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Analysis of an age structured model for tick populations subject to seasonal effects

Kaihui Liu[a], Yijun Lou[a], Jianhong Wu[b]

[a]Department of Applied Mathematics, The Hong Kong Polytechnic University, Kowloon, Hong Kong, China
[b]Centre for Disease Modelling, York Institute for Health Research, York University, Toronto, ON, M3J 1P3, Canada

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Abstract

We investigate an age-structured hyperbolic equation model by allowing the birth and death functions to be density dependent and periodic in time with the consideration of seasonal effects. By studying the integral form solution of this general hyperbolic equation obtained through the method of integration along characteristics, we give a detailed proof of the uniqueness and existence of the solution in light of the contraction mapping theorem. With additional biologically natural assumptions, using the tick population growth as a motivating example, we derive an age-structured model with time-dependent periodic maturation delays, which is quite different from the existing population models with time-independent maturation delays. For this periodic differential system with seasonal delays, the basic reproduction number $\mathcal{R}_0$ is defined as the spectral radius of the next generation operator. Then, we show the tick population tends to die out when $\mathcal{R}_0 < 1$ while remains persistent if $\mathcal{R}_0 > 1$. When there is no intra-specific competition among immature individuals due to the sufficient availability of immature tick hosts, the global stability of the positive periodic state for the whole model system of four delay differential equations can be obtained with the observation that a scalar subsystem for the adult stage size can be decoupled. The challenge for the proof of such a global stability result can be overcome by introducing a new phase space, based on which, a periodic solution semiflow can be defined which is eventually strongly monotone and strictly subhomogeneous.

Keywords: age-structure; seasonal effects; periodic delay; tick population; uniform persistence; global stability

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1. Introduction

Mathematical modeling for population growth has an extensive history dated back to the eighteenth century when Leonhard Euler studied human population growth [1]. However, mathematical formulation of population ecology did not acquire extensive development until Lotka and Volterra pioneered the modern ecological theory [1, 2]. There are many different ways to derive the models in literatures including the Leslie matrix, difference equations, integral equations and functional differential equations [3]. Many models consisting of simple ordinary differential equations (such as the prototypical logistic differential equations)

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*Corresponding author
Email address: `yijun.lou@polyu.edu.hk` (Yijun Lou)

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may not be appropriate for fully understanding the complicated dynamics of most populations because they postulate that all individuals are the same as each other [4]. As a matter of fact, the individual growth rate in the real world varies with many biotic and abiotic factors and therefore, structured population models characterizing the differences between individuals may be a more realistic way to better describe complex population dynamics. One of the most important structuring variables in population dynamics is the chronological age as the reproduction and survival capabilities among individuals differ from age to age. Age-structured modeling framework was first introduced by Lotka and Mackendrick with the incorporation of age-dependent birth and death rates [5]. Since then, age-structured models have been widely studied and applied to population ecology and epidemiology [6, 7]. As the research moves along, other factors such as environmental aspects have been integrated into age-structured models.

Seasonality due to variations of weather conditions is known as the pervasive external environmental factor affecting the annual trends of population dynamics and transmission of infectious diseases. For example, mosquito-borne diseases such as dengue fever always pose high prevalence in the summer when the humidity and temperature are appropriate for the breeding of mosquitoes, while the incidence rate of dengue fever declines to the lowest level during winter due to the low temperature and dry weather [8]. Many researchers have explored the impact of seasonality on influenza [9], dengue fever [8] and respiratory tract infections [10] and so on. In particular, authors in [11] reviewed some examples of human and wildlife diseases to interpret the roles of seasonal variations on the dynamics of infectious diseases from different aspects. In the current study, we investigate the age-structured population dynamics subject to seasonal effects by incorporating periodic birth, death and maturation rates. Our main focus is on the mathematical modeling and analysis of the population size evolution, with the tick growth as the motivating example.

The population growth of ticks, the primary vector transmitting the tick-borne diseases such as Lyme disease, babesiosis, anaplasmosis, tularemia and so on [12], has attracted a growing body of studies in order to evaluate the disease risk. Seasonality is considered as the driving factor to generate annual patterns of tick dynamics especially the survival during non-parasitic periods [13]. The lifecycle of ticks can be divided into four main stages including egg, larval, nymphal and adult. Ogden and coauthors formulated a computational model with temperature dependent delays, which takes into account the twelve tick stages to illustrate the temperature effect on population growth by dividing each post-egg stage into three substages including questing, feeding and engorged [14]. Since then, a number of age-structured models incorporating seasonal variations have been developed. Authors in [15] proposed an ordinary differential model consisting of twelve ordinary differential equations and studied tick persistence and the existence and local stability of unique endemic equilibrium in terms of basic reproduction number $\mathcal{R}_0$. A similar deterministic model involving twelve periodic ordinary differential equations was developed in [16], where the seasonal temperature-driven development rates and host biting rates were estimated via temperature normals smoothened by Fourier analysis and the values of $\mathcal{R}_0$ were evaluated for the model with various locations in Eastern Canada. A system of delay differential equations was built in [17] to investigate the self-regulation dynamics of tick population. Considering the fact that interstadial developmental time is affected by temperature, authors in [18] formulated an elegant link between time-dependent maturation delays and the development durations. They further evaluated the basic reproduction number for such a system with applications to different scenarios. However, few theoretical results related to the global dynamics, including the extinction, persistence and the global stability of the model system in terms of $\mathcal{R}_0$ were performed in [18], and this fact constitutes the main motivation of the current study. In particular, we will provide a rigorous mathematical framework to study the population growth subject to seasonal variations on birth, death and development durations. Although the study is presented in terms of tick population, it is worth remarking that the theoretical framework is general enough for investigating population growths of other species.

The goal of the present study is twofold. On one side, it is necessary to provide a comprehensive study for the topic through the modeling population growth subject to seasonal factors with a hyperbolic equation and its reduction to a periodic differential system with periodic delays. However, it is not always the case that rigorous biological and mathematical arguments are included. On the other side, detailed analysis is needed for hyperbolic equations on the existence and uniqueness of solutions in a general biological setting and the global analysis of the delay differential systems should be performed from the perspective of global extinction, persistence and global stability of a positive periodic solution. The rest of this paper is organized as follows. A periodic age structured hyperbolic equation, known as McKendrick-von Foerster equation is presented in Section 2 and some preliminary results on the existence and uniqueness of the solution are shown. Section 3 derives an age-structured model in the form of periodic differential equations with periodic delays from the general hyperbolic model. In Section 4, the definition of $\mathcal{R}_0$ and detailed proof of tick extinction and persistence in terms of $\mathcal{R}_0$ are established. When the host populations for immature ticks, such as deers , white-footed mice, chipmunks and shrews [19], are abundant and the density-dependent regulation of immature ticks can be ignored, existence and global attractivity of a positive periodic solution is shown by using the theory of monotone dynamical systems for the case $\mathcal{R}_0 > 1$. A brief discussion is presented in the last section. We defer some mathematical arguments to the Appendix section.

2. Model formulation and well-posedness

2.1. A hyperbolic model for age-structured population growth with seasonal effects

Let $\rho(t, a)$ be the population density with respect to age a at time t. Considering the effects of seasonal biotic and abiotic factors on population growth, the well-known McKendrick-von Foerster equation (also called Lotka-McKendrick equation sometimes [20, 21, 22]) as a modeling framework for age structured population growth can be extended to

$$\begin{cases} (\frac{\partial}{\partial t} + \frac{\partial}{\partial a})\rho(t, a) = -\mu\left(t, a, \int_0^\infty q(t, s)\rho(t, s)ds\right)\rho(t, a), \\ \rho(0, a) = \phi(a), \ a \geq 0, \\ \rho(t, 0) = b\left(t, \int_0^\infty p(t, s)\rho(t, s)ds\right), \ t \geq 0. \end{cases} \tag{2.1}$$

Here the egg fecundity rate $b\left(t, \int_0^\infty p(t,s)\rho(t,s)ds\right)$ is dependent on time t and population density with a weight function $p(t,a)$, the per-capita mortality rate $\mu\left(t, a, \int_0^\infty q(t,s)\rho(t,s)ds\right)$ varies with time t, age a and the population density with another weight function $q(t,a)$. Here and in what follows, the variable parameter functions including the birth rate $b(t,\cdot)$, per-capita death rate $\mu(t,\cdot,\cdot)$ and weight functions $q(t,\cdot)$ and $p(t,\cdot)$ are all periodic in time t with the same period T, taking the seasonal effects on population growth into account [16, 18]. The function $\phi(\cdot)$ gives the non-negative initial age distribution of the population. It is very natural to have the following general assumptions on the birth rate, death rate, initial and boundary conditions as well as kernel functions:

(B1) Both the birth rate $b(t,x)$ and the per-capita death rate $\mu(t,a,x)$ are non-negative and Lipschitzian functions with respect to the x variable with Lipschitzian constants $\bar{b}$ and $\bar{\mu}$ respectively. Moreover, there exists a positive constant $\mu_{\min}$ such that $\mu(t,a,x) \geq \mu_{\min} > 0$ for all x, $t \geq 0$ and $a \geq 0$.

(B2) The inherent relationships between boundary and initial condition must be satisfied, that is

$$\rho(0,0) = \phi(0) = b\left(0, \int_0^\infty p(0,s)\phi(s)ds\right).$$

(B3) $q(t,\cdot)$ and $p(t,\cdot)$ are assumed to be non-negative in $L[0,\infty)$.

Based on these assumptions, we can establish some preliminary results for the hyperbolic equation (2.1) as below.

2.2. Existence and non-negativeness of solutions

In order to obtain the formulation of solutions for system (2.1), we will follow a more readily comprehensible method of characteristics (for example Li and Brauer [20] and [22]). Since the time variable t is involved in the right hand side of the hyperbolic equation and the boundary condition, a careful argument is needed and for reader's convenience, we present the details in Appendix A. Then, (2.1) can be written as the following equivalent integral equation:

$$\begin{aligned}\rho(t,a) =& b\left(t-a, \int_0^\infty p(t-a,s)\rho(t-a,s)ds\right)\exp\left(-\int_0^a \mu(t-a+r, r, \int_0^\infty q(t-a+r,s)\rho(t-a+r,s)ds)dr\right)\mathbf{1}_{\{t>a\}} \\ &+ \phi(a-t)\exp\left(-\int_0^t \mu(r, a-t+r, \int_0^\infty q(r,s)\rho(r,s)ds)dr\right)\mathbf{1}_{\{a\geq t\}},\end{aligned} \tag{2.2}$$

where the indicator function is shown as follows:

$$\mathbf{1}_{\{t>a\}} = \begin{cases} 1, & t > a \geq 0, \\ 0, & a \geq t \geq 0, \end{cases} \quad \text{and} \quad \mathbf{1}_{\{a\geq t\}} = \begin{cases} 0, & t > a \geq 0, \\ 1, & a \geq t \geq 0. \end{cases}$$

Next, we prove local existence and uniqueness of solutions to system (2.2) and hence to system (2.1) in view of Theorem 2.1 in [23].

Theorem 2.1. *Let* $x_0 = \phi(\cdot) \in L_+[0,\infty)$*. Then, there exists* $\epsilon > 0$ *and an open neighborhood* $B_0 \subset L[0,\infty)$ *with* $x_0 \in B_0$ *such that there exists a unique continuous function,* $\chi : [0,\epsilon] \times B_0 \to L[0,\infty)$ *that satisfies (2.2) with* $\chi(0,x) = x$ *for* $x \in B_0$*.*

Proof. Set $Y = C([0,\epsilon] \times B_0, L[0,\infty))$, the set of all continuous functions from $[0,\epsilon] \times B_0$ to $L[0,\infty)$ with the norm $\|\cdot\|_Y$ defined by

$$\|\psi\|_Y = \sup_{t\in[0,\epsilon],\ x\in B_0} \int_0^\infty |\psi(t,x)(a)| da,$$

where $\epsilon > 0$ and $B_0 \subset L[0,\infty)$ is a neighborhood of x_0, which will be determined later. Let $\mathcal{B}$ be a subset of Y containing functions whose ranges lie in $B \subset L[0,\infty)$, where $B = \overline{U}(\phi(\cdot), r)$ is the closed ball of radius r centered around the initial function with the value of r to be determined later. Then, $\mathcal{B}$ is a closed subset of the complete metric space Y. Define an operator Λ on $\mathcal{B}$ as follows: for any $x = x(\cdot) \in B_0$, $\eta(t,x)(\cdot) \in \mathcal{B}$,

$$\begin{aligned}\Lambda(\eta)(t,x)(a) = b&\left(t-a, \int_0^\infty p(t-a,s)\eta(t-a,x)(s)ds\right)\\ &\exp\left(-\int_0^a \mu(t-a+r, r, \int_0^\infty q(t-a+r,s)\eta(t-a+r,x)(s)ds)dr\right)\mathbf{1}_{\{t>a\}}\\ &+ x(a-t)\exp\left(-\int_0^t \mu(r, a-t+r, \int_0^\infty q(r,s)\eta(r,x)(s)ds)dr\right)\mathbf{1}_{\{a\geq t\}}.\end{aligned} \tag{2.3}$$

If Λ admits a fixed point u in $\mathcal{B}$, i.e. $\Lambda u = u$, then $\Lambda u(t,x)(\cdot) = u(t,x)(\cdot)$. Let $\tilde{\rho}(t,a) = u(t,x)(a)$, $\forall a \geq 0$, then we have

$$\begin{aligned}\tilde{\rho}(t,a) =b&\left(t-a, \int_0^\infty p(t-a,s)\tilde{\rho}(t-a,s)ds\right)\\ &\exp\left(-\int_0^a \mu(t-a+r, r, \int_0^\infty q(t-a+r,s)\tilde{\rho}(t-a+r,s)ds)dr\right)\mathbf{1}_{\{t>a\}}\\ &+ x(a-t)\exp\left(-\int_0^t \mu(r, a-t+r, \int_0^\infty q(r,s)\tilde{\rho}(r,s)ds)dr\right)\mathbf{1}_{\{a\geq t\}}.\end{aligned}$$

Hence, $\tilde{\rho}(t,a)$ satisfies equation (2.2), i.e. $\tilde{\rho}(t,a)$ is a solution to (2.2) with $\tilde{\rho}(0,a) = x(a)$.

The subsequent proof is to show that Λ is a contraction mapping on $\mathcal{B}$, which ensures the existence of a unique fixed point of Λ on $\mathcal{B}$. This conclusion can be achieved by the following three steps (details of these three steps are presented in the Appendix B):

(I) For any $\eta \in \mathcal{B}$, we first show $\Lambda(\eta) \in Y$, that is $\Lambda : \mathcal{B} \to Y$;
(II) For any $\eta \in \mathcal{B}$, we further claim $\Lambda(\eta) \in \mathcal{B}$, that is $\Lambda : \mathcal{B} \to \mathcal{B}$;
(III) Λ is a contraction mapping on $\mathcal{B}$.

Thus, the contraction mapping theorem guarantees the existence of a unique fixed point of Λ in $\mathcal{B}$, denoted by χ. In conclusion, $\chi(t,x)$ is the continuous solution to (2.2) on $[0,\epsilon] \times B_0$ with $\chi(0,x) = x$ for any $x \in B_0$. □

We can easily check from the integral form (2.2) that this solution to (2.1) remains nonnegative whenever it exists for any nonnegative initial value $\rho(0,\cdot)$. Hence the following theorem holds.

Theorem 2.2. *Any solution to (2.2) through a non-negative initial value remains non-negative for every* $a \geq 0$ *and all* $t \geq 0$ *on the interval of existence.*

To obtain the existence and uniqueness of the solution, we employ the classical approach, by rewriting the partial differential equation to an integral equation through integration along the characteristics. However, we would like to mention that other approaches are applicable, for example, by considering the equation as a Cauchy problem, the integral solution of which can be investigated by the integrated semigroups theory [24, 25].

3. Reduction to DDE model with periodic delays

In this section, we shall reduce the hyperbolic equation (2.1) into a system of delay differential equations, for which the tick population dynamics is easier to infer. However, the reduction process involves careful biological justifications. We first assume some age thresholds in order to stratify the tick growth into some discrete age stages, and in this paper, we divide the ticks into four stages, including egg, larval, pupal and adult ones. Since the maturation age is determined by weather conditions, two classes of periodically time-dependent terms are introduced, which are the developmental period and the chronological age thresholds. At time t, denote by $\tau_i(t)$ the time period needed for ticks to develop from the i-th stage ($i = E, L, N$, denoting egg-stage, larval-stage and nymphal-stage respectively) to the $(i+1)$-th stage ($i + 1 = L, N, A$, representing larval-stage, nymphal-stage and adult-stage respectively). In general, $\tau_i(t)$ is determined by ambient environment conditions and can be implicitly considered as a periodic function of time t with the period T, being one year. That is, the ticks developing to the $(i+1)$-th stage at time t were entering the i-th stage at time $t - \tau_i(t)$. Likewise, we assume the maximum chronological ages at time t are $f_E(t)$, $f_L(t)$ and $f_N(t)$ for egg, larval and nymphal stages respectively, which are in order of increasing maturity, that is $f_N(t) \geq f_L(t) \geq f_E(t)$ for every $t \geq 0$. Meanwhile, the threshold ages for each stage at the instant time t are assumed to be periodic functions of t with the same period T. The relationships between time dependent threshold ages and time-varying delays can be formulated as follows:

$$\begin{cases} f_E(t) = \tau_E(t), \\ f_L(t) = \tau_L(t) + \tau_E\left(t - \tau_L(t)\right) = \tau_L(t) + f_E\left(t - \tau_L(t)\right), \\ f_N(t) = \tau_N(t) + \tau_L(t - \tau_N(t)) + \tau_E(t - \tau_N(t) - \tau_L(t - \tau_N(t))) = \tau_N(t) + f_L(t - \tau_N(t)), \\ 1 - f_L'(t) = (1 - \tau_L'(t))(1 - f_E'(t - \tau_L(t))), \\ 1 - f_N'(t) = (1 - \tau_N'(t))(1 - f_L'(t - \tau_N(t))). \end{cases} \tag{3.1}$$

These relationships are illustrated in Figure 1 and interested readers can also find another derivation for these relationships in [18].

Moreover, the following arguments guarantee that $\tau_i(t)$ must satisfy $1 - \tau_i'(t) > 0$ ($i = E, L, N$). Indeed, (a)(b)(c)

Figure 1: (a) At time t, the ticks reach the threshold age $f_E(t)$ and develop into the larval stage. These newly developed larvae are grown from eggs laid at previous time $t-\tau_E(t)$. Thus, the threshold age at time t is $f_E(t) = t-(t-\tau_E(t)) = \tau_E(t)$. (b) At time t, the ticks reach the threshold age $f_L(t)$ and develop into the nymphal stage. These newly developed nymphs are grown from ticks entering larval-stage at previous time $t-\tau_L(t)$ which were developed from eggs laid at earlier time $t^*(t) = t-\tau_L(t)-\tau_E(t-\tau_L(t))$. Thus, the threshold age at time t admits $f_L(t) = t - t^*(t) = \tau_L(t) + \tau_E(t - \tau_L(t)) = \tau_L(t) + f_E(t - \tau_L(t))$. (c) At time t, the ticks reach the threshold age $f_N(t)$ and mature into adults. These newly developed adults are grown from ticks entering nymphal-stage at previous time $t - \tau_N(t)$ which were developed from larvae at earlier time $t_1(t) = t - \tau_N(t) - \tau_L(t - \tau_N(t))$. Likewise, these larvae stem from eggs laid at previous time $t_2(t) = t-\tau_N(t)-\tau_L(t-\tau_N(t))-\tau_E(t-\tau_N(t)-\tau_L(t-\tau_N(t)))$. Thus, the threshold age at time t is $f_N(t) = t-t_2(t) = \tau_N(t)+\tau_L(t-\tau_N(t))+\tau_E(t-\tau_N(t)-\tau_L(t-\tau_N(t))) = \tau_N(t)+f_L(t-\tau_N(t))$.

this assumption is biologically reasonable since the following relationship holds:

$$\int_{t-\tau_i(t)}^{t} \sigma(r)dr = 1, \quad i = E, L, N,$$

where $\sigma(r)$ is the developmental proportion at time r. After taking the derivative with respect to t, we have

$$1 - \tau_i'(t) = \frac{\sigma(t)}{\sigma(t - \tau_i(t))}, \quad i = E, L, N,$$

which indicates $1 - \tau_i'(t) > 0$. Then, it is easy to check that $1 - f_i'(t) > 0$ ($i = E, L, N$). Experimentally, we can measure the developmental proportion to evaluate the development duration $\tau_i(t)$ by using the above relationship, from which chronological age thresholds $f_i(t)$ can be derived through the identities in (3.1).

The population size for each stage can be computed as the accumulative density between two age thresholds, and in particular, we have the following mathematical expressions for the numbers of individuals within the egg ($E(t)$), larval ($L(t)$), nymphal ($N(t)$) and adult ($A(t)$) stages:

$$E(t) = \int_0^{f_E(t)} \rho(t,a)da, \quad L(t) = \int_{f_E(t)}^{f_L(t)} \rho(t,a)da, \quad N(t) = \int_{f_L(t)}^{f_N(t)} \rho(t,a)da, \quad A(t) = \int_{f_N(t)}^{a_{\max}} \rho(t,a)da, \tag{3.2}$$

where $a_{\max}$ is the maximum chronological age of adult ticks, rather than infinity as the life span of ticks is between 2 to 4 years [26]. Since the solution of equation (2.1) is in $L_+[0,\infty)$ based on results in Section 2, the above terms are all well-defined and remain nonnegative when it exists.

Next, we propose natural biological assumptions for the birth and death rates in the hyperbolic equation (2.1). Since only adults give birth, $b\left(t, \int_0^{a_{\max}} p(t,s)\rho(t,s)ds\right)$ can be rewritten as $b(t,A)$, a periodic function in t. This can be done by choosing an appropriate weight function $p(t,a)$ in the general model (2.1) as follows:

$$p(t,a) = \begin{cases} 1, & \text{if } f_N(t) < a < a_{\max}, \\ 0, & \text{otherwise.} \end{cases}$$

For individuals in each stage, they are subject to natural death rates $\mu_i(t)$ (i=E, L, N, A) and possible density dependent death rates (except eggs) $D_i(t, i(t))i(t)$ (i=L, N, A) due to intra-specific stage competition [27]. This assumption can be formulated in the general PDE equation by choosing an appropriate kernel

$q(t,a)$ in $\mu\left(t,a,\int_0^{a_{\max}} q(t,s)\rho(t,s)ds\right)$, that is

$$q(t,a) = \begin{cases} q_E(t,a), & \text{if } 0 \le a \le f_E(t), \\ q_L(t,a), & \text{if } f_E(t) < a \le f_L(t), \\ q_N(t,a), & \text{if } f_L(t) < a \le f_N(t), \\ q_A(t,a), & \text{if } f_N(t) < a < a_{\max}. \end{cases}$$

The value of q_i (i=E, L, N, A represent egg, larval, nymphal and adult stages respectively) is 1 if the ticks develop into the i-th stage, otherwise the value takes 0. Therefore, the function $\mu\left(t,a,\int_0^{a_{\max}} q(t,s)\rho(t,s)ds\right)$ takes the following form:

$$\mu(t,a,\int_0^{a_{\max}} q(t,s)\rho(t,s)ds) = \begin{cases} \mu_E(t), & \text{if} \quad 0 \le a \le f_E(t), \\ \mu_L(t) + D_L(t,L(t))L(t), & \text{if} \quad f_E(t) < a \le f_L(t), \\ \mu_N(t) + D_N(t,N(t))N(t), & \text{if} \quad f_L(t) < a \le f_N(t), \\ \mu_A(t) + D_A(t,A(t))A(t), & \text{if} \quad f_N(t) < a < a_{\max}. \end{cases}$$

Differentiating the equations in system (3.2) with respect to time t on both sides yields

$$\begin{aligned} \frac{dE(t)}{dt} &= b(t,A(t)) - \mu_E(t)E(t) - (1-f_E'(t))\rho(t,f_E(t)), \\ \frac{dL(t)}{dt} &= (1-f_E'(t))\rho(t,f_E(t)) - \mu_L(t)L(t) - D_L(t,L(t))L^2(t) - (1-f_L'(t))\rho(t,f_L(t)), \\ \frac{dN(t)}{dt} &= (1-f_L'(t))\rho(t,f_L(t)) - \mu_N(t)N(t) - D_N(t,N(t))N^2(t) - (1-f_N'(t))\rho(t,f_N(t)), \\ \frac{dA(t)}{dt} &= (1-f_N'(t))\rho(t,f_N(t)) - \mu_A(t)A(t) - D_A(t,A(t))A^2(t). \end{aligned}$$

To obtain the closed form of the above system, $\rho(t,f_i(t))$ ($i = E$, L, N) will be evaluated by the method of integration along characteristics, as processed in Appendix C. There are different expressions for $\rho(t,f_i(t))$ for $t \ge f_i(t)$ and $t < f_i(t)$ respectively. Since we focus on the long-term dynamics, without the loss of generality, we study the case when $t \ge f_i(t)$, which is feasible due to the boundedness of $f_i(t)$. It follows from the integral form of the solution (2.2) that when $t \ge f_N(t)$ (note that $f_N(t) > f_L(t) > f_E(t)$), we have:

$$\rho(t,f_i(t)) = b(t-f_i(t),A(t-f_i(t)))e^{-\int_0^{f_i(t)} \mu\left(t-f_i(t)+r,r,\int_0^{a_{\max}} q(t-f_i(t)+r,s)\rho(t-f_i(t)+r,s)ds\right)dr},$$

for $i = E, L, N$. Therefore, we can obtain a closed form, in terms of delay differential equations, to describe the tick population growth when $t \geq f_N(t)$ (see Appendix C for detailed derivation):

$$\begin{aligned}
\frac{dE(t)}{dt} &= b(t, A(t)) - \mu_E(t)E(t) - (1 - f_E'(t))h_1(t)b(t - f_E(t), A(t - f_E(t))), \\
\frac{dL(t)}{dt} &= (1 - f_E'(t))h_1(t)b(t - f_E(t), A(t - f_E(t))) - \mu_L(t)L(t) - D_L(t, L(t))L^2(t) \\
&\quad - (1 - f_L'(t))h_2(t)g_1(t, L(t))b(t - f_L(t), A(t - f_L(t))), \\
\frac{dN(t)}{dt} &= (1 - f_L'(t))h_2(t)g_1(t, L(t))b(t - f_L(t), A(t - f_L(t))) - \mu_N(t)N(t) - D_N(t, N(t))N^2(t) \\
&\quad - (1 - f_N'(t))h_3(t)g_2(t, L(t), N(t))b(t - f_N(t), A(t - f_N(t))), \\
\frac{dA(t)}{dt} &= (1 - f_N'(t))h_3(t)g_2(t, L(t), N(t))b(t - f_N(t), A(t - f_N(t))) - \mu_A(t)A(t) - D_A(t, A(t))A^2(t),
\end{aligned} \tag{3.3}$$

where

$$\begin{aligned}
h_1(t) &= \exp\left(-\int_{t-f_E(t)}^{t} \mu_E(r)dr\right), \\
h_2(t) &= \exp\left(-\int_{t-\tau_L(t)}^{t} \mu_L(r)dr - \int_{t-f_L(t)}^{t-\tau_L(t)} \mu_E(r)dr\right), \\
h_3(t) &= \exp\left(-\int_{t-\tau_N(t)}^{t} \mu_N(r)dr - \int_{t-\tau_N(t)-\tau_L(t-\tau_N(t))}^{t-\tau_N(t)} \mu_L(r)dr - \int_{t-f_N(t)}^{t-\tau_N(t)-\tau_L(t-\tau_N(t))} \mu_E(r)dr\right)
\end{aligned}$$

are probabilities surviving through natural death during development while

$$\begin{aligned}
g_1(t, L(t)) &= \exp\left(-\int_{t-\tau_L(t)}^{t} D_L(r, L(r))L(r)dr\right), \\
g_2(t, L(t), N(t)) &= \exp\left(-\int_{t-\tau_N(t)}^{t} D_N(r, N(r))N(r)dr - \int_{t-\tau_N(t)-\tau_L(t-\tau_N(t))}^{t-\tau_N(t)} D_L(r, L(r))L(r)dr\right)
\end{aligned}$$

represent the probabilities surviving through additional death due to competition.

Alternatively, $E(t)$, $L(t)$, $N(t)$ and $A(t)$ can be expressed into integral forms. Note that $\tau_E(t)$ is the developmental time for eggs at time t. Hence, the eggs at time t consist of all eggs laid at previous time ξ with $\xi \in (t - \tau_E(t), t)$ and survived to time t. Therefore, we have

$$\begin{aligned}
E(t) &= \int_{t-\tau_E(t)}^{t} \exp\left(-\int_{\xi}^{t} \mu\left(r, a, \int_0^{a_{\max}} q(t, s)\rho(t, s)ds\right) dr\right) b(\xi, A(\xi))d\xi \\
&= \int_{t-\tau_E(t)}^{t} \exp\left(-\int_{\xi}^{t} \mu_E(r)dr\right) b(\xi, A(\xi))d\xi.
\end{aligned} \tag{3.4}$$

All the larvae at time t are developed from eggs laid at previous time $(\xi - f_E(\xi))$ with $\xi \in (t - \tau_L(t), t)$ and successfully survived in the egg stage for $\tau_E(\xi)$ (i.e. $f_E(\xi)$) time period, then matured into larvae with a "maturation rate" $(1 - \tau_E'(\xi))$ at time ξ and remain alive in the larval stage until time t. Thus, the number of larvae at time t can be expressed as follows:

$$
\begin{aligned}
L(t) =& \int_{t-\tau_L(t)}^{t} \exp\left(-\int_{\xi-f_E(\xi)}^{t} \mu\left(r, a, \int_0^{a_{\max}} q(t,s)\rho(t,s)ds\right) dr\right) b(\xi - f_E(\xi), A(\xi - f_E(\xi)))(1-\tau_E'(\xi))d\xi \\
=& \int_{t-\tau_L(t)}^{t} \exp\left(-\int_{\xi}^{t} (\mu_L(r) + D_L(r, L(r))L(r))dr - \int_{\xi-f_E(\xi)}^{\xi} \mu_E(r)dr\right) \\
& b(\xi - f_E(\xi), A(\xi - f_E(\xi)))(1-f_E'(\xi))d\xi.
\end{aligned}
\tag{3.5}
$$

Similarly, nymphs at time t contain all newly developed nymphs at previous time ξ with $\xi \in (t-\tau_N(t), t)$ and survived to time t. These newly developed nymphs are grown from larvae produced at time $(\xi - \tau_L(\xi))$, which developed through $\tau_L(\xi)$ time period in the larval stage and matured into nymphs at time ξ with "maturation rate" $(1-\tau_L'(\xi))$. Likewise, the larvae produced at time $(\xi - \tau_L(\xi))$ come from the eggs laid at time $(\xi - \tau_L(\xi) - \tau_E(\xi - \tau_L(\xi)))$, i.e. $(\xi - f_L(\xi))$, which survived through $(\tau_E(\xi - \tau_L(\xi)))$ time period and matured into larvae at time $(\xi - \tau_L(\xi))$ with "maturation rate" $(1 - \tau_E'(\xi - \tau_L(\xi)))$. Therefore, the total number of nymphs at time t is given as follows:

$$
\begin{aligned}
N(t) =& \int_{t-\tau_N(t)}^{t} \exp\left(-\int_{\xi-f_L(\xi)}^{t} \mu\left(r, a, \int_0^{a_{\max}} q(r,s)\rho(t,s)ds\right) dr\right) \\
& b(\xi - f_L(\xi), A(\xi - f_L(\xi)))(1-\tau_L'(\xi))(1-\tau_E'(\xi-\tau_L(\xi)))d\xi \\
=& \int_{t-\tau_N(t)}^{t} \exp\left(-\int_{\xi}^{t} (\mu_N(r) + D_N(r, N(r))N(r))dr - \int_{\xi-\tau_L(\xi)}^{\xi} (\mu_L(r) + D_L(r, L(r))L(r))dr \right. \\
& \left. - \int_{\xi-f_L(\xi)}^{\xi-\tau_L(\xi)} \mu_E(r)dr\right) b(\xi - f_L(\xi), A(\xi - f_L(\xi)))(1-f_L'(\xi))d\xi.
\end{aligned}
\tag{3.6}
$$

Similarly, the total number $A(t)$ can be computed in the following integral form:

$$
\begin{aligned}
A(t) =& \exp\left(-\int_0^t (\mu_A(\xi) + D_A(\xi, A(\xi))A(\xi))d\xi\right) \left[\int_0^t (1-f_N'(\xi))b(\xi - f_N(\xi), A(\xi - f_N(\xi)))\right. \\
& \exp\left(-\int_{\xi-\tau_N(\xi)}^{\xi} (\mu_N(r) + D_N(r, N(r))N(r))dr - \int_{\xi-\tau_N(\xi)-\tau_L(\xi-\tau_N(\xi))}^{\xi-\tau_N(\xi)} (\mu_L(r) + D_L(r, L(r))L(r))dr \right. \\
& \left.\left. - \int_{\xi-f_N(\xi)}^{\xi-\tau_N(\xi)-\tau_L(\xi-\tau_N(\xi))} \mu_E(r)dr\right) \exp\left(\int_0^{\xi} \mu_A(r) + D_A(r, A(r))A(r)dr\right) d\xi + A_0\right],
\end{aligned}
\tag{3.7}
$$

where $A_0 = A(0)$ is the initial value of $A(t)$.

Combining with the relationships between $f_i(t)$ and $\tau_i(t)$ $(i = E, L, N)$ shown in (3.1), it is easy to check by differentiation that the system of integral equations consisting of (3.4), (3.5), (3.6) and (3.7) is equivalent to the system (3.3).

We would like to draw readers' attention to the fact that a similar model system was formulated in paper [18]. The main focus of the current paper is on the mathematical analysis of this kind of systems to get the global properties of solutions. Moreover, we will link the relationships between the basic reproduction number and the population dynamics of ticks. Here, we reformulate the model system for readers' convenience.

4. Analysis of the model

To investigate the long-term dynamics of system (3.3), we make the following assumptions, justified with the tick growth biology [18]:

(C1) All the mortality rates including per-capita natural death rates $\mu_i(t)$ $(i = E, L, N, A)$ and density dependent death coefficients $D_i(t, i)$ $(i = L, N, A)$ are non-negative T-periodic continuous functions with respect to time t. In addition, $D_i(t, i)$ is non-decreasing with respect to i for $i = L, N, A$.

(C2) The birth rate $b(t, A)$ satisfies:

- (i) $b(t, 0) \equiv 0$, $\frac{\partial b(t,0)}{\partial A} = \beta(t) > 0$ for all $t \in \mathbb{R}$, where $\beta(t)$ is a T-periodic continuous function;
- (ii) $b(t, A)$ is increasing with respect to A for all $A > 0$ and $b(t, A) \leq \frac{\partial b(t,0)}{\partial A} A = \beta(t)A$ for all $(t, A) \in \mathbb{R} \times \mathbb{R}_+$.

(C3) There exist positive constants $D_{\min}$ and A^* such that $D_A(t, A) > D_{\min}$ hold for all $t \in [0, T]$ when $A > A^*$.

Let $\hat{f} = \max_{t\in[0,T]} f_N(t)$, define $C_{\hat{f}} = C([-\hat{f}, 0], \mathbb{R}^4)$. For any $\phi \in C_{\hat{f}}$, define the norm $\|\phi\| = \max\limits_{\theta\in[-\hat{f},0]} \|\phi(\theta)\|_{\mathbb{R}^4}$. Then $C_{\hat{f}}$ is a Banach space. Let $C^+_{\hat{f}} = C([-\hat{f}, 0], \mathbb{R}^4_+)$, then $(C_{\hat{f}}, C^+_{\hat{f}})$ is a strongly ordered space. Given a function $u(t) : [-\hat{f}, \sigma) \to \mathbb{R}^4$ for $\sigma > 0$, define $u_t \in C_{\hat{f}}$ by $u_t(\theta) = u(t + \theta)$, for all $\theta \in [-\hat{f}, 0]$ and $t \in [0, \sigma)$.

Before exploring the long-term dynamics, we firstly verify the global existence of solutions to system (3.3).

Lemma 4.1. *A unique solution* $(E(t), L(t), N(t), A(t))$ *of system (3.3) exists globally on* $[0, \infty)$ *with the initial data* $\phi(\theta) \in C^+_{\hat{f}}$. *Moreover, system (3.3) generates a* T*-periodic semiflow* $\Phi_t : C^+_{\hat{f}} \to C^+_{\hat{f}}$, *i.e.* $\Phi_t(\phi)(\theta) = (E(t + \theta; \phi), L(t + \theta; \phi), N(t + \theta; \phi), A(t + \theta; \phi))$, $\forall \phi \in C^+_{\hat{f}}$, $t \geq 0$, $\theta \in [-\hat{f}, 0]$.

Proof. Set $A^{**} = \max\{\frac{\hat{\beta}}{D_{\min}}\hat{\gamma}_N, A^*\}$, where $\hat{\gamma}_N = \max\limits_{t\in[0,T]}(1 - f'_N(t))$ and $\hat{\beta} = \max\limits_{t\in[0,T]} \beta(t)$. Based on assumptions (C2) and (C3), we can show that $[0, \rho A^{**}]$ is positively invariant for the last equation of system (3.3) with any given $\rho \geq 1$, that is, the unique solution $A(t)$ with $0 \leq A(\theta) \leq \rho A^{**}$ satisfies $0 \leq A(t) \leq \rho A^{**}$ for all $t \geq 0$ and for any $\theta \in [-\hat{f}, 0]$. It easily follows from Theorem 2.2 that $A(t)$ is nonnegative. We claim $A(t) \leq \rho A^{**}$ by the argument of contradiction. Assume the contrary, there exists t_0 such that $A(t) < \rho A^{**}$ when $t < t_0$, while $A(t_0) = \rho A^{**}$, then $\frac{dA(t)}{dt}\Big|_{t_0} \geq 0$. However, it follows from assumptions (C2) and (C3) that

$$\begin{aligned}\frac{dA(t)}{dt}\Big|_{t_0} &\leq (1 - f'_N(t_0))b(t_0 - f_N(t_0), A(t_0 - f_N(t_0))) - D_A(t_0, A(t_0))A^2(t_0) \\ &\leq \hat{\gamma}_N \hat{\beta} \rho A^{**} - D_{\min}(\rho A^{**})^2 < 0.\end{aligned}$$

Therefore, $A(t) \in [0, \rho A^{**}]$ for all t provided that $0 \leq A(\theta) \leq \rho A^{**}$ for any $\theta \in [-\hat{f}, 0]$.

Likewise, $E(t)$, $L(t)$ and $N(t)$ are bounded since

$$\begin{aligned}
E(t) &\le \int_{t-\tau_E(t)}^{t} b(\xi, A(\xi))d\xi \le \int_{t-\tau_E(t)}^{t} \beta(\xi)A(\xi)d\xi \le \rho\hat{\tau}_E\hat{\beta}A^{**},\\
L(t) &\le \int_{t-\tau_L(t)}^{t} (1-f_E'(\xi))b(\xi - f_E(\xi), A(\xi - f_E(\xi)))d\xi\\
&\le \int_{t-\tau_L(t)}^{t} (1-f_E'(\xi))\beta(\xi - f_E(\xi))A(\xi - f_E(\xi))d\xi \le \rho\hat{\tau}_L\hat{\gamma}_E\hat{\beta}A^{**},\\
N(t) &\le \int_{t-\tau_N(t)}^{t} (1-f_L'(\xi))b(\xi - f_L(\xi), A(\xi - f_L(\xi)))d\xi\\
&\le \int_{t-\tau_N(t)}^{t} (1-f_L'(\xi))\beta(\xi - f_L(\xi))A(\xi - f_L(\xi))d\xi \le \rho\hat{\tau}_N\hat{\gamma}_L\hat{\beta}A^{**},
\end{aligned}$$

where $\hat{\tau}_E = \max\limits_{t\in[0,T]}\tau_E(t)$, $\hat{\tau}_L = \max\limits_{t\in[0,T]}\tau_L(t)$, $\hat{\tau}_N = \max\limits_{t\in[0,T]}\tau_N(t)$, $\hat{\gamma}_E = \max\limits_{t\in[0,T]}(1-f_E'(t))$ and $\hat{\gamma}_L = \max\limits_{t\in[0,T]}(1-f_L'(t))$. Hence,

$$S := C([-\hat{f}, 0], [0, \rho\hat{\tau}_E\hat{\beta}A^{**}] \times [0, \rho\hat{\tau}_L\hat{\gamma}_E\hat{\beta}A^{**}] \times [0, \rho\hat{\tau}_N\hat{\gamma}_L\hat{\beta}A^{**}] \times [0, \rho A^{**}]),$$

is positively invariant for system (3.3). This further indicates the non-negativity and boundedness of solutions hold in $[0, \infty)$. Thus, a unique solution $(E(t), L(t), N(t), A(t))$ of system (3.3) exists globally on $[0, \infty)$ with the initial data $\phi(\theta) \in C_{\hat{f}}^{+}$.

Define the solution map of system (3.3) as

$$\Phi_t(\phi)(\theta) = (E(t+\theta;\phi), L(t+\theta;\phi), N(t+\theta;\phi), A(t+\theta;\phi)), \quad \forall t \ge 0,\ \theta \in [-\hat{f}, 0],\ \phi \in C_{\hat{f}}^{+},$$

where $(E(t;\phi), L(t;\phi), N(t;\phi), A(t;\phi))$ is the solution of system (3.3) with the initial data $\phi(\theta)$ for all $\theta \in [-\hat{f}, 0]$. Due to the periodicity of the variable coefficients, it easily follows that Φ_t is a T-periodic semiflow on $C_{\hat{f}}^{+}$. □

4.1. Extinction and persistence

It follows from the assumption (C2) that system (3.3) has the extinction equilibrium $(0, 0, 0, 0)$. The linearized system of system (3.3) at the population extinction equilibrium is:

$$\begin{aligned}
\frac{dE(t)}{dt} &= \beta(t)A(t) - \mu_E(t)E(t) - (1-f_E'(t))h_1(t)\beta(t-f_E(t))A(t-f_E(t)),\\
\frac{dL(t)}{dt} &= (1-f_E'(t))h_1(t)\beta(t-f_E(t))A(t-f_E(t)) - \mu_L(t)L(t)\\
&\quad - (1-f_L'(t))h_2(t)\beta(t-f_L(t))A(t-f_L(t)),\\
\frac{dN(t)}{dt} &= (1-f_L'(t))h_2(t)\beta(t-f_L(t))A(t-f_L(t)) - \mu_N(t)N(t)\\
&\quad - (1-f_N'(t))h_3(t)\beta(t-f_N(t))A(t-f_N(t)),\\
\frac{dA(t)}{dt} &= (1-f_N'(t))h_3(t)\beta(t-f_N(t))A(t-f_N(t)) - \mu_A(t)A(t).
\end{aligned} \tag{4.1}$$

The last equation in (4.1) is decoupled, giving a linear scalar delay differential equation as below:

$$\frac{dA(t)}{dt} = (1 - f_N'(t))h_3(t)\beta(t - f_N(t))A(t - f_N(t)) - \mu_A(t)A(t). \tag{4.2}$$

Since all time-dependent coefficients are non-negative T-periodic functions, both systems (3.3) and (4.1) are T-periodic. Let C_T be the ordered Banach space of all T-periodic continuous functions from $\mathbb{R}$ to $\mathbb{R}$, which is equipped with the maximum norm $\|\cdot\|$ and the positive cone

$$C_T^+ := \{\phi \in C_T : \phi(t) \geq 0, \quad \forall t \in \mathbb{R}\}.$$

Let $F(t)(\phi) = (1 - f_N'(t))h_3(t)\beta(t - f_N(t))\phi(-f_N(t))$ and $V(t) = \mu_A(t)$, then the next generation operator $\mathcal{L} : C_T \to C_T$ is defined as [28]

$$\begin{aligned} [\mathcal{L}\phi](t) &= \int_0^\infty e^{-\int_{t-s}^t V(r)dr} F(t-s)\phi(t-s+\cdot)ds \\ &= \int_0^\infty e^{-\int_{t-s}^t \mu_A(r)dr}(1 - f_N'(t-s))h_3(t-s)\beta(t-s-f_N(t-s))\phi(t-s-f_N(t-s))ds. \end{aligned}$$

We then define the basic reproduction number as the spectral radius of $\mathcal{L}$, i.e. $\mathcal{R}_0 = r(\mathcal{L})$. Let $P(t)$ be the solution map of the linear periodic equation (4.2) on $Y := C([-\hat{f}, 0], \mathbb{R})$, that is, $P(t)\phi = w_t(\phi)$, $t \geq 0$, where $w_t(\phi)(\theta) = w(t+\theta; \phi)$, $\forall \theta \in [-\hat{f}, 0]$, is the solution semiflow of (4.2) satisfying $w_0 = \phi \in Y$. Hence, $P := P(T)$ is the Poincaré map associated with system (4.2). Let $r(P)$ be the spectral radius of P. The following Lemma shows that the system admits a special solution, which is the key technique for investigating the long-term dynamics in later proofs. The argument below is motivated by the treatment in [29].

Lemma 4.2. *There exists a positive T-periodic function $v(t)$ such that $w(t) = e^{\mu t}v(t)$ is a positive solution of (4.2), where $\mu = \frac{\ln r(P)}{T}$.*

Proof. Since $(1 - f_N'(t))h_3(t)\beta(t - f_N(t)) > 0$, then P is a positive operator on Y. It then follows from Krein-Rutman theorem [30, Theorem 3.1] that $r(P)$ is an eigenvalue of P with a positive eigenfunction ψ^*. Let $\mu = \frac{\ln r(P)}{T}$. Suppose $w(t)$ is the particular solution of (4.2) through ψ^*, that is $w(\theta) = \psi^*(\theta)$ and $w(T+\theta) = P(\psi^*)(\theta) = r(P)\psi^*(\theta)$ for all $\theta \in [-\hat{f}, 0]$. Let $v(t) = e^{-\mu t}w(t)$, then $v(\theta) = e^{-\mu\theta}w(\theta) = e^{-\mu\theta}\psi^*(\theta)$ for all $\theta \in [-\hat{f}, 0]$. Furthermore, for all $\theta \in [-\hat{f}, 0]$, we have

$$v(T+\theta) = e^{-\mu(T+\theta)}w(T+\theta) = e^{-\mu(T+\theta)}r(P)\psi^*(\theta) = e^{-\mu\theta}\psi^*(\theta) = v(\theta).$$

Hence, $v(t)$ is periodic and (4.2) admits a special solution $w(t) = e^{\mu t}v(t)$. Moreover, it is very easy to see that $v(t) > 0$ for all $t \in [0, T]$. □

The following theorem deals with extinction and uniform persistence in terms of $\mathcal{R}_0$. Let

$$M_0 := \{\phi = (\phi_1, \phi_2, \phi_3, \phi_4) \in C_{\hat{f}} : \phi_4(0) > 0\},$$

and

$$\partial M_0 := C_{\hat{f}} \setminus M_0 = \{\phi = (\phi_1, \phi_2, \phi_3, \phi_4) \in C_{\hat{f}} : \phi_4(0) = 0\}.$$

Theorem 4.3. *Let (C1), (C2) and (C3) hold. Then, the following statements are valid:*

(1) If $\mathcal{R}_0 < 1$, then the population extinction equilibrium $(0,0,0,0)$ is globally attractive for system (3.3) on $C_{\hat{f}}$.

(2) If $\mathcal{R}_0 > 1$, then system (3.3) admits a positive T-periodic solution $(E^*(t), L^*(t), N^*(t), A^*(t))$ in M_0 and there exists a real number $\eta > 0$ such that the solution $(E(t), L(t), N(t), A(t))$ with $\phi \in M_0$ satisfies $\liminf_{t\to\infty} i(t) \geq \eta$ for $i = E, L, N, A$.

Proof. In the case where $\mathcal{R}_0 < 1$, we have $r(P) < 1$ since $sign(\mathcal{R}_0 - 1)$=$sign(r(P) - 1)$ in light of [28, Theorem 2.1]. Based on Lemma 4.2, there is a positive T-periodic function $v(t)$ such that $w(t) = e^{\mu t}v(t)$ is a positive solution of (4.2), where $\mu = \frac{\ln r(P)}{T} < 0$. Then, the positivity of $A(t)$ and assumption (C2) indicate that

$$\begin{aligned}\frac{dA(t)}{dt} &\leq (1 - f_N'(t))h_3(t)b(t - f_N(t), A(t - f_N(t))) - \mu_A(t)A(t)\\ &\leq (1 - f_N'(t))h_3(t)\beta(t - f_N(t))A(t - f_N(t)) - \mu_A(t)A(t).\end{aligned}$$

Hence, the comparison theorem [31, Theorem 5.1.1] implies that

$$A(t) \leq Kw(t) = Ke^{\mu t}v(t),$$

with constant $K > 0$ satisfying $A(\theta) \leq Ke^{\mu\theta}v(\theta)$ for all $-\hat{f} \leq \theta \leq 0$. Hence $\lim_{t\to\infty} A(t) = 0$.

Besides, based on equation (3.4), (3.5) and (3.6), it follows from assumption (C3) that

$$\begin{aligned}E(t) &\leq \int_{t-\tau_E(t)}^{t} b(\xi, A(\xi))d\xi \leq \int_{t-\tau_E(t)}^{t} \beta(\xi)A(\xi)d\xi,\\ L(t) &\leq \int_{t-\tau_L(t)}^{t} (1 - f_E'(\xi))b(\xi - f_E(\xi), A(\xi - f_E(\xi)))d\xi \leq \int_{t-\tau_L(t)}^{t} \hat{\gamma}_E\beta(\xi - f_E(\xi))A(\xi - f_E(\xi))d\xi,\\ N(t) &\leq \int_{t-\tau_N(t)}^{t} (1 - f_L'(\xi))b(\xi - f_L(\xi), A(\xi - f_L(\xi)))d\xi \leq \int_{t-\tau_N(t)}^{t} \hat{\gamma}_L\beta(\xi - f_L(\xi))A(\xi - f_L(\xi))d\xi.\end{aligned}$$

Thus, when $\mathcal{R}_0 < 1$,

$$\lim_{t\to\infty}(E(t), L(t), N(t), A(t)) = (0,0,0,0).$$

In the case where $\mathcal{R}_0 > 1$, we have $r(P) > 1$. Then, there exists a sufficiently small $\epsilon > 0$, such that r_ϵ, the spectral radius of the Poincaré map corresponding to

$$u'(t) = (1 - f'_N(t))h_3(t)(\beta(t - f_N(t)) - \epsilon)u(t - f_N(t)) - (\mu_A(t) + \epsilon)u(t), \tag{4.3}$$

satisfies $r_\epsilon > 1$ [28]. Similarly, there is a positive T-periodic function $v^\epsilon(t)$ such that $u(t) = e^{\lambda t}v^\epsilon(t)$ is a positive solution of equation (4.3) with $\lambda = \frac{\ln r_\epsilon}{T} > 0$.

Based on the continuity of $g_2(t, \cdot, \cdot)$ and differentiability of $b(t, \cdot)$, for any $\epsilon > 0$, we can choose a sufficiently small number $\eta_1 > 0$ such that for all $i \in [0, \eta_1]$ $(i = L, N, A)$

$$g_2(t, L, N)b(t, A) \geq (g_2(t, 0, 0)\frac{\partial b(t, 0)}{\partial A} - \epsilon)A = (\beta(t) - \epsilon)A,$$

and $D_A(t, A)A < D_A(t, \eta_1)\eta_1 < \epsilon$ hold according to assumption (C1).

Recall that the solution semiflow $\Phi_t(\phi)$ (defined in Lemma 4.1) tends to 0 uniformly for all $t \in [0, T]$ when ϕ approaches to 0, then there exists $\eta_0 > 0$ such that for any $\|\phi\| \leq \eta_0$, we have

$$\|\Phi_t(\phi)\| \leq \eta_1, \ \forall t \in [0, T].$$

Furthermore, we can prove the following weak persistence claim when $\mathcal{R}_0 > 1$:

Claim: $\limsup_{n\to\infty}\|\Phi_{nT}(\phi)\| \geq \eta_0$ **for all** $\phi \in M_0$**.**

Suppose the claim is false, then $\limsup_{n\to\infty}\|\Phi_{nT}(\phi)\| < \eta_0$ for some $\phi \in M_0$. Hence, there exists a positive integer N_1, such that $\|\Phi_{nT}(\phi)\| < \eta_0$ when $n \geq N_1$. Thus, for any $t = nT + t_1$ with $n \geq N_1$ and $t_1 \in [0, T]$, we have $\|\Phi_t(\phi)\| = \|\Phi_{t_1}(\Phi_{nT}(\phi))\| \leq \eta_1$ and

$$\frac{dA(t)}{dt} \geq (1 - f'_N(t))h_3(t)(\beta(t - f_N(t)) - \epsilon)A(t - f_N(t)) - (\mu_A(t) + \epsilon)A(t).$$

Again, by the comparison theorem [31, Theorem 5.1.1], we can conclude that

$$A(t) \geq Ku(t) = Ke^{\lambda t}v^\epsilon(t),$$

with constant $K > 0$ satisfying $A(\theta) \geq Ke^{\lambda\theta}v^\epsilon(\theta)$ for all $-\hat{f} \leq \theta \leq 0$ (If $A(\theta) = 0$ for some $\theta \in [-\hat{f}, 0]$, a time shift of $nT > \hat{f}$ for some integer n is sufficient to ensure the initial value of $A(\cdot)$ is strongly positive). This implies

$$\lim_{t\to\infty} A(t) \geq \lim_{t\to\infty} K\ e^{\lambda t}v^\epsilon(t) = \infty,$$

contradicting to the uniform boundedness of $A(t)$.

Let $M_1 = (0, 0, 0, 0)$. It then follows from the above claim that M_1 is an isolated invariant set for P on $C_{\hat{f}}$ and $W^s(M_1) \cap M_0 = \varnothing$, where $W^s(M_1)$ is the stable set of M_1 for P. Define

$$M_\partial := \{\phi \in \partial M_0 : P^n(\phi) \in \partial M_0, \forall n \geq 0\}.$$

Then $\cup_{\phi \in M_\partial} \omega(\phi) = M_1$. In addition, it is easy to see that no subset of M_1 forms a cycle in M_∂, which also holds in ∂M_0. Further, the proof of Lemma 4.1 implies that Φ_t is point dissipative. According to the acyclicity theorem on uniform persistence for maps in [32], we have $P : C_{\hat{f}} \to C_{\hat{f}}$ is uniformly persistent with respect to M_0. Thus, Theorem 3.1.1 of [32] implies that the semiflow $\Phi_t : C_{\hat{f}} \to C_{\hat{f}}$ is also uniformly persistent with respect to M_0. Based on [33, Theorem 3.1], it can be concluded that system (3.3) admits a T-periodic solution $(E^*(t), L^*(t), N^*(t), A^*(t))$ with $(E^*(\theta), L^*(\theta), N^*(\theta), A^*(\theta)) \in M_0$.

In order to obtain the practical uniform persistence, we define a continuous function $p : C_{\hat{f}} \to \mathbb{R}_+$ by

$$p(\phi) = \phi_4(0), \qquad \forall \phi = (\phi_1, \phi_2, \phi_3, \phi_4) \in C_{\hat{f}}.$$

By applying similar arguments to the proof of [34, Theorem 3.2], we can obtain the practical uniform persistence, that is, there exists $\eta_1 > 0$ such that $\liminf_{t\to\infty} A(t, \phi) \geq \eta_1$. By using the equations for other variables, there exists $\eta > 0$ such that

$$\liminf_{t\to\infty} \min(E(t,\phi), L(t,\phi), N(t,\phi), A(t,\phi)) \geq \eta, \ \forall \phi \in M_0.$$

□

4.2. Global stability of the positive periodic solution

We will establish the global stability in terms of the basic reproduction number for a special case when there is no intra-specific competition in the immature stages, which means the density dependent death coefficients $D_i(t,i)$ $(i = L, N)$ take 0. Indeed, this assumption makes sense in biology when the host community, which includes a group of small mammals such as white-footed mice, chipmunks and shrews [19], is very rich. If the host density is very high, the intra-specific competition during immature stages can be ignored and system (3.3) reduces to the following one:

$$\begin{aligned}
\frac{dE(t)}{dt} &= b(t, A(t)) - \mu_E(t)E(t) - (1 - f_E'(t))h_1(t)b(t - f_E(t), A(t - f_E(t))), \\
\frac{dL(t)}{dt} &= (1 - f_E'(t))h_1(t)b(t - f_E(t), A(t - f_E(t))) - \mu_L(t)L(t) \\
&\quad - (1 - f_L'(t))h_2(t)b(t - f_L(t), A(t - f_L(t))), \\
\frac{dN(t)}{dt} &= (1 - f_L'(t))h_2(t)b(t - f_L(t), A(t - f_L(t))) - \mu_N(t)N(t) \\
&\quad - (1 - f_N'(t))h_3(t)b(t - f_N(t), A(t - f_N(t))), \\
\frac{dA(t)}{dt} &= (1 - f_N'(t))h_3(t)b(t - f_N(t), A(t - f_N(t))) - \mu_A(t)A(t) - D_A(t, A(t))A^2(t).
\end{aligned} \tag{4.4}$$

Since variables E, L and N in system (4.4) do not appear in equation related to A, it suffices to study the decoupled system:

$$\frac{dA(t)}{dt} = (1 - f_N'(t))h_3(t)b(t - f_N(t), A(t - f_N(t))) - \mu_A(t)A(t) - D_A(t, A(t))A^2(t). \tag{4.5}$$

Note that the linearized system for equation (4.5) at the population extinction equilibrium is precisely (4.2). Therefore, the previous theoretical results including the formulation of $\mathcal{R}_0$ and Theorem 4.3 remain valid.

We can further show that the positive periodic solution is globally attractive when $\mathcal{R}_0 > 1$, which is the main focus of this subsection. To do this, we will employ the theory of monotone and subhomogeneous semiflows [32, Section 2.3]. To explore this result, the key idea is to show that the periodic semiflow of the decoupled system (4.5) is (eventually) strongly monotone in a suitable phase space. However, in the natural space $Y := C([-\hat{f}, 0], \mathbb{R})$, the periodic semiflow is monotone but not strongly monotone. As a matter of fact, a solution periodic semiflow $\tilde{\Phi}_t$ can also be defined through a new phase space $X := C([-f_N(0), 0], \mathbb{R})$, see [35]. Then we can show that the periodic semiflow $\tilde{\Phi}_t$ is strongly monotone and strictly subhomogeneous. Now we have two phase spaces for (4.5), X and Y with the following observation for the solution in these two phase spaces [35, Lemma 3.3 and 3.5]:

$$A(t;\phi) = A(t;\psi), \forall \phi \in Y,\ \forall \psi \in X, \quad \text{provided that } \phi(\theta) = \psi(\theta),\ \forall \theta \in [-f_N(0), 0].$$

However, since different phase spaces are used, $\mathcal{R}_0$ may not determine the stability of the linear periodic system of (4.5) on X. It is necessary to prove the equivalence of stability properties for the linear periodic system of (4.5) in two different spaces. Recall that $P(t)$ is already defined as the solution map of linear periodic system (4.2) on Y in the above proof. Then, we denote $\tilde{Q}(t)$ as the solution map of the linear periodic system of (4.5) on X. The following lemma reveals the equivalence of stability properties for the linear periodic system in these two spaces, which can be obtained by an argument similar to that in [35].

Lemma 4.4. *Poincaré maps $P(T)$ and $\tilde{Q}(T)$ have the same spectral radius, that is, $r(P(T)) = r(\tilde{Q}(T))$.*

Let $X_+ := C([-f_N(0), 0], \mathbb{R}_+)$. The subsequent two theorems show that $\tilde{\Phi}_t$ is a strongly monotone and strictly subhomogeneous periodic semiflow in X.

Theorem 4.5. *For any ϕ_1 and ϕ_2 in X_+ with $\phi_1 > \phi_2$ (that is, $\phi_1 \geq \phi_2$ but $\phi_1 \neq \phi_2$), the solutions $u_1(t)$ and $u_2(t)$ of system (4.5) with $u_1(\cdot) = \phi_1$ and $u_2(\cdot) = \phi_2$, respectively, satisfy $u_1(t) > u_2(t)$ for all $t > \hat{f}$, and hence $\tilde{\Phi}_t(\phi_1) \gg \tilde{\Phi}_t(\phi_2)$ in X for all $t > 2\hat{f}$.*

Proof. It is easy to prove $u_1(t) \geq u_2(t)$ for all $t \geq 0$ by a repeated comparison argument on each interval $[nf_N(0), (n+1)f_N(0)]$, $n \in \mathbb{N}$. Since $u_i(t)$ $(i = 1, 2)$ is bounded on $[0, \infty)$, then $u_i(t)$ $(i = 1, 2)$ can be restricted in an order interval $[0, h]$ for all $t \geq 0$, where h is a positive real number. Hence, we can construct a function $g(t,A) = -\mu_A(t)A - D_A(t,A)A^2 + HA$, where $H > 0$ is a large number to guarantee g is increasing with respect to A when $A \in [0,h]$. It is noted that $u_i(t)$ $(i = 1,2)$ satisfy the integral equation:

$$A(t) = e^{-Ht}A(0) + \int_0^t e^{-H(t-s)}g(s,A(s))ds + \int_0^t e^{-H(t-s)}(1 - f_N'(s))h_3(s)b(s - f_N(s), A(s - f_N(s)))ds. \tag{4.6}$$

It is apparent that $[-f_N(0),0] \subset [-f_N(0), \hat{f} - f_N(\hat{f})]$. Since $\phi_1 > \phi_2$, there exists an $\eta \in [-f_N(0),0]$ such that $u_1(\eta) > u_2(\eta)$. It follows from equation (4.6) and the comparison theorem [31, Theorem 5.1.1] that $u_1(t) > u_2(t)$ for all $t > \hat{f}$. Thus, the solution map $\tilde{\Phi}_t$ is strongly monotone if $t > 2\hat{f}$. □

Before establishing the next result, we propose an additional assumption about the birth rate $b(t,A)$, that is,

(S1) The birth rate $b(t,A)$ can be expressed as follows,

$$b(t,A) = B(t,A)A,$$

where $B(t,A)$ is the per-capita birth rate and non-increasing in A for all $t \in \mathbb{R}$.

This assumption is reasonable for ticks according to [14], as the per-capita birth rate for ticks is decreasing with respect to the number of adults due to host grooming or host resistance. With this assumption, we can show that $\tilde{\Phi}_t$ is strictly subhomogeneous through the following theorem.

Theorem 4.6. *For any $\psi \gg 0$ in X and any $r \in (0,1)$, the following two results hold, that is,*

(i) $u(t; r\psi) > ru(t;\psi)$ for all $t > \hat{f}$;

(ii) $\tilde{\Phi}_T^n(r\psi) \gg r\tilde{\Phi}_T^n(\psi)$ in X, for all integer n satisfing $nT > 2\hat{f}$.

Proof. Let $u(t;\psi)$ be the unique solution of system (4.5) with $u_0 = \psi \gg 0$ in X. For notational simplification, we use $w(t) = u(t; r\psi)$ and $v(t) = ru(t;\psi)$. It then follows from Theorem 2.2 that $w(t) > 0$ and $v(t) > 0$ for all $t \geq 0$ and $w(\theta) = r\psi(\theta) = v(\theta)$ for all $\theta \in [-f_N(0), 0]$.

Note that

$$\begin{aligned}
\frac{dv}{dt}\Big|_{t=0} &= r(1 - f_N'(0))h_3(0)B(0 - f_N(0), u(0 - f_N(0)))u(0 - f_N(0)) - \mu_A(0)v(0) - \frac{D_A(0,u(0))}{r}v^2(0) \\
&< (1 - f_N'(0))h_3(0)B(-f_N(0), ru(-f_N(0)))v(-f_N(0)) - \mu_A(0)v(0) - D_A(0,u(0))v^2(0) \\
&\leq (1 - f_N'(0))h_3(0)B(-f_N(0), ru(-f_N(0)))v(-f_N(0)) - \mu_A(0)v(0) - D_A(0,ru(0))v^2(0) \\
&= (1 - f_N'(0))h_3(0)b(-f_N(0), w(-f_N(0))) - \mu_A(0)w(0) - D_A(0,w(0))w^2(0) \\
&= \frac{dw}{dt}\Big|_{t=0}.
\end{aligned}$$

It follows from $w(0) = v(0) > 0$ that there must be an $\xi \in (0,\hat{f})$ such that $w(t) > v(t) > 0$ holds for all $t \in (0,\xi)$. We can further conclude that $w(t) > v(t)$ holds for all $0 < t \leq f_N(0)$. If we assume the contrary, then there is a $\tilde{t} \in (0, f_N(0)]$ such that $w(t) > v(t)$ for all $t \in (0, \tilde{t})$ and $w(\tilde{t}) = v(\tilde{t})$, which indicates $\frac{dv}{dt}\Big|_{t=\tilde{t}} \geq \frac{dw}{dt}\Big|_{t=\tilde{t}}$. However,

$$\begin{aligned}
\frac{dv}{dt}\Big|_{t=\tilde{t}} &= r(1 - f'_N(\tilde{t}))h_3(\tilde{t})B(\tilde{t} - f_N(\tilde{t}), u(\tilde{t} - f_N(\tilde{t})))u(\tilde{t} - f_N(\tilde{t})) - \mu_A(\tilde{t})v(\tilde{t}) - \frac{D_A(\tilde{t}, u(\tilde{t}))}{r}v^2(\tilde{t}) \\
&< (1 - f'_N(\tilde{t}))h_3(\tilde{t})B(\tilde{t} - f_N(\tilde{t}), u(\tilde{t} - f_N(\tilde{t})))v(\tilde{t} - f_N(\tilde{t})) - \mu_A(\tilde{t})v(\tilde{t}) - D_A(\tilde{t}, u(\tilde{t}))v^2(\tilde{t}) \\
&\leq (1 - f'_N(\tilde{t}))h_3(\tilde{t})B(\tilde{t} - f_N(\tilde{t}), ru(\tilde{t} - f_N(\tilde{t})))v(\tilde{t} - f_N(\tilde{t})) - \mu_A(\tilde{t})v(\tilde{t}) - D_A(\tilde{t}, ru(\tilde{t}))v^2(\tilde{t}) \\
&= (1 - f'_N(\tilde{t}))h_3(\tilde{t})b(\tilde{t} - f_N(\tilde{t}), w(\tilde{t} - f_N(\tilde{t}))) - \mu_A(\tilde{t})w(\tilde{t}) - D_A(\tilde{t}, w(\tilde{t}))w^2(\tilde{t}) \\
&= \frac{dw}{dt}\Big|_{t=\tilde{t}},
\end{aligned}$$

which is a contradiction. Similarly, we can repeat this procedure to prove $w(t) > v(t)$ for all $t \in (nf_N(0), (n+1)f_N(0)]$, where n can be any positive integer. Note that $t - f_N(t) > 0$ when $t > \hat{f}$. Thus, $u(t; r\psi) > ru(t; \psi)$ for all $t > \hat{f}$ and $\tilde{\Phi}^n_T(r\psi) = \tilde{\Phi}_{nT}(r\psi) \gg r\tilde{\Phi}_{nT}(\psi) = r\tilde{\Phi}^n_T(\psi)$ in X, where the integer n satisfies $nT > 2\hat{f}$. $\square$

We now prove the global stability of system (4.5) when $\mathcal{R}_0 > 1$ by focusing on the positive cone X_+.

Theorem 4.7. *If $\mathcal{R}_0 > 1$, then system (4.5) has a unique positive T-periodic solution $A^*(t)$, which is globally asymptotically stable in $X_+ \setminus \{0\}$.*

Proof. Note that $\tilde{\Phi}_t$ can be regarded as an n_0T-periodic semiflow in X_+ if we choose proper integer n_0 such that $n_0T > 2\hat{f}$. It follows from Theorems 4.5 and 4.6 that $\tilde{\Phi}_{n_0T}$ is a strongly monotone and strictly subhomogeneous map on X_+. It is shown that the sign of $R_0 - 1$ is the same as $r(D\tilde{\Phi}_{n_0T}(0)) - 1$ [28], where $r(D\tilde{\Phi}_{n_0T}(0)) = r(\tilde{Q}(n_0T)) = (r(\tilde{Q}(T)))^{n_0}$. Based on [32, Theorem 2.3.4] for periodic maps, if $r(D\tilde{\Phi}_{n_0T}(0)) > 1$, system (4.5) admits a unique positive n_0T-periodic solution $A^*(t)$, which is globally asymptotically stable for system (4.5) in $X_+ \setminus \{0\}$. In addition, $A^*(t)$ is T-periodic. This is true since

$$\tilde{\Phi}^{n_0}_T(\tilde{\Phi}_T\psi^*) = \tilde{\Phi}_T(\tilde{\Phi}^{n_0}_T\psi^*) = \tilde{\Phi}_T(\tilde{\Phi}_{n_0T}\psi^*) = \tilde{\Phi}_T(\psi^*),$$

where $\psi^* = A^*_0 \in X$ guarantees $\tilde{\Phi}_{n_0T}\psi^* = \psi^*$. It follows from the uniqueness of the positive fixed point for $\tilde{\Phi}^{n_0}_T = \tilde{\Phi}_{n_0T}$ that $\tilde{\Phi}_T\psi^* = \psi^*$ holds. Thus, $A^*(t)$ is a T-periodic solution of system (4.5). $\square$

Based on the information about the decoupled variable $A(t)$, we can also deduce the solution property for other variables $E(t)$, $L(t)$ and $N(t)$ by their integral expressions:

$$\begin{aligned}
E(t) &= \int_{t-\tau_E(t)}^{t} \exp\left(-\int_{\xi}^{t} \mu_E(r)dr\right) b(\xi, A(\xi))d\xi,\\
L(t) &= \int_{t-\tau_L(t)}^{t} (1-f_E'(\xi)) \exp\left(-\int_{\xi}^{t} \mu_L(r)dr - \int_{\xi-f_E(\xi)}^{\xi} \mu_E(r)dr\right) b(\xi - f_E(\xi), A(\xi - f_E(\xi)))d\xi,\\
N(t) &= \int_{t-\tau_N(t)}^{t} (1-f_L'(\xi)) \exp\left(-\int_{\xi}^{t} \mu_N(r)dr - \int_{\xi-\tau_L(\xi)}^{\xi} \mu_L(r)dr - \int_{\xi-f_L(\xi)}^{\xi-\tau_L(\xi)} \mu_E(r)dr\right)\\
&\qquad b(\xi - f_L(\xi), A(\xi - f_L(\xi)))d\xi.
\end{aligned}$$

It easily follows from the global attractivity of $A(t)$ that

$$\lim_{t\to\infty}[E(t)-E^*(t)] = 0,\ \lim_{t\to\infty}[L(t)-L^*(t)] = 0 \text{ and } \lim_{t\to\infty}[N(t)-N^*(t)] = 0,$$

where

$$\begin{aligned}
E^*(t) &= \int_{t-\tau_E(t)}^{t} \exp\left(-\int_{\xi}^{t} \mu_E(r)dr\right) b(\xi, A^*(\xi))d\xi,\\
L^*(t) &= \int_{t-\tau_L(t)}^{t} (1-f_E'(\xi)) \exp\left(-\int_{\xi}^{t} \mu_L(r)dr - \int_{\xi-f_E(\xi)}^{\xi} \mu_E(r)dr\right) b(\xi - f_E(\xi), A^*(\xi - f_E(\xi)))d\xi,\\
N^*(t) &= \int_{t-\tau_N(t)}^{t} (1-f_L'(\xi)) \exp\left(-\int_{\xi}^{t} \mu_N(r)dr - \int_{\xi-\tau_L(\xi)}^{\xi} \mu_L(r)dr - \int_{\xi-f_L(\xi)}^{\xi-\tau_L(\xi)} \mu_E(r)dr\right)\\
&\qquad b(\xi - f_L(\xi), A^*(\xi - f_L(\xi)))d\xi,
\end{aligned}$$

are all positive T-periodic functions. Thus, the global attractivity of the full system (4.4) can be obtained.

Theorem 4.8. *If $\mathcal{R}_0 > 1$, then system (4.4) has a unique positive T-periodic solution ($E^*(t)$, $L^*(t)$, $N^*(t)$, $A^*(t)$), which is globally attractive for all nontrivial solutions.*

5. Discussion

This paper starts from a periodic version of McKendrick-von Foerster equation with periodic coefficients to describe the population growth with seasonal effects. Using the equivalent integral equation obtained by the method of integration along characteristics, we present a detailed proof of the uniqueness and existence of the solution in light of contraction mapping theorem. It is worth noting that the age-dependent models can also be studied by using the semigroup theory [36] and similar models have been extensively studied in [22]. Our approach is highly motivated by [22, 23].

Then the hyperbolic equation is reduced to a periodic differential system with periodic delays through rigorous biological and mathematical arguments, with the tick population growth as our motivating example. The derived age-structured model with time-dependent periodic delays is quite different from previous time-independent delay system and challenging to conduct global analysis. The basic reproduction number $\mathcal{R}_0$ is defined as the spectral radius of the next generation operator following the work [28]. We should mention that the study [18] has also used the approach in [37] to define and derive the basic reproduction number for tick population dynamics, with some numerical computations for the model parameterized by the blacklegged ticks. The formulation of the basic reproduction number for models with periodic coefficients has been extensively studied and interesting readers can find more details from [38, 39, 40, 41] and references therein.

Even though the specific form of $\mathcal{R}_0$ is not known, it is shown that $\mathcal{R}_0$ is a threshold value for the stability of zero solution of the corresponding linear equation [28, Theorem 2.1]. Given this, the extinction and uniform persistence of tick population can be proved in terms of $\mathcal{R}_0$. Other than that, we acquire the existence of at least one positive periodic solution. When the host community for immature ticks is very rich, the intra-specific competition between immature stages of ticks is negligible. In this scenario, we further obtain the global stability of the positive periodic solution with the following two steps. Firstly, we investigate the global attractivity of the equation for the adult stage when $\mathcal{R}_0 > 1$ by applying the theory of monotone systems. We can show that the solution semiflow is strongly monotone and strictly subhomogeneous in a novel space $X := C([-f_N(0), 0], \mathbb{R})$, different from the usual space $Y := C([-\hat{f}, 0], \mathbb{R})$. Then, we extend the result to the full system as the other variables can be represented as integral forms of the adult size. However, the introduction of novel phase space gives rise new challenges and we need to argue the following facts: (1) the solution map can define a periodic semiflow; (2) the basic reproduction number $\mathcal{R}_0$ can not only determine the stability of the system on Y, but also indicate the stability in X; and (3) the periodic semilfow is (eventually) strongly monotone and strictly subhomogeneous.

In this paper, the basic reproduction number $\mathcal{R}_0$ is defined through a scalar periodic delay equation. However, we can not conclude that its value is equal to the coefficient-averaged system as that for a periodic ordinary differential equation in [41, Lemma 2.2] since a delay is involved. This remains a future question. This paper is focusing on the mathematical analysis of the model and simulations have not been presented. Interesting simulations can also be performed for the model system to study the effects of seasonal weather variations and global warming on the population growth, as done in [16, 42]. Furthermore, in the current study, the global stability of the positive periodic solution is obtained when $\mathcal{R}_0 > 1$, however with the condition that the intra-specific competition for immature ticks is negligible due to the sufficient availability of immature tick hosts. When the competition exists, we only show the uniform persistence of the system and existence of a positive periodic solution in this scenario. The number of the positive periodic solutions is an interesting question to address in the future.

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Appendix A: The derivation of integral form by integration along characteristic

Set $\hat{\rho}(h) := \rho(t_0+h, a_0+h)$ and $\hat{\mu}(h) := \mu(t_0+h, a_0+h, \int_0^\infty q(t_0+h,s)\rho(t_0+h,s)ds)$, where t_0 and a_0 are fixed. Differentiating $\hat{\rho}(h)$ with respect to h yields

$$\begin{aligned}\frac{d\hat{\rho}(h)}{dh} &= (\frac{\partial}{\partial t}+\frac{\partial}{\partial a})\rho(t_0+h, a_0+h)\\ &= -\mu(t_0+h, a_0+h, \int_0^\infty q(t_0+h,s)\rho(t_0+h,s)ds)\\ &= -\hat{\mu}(h)\hat{\rho}(h).\end{aligned} \tag{5.1}$$

Integrating (5.1) from 0 to h, we have

$$\hat{\rho}(h) = \hat{\rho}(0)\exp\left(-\int_0^h \hat{\mu}(r)dr\right),$$

that is

$$\rho(t_0+h, a_0+h) = \rho(t_0,a_0)\exp\left(-\int_0^h \mu(t_0+r, a_0+r, \int_0^\infty q(t_0+r,s)\rho(t_0+r,s)ds)dr\right).$$

In case where $a \geq t$, setting $(t_0,a_0) = (0, a-t)$ and $h = t$, it follows that

$$\begin{aligned}\rho(t,a) &= \rho(0,a-t)\exp\left(-\int_0^t \mu(r, a-t+r, \int_0^\infty q(r,s)\rho(r,s)ds)dr\right)\\ &= \phi(a-t)\exp\left(-\int_0^t \mu(r, a-t+r, \int_0^\infty q(r,s)\rho(r,s)ds)dr\right).\end{aligned}$$

Similarly, in case where $t \geq a$, setting $(t_0,a_0) = (t-a, 0)$ and $h = a$ yields

$$\begin{aligned}\rho(t,a) &= \rho(t-a,0)\exp\left(-\int_0^a \mu\left(t-a+r, r, \int_0^\infty q(t-a+r,s)\rho(t-a+r,s)ds\right)dr\right)\\ &= b\left(t-a, \int_0^\infty p(t-a,s)\rho(t-a,s)ds\right)\exp\left(-\int_0^a \mu\left(t-a+r, r, \int_0^\infty q(t-a+r,s)\rho(t-a+r,s)ds\right)dr\right).\end{aligned}$$

Appendix B: Three steps in the proof of Theorem 2.1

Step (I): For any $\eta \in \mathcal{B}$, it follows from equation (2.3) that

$$
\begin{aligned}
&\int_0^\infty |\Lambda(\eta)(t,x)(a)|\, da = \int_0^\infty \Bigg| b\left(t-a, \int_0^\infty p(t-a,s)\eta(t-a,x)(s)ds\right) \\
&\exp\left(-\int_0^a \mu(t-a+r, r, \int_0^\infty q(t-a+r,s)\eta(t-a+r,x)(s)ds)dr\right)\mathbf{1}_{\{t>a\}} \\
&+x(a-t)\exp\left(-\int_0^t \mu(r, a-t+r, \int_0^\infty q(r,s)\eta(r,x)(s)ds)dr\right)\mathbf{1}_{\{a\ge t\}}\Bigg| da \\
\le & b_{\max}\int_0^t e^{-\mu_{\min} a} da + \int_t^\infty \exp\left(-\int_0^t \mu(r, a-t+r, \int_0^\infty q(r,s)\eta(r,x)(s)ds)dr\right)|x(a-t)|\, da \\
\le & b_{\max}\frac{1-e^{-\mu_{\min} t}}{\mu_{\min}} + \int_t^\infty e^{-\mu_{\min} t}|x(a-t)|da \\
\le & b_{\max}\frac{1-e^{-\mu_{\min} t}}{\mu_{\min}} + \|x\| < \infty,
\end{aligned}
$$

for all $t \in [0,\epsilon]$, where ϵ is sufficiently small number, $\|\cdot\|$ is defined as $\int_0^\infty |x(a)|da$, and $b_{\max} > 0$ is the maximal value of $b\left(t, \int_0^\infty p(t,s)\eta(t,x)(s)ds\right)$ on B_0 since the birth function is continuous in the closed region. Therefore, it can be concluded that $\Lambda(\eta) \in Y$ for any $\eta \in \mathcal{B}$.

Step (II): Set $B_0 = U(x_0, \frac{r}{2})$, a ball in $L[0,\infty)$ with radius $\frac{r}{2}$ and $x_0 = \rho(0,\cdot)$, then it follows that for all $x \in B_0$, we have

$$
\begin{aligned}
&\|\Lambda(\eta)(t,x) - x_0\| \\
=&\int_0^\infty \Bigg| b\left(t-a, \int_0^\infty p(t-a,s)\eta(t-a,x)(s)ds\right) \\
&\exp\left(-\int_0^a \mu(t-a+r, r, \int_0^\infty q(t-a+r,s)\eta(t-a+r,x)(s)ds)dr\right)\mathbf{1}_{\{t>a\}} \\
&+x(a-t)\exp\left(-\int_0^t \mu(r, a-t+r, \int_0^\infty q(r,s)\eta(r,x)(s)ds)dr\right)\mathbf{1}_{\{a\ge t\}} - \rho(0,a)\Bigg| da \\
\le & b_{\max}\frac{1-e^{-\mu_{\min} t}}{\mu_{\min}} + \int_0^\infty \left| x(a-t)\exp\left(-\int_0^t \mu(r, a-t+r, \int_0^\infty q(r,s)\eta(r,x)(s)ds)dr\right)\mathbf{1}_{\{a\ge t\}} - \rho(0,a)\right| da \\
\le & b_{\max}\frac{1-e^{-\mu_{\min} t}}{\mu_{\min}} + \int_0^\infty \exp\left(-\int_0^t \mu(r, a-t+r, \int_0^\infty q(r,s)\eta(r,x)(s)ds)dr\right)\mathbf{1}_{\{a\ge t\}}\, |x(a-t) - \rho(0,a-t)|\, da \\
&+\int_0^\infty \left| \exp\left(-\int_0^t \mu(r, a-t+r, \int_0^\infty q(r,s)\eta(r,x)(s)ds)dr\right)\mathbf{1}_{\{a\ge t\}}\rho(0,a-t) - \rho(0,a)\right| da.
\end{aligned}
$$

Note that

$$
\int_0^\infty \exp\left(-\int_0^t \mu(r, a-t+r, \int_0^\infty q(r,s)\eta(r,x)(s)ds)dr\right)\mathbf{1}_{\{a\ge t\}}|x(a-t) - \rho(0,a-t)|da \le \|x(\cdot) - \rho(0,\cdot)\|,
$$

and

$$\begin{aligned}&\int_0^\infty \left|\exp\left(-\int_0^t \mu(r, a-t+r, \int_0^\infty q(r,s)\eta(r,x)(s)ds)dr\right)\mathbf{1}_{\{a\geq t\}}\rho(0,a-t)-\rho(0,a)\right| da\\ &\leq \int_0^\infty \mathbf{1}_{\{a\geq t\}}\rho(0,a-t)\left|\exp\left(-\int_0^t \mu(r, a-t+r, \int_0^\infty q(r,s)\eta(r,x)(s)ds)dr\right)-1\right| da\\ &\quad+\int_0^\infty \left|\rho(0,a-t)\mathbf{1}_{\{a\geq t\}}-\rho(0,a)\right| da.\end{aligned}$$

Hence the dominated-convergence theorem implies

$$\lim_{t\to 0}\int_0^\infty \mathbf{1}_{\{a\geq t\}}\rho(0,a-t)\left|\exp\left(-\int_0^t \mu(r, a-t+r, \int_0^\infty q(r,s)\eta(r,x)(s)ds)dr\right)-1\right| da=0.$$

Therefore, if ϵ is sufficiently small, the following inequality holds for all $t\in[0,\epsilon]$:

$$\int_0^\infty \mathbf{1}_{\{a\geq t\}}\rho(0,a-t)\left|\exp\left(-\int_0^t \mu(r, a-t+r, \int_0^\infty q(r,s)\eta(r,x)(s)ds)dr\right)-1\right| da<\frac{r}{16}.$$

Since the set of all continuous functions with compact support is dense in $L[0,\infty)$, there exists a continuous function ξ with compact support in $[0,\ \infty)$ such that $\|\rho(0,\cdot)-\xi\|\leq\frac{r}{16}$. Besides, the function with compact support vanishes at the boundary, which indicates there exists a bounded and closed interval $I\subset[0,\infty)$ such that $\xi(y)=0$ for $\forall y\notin I$. Then,

$$\begin{aligned}&\int_0^\infty |\rho(0,a-t)\mathbf{1}_{\{a\geq t\}}-\rho(0,a)|da\\ &\leq\int_0^t|\rho(0,a)|da+\int_t^\infty|\rho(0,a-t)-\rho(0,a)|da\\ &\leq\int_0^t|\rho(0,a)|da+\int_t^\infty|\rho(0,a-t)-\xi(a-t)|da+\int_t^\infty|\xi(a-t)-\xi(a)|da+\int_t^\infty|\xi(a)-\rho(0,a)|da\\ &\leq\int_0^t|\rho(0,a)|da+2\int_0^\infty|\xi(a)-\rho(0,a)|da+\int_I|\xi(a-t)-\xi(a)|da\\ &\leq\frac{r}{32}+\frac{r}{8}+\frac{r}{32}=\frac{3r}{16},\end{aligned}$$

where ϵ should be very small.

Hence,

$$\begin{aligned}&\int_0^\infty \left|\exp\left(-\int_0^t \mu(r, a-t+r, \int_0^\infty q(r,s)\eta(r,x)(s)ds)dr\right)\mathbf{1}_{\{a\geq t\}}\rho(0,a-t)-\rho(0,a)\right| da\\ &\leq \int_0^\infty \mathbf{1}_{\{a\geq t\}}\rho(0,a-t)\left|\exp\left(-\int_0^t \mu(r, a-t+r, \int_0^\infty q(r,s)\eta(r,x)(s)ds)dr\right)-1\right| da\\ &+\int_0^\infty \left|\rho(0,a-t)\mathbf{1}_{\{a\geq t\}}-\rho(0,a)\right| da\\ &<\frac{r}{16}+\frac{3r}{16}=\frac{r}{4}.\end{aligned}$$

In summary, we have

$$\|\Lambda(\eta)(t,x) - x_0\| \leq b_{\max}\frac{1-e^{-\mu_{\min}t}}{\mu_{\min}} + \|x(\cdot) - \rho(0,\cdot)\| + \frac{r}{4} < \frac{r}{4} + \frac{r}{2} + \frac{r}{4} = r,$$

for all $t \in [0,\epsilon]$, where constant $\epsilon > 0$ is small enough. Therefore, for any $\eta \in \mathcal{B}$, we have $\Lambda(\eta) \in \mathcal{B}$, that is $\Lambda : \mathcal{B} \to \mathcal{B}$.

Step (III): In the final step, we will show that Λ is a contraction mapping on $\mathcal{B}$ for ϵ small enough. For any $\eta_1, \eta_2 \in \mathcal{B}$, it then follows that

$$
\begin{aligned}
&\|\Lambda(\eta_1)(t,x) - \Lambda(\eta_2)(t,x)\| \leq \int_0^\infty \Bigg| b\left(t-a, \int_0^\infty p(t-a,s)\eta_1(t-a,x)(s)ds\right) \\
&\exp\left(-\int_0^a \mu(t-a+r, r, \int_0^\infty q(t-a+r,s)\eta_1(t-a+r,x)(s)ds)dr\right) \\
&-b\left(t-a, \int_0^\infty p(t-a,s)\eta_2(t-a,x)(s)ds\right)\exp\left(-\int_0^a \mu(t-a+r,r,\int_0^\infty q(t-a+r,s)\eta_2(t-a+r,x)(s)ds)dr\right)\Bigg| \\
&\mathbf{1}_{\{t>a\}}da + \int_0^\infty \Bigg| x(a-t)\exp\left(-\int_0^t \mu(r, a-t+r, \int_0^\infty q(r,s)\eta_1(r,x)(s)ds)dr\right)\mathbf{1}_{\{a\geq t\}} \\
&-x(a-t)\exp\left(-\int_0^t \mu(r,a-t+r,\int_0^\infty q(r,s)\eta_2(r,x)(s)ds)dr\right)\mathbf{1}_{\{a\geq t\}}\Bigg| da \\
&\leq \int_0^t \Bigg| b\left(t-a, \int_0^\infty p(t-a,s)\eta_1(t-a,x)(s)ds\right) - b\left(t-a,\int_0^\infty p(t-a,s)\eta_2(t-a,x)(s)ds\right)\Bigg| \\
&\exp\left(-\int_0^a \mu(t-a+r,r,\int_0^\infty q(t-a+r,s)\eta_1(t-a+r,x)(s)ds)dr\right)da \\
&+\int_0^t b\left(t-a,\int_0^\infty p(t-a,s)\eta_2(t-a,x)(s)ds\right) \\
&\Bigg|\exp\left(-\int_0^a \mu(t-a+r,r,\int_0^\infty q(t-a+r,s)\eta_1(t-a+r,x)(s)ds)dr\right) \\
&-\exp\left(-\int_0^a \mu(t-a+r,r,\int_0^\infty q(t-a+r,s)\eta_2(t-a+r,x)(s)ds)dr\right)\Bigg| da \\
&+\int_t^\infty |x(a-t)|\Bigg|\exp\left(-\int_0^t \mu(r,a-t+r,\int_0^\infty q(r,s)\eta_1(r,x)(s)ds)dr\right) \\
&-\exp\left(-\int_0^t \mu(r,a-t+r,\int_0^\infty q(r,s)\eta_2(r,x)(s)ds)dr\right)\Bigg| da \\
&\leq \bar{b}\int_0^t e^{-\mu_{\min}a}\int_0^\infty p(t-a,s)\left|\eta_1(t-a,x)(s) - \eta_2(t-a,x)(s)\right| dsda \\
&+\int_0^t b_{\max}\int_0^a \Bigg|\mu\left(t-a+r,r,\int_0^\infty q(t-a+r,s)\eta_1(t-a+r,x)(s)ds\right) \\
&-\mu\left(t-a+r,r,\int_0^\infty q(t-a+r,s)\eta_2(t-a+r,x)(s)ds\right)\Bigg| drda \\
&+\int_t^\infty |x(a-t)|\int_0^t \Bigg|\mu\left(r,a-t+r,\int_0^\infty q(r,s)\eta_1(r,x)(s)ds\right) - \mu\left(r,a-t+r,\int_0^\infty q(r,s)\eta_2(r,x)(s)ds\right)\Bigg| drda \\
&\leq \bar{b}\int_0^t e^{-\mu_{\min}a}p_{\sup}\|\eta_1-\eta_2\|da + b_{\max}\int_0^t\int_0^a q_{\sup}\bar{\mu}\|\eta_1-\eta_2\|drda \\
&+\int_t^\infty |x(a-t)|\int_0^t q_{\sup}\bar{\mu}\|\eta_1-\eta_2\|drda \\
&\leq p_{\sup}\bar{b}\frac{1-e^{-\mu_{\min}t}}{\mu_{\min}}\|\eta_1-\eta_2\| + \frac{t^2}{2}q_{\sup}\bar{\mu}b_{\max}\|\eta_1-\eta_2\| + q_{\sup}t\bar{\mu}\|x\|\|\eta_1-\eta_2\| \\
&\leq \left(p_{\sup}\bar{b}\frac{1-e^{-\mu_{\min}t}}{\mu_{\min}} + \frac{t^2}{2}q_{\sup}\bar{\mu}b_{\max} + q_{\sup}t\bar{\mu}\|x\|\right)\|\eta_1-\eta_2\| \\
&\leq \epsilon M\|\eta_1-\eta_2\|,
\end{aligned}
$$

with some constant $M > 0$, $p_{\sup} = \sup_{a\geq 0, t\geq 0}\{p(t,a)\}$ and $q_{\sup} = \sup_{a\geq 0,t\geq 0}\{q(t,a)\}$. It is noted that, in the above proof, $|e^{-x} - e^{-y}| \leq |x-y|$, $\forall x, y > 0$.

Appendix C: Detailed derivation of the system (3.3) of delay differential equations

Differentiating the equations in system (3.2) with respect to time t on both sides yields

$$\begin{aligned}
\frac{dE(t)}{dt} &= \int_0^{f_E(t)} \frac{\partial \rho(t,a)}{\partial t} da + \rho(t, f_E(t)) f_E'(t) \\
&= \rho(t,0) - \rho(t, f_E(t)) - \mu_E(t)E(t) + \rho(t, f_E(t)) f_E'(t) \\
&= b(t, A(t)) - \mu_E(t)E(t) - (1 - f_E'(t))\rho(t, f_E(t)), \\
\frac{dL(t)}{dt} &= \int_{f_E(t)}^{f_L(t)} \frac{\partial \rho(t,a)}{\partial t} da + \rho(t, f_L(t)) f_L'(t) - \rho(t, f_E(t)) f_E'(t) \\
&= \rho(t, f_E(t)) - \rho(t, f_L(t)) - \mu_L(t)L(t) - D_L(t, L(t))L^2(t) + \rho(t, f_L(t)) f_L'(t) - \rho(t, f_E(t)) f_E'(t) \\
&= (1 - f_E'(t))\rho(t, f_E(t)) - \mu_L(t)L(t) - D_L(t, L(t))L^2(t) - (1 - f_L'(t))\rho(t, f_L(t)),
\end{aligned}$$

$$\begin{aligned}
\frac{dN(t)}{dt} &= \int_{f_L(t)}^{f_N(t)} \frac{\partial \rho(t,a)}{\partial t} da + \rho(t, f_N(t)) f_N'(t) - \rho(t, f_L(t)) f_L'(t) \\
&= \rho(t, f_L(t)) - \rho(t, f_N(t)) - \mu_N(t)N(t) - D_N(t, N(t))N^2(t) + \rho(t, f_N(t)) f_N'(t) - \rho(t, f_L(t)) f_L'(t) \\
&= (1 - f_L'(t))\rho(t, f_L(t)) - \mu_N(t)N(t) - D_N(t, N(t))N^2(t) - (1 - f_N'(t))\rho(t, f_N(t)), \\
\frac{dA(t)}{dt} &= \int_{f_N(t)}^{a_{\max}} \frac{\partial \rho(t,a)}{\partial t} da - \rho(t, f_N(t)) f_N'(t) \\
&= \rho(t, f_N(t)) - \mu_A(t)A(t) - D_A(t, A(t))A^2(t) - \rho(t, f_N(t)) f_N'(t) \\
&= (1 - f_N'(t))\rho(t, f_N(t)) - \mu_A(t)A(t) - D_A(t, A(t))A^2(t).
\end{aligned}$$

To get the closed form of the above system, $\rho(t, f_i(t))$(for $i = E, L, N$) is evaluated by the method of integration along characteristics. Setting $t = t_0 + h$, $a = a_0 + h$ and $V(h) = \rho(t_0 + h, a_0 + h)$. Then,

$$\begin{aligned}
\frac{dV(h)}{dh} &= (\frac{\partial}{\partial t} + \frac{\partial}{\partial a})\rho(t,a) \\
&= -\mu\left(t_0 + h, a_0 + h, \int_0^{a_{\max}} q(t_0 + h, s)\rho(t_0 + h, s) ds\right) \rho(t_0 + h, a_0 + h) \\
&= -\mu\left(t_0 + h, a_0 + h, \int_0^{a_{\max}} q(t_0 + h, s)\rho(t_0 + h, s) ds\right) V(h).
\end{aligned} \tag{5.2}$$

Integrating equation (5.2) from h_1 to h_2 yields,

$$V(h_2) = V(h_1) e^{-\int_{h_1}^{h_2} \mu\left(t_0 + r, a_0 + r, \int_0^{a_{\max}} q(t_0 + r, s)\rho(t_0 + r, s) ds\right) dr}.$$

For $t \geq f_i(t)$, setting $t_0 = t - f_i(t)$, $h = f_i(t)$ and $a_0 = 0$, for $i = E, L, N$, we have

$$\begin{aligned}
\rho(t, f_i(t)) &= \rho(t - f_i(t), 0) e^{-\int_0^{f_i(t)} \mu\left(t - f_i(t) + r, r, \int_0^{a_{\max}} q(t - f_i(t) + r, s)\rho(t - f_i(t) + r, s) ds\right) dr} \\
&= b(t - f_i(t), A(t - f_i(t))) e^{-\int_0^{f_i(t)} \mu\left(t - f_i(t) + r, r, \int_0^{a_{\max}} q(t - f_i(t) + r, s)\rho(t - f_i(t) + r, s) ds\right) dr}.
\end{aligned}$$

Since we focus on the long-term behavior of population dynamics, the closed form of the model for $t \geq f_N(t)$ is obtained as follows.

$$
\begin{aligned}
\frac{dE(t)}{dt} &= b(t, A(t)) - \mu_E(t)E(t) - (1 - f_E'(t))b(t - f_E(t), A(t - f_E(t))) \\
&\quad \exp\left(-\int_0^{f_E(t)} \mu\left(t - f_E(t) + r, r, \int_0^{a_{\max}} q(t - f_E(t) + r, s)\rho(t - f_E(t) + r, s)ds\right) dr\right) \\
&= b(t, A(t)) - \mu_E(t)E(t) - (1 - f_E'(t))b(t - f_E(t), A(t - f_E(t))) \exp\left(-\int_0^{f_E(t)} \mu_E(t - f_E(t) + r)dr\right) \\
&= b(t, A(t)) - \mu_E(t)E(t) - (1 - f_E'(t))b(t - f_E(t), A(t - f_E(t))) \exp\left(-\int_{t-f_E(t)}^{t} \mu_E(r)dr\right),
\end{aligned}
$$

$$
\begin{aligned}
\frac{dL(t)}{dt} &= (1 - f_E'(t))b(t - f_E(t), A(t - f_E(t))) \exp\left(-\int_{t-f_E(t)}^{t} \mu_E(r)dr\right) - \mu_L(t)L(t) - D_L(t, L(t))L^2(t) \\
&- (1 - f_L'(t))b(t - f_L(t), A(t - f_L(t))) \\
&\exp\left(-\int_0^{f_L(t)} \mu\left(t - f_L(t) + r, r, \int_0^{a_{\max}} q(t - f_L(t) + r, s)\rho(t - f_L(t) + r, s)ds\right) dr\right) \\
&= (1 - f_E'(t))b(t - f_E(t), A(t - f_E(t))) \exp\left(-\int_{t-f_E(t)}^{t} \mu_E(r)dr\right) - \mu_L(t)L(t) - D_L(t, L(t))L^2(t) \\
&- (1 - f_L'(t))b(t - f_L(t), A(t - f_L(t))) \exp\left(-\int_{t-f_L(t)}^{t} \mu\left(r, r - (t - f_L(t)), \int_0^{a_{\max}} q(r, s)\rho(r, s)ds\right) dr\right) \\
&= (1 - f_E'(t))b(t - f_E(t), A(t - f_E(t))) \exp\left(-\int_{t-f_E(t)}^{t} \mu_E(r)dr\right) - \mu_L(t)L(t) - D_L(t, L(t))L^2(t) \\
&- (1 - f_L'(t))b(t - f_L(t), A(t - f_L(t))) \exp\left(-\int_{t-\tau_L(t)}^{t} (\mu_L(r) + D_L(r, L(r))L(r))dr - \int_{t-f_L(t)}^{t-\tau_L(t)} \mu_E(r)dr\right) \\
&= (1 - f_E'(t))b(t - f_E(t), A(t - f_E(t))) \exp\left(-\int_{t-f_E(t)}^{t} \mu_E(r)dr\right) - \mu_L(t)L(t) - D_L(t, L(t))L^2(t) \\
&- (1 - f_L'(t))b(t - f_L(t), A(t - f_L(t))) \exp\left(-\int_{t-\tau_L(t)}^{t} \mu_L(r)dr - \int_{t-f_L(t)}^{t-\tau_L(t)} \mu_E(r)dr\right) \\
&\exp\left(-\int_{t-\tau_L(t)}^{t} D_L(r, L(r))L(r)dr\right),
\end{aligned}
$$

$$
\begin{aligned}
\frac{dN(t)}{dt} &= (1-f_L'(t))b(t-f_L(t),A(t-f_L(t)))\exp\left(-\int_{t-\tau_L(t)}^{t}\mu_L(r)dr-\int_{t-f_L(t)}^{t-\tau_L(t)}\mu_E(r)dr\right)\\
&\exp\left(-\int_{t-\tau_L(t)}^{t}D_L(r,L(r))L(r)dr\right)-\mu_N(t)N(t)-D_N(t,N(t))N^2(t)\\
&-(1-f_N'(t))b(t-f_N(t),A(t-f_N(t)))\\
&\exp\left(-\int_0^{f_N(t)}\mu\left(t-f_N(t)+r,r,\int_0^{a_{\max}}q(t-f_N(t)+r,s)\rho(t-f_N(t)+r,s)ds\right)dr\right)\\
&=(1-f_L'(t))b(t-f_L(t),A(t-f_L(t)))\exp\left(-\int_{t-\tau_L(t)}^{t}\mu_L(r)dr-\int_{t-f_L(t)}^{t-\tau_L(t)}\mu_E(r)dr\right)\\
&\exp\left(-\int_{t-\tau_L(t)}^{t}D_L(r,L(r))L(r)dr\right)-\mu_N(t)N(t)-D_N(t,N(t))N^2(t)\\
&-(1-f_N'(t))b(t-f_N(t),A(t-f_N(t)))\exp\left(-\int_{t-\tau_N(t)}^{t}(\mu_N(r)+D_N(r,N(r))N(r))dr\right.\\
&\left.-\int_{t-\tau_N(t)-\tau_L(t-\tau_N(t))}^{t-\tau_N(t)}(\mu_L(r)+D_L(r,L(r))L(r))dr-\int_{t-f_N(t)}^{t-\tau_N(t)-\tau_L(t-\tau_N(t))}\mu_E(r)dr\right)\\
&=(1-f_L'(t))b(t-f_L(t),A(t-f_L(t)))\exp\left(-\int_{t-\tau_L(t)}^{t}\mu_L(r)dr-\int_{t-f_L(t)}^{t-\tau_L(t)}\mu_E(r)dr\right)\\
&\exp\left(-\int_{t-\tau_L(t)}^{t}D_L(r,L(r))L(r)dr\right)-\mu_N(t)N(t)-D_N(t,N(t))N^2(t)\\
&-(1-f_N'(t))b(t-f_N(t),A(t-f_N(t)))\exp\left(-\int_{t-\tau_N(t)}^{t}\mu_N(r)dr-\int_{t-\tau_N(t)-\tau_L(t-\tau_N(t))}^{t-\tau_N(t)}\mu_L(r)dr\right.\\
&\left.-\int_{t-f_N(t)}^{t-\tau_N(t)-\tau_L(t-\tau_N(t))}\mu_E(r)dr\right)\\
&\exp\left(-\int_{t-\tau_N(t)}^{t}D_N(r,N(r))N(r)dr-\int_{t-\tau_N(t)-\tau_L(t-\tau_N(t))}^{t-\tau_N(t)}D_L(r,L(r))L(r)dr\right),\\
\frac{dA(t)}{dt} &= (1-f_N'(t))b(t-f_N(t),A(t-f_N(t)))\exp\left(-\int_{t-\tau_N(t)}^{t}\mu_N(r)dr-\int_{t-\tau_N(t)-\tau_L(t-\tau_N(t))}^{t-\tau_N(t)}\mu_L(r)dr\right.\\
&\left.-\int_{t-f_N(t)}^{t-\tau_N(t)-\tau_L(t-\tau_N(t))}\mu_E(r)dr\right)\exp\left(-\int_{t-\tau_N(t)}^{t}D_N(r,N(r))N(r)dr\right.\\
&\left.-\int_{t-\tau_N(t)-\tau_L(t-\tau_N(t))}^{t-\tau_N(t)}D_L(r,L(r))L(r)dr\right)-\mu_A(t)A(t)-D_A(t,A(t))A^2(t).
\end{aligned}
$$

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