CANADIAN APPLIED
MATHEMATICS QUARTERLY
Volume 19, Number 1, Spring 2011

GLOBAL DYNAMICS OF A TICK *IXODES SCAPULARIS* MODEL

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ABSTRACT. Lyme disease remains the world's most frequently recorded vector-borne disease in the temperate zone, with the black-legged tick, *Ixodes scapularis Say*, as the primary vector in eastern and mid-western United States and Canada. A preliminary to determine the Lyme disease risk is providing detailed information on the tick population. This paper establishes the global dynamics of a tick population model developed to capture dynamical temperature influences on the tick population. It is shown that if the reproduction number for ticks $\mathcal{R}_{tick}$ is less than one, then ticks are doomed to extinction, and it is confirmed that $\mathcal{R}_{tick} > 1$ implies that ticks can invade into the study region and a positive equilibrium exists. We also use a fluctuation argument to establish the global stability of the positive equilibrium.

1 Introduction Lyme disease, a tick-borne zoonotic disease, remains the world's most commonly recorded tick-borne disease, and the most frequently reported vector-borne disease in the temperate zone [**10**]. More than 20,000 cases of Lyme disease are reported in the United States each year [**3, 10**] and Lyme disease is declared as an emerging disease in Canada due to the ongoing northward range expansion of its primary vector, *Ixodes scapularis Say* (1821), which is driven by the climate change [**15, 16**]. Lyme disease is caused by a bacteria called *Borrelia*. Different strains of *Borrelia* and different species of tick vectors are responsible for Lyme disease in different geographical regions. In the eastern and mid-western United States and Canada, the Lyme

Research was partially supported by the Canada Research Chairs program (CRC), the Natural Sciences and Engineering Research Council of Canada (NSERC), the Mathematics for Information Technology and Complex Systems (MITACS), Mprime and the GEOmatics for Informed Decision (GEOIDE).

Keywords: Lyme disease, tick, reproduction number, global stability, fluctuation argument.

disease is mainly caused by *Borrelia burgdorferi* bacterium and transmitted by the black-legged tick, *Ixodes scapularis*. Lyme disease may result when a human is inadvertently bitten by an infectious nymph. The primary ecological risk factor in the Lyme disease epidemic is the number of infected nymphs within areas where people use recreationally and domestically from late spring to midsummer [**17**]. Since complex interactions between seemingly unconnected phenomena determine the risk of exposure to the expanding Lyme disease [**17**], a preliminary step to understand the disease risk is to study the population dynamics of its vector, *Ixodes scapularis* ticks.

The life cycle of *Ixodes scapularis* ticks is complex, proceeding through four developmental stages: egg, larva, nymph and adult. At each post-egg stage (larva, nymph and adult), the tick should attach to a host and get one blood meal for development. Various mathematical models have been formulated to track tick development dynamics and the tick-borne disease transmission; see [**1, 2, 5, 6, 7, 9, 13, 14, 15**] for some of these models. The authors in [**15**] proposed a process-based dynamic model to investigate effects of climate on the geographic range and seasonality of the tick *Ixodes scapularis*. Based on the given modeling framework in [**15**] (reproduced in Figure 1), the authors in [**25**] formulated a dynamic model, derived the tick reproduction number $\mathcal{R}_{tick}$ and determined the local stability property for the tick free equilibrium and the tick endemic equilibrium. An unanswered question is the global stability of the equilibria for the tick population model. The main purpose of this work is to extend the results in [**25**] to answer the question concerning the global dynamics of the model.

The rest of this paper is organized as follows. The next section presents the model and some results given in [**25**]. Global dynamics when $\mathcal{R}_{tick} < 1$ and $\mathcal{R}_{tick} > 1$ are established in Sections 3 and 4, respectively. A short discussion about the mathematical techniques used in the paper is presented in the final section.

2 The model, reproduction number and local stability Generally speaking, *Ixodes scapularis* ticks have four stages: egg, larva, nymph and adult. To be capable of investigating effects of climate on tick populations, the model proposed in [**15**] contains 12 mutually exclusive states in the tick life cycle: egg-lying adult females (x_1); eggs (x_2); hardening larvae (x_3); questing larvae (x_4); feeding larvae (x_5); engorged larvae (x_6); questing nymphs (x_7); feeding nymphs (x_8); engorged nymphs (x_9); questing adults (x_{10}); feeding adult females (x_{11})

and engorged adult females (x_{12}). Each state represents a specific point in the life cycle of the tick population and flows from one stage to the next represent the essential sequential steps of development (from engorged ticks of one instar to questing ticks of the next), host attaching (from questing to feeding ticks of the same instar), and detaching (from feeding ticks to engorged, developing ticks) [**15**]. Based on the modeling framework in [**15**] (also see Figure 1), the tick developmental dynamics is described by the following system of ordinary differential equations [**25**]:

$$
\begin{aligned}
&x_1' = d_{12}x_{12} - \mu_1 x_1, && x_2' = pf(x_{11})x_1 - (d_2+\mu_2)x_2,\\
&x_3' = d_2x_2 - (d_3+\mu_3)x_3, && x_4' = d_3x_3 - (d_4+\mu_4)x_4,\\
&x_5' = d_4x_4 - (d_5+\mu_5(x_5))x_5, && x_6' = d_5x_5 - (d_6+\mu_6)x_6,\\
&x_7' = d_6x_6 - (d_7+\mu_7)x_7, && x_8' = d_7x_7 - (d_8+\mu_8(x_8))x_8,\\
&x_9' = d_8x_8 - (d_9+\mu_9)x_9, && x_{10}' = d_9x_9 - (d_{10}+\mu_{10})x_{10},\\
&x_{11}' = \frac{1}{2}d_{10}x_{10} - (d_{11}+\mu_{11}(x_{11}))x_{11},\\
&x_{12}' = d_{11}x_{11} - (d_{12}+\mu_{12})x_{12}.
\end{aligned}
\tag{1}
$$

Here, d_i is the progression rate from the i-th stage to the next stage, μ_i is the death rate for stage i, and p is the per-capita egg reproduction rate by egg-laying females. Note that in this model, we have three density-dependent death rates $\mu_5(x_5)$, $\mu_8(x_8)$, $\mu_{11}(x_{11})$ and we assume that each $\mu_j(x_j)$ is an increasing function of x_j for $j = 5, 8, 11$. To account for the density dependent reduction in fecundity of egg laying females, we suppose that $f(x_{11})$ is a decreasing function of x_{11}. The parameter values for the tick model (1) are summarized in Table 2.

Denote

$$
T = \begin{pmatrix}
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & d_{12}\\
f(0)\times p & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0\\
0 & d_2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0\\
0 & 0 & d_3 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0\\
0 & 0 & 0 & d_4 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0\\
0 & 0 & 0 & 0 & d_5 & 0 & 0 & 0 & 0 & 0 & 0 & 0\\
0 & 0 & 0 & 0 & 0 & d_6 & 0 & 0 & 0 & 0 & 0 & 0\\
0 & 0 & 0 & 0 & 0 & 0 & d_7 & 0 & 0 & 0 & 0 & 0\\
0 & 0 & 0 & 0 & 0 & 0 & 0 & d_8 & 0 & 0 & 0 & 0\\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & d_9 & 0 & 0 & 0\\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{d_{10}}{2} & 0 & 0\\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & d_{11} & 0
\end{pmatrix}
\tag{2}
$$

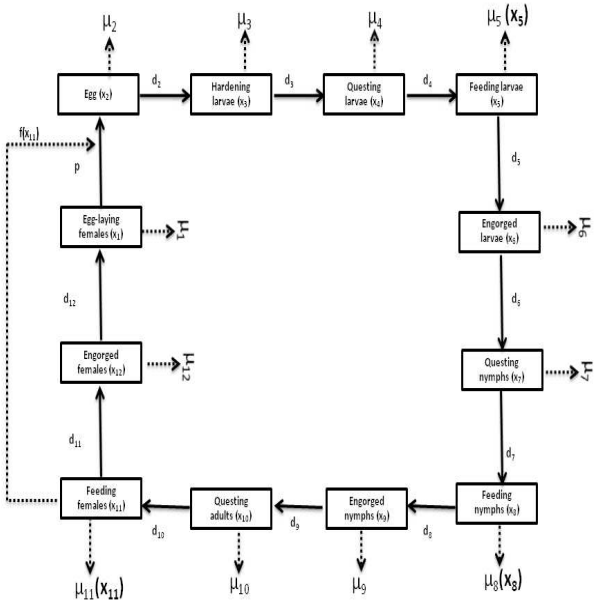

FIGURE 1: The flowchart of the Ogden's tick population model [**15**] that predicts the specific states of the tick life cycle, progressive movement and rates of movement.

and

$$
\begin{aligned}
(3) \qquad D =& \operatorname{diag}(\mu_1; d_2+\mu_2; d_3+\mu_4; d_4+\mu_4; \\
& d_5+\mu_5(0); d_6+\mu_6; d_7+\mu_7; d_8+\mu_8(0); \\
& d_9+\mu_9; d_{10}+\mu_{10}; d_{11}+\mu_{11}(0); d_{12}+\mu_{12}).
\end{aligned}
$$

Using a variation of the next generation matrix method [**4, 24**], the authors in [**25**] derived the tick reproduction number $\mathcal{R}_{tick}$, which represents the number of new female ticks produced by a female tick when there are no density dependent constraints acting anywhere in the life cycle of the tick population, given by

Parameter	Description
μ_1	Per capita mortality rate of egg-laying adult females
μ_2	Per capita mortality rate of eggs
μ_3	Per capita mortality rate of hardening larvae
μ_4	Per capita mortality rate of questing larvae
$\mu_5(x_5)$	Per capita mortality rate of feeding larvae on rodents
μ_6	Per capita mortality rate of engorged larvae
μ_7	Per capita mortality rate of questing nymphs
$\mu_8(x_8)$	Per capita mortality rate of feeding nymphs on rodents
μ_9	Per capita mortality rate of engorged nymphs
μ_{10}	Per capita mortality rate of questing adults
$\mu_{11}(x_{11})$	Per capita mortality rate of feeding adults on deer
μ_{12}	Per capita mortality rate of engorged adult females
p	Per capita egg production by egg-laying adult females
$f(x_{11})$	Reduction in fecundity of egg-laying adult females
d_2	Development rate from eggs to hardening larvae
d_3	Development rate from hardening larvae to questing larvae
d_4	Host attaching rate for questing larvae
d_5	Development rate from feeding larvae to engorged larvae
d_6	Development rate from engorged larvae to questing nymphs
d_7	Host attaching rate for questing nymphs
d_8	Development rate from feeding nymphs to engorged nymphs
d_9	Development rate from engorged nymphs to questing adults
d_{10}	Host attaching rate for questing adults
d_{11}	Development rate from feeding adult females to engorged females
d_{12}	Development rate from engorged females to egg-laying females

TABLE 1: Parameter definitions

$$\mathcal{R}_{tick} = \frac{d_2}{d_2+\mu_2}\frac{d_3}{d_3+\mu_3}\frac{d_4}{d_4+\mu_4}\frac{d_5}{d_5+\mu_5(0)}\frac{d_6}{d_6+\mu_6}\frac{d_7}{d_7+\mu_7} \cdot \frac{d_8}{d_8+\mu_8(0)}\frac{d_9}{d_9+\mu_9}\frac{d_{10}/2}{d_{10}+\mu_{10}}\frac{d_{11}}{d_{11}+\mu_{11}(0)}\frac{d_{12}}{d_{12}+\mu_{12}}\frac{pf(0)}{\mu_1}. \tag{4}$$

Based on $\mathcal{R}_{tick}$, they also proved the following result for the tick model (1):

Theorem 1. *The tick-free equilibrium* $E_0 = (0,0,0,0,0,0,0,0,0,0,0,0)$ *is asymptotically stable if* $\mathcal{R}_{tick} < 1$. *A unique tick endemic equilibrium* E^* *exists and it is locally asymptotically stable when* $\mathcal{R}_{tick} > 1$.

In the next two sections, we will extend this theorem with respect to the global dynamics of the tick model (1). We start with the case where $\mathcal{R}_{tick} < 1$.

3 Global stability of the tick-free equilibrium when $\mathcal{R}_{tick} < 1$

In this section, we study the global dynamics in the case where the reproduction number is less than unity. As stated in Theorem 1, the tick-free equilibrium is locally stable. This implies that the tick population could not sustain itself in the habitat (when $\mathcal{R}_{tick} < 1$) if the initial size is in the attraction basin of the tick-free equilibrium. To ensure that the tick elimination is independent of the initial size of each stage, it is necessary to show that the tick-free equilibrium is also globally asymptotically stable if $\mathcal{R}_{tick} < 1$. This result is established in the following theorem.

Theorem 2. *If $\mathcal{R}_{tick} < 1$, then the tick-free equilibrium $E_0 = (0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0)$ is globally stable.*

Proof. Since the tick-free equilibrium is locally asymptotically stable when $\mathcal{R}_{tick} < 1$, we just need to check it is also globally attractive. To prove this, we use a comparison argument arising from the monotone dynamical systems theory (see [**18**]). Consider the linear system

$$\frac{dx(t)}{dt} = (T - D)x(t), \tag{5}$$

where matrices T and D are defined in equations (2) and (3), respectively. Since $\mathcal{R}_{tick} < 1$, then the stability modulus of the matrix $T - D$, $s(T - D) = \max\{\operatorname{Re}\lambda : \det(\lambda I - (T - D)) = 0\} < 0$, where I is the identity matrix. Therefore, the zero solution is globally stable for the linear system (5). For every solution $x(t)$ of the system (1), $x(t) \geq 0$ for every $t \geq 0$. Thus the 11th element of $x(t)$, $x_{11}(t) \geq 0$. Because $f(z)$ is a decreasing function of the variable z, we have $f(x_{11}(t)) \leq f(0)$, $\forall t \geq 0$. Moreover, since $x_i(t) \geq 0$ for $i = 5, 8, 11$, we also have $\mu_i(x_i(t)) \geq \mu_i(0)$. Thus, system (1) can be controlled by the linear system (5) from above. By applying the comparison principle (see, e.g., [**21,** Theorem B.1]), we have $x(t) \to 0$ as $t \to \infty$. □

Since abiotic and biotic factors influence the tick development process, thereby altering the parameters in the model system (1), these factors change the value of the reproduction number $\mathcal{R}_{tick}$. An unfavorable habitat, where the biotic and abiotic environments are disadvantageous

for the tick development, brings the reproduction number $\mathcal{R}_{tick}$ to a value less than unity, thus forcing the tick population to extinction in the habitat. However, our results in the next section show that for a favorable habitat, where the abiotic and biotic factors make $\mathcal{R}_{tick} > 1$, the population size of each tick stage always remains above a certain positive level. Thus, if the environment-determined parameter $\mathcal{R}_{tick}$ is greater than unity, then the tick population can remain endemic in the study region.

4 Global dynamics when $\mathcal{R}_{tick} > 1$ In this section, we will establish the global dynamics of the tick model when $\mathcal{R}_{tick} > 1$. Before introducing our main results, we make a few observations. For two vectors x, $y \in \mathbb{R}^{12}$, we write $x \geq y$ if $x_i \geq y_i$; $x > y$ if $x \geq y$ and $x \neq y$; and $x \gg y$ if $x_i > y_i$, $\forall i \in [1, 12]$. For any $x \in \mathbb{R}^{12}_+$ and $g \geq 0$, set

$$
\begin{aligned}
(6) \qquad G(x,g) = (&d_{12}x_{12} - \mu_1 x_1, x_1 \times g \times p - (d_2 + \mu_2)x_2,\\
&d_2 x_2 - (d_3 + \mu_3)x_3, d_3 x_3 - (d_4 + \mu_4)x_4,\\
&d_4 x_4 - (d_5 + \mu_5(x_5))x_5, d_5 x_5 - (d_6 + \mu_6)x_6,\\
&d_6 x_6 - (d_7 + \mu_7)x_7, d_7 x_7 - (d_8 + \mu_8(x_8))x_8,\\
&d_8 x_8 - (d_9 + \mu_9)x_9, d_9 x_9 - (d_{10} + \mu_{10})x_{10},\\
&d_{10}x_{10}/2 - (d_{11} + \mu_{11}(x_{11}))x_{11},\\
&d_{11}x_{11} - (d_{12} + \mu_{12})x_{12})^T,
\end{aligned}
$$

where T denotes the transpose of a vector, $\mu_j(x_j)$ is a positive increasing function of x_j for $j = 5$, 8, 11 and other parameters are positive. It then follows from [**29,** Corollary 3.2] that the system $dx/dt = G(x, g)$ possesses the following properties:

Lemma 1. *Consider the system $dx/dt = G(x, g)$. If $s(DG(0, g)) = s(\partial G(0, g)/\partial x) = \max\{Re\lambda : det(\lambda I - Df(0, g)) = 0\} \leq 0$, then $x = 0$ is globally asymptotically stable with respect to $\mathbb{R}^{12}_+$; if $s(DG(0, g)) > 0$, then system $dx/dt = G(x, g)$ admits a unique positive equilibrium $x^*(g)$ which is globally asymptotically stable with respect to $\mathbb{R}^{12}_+ \setminus \{0\}$.*

Remark 1. In the case where $s(DG(0, g)) > 0$, we have a positive equilibrium $x^*(g)$, which is an increasing function of g. More precisely, if $g_1 > g_2$, then $x^*(g_1) \gg x^*(g_2)$. To show this, we first use the comparison principle (see, e.g., [**21,** Theorem B. 1]) to prove that $x^*(g_1) \geq x^*(g_2)$,

from which it follows easily that $x^*(g_1) \gg x^*(g_2)$. Moreover, by setting $g = f(0)$, Lemma 1 implies that if $s(DG(0, f(0))) > 0$ (which is equivalent to $\mathcal{R}_{tick} > 1$), there is a positive equilibrium $x^*(f(0))$ which is globally stable for the system $dx/dt = G(x, f(0))$.

Our next result indicates that the tick population remains persistent if the habitat-determined reproduction number is greater than unity.

Theorem 3. *If $\mathcal{R}_{tick} > 1$, then the system is uniformly persistent, that is, there exists an $\epsilon > 0$ such that every solution $x(t, x^0)$ of system (1) with initial value $x^0 \neq 0$ satisfies $\liminf_{t\to\infty} x_i(t, x^0) > \epsilon$, $\forall i \in [1, 12]$.*

Proof. Since $\mathcal{R}_{tick} > 1$, we have $s(T - D) = \max\{\lambda : det(\lambda I - (T - D)) = 0\} > 0$. Hence, there exists small $\delta > 0$ such that $s(T(\delta) - D) > 0$, where $T(\delta)$ is generated by replacing $f(0)$ with $f(\delta)$ in the matrix T defined by (2). It then follows from Lemma 1 that the system (1) with $f(x_{11})$ replaced by $f(\delta)$ has a positive equilibrium $x^*(f(\delta))$, which is globally asymptotically stable with respect to $\mathbb{R}^{12}_+ \setminus \{0\}$. Since $x^*(f(\delta)) \to x^*(f(0)) \gg 0$ as $\delta \to 0$, we can choose $\delta_0 < \delta$ small enough such that $x^*_{11}(f(\delta_0)) > \delta_0$, where $x^*_{11}(f(\delta_0))$ is the 11th element of $x^*(f(\delta_0))$.

Define $X = \mathbb{R}^{12}_+$ and $X_0 = Int\mathbb{R}^{12}_+ = \{x \in \mathbb{R}^{12}_+ : x_i > 0, i = 1, 2, \ldots, 12\}$. Then the boundary $\partial X_0 := X \setminus X_0 = \{x \in \mathbb{R}^{12}_+ : \Pi^{12}_{i=1} x_i = 0\}$. Suppose $\Phi(t)$ is the solution semiflow of system (1), i.e., $\Phi(t)x_0 = x(t, x_0)$. It is easy to see that $\Phi(t)x \in X_0$ if $x \in X_0$, $\forall t \geq 0$ and $\Phi(t)x \gg 0$ if $x \in X \setminus \{0\}$, $\forall t > 0$. If we define $M_\partial = \{x \in \mathbb{R}^{12}_+ : \Phi(t)x \in \partial X_0, \forall t > 0\}$, then $M_\partial = \{0\}$. Our next claim shows that $\{0\}$ is a uniformly weak repeller for X_0.

Claim. $\limsup_{t\to\infty} \|\Phi(t)x\| > \delta_0/2$, $\forall x \in X_0$. Suppose, by contraction, that $\limsup_{t\to\infty} \|\Phi(t)x_0\| \leq \delta_0/2$ for some $x_0 \in X_0$. Then there exists a $T_1 > 0$ such that $\|\Phi(t)x_0\| \leq \delta_0$ for all $t \geq T_1$. Thus, we have the following inequality $dx_2/dt \geq x_1 f(\delta_0)p - (d_2 + \mu_2)x_2$, $\forall t \geq T_1$. Hence, $dx/dt \geq G(x, f(\delta_0))$, $\forall t \geq T_1$. By the comparison principle, we have $\limsup_{t\to\infty} x_{11}(t, x_0) \geq x^*_{11}(f(\delta_0)) > \delta_0$, a contradiction to $\limsup_{t\to\infty} \|\Phi(t)x_0\| \leq \delta_0/2$.

Using Lemma 1 and a comparison argument, we can easily show that system (1) is point dissipative. By the acyclicity theorem on uniform persistence for maps (see [**27,** Theorem 1.3.1 and Remark 1.3.1]), it follows that $\Phi(t)$ is uniformly persistent with respect to X_0. □

The previous theorem ensures that ticks can invade into the habitat if $\mathcal{R}_{tick} > 1$. Our next result confirms that the tick population will eventu-

ally stabilize at an equilibrium level. Suppose $\mathcal{R}_{tick} > 1$, then there exists a unique positive equilibrium $x^*(f(0))$ for $dx/dt = G(x, f(0))$ which is globally asymptotically stable with respect to $\mathbb{R}^{12}_+ \setminus \{0\}$ according to Lemma 1 and Remark 1. Denote $y^{(1)} = x^*(f(0))$ and $y^{(1)}_{11} = x^*_{11}(f(0))$, the 11th element of $y^{(1)}$.

Theorem 4. *Suppose $\mathcal{R}_{tick} > 1$. If the zero solution of system (1) with $f(x_{11})$ being replaced by $f(y^{(1)}_{11})$ is unstable, then the positive equilibrium E^* of system (1) is globally asymptotically stable. Here, $y^{(1)}$ is the positive equilibrium of system (1) with $f(x_{11})$ replaced by $f(0)$.*

Proof. To prove this theorem, we will use a fluctuation argument, previously used in different settings by [**11, 12, 19, 23, 26, 28**].

According to Lemma 1 and Remark 1, system $dx_2/dt = G(x, f(0))$ admits a globally stable equilibrium $x^*(f(0))$ when $\mathcal{R}_{tick} > 1$. Since $dx_2/dt \leq x_1 f(0)p - (d_2 + \mu_2)x_2$, system (1) can be controlled from above by the cooperative system $dx/dt = G(x, f(0))$. It then follows from the comparison principle and the global stability of $x^*(f(0))$ for the system $dx/dt = G(x, f(0))$ that for any $\epsilon > 0$, there exists a $T_1 > 0$ such that $x(t) \leq x^*(f(0)) + \epsilon = y^{(1)} + \epsilon$, $\forall t > T_1$. Since the stability modulus of the matrix $T - D$ with $f(0)$ replaced by $f(y^{(1)}_{11})$ is greater than zero, we can choose ϵ small enough such that the same statement holds for the matrix $T - D$ with $f(0)$ replaced by $f(y^{(1)}_{11} + \epsilon)$. It then follows from Lemma 1 that there exists a unique positive equilibrium $x^*(f(y^{(1)}_{11} + \epsilon))$ for $dx/dt = G(x, f(y^{(1)}_{11} + \epsilon))$ which is globally asymptotically stable with respect to $\mathbb{R}^{12}_+ \setminus \{0\}$. Denote $z^{(1)} = x^*(f(y^{(1)}_{11} + \epsilon))$. Since $x_{11}(t) \leq y^{(1)}_{11} + \epsilon$, $\forall t > T_1$, we have $f(x_{11}(t)) \geq f(y^{(1)}_{11} + \epsilon)$ for $t > T_1$. Hence, $dx_2/dt \geq x_1 f(y^{(1)}_{11} + \epsilon)p - (d_2 + \mu_2)x_2$, $\forall t \geq T_1$. Therefore, the model system (1) can be controlled from below by the cooperative system $dx/dt = G(x, f(y^{(1)}_{11} + \epsilon))$, $\forall t > T_1$. Thus, the comparison principle and the global stability of $z^{(1)} = x^*(f(y^{(1)}_{11} + \epsilon))$ imply that for any $\epsilon > 0$ with $z^{(1)} - \epsilon \gg 0$, there exists $T_2 > T_1$ such that $x(t) \geq z^{(1)} - \epsilon$, $\forall t > T_2$. Moreover, it is easy to see that $z^{(1)} \ll y^{(1)}$ from Remark 1.

Continuing this process, we can construct two vectors $y^{(2)} = x^*(f(z^{(1)}_{11} - \epsilon))$ and $z^{(2)} = x^*(f(y^{(2)}_{11} + \epsilon))$. Moreover, there exists a $T_4 > 0$ such that $z^{(2)} - \epsilon \leq x(t) \leq y^{(2)} + \epsilon$, $\forall t > T_4$. We claim that the relationship $z^{(1)} \ll z^{(2)} \ll y^{(2)} \ll y^{(1)}$ holds. Since $f(z^{(1)}_{11} - \epsilon) < f(0)$, we have $y^{(2)} = x^*(f(z^{(1)}_{11} - \epsilon)) \ll x^*(f(0)) = y^{(1)}$. Similarly, since $f(y^{(2)}_{11} + \epsilon) > f(y^{(1)}_{11} + \epsilon)$, we have $z^{(2)} = x^*(f(y^{(2)}_{11} + \epsilon)) \gg x^*(f(y^{(1)}_{11} + \epsilon)) = z^{(1)}$. Since

$f(z_{11}^{(1)}-\epsilon) > f(y_{11}^{(1)}+\epsilon)$, we have $y^{(2)} = x^*(f(z_{11}^{(1)}-\epsilon)) \gg x^*(f(y_{11}^{(1)}+\epsilon)) = z^{(1)}$. Thus we get $f(y_{11}^{(2)}+\epsilon) < f(z_{11}^{(1)}-\epsilon)$, and consequently, $z^{(2)} = x^*(f(y_{11}^{(2)}+\epsilon)) \ll x^*(f(z_{11}^{(1)}-\epsilon)) = y^{(2)}$. Therefore, $z^{(1)} \ll z^{(2)} \ll y^{(2)} \ll y^{(1)}$.

Using a similar idea, we can construct two monotone sequences of vectors $\{z^{(n)}\}$ and $\{y^{(n)}\}$ such that $0 \ll z^{(1)} \ll z^{(2)} \ll \cdots z^{(n)} \ll y^{(n)} \ll \cdots \ll y^{(2)} \ll y^{(1)}$, $G(z^{(n)}, f(y_{11}^{(n)}+\epsilon)) = 0$ and $G(y^{(n)}, f(z_{11}^{(n-1)}-\epsilon)) = 0$, $\forall n \geq 2$. Moreover, there exists T_{2n} such that $z^{(n)} - \epsilon \leq x(t) \leq y^{(n)} + \epsilon$, $\forall t \geq T_{2n}$. Hence, there exist two positive vectors Y and Z with $Y \geq Z$ such that $\lim_{t\to\infty} z^{(n)} = Z$ and $\lim_{t\to\infty} y^{(n)} = Y$. Moreover, the ordered interval $[Z, Y]$ is positively invariant and the positive equilibrium E^* is in this interval, that is $Z \leq E^* \leq Y$. For any $x \neq 0$, the omega limit set $\omega(x) \in [Z, Y]$.

If $Z = Y$, then we proved that $Z = Y = E^*$ and this equilibrium is globally asymptotically stable.

If $Z \neq Y$, that is $Z < Y$, then it is easy to see that $Z \ll Y$. Moreover, a persistence argument shows that there exists an $\eta > 0$ such that $\omega(x)$ is in the ordered interval $[Z, Y]$ with $Z_{11} + \eta \leq (\omega(x))_{11} \leq Y_{11} - \eta$, where $(\omega(x))_{11}$ is the 11-th variable of $\omega(x)$. By repeating the previous procedure, we can construct two vectors $Z^{(1)}$ and $Y^{(1)}$ such that for any nonzero point x,

$$Z \ll Z^{(1)} \leq E^* \leq Y^{(1)} \ll Y \quad \text{and} \quad \omega(x) \in [Z^{(1)}, Y^{(1)}].$$

If $Z^{(1)} = Y^{(1)}$ then we finish the proof. If $Z^{(1)} < Y^{(1)}$, then $Z^{(1)} \ll Y^{(1)}$. Repeating the procedure, we can eventually construct two series $Y^{(n)}$ and $Z^{(n)}$ such that

$$Z^{(n-1)} \leq Z^{(n)} \leq E^* \leq Y^{(n)} \leq Y^{(n-1)}$$

and

$$\lim_{n\to\infty} Z^{(n)} = \lim_{n\to\infty} Y^{(n)} = E^*,$$

which implies that the omega limit set of every nonzero point x is E^* and thus E^* is globally stable. □

5 Discussion In this paper, we have investigated the long-term behavior of a tick model formulated in [**25**]. Our results confirm that the tick reproduction number $\mathcal{R}_{tick}$ serves as a threshold condition for tick establishment and extinction: ticks are doomed to extinction when $\mathcal{R}_{tick} < 1$ and invading into the habitat when $\mathcal{R}_{tick} > 1$. Moreover,

under a minor technical condition, $\mathcal{R}_{tick} > 1$ implies that the tick population will eventually stabilize at a constant level.

Mathematical techniques in this paper involve the monotone dynamical systems theory [**18**], the uniform persistence theory [**20, 22, 27**] and a fluctuation argument motivated by previous studies [**11, 12, 19, 22, 23, 26, 28**]. Since the system (1) is not a cooperative system and the nonlinear terms $f(x_{11})$, $\mu_5(x_5)$, $\mu_8(x_8)$ and $\mu_{11}(x_{11})$ may be very complicated (see parameters in [**25**] for examples), it is highly motivated to derive the global stability of the positive equilibrium by using the monotone dynamical systems theory or the Lyapunov function method directly. To get a global stability result when $\mathcal{R}_{tick} > 1$, here we use a fluctuation technique instead. The main idea is to construct two sequences of monotone systems, with each series controlling the original system from below and above, respectively. If all nonzero solutions of a specific system converge to a corresponding positive equilibrium, then we get an upper bound and lower bound for nonzero solutions of the original system according to the comparison principle. To show the global attractivity of the positive equilibrium, it is sufficient to prove that the upper bound and lower bound tend to the same vector (see the proof of Theorem 4).

In fact, the argument of the fluctuation idea was used previously to yield information of dynamics of a differential system. It was developed and used to study asymptotic behaviors of some parasitic models by Hirsch, Hanisch and Gabriel [**8**]. Thieme employed this method to prove the uniform persistence of a dynamic system [**22**]. In [**12, 23, 28**], this idea was used to prove the global stability of the positive equilibrium for nonmonotone reation-diffusion systems with time delays. The authors in [**11**] proved the global attractivity of the interior equilibrium for a stage-structured predator-prey model by using the fluctuation method. Another modification of the fluctuation method was used in [**19**] to establish the global stability of a fixed point for discrete maps. This idea seems to have great potential to be used for the global dynamics of differential equations where the widely used comparison principle and Lyapunov method may fail to yield the global attractivity property.

Acknowledgement We are grateful to the referees for helpful comments which led to an improvement of our original manuscript.

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