutions of (21) and (22) with initial distribution $\phi \in \mathbb{C}_{M^+}$ respectively. From the construction of $F^\pm$, we know that equations (21) and (22) are monotone and satisfy Lemma 4.1 in $\mathbb{C}_{M^+}$. Moreover, it follows from the comparison principle that

$$u^-(t, x; \phi) \leq u(t, x; \phi) \leq u^+(t, x; \phi), \quad \forall t > 0, \ x \in \mathbb{R}.$$

Note that equations (16), (21) and (22) have the same linearization at $u \equiv 0$. Then (21) and (22) admit the same spreading speed c^* in the sense as given in Theorem 4.2 with $u(t, x; \phi)$ and M^* replaced by $u^\pm(t, x; \phi)$ and $M^\pm$, respetively. Therefore, the result is easily verified by the comparison principle. Moreover, if f is nondecreasing on $[0, M^+]$, then we have $M^\pm = M^*$, which implies that $\lim\limits_{t \to \infty, |x| \leq ct} u(t, x; \phi) = M^*$ for any $\phi \in \mathbb{C}_{M^+} \setminus \{0\}$. $\qquad \square$

In order to study the existence of traveling waves, other suitable upper and lower solutions should be constructed. Here, we further propose the following assumption.

(A3) There exists $\delta \in (0, M^+]$, $\rho > 0$, and $\sigma > 1$ such that $f(N) \geq f'(0)N - \rho N^\sigma$ for any $N \in [0, \delta]$.

This s a technical assumption, however, it is a weak one. For example, if the birth rate function f is twice differentiable at zero, then this assumption naturally holds.

Substituting $u(x, t) = U(\xi)$ with $\xi = x + ct$ into (16), we get the following wave equation:

$$D_M U''(\xi) - cU'(\xi) - \mu U(\xi) - g(U(\xi))U(\xi) + H(U)(\xi) = 0, \qquad (23)\ \boxed{\texttt{waveeq}}$$

where

$$H(U)(\xi) = pe^{-d_1\tau_1} \int_\mathbb{R} \Gamma(D_1\tau_1, y)f(U(\xi - y - c\tau_1))dy$$

$$+ (1 - p)e^{-d_2\tau_2} \int_\mathbb{R} \Gamma(D_2\tau_2, y)f(U(\xi - y - c\tau_2))dy.$$

Similarly, we can get the following wave equations for (21) and (22):

$$D_M U''(\xi) - cU'(\xi) - \mu U(\xi) - g(U(\xi))U(\xi) + H^+(U)(\xi) = 0, \qquad (24)\ \boxed{\texttt{waveequpp}}$$

and

$$D_M U''(\xi) - cU'(\xi) - \mu U(\xi) - g(U(\xi))U(\xi) + H^-(U)(\xi) = 0, \qquad (25)\ \boxed{\texttt{waveeqlow}}$$

where H^+ and H^- are defined by replacing f with f^+ and f^- in the formula of H, respectively. Then we establish the following result on the existence of traveling wave solutions.

$\langle\texttt{thm:TWS}\rangle$
Theorem 4.5. *Assume (A1)-(A3) and $R_0 > 1$ hold, and $M^+ > N^*$. Then the following statements are valid:*

(i) *For any $c > c^*$, (16) has a traveling wave solution $U(x + ct)$ such that $U(-\infty) = 0$ and*

$$M^- \leq \liminf_{\xi \to \infty} U(\xi) \leq \limsup_{\xi \to \infty} U(\xi) \leq M^+.$$

Moreover, if f is nondecreasing on $[0, M^+]$, then $\lim_{\xi \to \infty} U(\xi) = M^*$.

(ii) *For any $c \in (0, c^*)$, (16) has no traveling wave $U(x + ct)$ connecting 0 to M^*.*

Proof. For $c > c^*$, we first prove (i) in the case that f is nondecreasing in $[0, M^+]$. From (A1), we know that $f(N) \equiv f(N^*)$ for any $N \in [N^*, M^+]$ and $M^\pm = M^*$. Then the equation (16) is monotone in $\mathbb{C}_{M^+}$. Let $\nu_1 := \nu_1(c)$ be given in Lemma 4.3, and $\varepsilon > 0$ small enough such that $P(c, \nu_1 + \varepsilon) < 0$. Then for any $\varrho \in (0, \delta)$, we can verify $(\bar\psi, \underline\psi)$ with

$$\bar\psi(\xi) := \min\{M^*, \varrho e^{\nu_1 \xi}\}, \quad \underline\psi(\xi) := \max\{0, \varrho e^{\nu_1 \xi}(1 - Le^{\varepsilon\xi})\},$$

is a pair of upper and lower solutions of (23) provided constant $L > 1$ is large enough. Following the procedure similar to the proof of [16, Lemma 2.3], we can see that for

any $c > c^*$, (23) admits a nondecreasing traveling wave solution $U(x + ct)$ satisfying $U(+\infty) = M^*$ and

$$\lim_{\xi \to -\infty} U(\xi)e^{-\nu_1 \xi} = \varrho.$$

If there exists $N_0 \in [N^*, M^+]$ such that $f(N) \neq f(N^*)$, then (A1) implies $M^+ > M^* \geq M^-$. Define

$$\bar{\psi}^+(\xi) := \min\{M^+, \varrho e^{\nu_1 \xi}\}, \quad \bar{\psi}^-(\xi) := \min\{M^-, \varrho e^{\nu_1 \xi}\}.$$

Then we can verify that $(\bar{\psi}^+, \underline{\psi})$, $(\bar{\psi}^-, \underline{\psi})$ are pairs of upper-lower solutions of (24) and (25), respectively. It follows from similar arguments as used above that (24) and (25) admit nondecreasing traveling waves $U^\pm(\xi)$ such that $U^\pm(+\infty) = M^\pm$. Moreover, we have

$$\lim_{\xi \to -\infty} U^+(\xi)e^{-\nu_1 \xi} = \lim_{\xi \to -\infty} U^-(\xi)e^{-\nu_1 \xi} = \varrho.$$

Since $M^+ > M^-$, there exists $l_1 > 0$ such that $U^+(\xi) > U^-(\xi)$ for any $\xi > l_1$. Taking $\xi_0 > 0$ such that $e^{\nu_1 \xi_0} > 2$, then we have

$$\lim_{\xi \to -\infty} U^+(\xi + \xi_0)e^{-\nu_1 \xi} = \varrho e^{\nu_1 \xi_0} > 2\varrho > \lim_{\xi \to -\infty} U^-(\xi)e^{-\nu_1 \xi}.$$

Therefore, there exists $l_2 > 0$ such that $U^+(\xi + \xi_0) > U^-(\xi)$ for any $\xi < -l_2$. It follows from the monotonicity of $U^\pm$ that there exists $\xi^* > 0$ large enough such that

$$U^+(\xi + \xi^*) > U^-(\xi), \ \forall \xi \in \mathbb{R}.$$

Then standard Schauder's fixed point arguments as used in the proof of [16, Theorem 1.1] show that (23) admits a traveling wave $U(\xi)$ such that

$$U^+(\xi + \xi^*) \geq U(\xi) \geq U^-(\xi), \forall \xi \in \mathbb{R},$$

which implies statement (i) holds.

For the proof of statement (ii), we can use an argument by contradiction as used in [10] and [5]. Suppose there exists a traveling wave $U(x + c_1 t)$ with some speed $c_1 \in (0, c^*)$ such that $U(-\infty) = 0$. Then by Theorem 4.4 (ii), we know that

$$\liminf_{t \to \infty, |x| \leq ct} U(x + c_1 t) \geq M^-, \ \forall c \in (0, c^*). \tag{26}$$ `contrad`

Taking $c_2 \in (c_1, c^*)$, and letting $x = -c_2 t$ in (26), we have

$$0 = \liminf_{t \to \infty} U((c_1 - c_2)t) \geq M^- > 0,$$

which is a contradiction. This completes the proof. $\qquad\square$

5. Numerical simulations

⟨sec:num⟩ For numerical simulations, we choose parameter values with the justifications from the tick ecology literatures [4, 19]. We would like to mention that this is just for illustrative purpose, as the tick ecology is more complicated, for example, we may need to consider the attaching and detaching processes as ticks can only diffuse with the help of host movement [30]. Unlike the usual sense, here we assume $I(t, x)$ in the model represents the density of feeding nymphs. We first assume a Ricker birth function $f(N) = rNe^{-\sigma N}$ for egg production and the density-dependent death rate $g(N) = \beta N$. Here $r = f'(0) > 0$ is the maximal egg number that an adult can produce per unit time, rescaled by multiplying with the survival probability of eggs to feeding nymphs, $\sigma > 0$ and $\beta > 0$ indicate the strength of the density dependence regulations in the birth and death rates. It is easy to check that assumptions (A1)-(A3) hold with $N^* = \frac{1}{\sigma}$. After some calculations, we know that $f(N^*) = \frac{r}{\sigma e}$ and the net reproduction number is

$$R_0 = \frac{(pe^{-d_1\tau_1} + (1-p)e^{-d_2\tau_2})r}{\mu}.$$

Then Theorem 3.4 implies that if $R_0 < 1$, then the population will eventually die out. If $R_0 > 1$, then (5) admits a unique positive equilibrium M^* satisfying

$$\mu + \beta M^* = (pe^{-d_1\tau_1} + (1-p)e^{-d_2\tau_2})re^{-\sigma M^*}.$$

Moreover, the population is strongly uniform persistent when the domain is bounded, and the spreading speed and traveling waves exist in an unbounded domain (Theorem 4.2, Threorem 4.4 and Theorem 4.5).

As there are three pre-mature tick stages, egg, larva and nymph, we need to rescale the parameters from experimental and observational studies. We set the first stage to be feeding nymph stage, which can be regarded as development from eggs reproduced by the second stage. Using the egg reproduction rate 3000 with no density-dependent self regulation, multiplied with the survival probabilities for those eggs surving to the feeding nymphs, r is set to be 2.4007 day^{-1} [4, 19] on tick population growth. The developmental delays τ_1 and τ_2 can be taken from a very wide interval, highly dependent on the abiotic factors such as temperature and photoperiodic exposure [2, 9]. For example, references [2, 4, 19] indicate that τ_1 and τ_2 can assume values in intervals [50 day, 360 day] or [63 day, 220 day]. In simulations, we set maturation delays with development diapause and no development diapause for nymphal *Ixodes scapularis* to be $\tau_1 = 100$ days and $\tau_2 = 220$ days [2, 4, 19], respectively. The average death rate for nymphs with short development duration is assumed to be $d_1 = 0.02$ day^{-1}. The death rate for feeding adults is assumed to be $\mu = 0.5$ per day. We assume parameters for the strength of negative feedback are $\beta = 0.001$ and $\sigma = 0.001$. Ticks diffuses when they are attaching on the hosts and we ignore the movement by themselves. On the other side, adult ticks prefer to feed on white-tailed deers while immature ticks normally feed on small mammals. The study [8] estimated that the diffusion rate for the short-tailed cane mouse in the study location is 200 ± 50 m^2 per day. In the simulation, we choose $D_1 = D_2 = 200$ m^2 per day. The

groups of deer display broad variations in movement behaviour and it is estimated in [21] that the diffusion rate for a deer group is 1.3362 m^2 per minute, which induces $D_M = 1924$ m^2 per day.

To distinguish the developmental strategy an individual will take, we choose a variable p values to illustrate different proportion allocations for the diapause strategy driven by the environmental conditions such as temperature and photoperiodic exposure [9]. To the best of our knowledge, there is no study on the death rates for the nymphs with development diapause, and in our simulations, we may illustratively assume reasonable values to represent different evolutionary benefits/costs for the development delay.

We first validate theoretical results with numerical simulations. As there are few biological studies on the exact values for the death rate d_2 and proportion $1 - p$ of the nymphs with delayed development, we may perform the uncertainty analysis on these two parameters later. First, we assume that $d_2 = d_1/10$ and $p = 0.6$. In this case, $R_0 = 1.6268 > 1$ and $M^* = 179.642$. However, if we choose $p = 0.9$, then $R_0 = 0.894 < 1$. Figure 1 shows solution evolution of the model in a bounded domain through the initial value $M(0, x) = 20 - \cos(2x)$, $x \in \bar{\Omega} = [0, \pi]$, with different p values, corresponding to two scenarios $R_0 > 1$ and $R_0 < 1$, respectively.


(a)   (b)
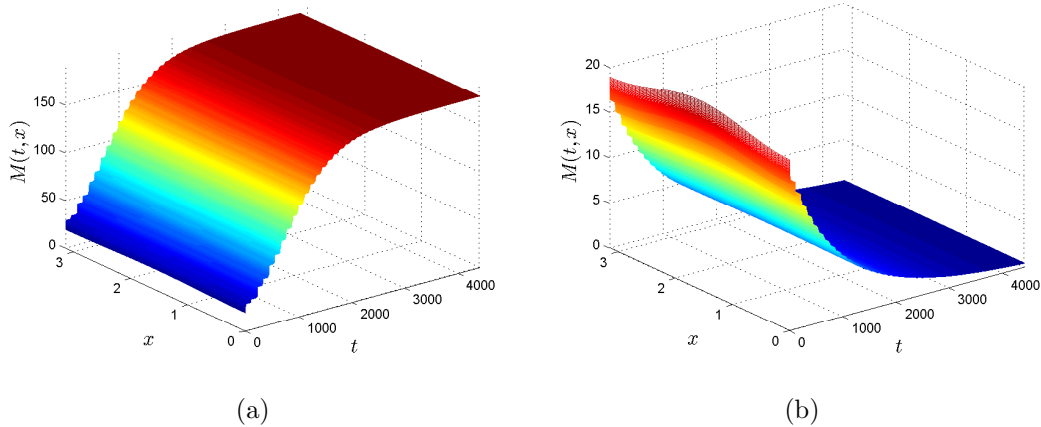
Figure 1. The evolution of M with $p = 0.6$ ($R_0 > 1$) and $p = 0.9$ ($R_0 < 1$), respectively.

fig:bd-mature⟩

Setting $p = 0.6$, then the species can establish in a bounded habitat. In this case, we further simulate the spreading of the adults in an unbounded domain, by truncating the infinite domain $\mathbb{R}$ to finite domain $[-L, L]$, with a large $L = 40$ and the initial data

$$M(0, x) = \begin{cases} 0, & |x| \geq 20; \\ 100 + 10 \times (|x| + 10), & 10 \leq |x| \leq 20; \\ 100, & |x| \leq 10. \end{cases}$$

The spreading of $M(t, x)$ as well as the traveling wave profiles are illustrated in Figure 2.

(a) (b)
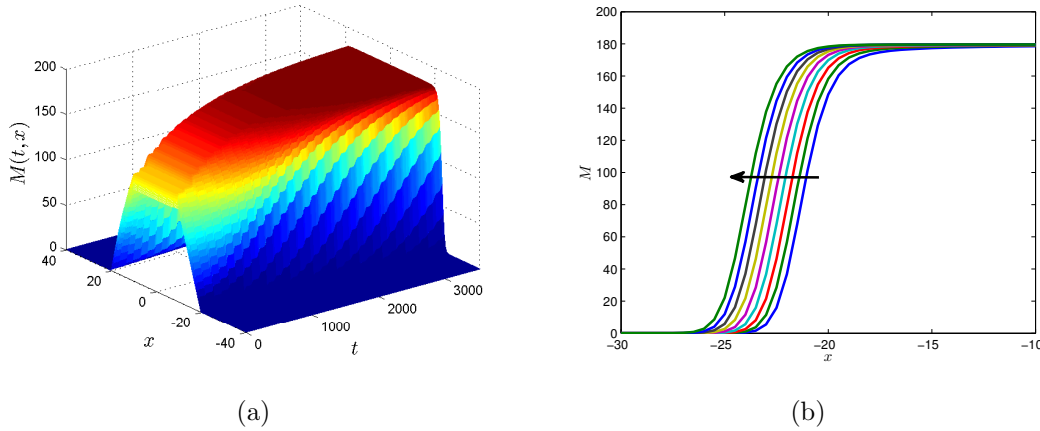
Figure 2. The spreading of M with $p = 0.6$ and the observed traveling wave profiles.

⟨fig:ubd⟩

We know that the system admits a spreading seed $c^* := \inf_{\nu \geq 0} \frac{\lambda(\nu)}{\nu}$, where $\lambda(\nu)$ is the principle eigenvalue of

$$\lambda = D_M \nu^2 - \mu + rpe^{-d_1\tau_1}e^{D_1\tau_1\nu^2}e^{-\lambda\tau_1} + r(1-p)e^{-d_2\tau_2}e^{D_2\tau_2\nu^2}e^{-\lambda\tau_2}.$$

With the given parameters, in Figure 3, we show that the spreading speed c^* is strictly decreasing with respect to p. This shows that when more individuals develop with shorter developmental duration, the species may spread at a slower speed.
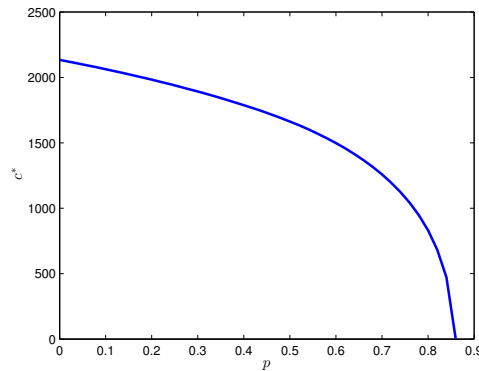

Figure 3. The spreading speed c^* with respect to p.

⟨ase1spreading⟩

Now we are going to investigate the following question: comparing two collective strategies: (a) most individuals mature at a smaller maturation duration τ_1, and (b) most individuals attain the sexual maturity at a longer maturation age τ_2, which one is in favor of species establishment and spreading? Here we are going to use different indices: the net reproduction number, the density of adults, and the density of immatures. This problem will be discussed by considering the tradeoff between early reproduction and survival probability to maturation: $e^{-d_i\tau_i}$, for $i = 1, 2$ representing different strategies. We first consider the case that individuals with delayed maturation have larger survival

probability to maturation, that is $d_1\tau_1 > d_2\tau_2$. Then Figure 4 shows that larger age-at maturity seems better for species establishment. As tick-borne disease risk can be measured through the density of nymphs in some sense, we can also illustrate the dynamics of nymph density, as indicated in Remark 3.1 and shown in Figure 5. Therefore, reproducing late may increase the nymph density, and pose larger disease risk. However, for the case $d_1\tau_1 < d_2\tau_2$, where individuals mature earlier have larger survival probability to maturation, a different prediction is illustrated in Figure 6 with $r = 9.6027$ day^{-1} and $d_2 \in (d_1\tau_1/\tau_2, d_1)$. It shows that earlier maturation strategy is better in terms of the net reproduction rate and the density of adults ticks. However, this monotone dependence result does not hold for the relationship between the density of immatures I^* and p, which may also depends on the immature death rate d_2, as shown in Figure 6(c)). For small d_2 values, for example $d_2 = 0.01$, the relationship between the density of immatures and the proportion p is decreasing, which implies that reproducing early is better to increase the immature population density. However, for relatively large d_2 value, say $d_2 = 0.015$, this relationship becomes a decreasing function, illustrating that having more individuals opt for reproducing later increases the immature population density. It is interesting to observe that at some death rate d_2, an intermediate value of the proportion p, instead of $p = 0$ and $p = 1$ can maximize the density of immatures (See Figure 6(d)).

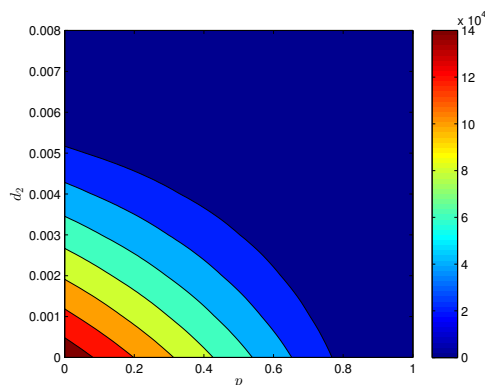(a)   (b)
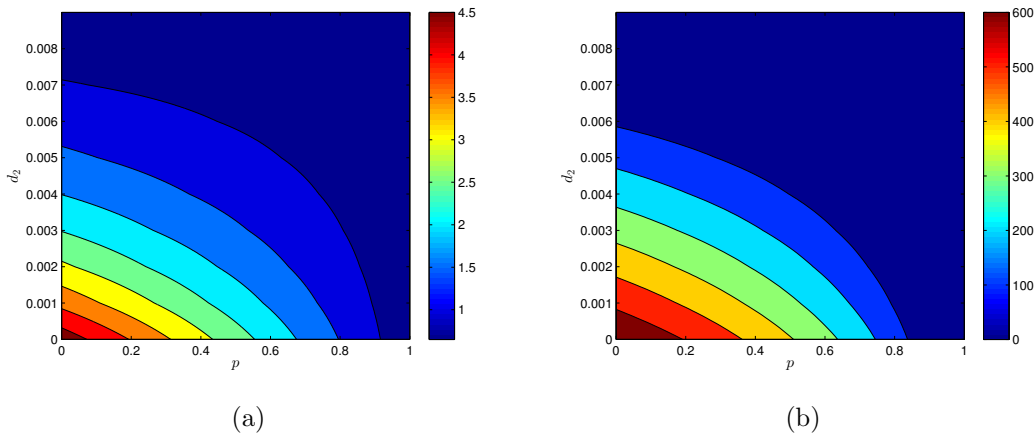
Figure 4. The contour plot for the case $d_1\tau_1 > d_2\tau_2$ to show relationship between the immature death rate d_2 and proportion $(1 - p)$ for immatures that have large age-at reproduction τ_2 to attain fixed values of the response variable: (a) the net reproduction number R_0, (b) the density of adults at equilibrium.

⟨tradeoff1⟩

6. Limitations and extensions of the study

⟨sec:dis⟩ The advantages of undergoing diapause, whether it is development diapause or behavior diapause, are characterized in the current model with different development durations and death rates. In the current study, we employ a simplified assumption that the early production may only correlated with the survival probability surviving to age-at

Figure 5. The contour plot for the case $d_1\tau_1 > d_2\tau_2$ to show relationship between d_2 and proportion p to attain fixed values of the density of immatures at equilibrium.

⟨tradeoff1-I⟩

(a)

(b)

(c)

(d)
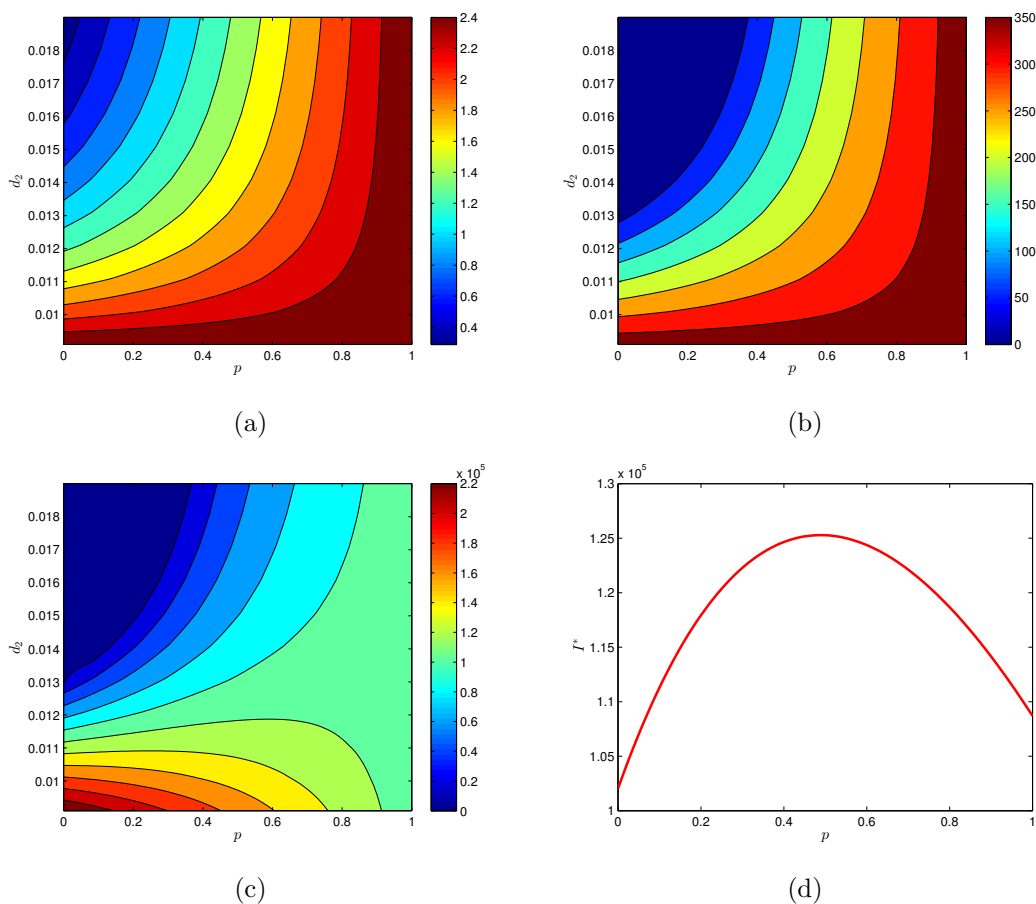
Figure 6. The contour plot for the case $d_1\tau_1 < d_2\tau_2$ to show relationship between the immature death rate d_2 and proportion $(1 - p)$ for immatures that have large age-at reproduction τ_2 to attain fixed values of the response variable: (a) the net reproduction number R_0, (b) the density of adults at equilibrium, (c) the density of immatures at equilibrium, (d) the density of immatures at equilibrium I^* with $d_2 = 0.0115$.

⟨tradeoff2⟩

reproduction. As a matter of fact, the lifetime tradeoffs between early reproductive allocation and late-life fitness includes late-life survival and reproduction [20]. For example, age at first reproduction can be negatively related to both reproductive performance and adult survival for some species [7]. Moreover, the advantages of having a longer development duration shall include but not limited to (a) the larger individual size at maturity, which will in turn increase the fecundity rate of adults; (b) longer reproduction duration and so on. Considering these realities, the model should be extended to two differential equations for M_1 and M_2 of various maturation delays, which can not be added into a scalar equation due to the difference in fecundity and death rates, and diffusion activity.

In many studies of tick population growth, various density-dependent effects should be considered, including but not limited to: the increased death rate during the feeding stages of ticks due to the immune response of hosts [19], the negative feedback to the birth rate of egg-laying adults induced by feeding adults [4] or all tick stages [22]. Therefore, other forms of birth and death rate functions to describe the self regulation may be employed [4]. Theoretical results derived in the current study hold when the strength of the negative feedback on the birth rate, although exists, is not so strong. For example, the analytical tools work well when the birth function takes the form of $f(N) = rNe^{-\sigma N}$, with a small σ. This is a reasonable assumption when the host population size for ticks, such as rodents and deers, are abundant. However, we highlight that it is a worthy topic for further study from the biological point of view as the negative feedback plays a very important role in the population dynamics of ticks. From the mathematical point of view, a strong self regulation on the fecundity rate, i.e., a large σ, will make the model not cooperative any more. In this case, some analytical arguments for the global dynamics, traveling waves and spreading speed fail, and we leave this interesting topic for further investigation.

We should also mention that our analysis is mainly focused on the monostable case, in other words, there is only one stable equilibrium in the spatially homogeneous environment. At the remaining part of this discussion, we would like to present some results on a bistable case. In theoretical ecology, the birth function may take the form of $f(N) = bN^2e^{-aN}$, with positive a and b values or

$$f(N) = \begin{cases} bN^2e^{-aN}, & 0 \leq N < \dfrac{2}{a}, \\ \dfrac{4b}{a^2e^2}, & N \geq \dfrac{2}{a}, \end{cases} \qquad (27) \boxed{\texttt{bistablef}}$$

(see for example [15, 17, 27]), which satisfies assumption (A1), but not (A2). To study this kind of birth functions, we propose the following conditions:

(A4) There exists $\widehat{N} \in (0, N^*)$ such that $f'(N)$ is strictly increasing for $0 < N \leq \widehat{N}$, and it is decreasing for $\widehat{N} < N \leq N^*$. Moreover, either $f'(N) = 0$ or $\mathcal{G}(N) \leq 0$ for all $N \geq N^*$.

(A5) Assume $\mu > (pe^{-d_1\tau_1} + (1-p)e^{-d_2\tau_2})f'(0)$, and (6) has two positive roots $M_1 < M_2$ such that $\mathcal{G}'(M_1) > 0$ and $\mathcal{G}'(M_2) < 0$.

Then it is easy to verify that (16) admits a bistable structure in the sense that the spatially homogeneous equation (18) has two stable equilibria $M_0 = 0$, M_2, and an unstable equilibrium M_1. We are going to search the bistable waves $U(\xi)$, $\xi = x + ct$, with $U(-\infty) = 0$ and $U(\infty) = M_2$. It follows from (A5) that (16) is quasi-monotone in $[0, M_2]_{\mathbb{C}}$. Then the comparison principle and squeezing technique as used in [17] and [27] can be applied to obtain the existence and uniqueness of bistable waves. Moreover, from the remark in [27, Section 6] and using similar arguments as in the proof of Theorems 3.3, 4.5, and 5.8 in [27], we can get the existence, uniqueness, and global stability of bistable waves for (16). Therefore, the following result holds and proof details are omitted.

⟨bistable⟩ **Theorem 6.1.** *Assume that (A1),(A4), and (A5) hold. Then (16) admits a strictly increasing traveling wave $U(\xi)$ with speed $\bar{c}$ satisfying $U(-\infty) = 0$ and $U(\infty) = M_2$. Moreover, $U(\xi)$ is globally asymptotically stable with phase shift in the sense that there exists $k > 0$ such that for any $\phi \in [0, M_2]_{\mathbb{C}}$ with*

$$\liminf_{x \to \infty} \min_{s \in [-\tau, 0]} \phi(s, x) > M_1, \quad \limsup_{x \to -\infty} \max_{s \in [-\tau, 0]} \phi(s, x) < M_1, \qquad (28) \boxed{\text{initial}}$$

the solution $u(t, x; \phi)$ of (16) with initial data ϕ satisfying

$$\mid u(t, x; \phi) - U(x + \bar{c}t + \bar{\xi}) \mid \leq K e^{-kt},$$

for some $K = K(\phi) > 0$ and $\bar{\xi} = \bar{\xi}(\phi) \in \mathbb{R}$.

It is well known that the sign of the bistable wave speed is critical to determine the propagation direction of waves. Biologically, the sign of the bistable wave speed can determine which stable equilibria can win the propagation. Moreover, from Theorem 6.1, we know that $\lim_{t \to \infty} u(t, x; \phi) = 0$ if $\bar{c} < 0$, and $\lim_{t \to \infty} u(t, x; \phi) = M_2$ if $\bar{c} > 0$ for any ϕ satisfying (28). However, it is not easy to determine the sign of the bistable wave speed for nonlocal and delayed equations. Fortunately, by constructing suitable upper and lower solutions, a recent work [15] successfully figured out some sufficient conditions to determine the sign of the bistable wave speed. Motivated by [15], we define the testing function

$$V(\xi) := \frac{1}{\frac{1}{m} + e^{-\bar{\nu}\xi}}, \quad m > 0, \quad \forall \xi \in \mathbb{R},$$

where $\bar{\nu}$ is the unique positive solution of

$$D_M \nu^2 - \mu + p e^{-d_1 \tau_1} f'(0) \gamma_1(\nu) + (1 - p) e^{-d_2 \tau_2} f'(0) \gamma_2(\nu) = 0. \qquad (29) \boxed{\text{chzero}}$$

Then $V(\xi)$ is increasing and satisfies $0 < V(\xi) < m$, $V(-\infty) = 0$ and $V(\infty) = m$. Substituting $V(\xi)$ to (23) with $c = 0$, we know that $V(\xi)$ is a strongly upper (lower) solution of (23) with $c = 0$ provided

$$\Theta(\xi) := -2 D_M \bar{\nu}^2 + \frac{J(V)(\xi) + (D_M \bar{\nu}^2 - \mu) V (1 - \frac{V}{m}) - \frac{\mu}{m} V^2 - g(V) V}{\frac{V^2}{m}(1 - \frac{V}{m})} < (>) 0,$$

where

$$J(V)(\xi) := pe^{-d_1\tau_1} \int_{\mathbb{R}} \Gamma(D_1\tau_1, y) f(V(\xi - y)) dy$$

$$+ (1-p)e^{-d_2\tau_2} \int_{\mathbb{R}} \Gamma(D_2\tau_2, y) f(V(\xi - y)) dy.$$

Then by similar arguments as in the proof of [15, Corollary 2.1 and Theorem 2.2], we get the following result for the determination of the sign of the wave speed $\bar{c}$.

⟨sign⟩ **Theorem 6.2.** *Let (A1), (A4) and (A5) hold. Then we have the following statements:*

(i) *If there exists $m \in (M_1, M_2]$ such that $\Theta(\xi) < 0$, $\forall \xi \in \mathbb{R}$, then $\bar{c} < 0$;*

(ii) *If there exists $m \in (M_1, M_2]$ such that $\Theta(\xi) > 0$, $\forall \xi \in \mathbb{R}$, then $\bar{c} > 0$.*

In order to have a better understanding on the sign of the wave speed. We take the birth function f given by (27) for example. Then we have $f'(0) = 0$, $N^* = \frac{2}{a}$ and (29) implies that $\bar{\nu} = \sqrt{\frac{\mu}{D_M}}$. For the simplicity of calculations, we assume the immature population is immobile, that is, $D_1 = D_2 = 0$. Then (16) is transformed to

$$\frac{\partial u(t,x)}{\partial t} = D_M \frac{\partial^2 u}{\partial x^2}(t,x) - (\mu + g(u))u + pe^{-d_1\tau_1} f(u(t - \tau_1, x))$$

$$+ (1-p)e^{-d_2\tau_2} f(u(t - \tau_2, x)).$$

Without loss of generality, we assume the density-dependent death rate is given by $g(N) = \beta N$ for some $\beta \geq 0$. Then for any $m \in (M_1, \frac{2}{a}]$, we have

$$\Theta(\xi) = -2\mu + \frac{b(pe^{-d_1\tau_1} + (1-p)e^{-d_2\tau_2})e^{-aV} - \frac{\mu}{m} - \beta}{\frac{1}{m}(1 - \frac{V}{m})}. \qquad (30)\ \boxed{\texttt{negative}}$$

If $M_2 > \frac{2}{a}$, then there exists a unique $\bar{m} \in (\frac{2}{a}, M_2)$ such that

$$b(pe^{-d_1\tau_1} + (1-p)e^{-d_2\tau_2})\bar{m}^2 e^{-a\bar{m}} = (\mu + \beta\bar{m})\bar{m}. \qquad (31)\ \boxed{\texttt{barm}}$$

Moreover, for any $m \in (\frac{2}{a}, M_2]$, we have

$$\Theta(\xi) \geq -2\mu + \frac{b(pe^{-d_1\tau_1} + (1-p)e^{-d_2\tau_2})e^{-aV} - \frac{\mu}{m} - \beta}{\frac{1}{m}(1 - \frac{V}{m})}. \qquad (32)\ \boxed{\texttt{positive}}$$

Then the following result holds.

Corollary 6.2.1. *Assume $D_1 = D_2 = 0$, $g(N) = \beta N$, and f is given by (27), then we have the following observations:*

(i) *If $M_2 \leq \frac{2}{a}$, and*

$$b(pe^{-d_1\tau_1} + (1-p)e^{-d_2\tau_2}) < \beta + \frac{3\mu}{M_2},$$

then $\bar{c} < 0$. In particular, if $\beta = 0$, then we have $\bar{c} < 0$ provided $M_2 < \frac{\ln 3}{a}$.

(ii) *If $M_2 > \frac{2}{a}$, then $\bar{c} > 0$.*

Proof. If $M_2 \leq \frac{2}{a}$, we choose $m = M_2$ in (30). Then Theorem 6.2(i) implies that $\bar{c} < 0$ provided $\Theta(\xi) < 0$, $\forall \xi \in \mathbb{R}$, which is equivalent to

$$b(pe^{-d_1\tau_1} + (1-p)e^{-d_2\tau_2})e^{-aV} < \beta + \frac{3\mu}{M_2} - \frac{2\mu}{M_2^2}V, \qquad (33)\boxed{\texttt{ineqone}}$$

for any $0 < V < M_2$. For any $N \geq 0$, we define

$$f_1(N) := b(pe^{-d_1\tau_1} + (1-p)e^{-d_2\tau_2})e^{-aN}, \quad f_2(N) := \beta + \frac{3\mu}{M_2} - \frac{2\mu}{M_2^2}N.$$

Note that $f_1(M_2) = f_2(M_2)$. Then the monotonicity of $f_i, i = 1, 2$ and the convexity of f_1 imply that (33) holds provided

$$b(pe^{-d_1\tau_1} + (1-p)e^{-d_2\tau_2}) = f_1(0) < f_2(0) = \beta + \frac{3\mu}{M_2}.$$

In particular, if $\beta = 0$, using

$$b(pe^{-d_1\tau_1} + (1-p)e^{-d_2\tau_2}) = \frac{\mu}{M_2}e^{aM_2},$$

it follows that $\bar{c} < 0$ provided $M_2 < \frac{\ln 3}{a}$.

In the case of $M_2 > \frac{2}{a}$, we take $m = \bar{m}$ in (32). Then Theorem 6.2(ii) implies that $\bar{c} > 0$ provided

$$b(pe^{-d_1\tau_1} + (1-p)e^{-d_2\tau_2})e^{-aV} > \beta + \frac{3\mu}{\bar{m}} - \frac{2\mu}{\bar{m}^2}V \qquad (34)\boxed{\texttt{ineqtwo}}$$

for any $0 < V < \bar{m}$. For any $N \geq 0$, we define

$$\bar{f}_1(N) := b(pe^{-d_1\tau_1} + (1-p)e^{-d_2\tau_2})e^{-aN}, \quad \bar{f}_2(N) := \beta + \frac{3\mu}{\bar{m}} - \frac{2\mu}{\bar{m}^2}N.$$

Note that $\bar{f}_1(\bar{m}) = \bar{f}_2(\bar{m})$. Then the properties of $\bar{f}_i, i = 1, 2$ imply that (34) holds provided $\bar{f}_1'(\bar{m}) < \bar{f}_2'(\bar{m})$, which is equivalent to

$$ab(pe^{-d_1\tau_1} + (1-p)e^{-d_2\tau_2})e^{-a\bar{m}} > \frac{2\mu}{\bar{m}^2}.$$

Using (31), we know that the above inequality is equivalent to $a(\mu + \beta\bar{m})\bar{m} > 2\mu$, which is always true since $\bar{m} > \frac{2}{a}$. Thus, the statement (ii) is valid. $\qquad\square$

Acknowledgments

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