A REACTION-DIFFUSION LYME DISEASE MODEL WITH SEASONALITY

YUXIANG ZHANG† AND XIAO-QIANG ZHAO‡

Abstract. This paper is devoted to the study of a reaction-diffusion Lyme disease model with seasonality. In the case of a bounded habitat, we obtain a threshold result on the global stability of either disease-free or endemic periodic solution. In the case of an unbounded habitat, we establish the existence of the disease spreading speed and its coincidence with the minimal wave speed for time-periodic traveling wave solutions. We also estimate parameter values based on some published data and use them to study the Lyme disease transmission in Port Dove, Ontario. Our numerical simulations are consistent with the obtained analytic results.

Key words. seasonality, basic reproduction ratio, periodic solutions, spreading speed, traveling waves

AMS subject classifications. 35K57, 37C65, 92D30

DOI. 10.1137/120875454

1. Introduction. Lyme disease is a commonly reported tick-borne illness, which was named after Lyme, Connecticut, where the first outbreak in humans in North America was recognized in 1975. The disease is caused by the bacterium Borrelia burgdorferi, which is transmitted to humans through the bite of infected ticks. The ticks live for about two years with three feeding stages: larva, nymph, and adult. Larval and nymphal ticks primarily feed on mice, and adult ticks feed on deer. Larvae that obtain a blood meal drop off their host (mice) and then grow into nymphs. These nymphs seek out their host (mice) for their blood meal. If they succeed, the nymphs pass the spirochete to susceptible mice and mature into adults. Adults feed almost exclusively on deer and mate there. Female adults eventually drop off the deer, lay their eggs nearby, and die. Larvae hatch and acquire the spirochete when they attack an infected mouse for their blood meal. Another tick-to-mouse-to-tick infection cycle happens again. For more information about the infection of Lyme disease, we refer the reader to [3, 4, 13, 15, 16, 17] and references therein.

In order to study the effect of a vector’s stage structure on the transmission dynamics and disease spreading velocity, Caraco et al. [4] proposed a reaction and diffusion model for Lyme disease in the northeast United States. The model treats population densities at locations $x := (x_1, x_2)$ in a continuous two-dimensional space $\Omega$, and parameters for birth, death, infection, and developmental advancement are all positive constants. Recently, Zhao [24] studied the global dynamics of this spatial model for Lyme disease. Note that this model ignores the seasonal pattern in abundance and activities of different stages. As mentioned in [1], seasonal variations in temperature, rainfall, and resource availability are ubiquitous and can exert strong...
pressures on population dynamics. For Lyme disease, the ticks develop slowly or become less active in colder temperatures (see [17]), and rainfall is also critically important for the development, survival, and activities of ticks (see [18]). According to the report from the Public Health Agency of Canada on Lyme disease cases in Ontario between 1999 and 2004 [5], most cases occurred in late spring and summer, when the young ticks are most active and people are outdoors more often. To take seasonal influences into account, we modify Caraco et al.’s model to a reaction and diffusion model in a periodic environment. Since tick development and activities are strongly affected by temperatures [15, 16, 17], we assume that the development rates of ticks and their activity rates (biting rates) are time-dependent. Another assumption is the self-regulation mechanism for the tick population, as discussed in [4]. We assume that the self-regulation process is mainly due to the carrying capacity of hosts and some density-dependent death terms.

Let \( M(t, x) \) and \( m(t, x) \) be the densities of susceptible and pathogen-infected mice, \( L(t, x) \) be the density of questing larvae, \( V(t, x) \) and \( v(t, x) \) be the densities of larvae infesting susceptible and pathogen-infected mice, \( N(t, x) \) and \( n(t, x) \) be the densities of susceptible and infectious nymphs, and \( A(t, x) \) and \( a(t, x) \) be the densities of uninfected and pathogen-infected adult ticks, at time \( t \) and location \( x \). In Figure 1.1, we use two schematic diagrams to illustrate the tick-mouse cycle of infection. Accordingly, our spatial model for Lyme disease is governed by the following periodic reaction-diffusion system:

\[
\begin{align*}
\frac{\partial M}{\partial t} &= D_M \Delta M + r_M(M + m) \left( 1 - \frac{M + m}{K_M} \right) - \mu_M M - \alpha_2(t) \beta M n, \\
\frac{\partial m}{\partial t} &= D_M \Delta m + \alpha_2(t) \beta M n - \mu_M m, \\
\frac{\partial L}{\partial t} &= r(t)(A + a) - \mu_L L - \alpha_1(t) L(M + m), \\
\frac{\partial V}{\partial t} &= D_M \Delta V + \alpha_1(t) M L - V(\sigma(t) + \mu_V) - \delta_V (V + v)V, \\
\frac{\partial v}{\partial t} &= D_M \Delta v + \alpha_1(t) m L - v(\sigma(t) + \mu_V) - \delta_V (V + v)v, \\
\frac{\partial N}{\partial t} &= \sigma(t)[V + (1 - \beta_T)v] - N[\gamma + \alpha_2(t)(M + m) + \mu_N], \\
\frac{\partial n}{\partial t} &= \beta_T \sigma(t)v - n[\gamma + \alpha_2(t)(M + m) + \mu_N], \\
\frac{\partial A}{\partial t} &= D_H \Delta A + \alpha_2(t) N[M + (1 - \beta_T)m] - \mu_A A - \delta_A(A + a)A, \\
\frac{\partial a}{\partial t} &= D_H \Delta a + \alpha_2(t)[(M + m)n + \beta_T m N] - \mu_A a - \delta_A(A + a)a,
\end{align*}
\]

where \( \Delta = \frac{\partial^2}{\partial x_1^2} + \frac{\partial^2}{\partial x_2^2} \) is the Laplacian operator on \( \mathbb{R}^2 \). All constant parameters are positive, and \( r(t), \alpha_1(t), \sigma(t), \) and \( \alpha_2(t) \) are nonnegative \( \omega \)-periodic functions. The biological interpretations for the parameters are listed in Table 1.1. We further assume that \( r_M > \mu_M, \beta \in (0, 1), \) and \( \beta_T \in (0, 1) \).

It is worth mentioning that the term \( \gamma n(t, x) \) represents the local risk of Lyme disease to humans under the assumption that nymphs biting humans do not feed long enough to mature into adults, and the diffusion coefficient \( D_H \) models dispersal of adult ticks while they infest deer. However, deer do not disperse the pathogen and cannot be infected. This also explains why we have ignored the dynamics for humans and deer in model (1.1).
Our main purpose in this paper is to study the global dynamics of system (1.1) in both bounded and unbounded spatial domains. In section 2, we obtain a threshold result on the global dynamics of (1.1) in a bounded domain \( \Omega \). In section 3, we establish the existence of the spreading speed of the disease and its coincidence with the minimal wave speed for periodic traveling waves of system (1.1) when \( \Omega \) is unbounded. In section 4, we present a case study on the transmission of Lyme disease in Port Dove, Ontario. A short discussion section completes the paper.

2. Threshold dynamics in a bounded domain. In this section, we consider system (1.1) in a bounded domain \( \Omega \subset \mathbb{R}^2 \) with smooth boundary \( \partial \Omega \). We assume that all populations remain confined to the domain \( \Omega \) for all time, and hence the model system (1.1) is subject to the Neumann boundary conditions

\[
\frac{\partial M}{\partial \nu} = \frac{\partial m}{\partial \nu} = \frac{\partial V}{\partial \nu} = \frac{\partial v}{\partial \nu} = \frac{\partial A}{\partial \nu} = \frac{\partial a}{\partial \nu} = 0,
\]

Fig. 1.1. The illustrative diagram for the tick-mouse cycle of infection.
where \( \frac{\partial}{\partial \nu} \) represents the differentiation along the outward normal \( \nu \) to \( \partial \Omega \).

For the convenience of mathematical analysis, we make a change of variables \( \mathcal{M} = M + m, \mathcal{V} = V + v, \mathcal{N} = N + n, \mathcal{A} = A + a \) for system (1.1). It then follows that system (1.1) is equivalent to the following:

\[
\begin{align*}
\frac{\partial M}{\partial t} &= D_M \Delta M + r_M M \left(1 - \frac{M}{K_M}\right) - \mu_M M, \\
\frac{\partial L}{\partial t} &= r(t)A - \mu_L L - \alpha_1(t)L M, \\
\frac{\partial V}{\partial t} &= D_M \Delta V + \alpha_1(t)L M - V(\sigma(t) + \mu_V) - \delta_V V^2, \\
\frac{\partial N}{\partial t} &= \sigma(t) V - N[\gamma + \alpha_2(t) M + \mu_N], \\
\frac{\partial A}{\partial t} &= D_H \Delta A + \alpha_2(t) N M - \mu_A A - \delta_A A^2, \\
\frac{\partial m}{\partial t} &= D_M \Delta m + \alpha_2(t) \beta(M - m) n - \mu_M m, \\
\frac{\partial v}{\partial t} &= D_M \Delta v + \alpha_1(t)L M - v(\sigma(t) + \mu_V) - \delta_V V v, \\
\frac{\partial n}{\partial t} &= \beta_T \sigma(t) v - n[\gamma + \alpha_2(t) M + \mu_N], \\
\frac{\partial a}{\partial t} &= D_H \Delta a + \alpha_2(t)[M n + \beta_T m(N - n)] - \mu_A a - \delta_A a a.
\end{align*}
\]

Note that the first five equations in (2.1) do not depend on the last four equations. In addition, by the condition \( r_M > \mu_M \) and a standard convergence result on the logistic type reaction-diffusion equation (see, e.g., Theorem 3.1.5 and the proof of Theorem 3.1.6 in [23]), it follows that for any \( \mathcal{M}(0, \cdot) \in C(\Omega, \mathbb{R}_+^2) \setminus \{0\} \), we have

\[
\lim_{t \to \infty} \mathcal{M}(t, \cdot) = K_M \left(1 - \frac{\mu_M}{r_M}\right) := Q
\]

uniformly for \( x = (x_1, x_2) \in \bar{\Omega} \). Thus, we first analyze the global dynamics of the

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Table 1.1

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>( r_M )</td>
<td>Individual birth rate of mice.</td>
</tr>
<tr>
<td>( K_M )</td>
<td>Carrying capacity for mice.</td>
</tr>
<tr>
<td>( \mu_M )</td>
<td>Mortality rate per mouse.</td>
</tr>
<tr>
<td>( D_M )</td>
<td>Diffusion coefficients for mice.</td>
</tr>
<tr>
<td>( D_H )</td>
<td>Diffusion coefficients for deer.</td>
</tr>
<tr>
<td>( \mu_L )</td>
<td>Mortality rate per questing tick larva.</td>
</tr>
<tr>
<td>( \mu_V )</td>
<td>Mortality rate per feeding tick larva.</td>
</tr>
<tr>
<td>( \mu_N )</td>
<td>Mortality rate per questing tick nymph.</td>
</tr>
<tr>
<td>( \mu_A )</td>
<td>Mortality rate per adult tick.</td>
</tr>
<tr>
<td>( \delta_V )</td>
<td>Self-regulation coefficient for tick larva.</td>
</tr>
<tr>
<td>( \delta_A )</td>
<td>Self-regulation coefficient for adult tick.</td>
</tr>
<tr>
<td>( \beta )</td>
<td>Susceptibility to infection in mice.</td>
</tr>
<tr>
<td>( \beta_T )</td>
<td>Susceptibility to infection in ticks.</td>
</tr>
<tr>
<td>( \gamma )</td>
<td>Biting rate per nymph to humans.</td>
</tr>
<tr>
<td>( r(t) )</td>
<td>Individual birth rate of tick at time ( t ).</td>
</tr>
<tr>
<td>( \sigma(t) )</td>
<td>Individual development rate of nymph at time ( t ).</td>
</tr>
<tr>
<td>( \alpha_1(t) )</td>
<td>Individual biting rate of larva to mice at time ( t ).</td>
</tr>
<tr>
<td>( \alpha_2(t) )</td>
<td>Individual biting rate of nymph to mice at time ( t ).</td>
</tr>
</tbody>
</table>
following limiting system:

\[
\begin{align*}
\frac{\partial L}{\partial t} &= r(t)A - L[\mu_L + \alpha_1(t)Q], \\
\frac{\partial V}{\partial t} &= D_M \Delta V + \alpha_1(t)QL - V(\sigma(t) + \mu_V) - \delta_V V^2, \\
\frac{\partial N}{\partial t} &= \sigma(t)V - N[\gamma + \alpha_2(t)Q + \mu_N], \\
\frac{\partial A}{\partial t} &= D_H \Delta A + \alpha_2(t)NQ - \mu_A A - \delta_A A^2.
\end{align*}
\]

(2.2)

Let \( X = C(\bar{\Omega}, \mathbb{R}^4), X^+ = C(\bar{\Omega}, \mathbb{R}^4_+) \), and \( \Gamma(t, x, y) \) be the Green function associated with the Laplacian operator \( \Delta \) and the Neumann boundary condition, and define

\[
\begin{align*}
[T_1(t, s)\phi_1](x) &= e^{-\int_0^t (\mu_L + \alpha_1(\tau)Q) d\tau} \phi_1(x), \\
[T_2(t, s)\phi_2](x) &= e^{-\int_0^t (\sigma(\tau) + \mu_V) d\tau} \int_\Omega \Gamma(D_M(t-s), x, y)\phi_2(y)dy, \\
[T_3(t, s)\phi_3](x) &= e^{-\int_0^t (\gamma + \alpha_2(\tau)Q + \mu_N) d\tau} \phi_3(x), \\
[T_4(t, s)\phi_4](x) &= e^{-\mu_A(t-s)} \int_\Omega \Gamma(D_H(t-s), x, y)\phi_4(y)dy.
\end{align*}
\]

Then system (2.2) can be written as the following integral equations:

\[
\begin{align*}
L(t, x) &= T_1(t, 0)L(0, x) + \int_0^t T_1(t, s)r(s)A(s, x)ds, \\
V(t, x) &= T_2(t, 0)V(0, x) + \int_0^t T_2(t, s)(\alpha_1(s)QL(s, x) - \delta_V V^2(s, x))ds, \\
N(t, x) &= T_3(t, 0)N(0, x) + \int_0^t T_3(t, s)\sigma(s)V(s, x)ds, \\
A(t, x) &= T_4(t, 0)A(0, x) + \int_0^t T_4(t, s)(\alpha_2(s)QN(s, x) - \delta_A A^2(s, x))ds.
\end{align*}
\]

(2.3)

By the theory of abstract semilinear integral equations in [14], it follows that for any \( \phi \in X^+ \), system (2.3) admits a unique nonnegative and noncontinuable solution

\[
\begin{align*}
u(t, x, \phi) := (L(t, x, \phi), V(t, x, \phi), N(t, x, \phi), A(t, x, \phi))
\end{align*}
\]

on \([0, \sigma_\phi] \) with \( u(0, \cdot, \phi) = \phi \). Moreover, it follows from [14, Proposition 1 and Remark 1.4] that system (2.3) admits the comparison principle.

Note that the spatially homogeneous system of (2.2) is the following periodic system of ordinary differential equations (ODEs):

\[
\begin{align*}
\frac{dL}{dt} &= r(t)L - L[\mu_L + \alpha_1(t)Q], \\
\frac{dV}{dt} &= \alpha_1(t)QL - V(\sigma(t) + \mu_V) - \delta_V V^2, \\
\frac{dN}{dt} &= \sigma(t)V - N[\gamma + \alpha_2(t)Q + \mu_N], \\
\frac{dA}{dt} &= \alpha_2(t)NQ - \mu_A A - \delta_A A^2.
\end{align*}
\]

(2.4)
and every nonnegative solution \((L(t), V(t), N(t), A(t))\) of \((2.4)\) satisfies
\[
\frac{d}{dt}(L(t) + V(t) + N(t) + A(t)) = (r(t) - \mu A - \delta A)A - \mu L L - \mu V V - \delta V V^2 - N(\gamma + \mu N) < 0
\]
provided \(A > (\max_{0 \leq t \leq \omega} r(t) - \mu A)/\delta A\). It then follows that solutions of \((2.4)\) are ultimately bounded in \(\mathbb{R}^4_+\) and exist for all \(t \in [0, \infty)\).

Linearizing system \((2.4)\) at \((0,0,0,0)\), we get the following linear cooperative system:
\[
\begin{align*}
\frac{dL}{dt} &= r(t)A - L[\mu_L + \alpha_1(t)Q], \\
\frac{dV}{dt} &= \alpha_1(t)QL - V(\sigma(t) + \mu V), \\
\frac{dN}{dt} &= \sigma(t)V - N[\gamma + \alpha_2(t)Q + \mu N], \\
\frac{dA}{dt} &= \alpha_2(t)NQ - \mu AA.
\end{align*}
\]

(2.5)

Let \(r_1\) be the principal Floquet multiplier of system \((2.5)\), that is, the spectral radius of the Poincaré map associated with system \((2.5)\). Then we have the following result.

**Lemma 2.1.** The following statements are valid:
(i) If \(r_1 \leq 1\), then \((0,0,0,0)\) is globally asymptotically stable for \((2.4)\) in \(\mathbb{R}^4_+\).
(ii) If \(r_1 > 1\), then \((2.4)\) admits a unique positive \(\omega\)-periodic solution \(u^*(t) := (L^*(t), V^*(t), N^*(t), A^*(t))\), which is globally asymptotically stable for \((2.4)\) in \(\mathbb{R}^4_+ \setminus \{0\}\).

**Proof.** Define \(f = (f_1, f_2, f_3, f_4) : \mathbb{R}^4 \to \mathbb{R}^4\) by
\[
\begin{align*}
f_1(x_1, x_2, x_3, x_4) &= r(t)x_4 - x_1[\mu_L + \alpha_1(t)Q], \\
f_2(x_1, x_2, x_3, x_4) &= \alpha_1(t)Qx_1 - x_2(\sigma(t) + \mu V) - \delta V x_2^2, \\
f_3(x_1, x_2, x_3, x_4) &= \sigma(t)x_2 - x_3[\gamma + \alpha_2(t)Q + \mu N], \\
f_4(x_1, x_2, x_3, x_4) &= \alpha_2(t)x_3Q - \mu A x_4 - \delta A x_4^2.
\end{align*}
\]

It is easy to verify that \(f_i \geq 0\) for any \(x = (x_1, x_2, x_3, x_4) \in \mathbb{R}^4_+\) with \(x_i = 0\), and the Jacobian matrix of \(f(x_1, x_2, x_3, x_4)\) is cooperative for any \(x \in \mathbb{R}^4_+\). Thus, the solution semiflow \(\{\Pi_t\}_{t \geq 0}\) determined by \((2.4)\) is monotone in the sense that \(\Pi_t(x) \geq \Pi_t(y)\) provided \(x \geq y\) in \(\mathbb{R}^4_+\). Next, we show that \(\Pi_t\) is strongly monotone for all \(t \geq 3\omega\), that is, \(\Pi_t(x) \gg \Pi_t(y)\) whenever \(t \geq 3\omega\) and \(x > y\). Let \(x(t) := (x_1(t), x_2(t), x_3(t), x_4(t)) = \Pi_t(x_0), y(t) := (y_1(t), y_2(t), y_3(t), y_4(t)) = \Pi_t(y_0)\), and \(z(t) := (z_1(t), z_2(t), z_3(t), z_4(t)) = x(t) - y(t)\). Then \(z(t)\) satisfies the following equations:
\[
\begin{align*}
\frac{dz_1}{dt} &= r(t)z_4 - z_1[\mu_L + \alpha_1(t)Q], \\
\frac{dz_2}{dt} &= \alpha_1(t)Qz_1 - z_2[\sigma(t) + \mu V + \delta V(x_2(t) + y_2(t))], \\
\frac{dz_3}{dt} &= \sigma(t)z_2 - z_3[\gamma + \alpha_2(t)Q + \mu N], \\
\frac{dz_4}{dt} &= \alpha_2(t)Qz_3 - z_4[\mu A + \delta A(x_4(t) + y_4(t))].
\end{align*}
\]

(2.6)

Now it suffices to prove \(z(t) \gg 0\) for all \(t \geq 3\omega\), whenever \(z(0) = x_0 - y_0 \geq 0\). Denote \(\frac{dz}{dt} = A(t)z\), where \(A(t) := (a_{ij}(t)), 1 \leq i, j \leq 4\), is the coefficient matrix of the right-hand side of \((2.6)\). Since \(a_{ij}(t) \geq 0, i \neq j\), we have \(\frac{dz_i}{dt} \geq a_{ii}(t)z_i, 1 \leq i \leq 4\). Using this...
Then Φ[24, Lemma 3.1], it follows that Φ is strongly monotone when $r \Phi$.

Furthermore, by the (2.2) are ultimately bounded in $t$.

And not identically zero, there must be some $t \in [0, \omega]$ such that $z_1(t) > 0$. Otherwise, we have $z_2(t) \equiv 0$ for all $t \in [0, \omega]$. From the $z_2$ equation in (2.6), we further derive that $a_1(t)Qz_1 \equiv 0$ for all $t \in [0, \omega]$. Since $a_1(t)$ is periodic and not identically zero, there must be some $t \in [0, \omega]$ such that $z_1(t) = 0$, which is a contradiction. Similarly, by the $z_3$ equation in (2.6) and the fact that $\sigma(t)$ is periodic and not identically zero, we can prove there exists $t_2 \in [t_1, t_1 + \omega]$ such that $z_3(t_2) > 0$.

Therefore, by the $z_4$ equation in (2.6) and the properties of $a_2(t)$, we see that there exists $t_4 \in [t_2, t_2 + \omega]$ such that $z_4(t_4) > 0$. Since $t_4 \in [0, 3\omega]$, we have proved that $\Pi_t$ is strongly monotone when $t \geq 3\omega$. Clearly, other cases can be proved in a similar way.

Note that $z(t) = \Pi_t(z(0))$ where $z(t)$ is a $3\omega$-periodic solution of (2.4) with initial data in $\mathbb{R}_+^3 \setminus \{0\}$. Clearly, $u^*(0)$ is unique fixed point of $\Pi_{3\omega}$. By the properties of the periodic semiflow, we further get

$$
\Pi_{3\omega}(\Pi_{\omega}(u^*(0))) = \Pi_{\omega}(\Pi_{3\omega}(u^*(0))) = \Pi_{\omega}(u^*(0)),
$$

which implies that $\Pi_{\omega}(u^*(0))$ is also a fixed point of $\Pi_{3\omega}$. By the uniqueness of the fixed point of $\Pi_{3\omega}$, it follows that $\Pi_{\omega}(u^*(0)) = u^*(0)$. Thus, $u^*(t)$ is an $\omega$-periodic solution of (2.4) and statement (ii) is valid.

To Lemma 2.1 and the comparison principle, we know that solutions of system (2.2) are ultimately bounded in $X^+$, and hence $\sigma_\phi = \infty$ for all $\phi \in X^+$. Let $\Phi_t : X^+ \to X^+$, $t > 0$, be the solution semiflow associated with (2.2), that is, $\Phi_t(\phi) = u(t, \cdot, \phi)$ for all $\phi \in X^+$. Define a linear operator $L(t)\phi = (T_1(t, 0)\phi_1, 0, T_3(t, 0)\phi_3, 0)$ and

$$
S(t)\phi = \left(\int_0^t T_1(t, s)r(s)A(s, \cdot, \phi)ds, V(t, \cdot, \phi), \int_0^t T_3(t, s)\sigma(s)V(s, \cdot, \phi)ds, A(t, \cdot, \phi)\right).
$$

Then $\Phi_t(\phi) = L(t)\phi + S(t)\phi$. By the same decomposition argument as in the proof of [24, Lemma 3.1], it follows that $\Phi_t$ is an $\alpha$-contraction operator for any given $t > 0$. Combining the arguments in Lemma 2.1 and the positivity result for reaction-diffusion equations, we can further show that $\Phi_t$ is strongly positive for all $t \geq 3\omega$, that is, $\Phi_t(\phi) \gg 0$ for any $t \geq 3\omega$ and initial data $\phi > 0$ in $X^+$. Note that solutions of system (2.4) are also solutions of the reaction-diffusion system (2.2) subject to Neumann boundary conditions. Thus, Lemma 2.1 and the standard comparison principle arguments give rise to the following result.

**Theorem 2.2.** For any given $\phi \in X^+$, let $u(t, \cdot, \phi)$ be the solution of (2.2) with $u(0, \cdot, \phi) = \phi$. Then the following two statements are valid:

(i) If $r_1 \leq 1$, then $(0, 0, 0, 0)$ is globally asymptotically stable for (2.2) in $X^+$.

(ii) If $r_1 > 1$, then $u^*(t)$ is globally asymptotically stable for (2.2) in $X^+ \setminus \{0\}$. 

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Next we consider the global dynamics of the following limiting system:

\[
\begin{align*}
\frac{\partial m}{\partial t} &= D_M \Delta m + \alpha_2(t)\beta(Q - m)n - \mu_M m, \\
\frac{\partial v}{\partial t} &= D_M \Delta v + \alpha_1(t)mL^*(t) - v(\sigma(t) + \mu_v) - \delta_v V^*(t)v, \\
\frac{\partial n}{\partial t} &= \beta_T \sigma(t)v - n[\gamma + \alpha_2(t)Q + \mu_N], \\
\frac{\partial a}{\partial t} &= D_H \Delta a + \alpha_2(t)[Qn + \beta_T m(N^*(t) - n)] - \mu_A a - \delta_A A^*(t)a.
\end{align*}
\]  

(2.7)

Let \( Y = C(\Omega, [0, Q] \times \mathbb{R}_+^2) \times C(\Omega, \mathbb{R}_+) \). It then follows that for any \( \phi \in Y \), system (2.7) admits a unique solution \( w(t, x, \phi) := (m(t, x, \phi), v(t, x, \phi), n(t, x, \phi), a(t, x, \phi)) \) on \([0, \infty) \) with \( w(0, \cdot, \phi) = \phi \), and \( w(t, x, \phi) \in Y \) for all \( t > 0 \). Moreover, by the ultimate boundedness of \( V, N, A \), we see that \( w(t, x, \phi) \) is also ultimately bounded.

Note that the spatially homogeneous system associated with (2.7) is the following system:

\[
\begin{align*}
\frac{\partial m}{\partial t} &= \alpha_2(t)\beta(Q - m)n - \mu_M m, \\
\frac{\partial v}{\partial t} &= \alpha_1(t)mL^*(t) - v(\sigma(t) + \mu_v) - \delta_v V^*(t)v, \\
\frac{\partial n}{\partial t} &= \beta_T \sigma(t)v - n[\gamma + \alpha_2(t)Q + \mu_N], \\
\frac{\partial a}{\partial t} &= \alpha_2(t)[Qn + \beta_T m(N^*(t) - n)] - \mu_A a - \delta_A A^*(t)a,
\end{align*}
\]

and \((0, 0, 0, 0)\) is an \( \omega \)-periodic solution of (2.8). Linearizing system (2.8) at \((0, 0, 0, 0)\), we get the linear system

\[
\begin{align*}
\frac{\partial m}{\partial t} &= \alpha_2(t)\beta Qn - \mu_M m, \\
\frac{\partial v}{\partial t} &= \alpha_1(t)mL^*(t) - v(\sigma(t) + \mu_v) - \delta_v V^*(t)v, \\
\frac{\partial n}{\partial t} &= \beta_T \sigma(t)v - n[\gamma + \alpha_2(t)Q + \mu_N], \\
\frac{\partial a}{\partial t} &= \alpha_2(t)Qn + \beta_T \alpha_2(t)N^*(t)m - \mu_A a - \delta_A A^*(t)a.
\end{align*}
\]  

(2.9)

In order to introduce the basic reproduction ratio for system (2.8), we follow the procedure in [21]. We rewrite system (2.9) as \( \frac{\partial \mathbf{u}}{\partial t} = (F(t) - V(t))\mathbf{u} \), where

\[
F(t) = \begin{pmatrix} 0 & 0 & \alpha_2(t)\beta Q & 0 \\ \alpha_1(t)L^*(t) & 0 & 0 & 0 \\ 0 & \beta_T \alpha_2(t)N^*(t) & 0 & 0 \\ \beta_T \alpha_2(t)N^*(t) & 0 & 0 & 0 \end{pmatrix},
\]

\[
V(t) = \begin{pmatrix} \mu_M & 0 & 0 & 0 \\ 0 & \sigma(t) + \mu_v + \delta_v V^*(t) & 0 & 0 \\ 0 & -\beta_T \sigma(t) & \gamma + \alpha_2(t)Q + \mu_N & 0 \\ 0 & 0 & -\alpha_2(t)Q & \mu_A + \delta_A A^*(t) \end{pmatrix}.
\]
Let \( Y(t, s), t \geq s \), be the evolution operator of the linear system \( \frac{dY}{dt} = -V(t)u \).
That is, for each \( s \in \mathbb{R} \), the matrix \( Y(t, s) \) satisfies
\[
\frac{d}{dt}Y(t, s) = -V(t)Y(t, s) \quad \forall t \geq s, \ Y(s, s) = I,
\]
where \( I \) is the \( 4 \times 4 \) identity matrix.

Let \( C_\omega \) be the Banach space of all \( \omega \)-periodic functions from \( \mathbb{R} \) to \( \mathbb{R}^2 \), equipped with the maximum norm. Suppose \( \phi(s) \in C_\omega \) is the initial distribution of infectious individuals in this periodic environment; then \( F(s)\phi(s) \) is the rate of new infections produced by the infected individuals who were introduced at time \( s \), and \( Y(t, s)F(s)\phi(s) \) represents the distribution of those infected individuals who were newly infected at time \( s \) and remain in the infected compartments at time \( t \) for \( t \geq s \). Hence,
\[
\int_{-\infty}^{t} Y(t, s)F(s)\phi(s)ds = \int_{0}^{\infty} Y(t, t-\tau)F(t-\tau)\phi(t-\tau)d\tau
\]
gives the distribution of accumulative new infection at time \( t \) produced by all those infected individuals \( \phi(s) \) introduced at the previous time. Define a linear operator \( L : C_\omega \to C_\omega \) by
\[
(L\phi)(t) = \int_{0}^{\infty} Y(t, t-\tau)F(t-\tau)\phi(t-\tau)d\tau \quad \forall t \in \mathbb{R}, \phi \in C_\omega.
\]
According to \([2, 21]\), we define the basic reproduction ratio to be \( R_0 := r(L) \), where \( r(L) \) is the spectral radius of \( L \).

Let \( r_2 \) be the principal Floquet multiplier of the linear system (2.9). Then \([21, \text{Theorem 2.2}]\) implies that \( R_0 - 1 \) has the same sign as \( r_2 - 1 \). Thus, \((0,0,0,0)\) is asymptotically stable if \( R_0 < 1 \) and unstable if \( R_0 > 1 \).

Since the first three equations in system (2.8) do not depend on the fourth, we consider the following subsystem of system (2.8):
\[
\begin{align*}
\frac{dm}{dt} &= \alpha_2(t)\beta(Q - m)n - \mu_M m, \\
\frac{dv}{dt} &= \alpha_1(t)mL^*(t) - v(\sigma(t) + \mu_V) - \delta_V V^*(t)v, \\
\frac{dn}{dt} &= \beta_T\sigma(t)v - n[\gamma + \alpha_2(t)Q + \mu_N].
\end{align*}
\]
Let \( r_3 \) be the principal Floquet multiplier of the following periodic linear system:
\[
\begin{align*}
\frac{dm}{dt} &= \alpha_2(t)\beta Qn - \mu_M m, \\
\frac{dv}{dt} &= \alpha_1(t)mL^*(t) - v(\sigma(t) + \mu_V) - \delta_V V^*(t)v, \\
\frac{dn}{dt} &= \beta_T\sigma(t)v - n[\gamma + \alpha_2(t)Q + \mu_N].
\end{align*}
\]
Comparing systems (2.9) and (2.11), it is easy to see that \( r_3 - 1 \) has the same sign as \( r_2 - 1 \). Then we have the following threshold result for system (2.8) in terms of \( R_0 \).

**Lemma 2.3.** The following statements are valid:

(i) If \( R_0 \leq 1 \), then \((0,0,0,0)\) is globally asymptotically stable for (2.8) in \([0, Q] \times \mathbb{R}_+^4\).
(ii) If $R_0 > 1$, then (2.8) admits a unique positive $\omega$-periodic solution $w^*(t) := (m^*(t), v^*(t), n^*(t), a^*(t))$, which is globally asymptotically stable for (2.8) in $([0, Q] \times \mathbb{R}_+^2 \setminus \{0\}) \times \mathbb{R}_+$.  

Proof. We first show that the following threshold result holds for system (2.10):

(a) If $r_3 \leq 1$, then $(0,0,0)$ is globally asymptotically stable for (2.10) in $[0, Q] \times \mathbb{R}_+^2$.

(b) If $r_3 > 1$, then (2.10) has a positive $\omega$-periodic solution $(m^*(t), v^*(t), n^*(t))$, which is globally asymptotically stable for (2.10) in $([0, Q] \times \mathbb{R}_+^2 \setminus \{0\})$.

Let $\bar{w}(t, \bar{w}_0)$ be the nonnegative solution of system (2.10) with initial data $\bar{w}_0 \in [0, Q] \times \mathbb{R}_+^2$. Denote $X(t) = \frac{\partial \bar{w}}{\partial \bar{w}_0}(t, \bar{w}_0)$. Then $X(t) = (x_{ij}(t))_{3 \times 3}$ satisfies

$$X'(t) = A(t)X(t), \quad X(0) = I,$$

where $A(t) = (a_{ij}(t))_{3 \times 3}$ is the Jacobian matrix of the right-hand side of system (2.10) evaluated at $(m,v,n) = \bar{w}(t, \bar{w}_0)$. Since $a_{ij}(t) \geq 0$, for all $t \geq 0$, we have $x_{ij}(t) \geq x_{ij}(t)$ for all $t \geq 0$, $1 \leq i,j \leq 3$. It then follows that $x_{ij}(t) > 0$ for all $t \geq t^*$ provided $x_{ij}(t^*) > 0$ for some $t^* > 0$. Since $x_{ii}(0) = 1$, we have $x_{ii}(t) > 0$ for all $t \geq 0$, $1 \leq i \leq 3$. We further prove that $x_{ij}(t) > 0$ for all $t \geq 2\omega$. Note that $x_{ij}(t)$, $i \neq j$, satisfy the following equations:

$$x_{12}'(t) = -(\alpha_2(t)\beta n(t) + \mu_3) x_{12}(t) + \alpha_2(t)\beta(Q - m(t)) x_{32}(t),$$
$$x_{13}'(t) = -(\alpha_2(t)\beta n(t) + \mu_3) x_{13}(t) + \alpha_2(t)\beta(Q - m(t)) x_{33}(t),$$
$$x_{21}'(t) = \alpha_1(t) L^*(t)x_{11}(t) - (\sigma(t) + \mu_1 + V^*(t) \delta V)x_{21}(t),$$
$$x_{23}'(t) = \alpha_1(t) L^*(t)x_{13}(t) - (\sigma(t) + \mu_1 + V^*(t) \delta V)x_{23}(t),$$
$$x_{31}'(t) = \beta_1 \sigma(t) x_{21}(t) + (\gamma + \alpha_2(t)Q + \mu_N) x_{31}(t),$$
$$x_{32}'(t) = \beta_1 \sigma(t) x_{22}(t) + (\gamma + \alpha_2(t)Q + \mu_N) x_{32}(t).$$

Since $x_{ii}(t) > 0$ for all $t \geq 0$, $1 \leq i \leq 3$, and $a_1(t), a_2(t), \sigma(t)$ are periodic but not identically zero, it follows from a contradiction argument that there exists $t_1 \in [0, \omega]$ such that $x_{13}(t), x_{21}(t), x_{32}(t) > 0$ for all $t \geq t_1$. Then we can prove that there exists $t_2 \in [t_1, t_1 + \omega]$ such that $x_{12}(t), x_{23}(t), x_{31}(t) > 0$ for all $t \geq t_2$. Since $t_2 \in [0, 2\omega]$, we have $X(t) \succ 0$ for all $t \geq 2\omega$. Then for any $\bar{w}_1, \bar{w}_2 \in \mathbb{R}_+^3$ satisfying $\bar{w}_2 > \bar{w}_1$, we have

$$\bar{w}(t, \bar{w}_2) - \bar{w}(t, \bar{w}_1) = \int_0^1 \frac{\partial \bar{w}}{\partial \bar{w}_0}(t, \bar{w}_1 + r(\bar{w}_2 - \bar{w}_1))(\bar{w}_2 - \bar{w}_1)dr \succ 0$$

provided $t \geq 2\omega$. This implies that $\bar{w}_1(\bar{w}_2) \succ \bar{w}_1(\bar{w}_2)$ for all $t \geq 2\omega$. In particular, we have that $\bar{w}_2(\cdot)$ is strongly monotone. By the same argument as in the proof of Lemma 2.1, we see that statements (a) and (b) hold.

By the theory of chain transitive sets (see [7] or [23, section 1.2]) and arguments similar to those in the proof of Theorem 2.5, it follows that $\lim_{t \to \infty} a(t) = 0$ in the case where $r_3 \leq 1$, and $\lim_{t \to \infty} (a(t) - a^*(t)) = 0$ in the case where $r_3 > 1$, where $a^*(t)$ is the unique positive $\omega$-periodic solution of the limiting equation

$$\frac{da}{dt} = \alpha_2(t)(Qn^*(t) + \beta r^*(t)(N^*(t) - n^*(t))) - (\mu_A + \delta A^*(t))a.$$

Since $r_3 - 1$ has the same sign as $R_0 - 1$, we then complete the proof. \[ \Box \]

The following result shows that $R_0$ is also the threshold value for the global dynamics of system (2.7).

**Theorem 2.4.** For any given $\phi \in \mathcal{Y}$, let $w(t, \cdot, \phi)$ be the solution of (2.7) with $w(0, \cdot, \phi) = \phi$. Then the following two statements are valid:

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is the unique solution of (2.1) with initial data

Lemma 2.3, together with the standard comparison argument, implies that the threshold result is valid for the following subsystem:

Proof. Since the first three equations in (2.7) do not depend on the fourth, it suffices to prove that the threshold result is valid for the following subsystem:

\[
\frac{\partial m}{\partial t} = D_M \Delta m + \alpha_2(t)\beta(Q - m)n - \mu_M m,
\]

\[
\frac{\partial v}{\partial t} = D_M \Delta v + \alpha_1(t)mL^*(t) - v(\sigma(t) + \mu_V) - \delta V^*(t)v,
\]

\[
\frac{\partial n}{\partial t} = \beta_T \sigma(t)v - n[\gamma + \alpha_2(t)Q + \mu_N].
\]

Let \( \hat{w}(t, \cdot, \cdot) \) be the unique solution of (2.12) with the initial data \( \hat{\phi} \in C(\Omega, [0, Q] \times \mathbb{R}_+^2) \setminus \{0\} \). By the positivity result for reaction-diffusion equations, it follows that \( \hat{w}(t, \cdot, \cdot) \gg 0 \) for all \( t \geq 2\omega \). Note that solutions of system (2.10) are also solutions of the reaction-diffusion system (2.12) subject to Neumann boundary conditions. Thus, Lemma 2.3, together with the standard comparison argument, implies that the threshold result is valid for system (2.12).

In the rest of this section, we use the theory of chain transitive sets (see [7] or [23, section 1.2]) to establish the following threshold result on the global dynamics for system (2.1).

Theorem 2.5. Let \( r_1 > 1 \). Then the following statements are valid:

(i) If \( R_0 \leq 1 \), then the disease-free periodic solution

\[
(Q, L^*(t), V^*(t), N^*(t), A^*(t), 0, 0, 0, 0)
\]

is globally attractive for system (2.1) in \( (C(\Omega, \mathbb{R}_+^4) \setminus \{0\}) \times (X^+ \setminus \{0\}) \times C(\Omega, \mathbb{R}_+^1) \).

(ii) If \( R_0 > 1 \), then system (2.1) has a unique positive \( \omega \)-periodic solution

\[
(Q, L^*(t), V^*(t), N^*(t), A^*(t), m^*(t), v^*(t), n^*(t), a^*(t)),
\]

which is globally attractive for system (2.1) in \( (C(\Omega, \mathbb{R}_+^4) \setminus \{0\}) \times (X^+ \setminus \{0\}) \times C(\Omega, \mathbb{R}_+^1) \).

Proof. Let \( \{\Psi_t\}_{t \geq 0} \) be the periodic semiflow associated with system (2.1). That is,

\[
\Psi_t(\psi)(x) := (M(t, x), L(t, x), V(t, x), N(t, x), A(t, x), m(t, x), v(t, x), n(t, x), a(t, x))
\]

is the unique solution of (2.1) with initial data \( \psi \in C(\Omega, \mathbb{R}_+^9) \). For any given \( \psi \in (C(\Omega, \mathbb{R}_+^4) \setminus \{0\}) \times (X^+ \setminus \{0\}) \times C(\Omega, \mathbb{R}_+^1) \), let \( \mathcal{L} \) be the omega limit set of the discrete-time orbit \( \{\Psi^n(\psi)\}_{n \geq 1} \). Since every solution is ultimately bounded, we know from [7, Lemma 2.1] (see also [23, Lemma 1.2.1]) that \( \mathcal{L} \) is an internally chain transitive set for \( \Psi_1 \). Since \( r_1 > 1 \), Theorem 2.2 implies that

\[
\lim_{n \to \infty} \left( (\Psi^n_1(\psi))_1, (\Psi^n_1(\psi))_2, (\Psi^n_1(\psi))_3, (\Psi^n_1(\psi))_4, (\Psi^n_1(\psi))_5 \right)
\]

\[
= (Q, L^*(0), V^*(0), N^*(0), A^*(0)).
\]

Thus, there exists a subset \( \mathcal{L}_1 \) of \( C(\Omega, \mathbb{R}_+^4) \) such that

\[
\mathcal{L} = \{(Q, L^*(0), V^*(0), N^*(0), A^*(0))\} \times \mathcal{L}_1.
\]
For any given \( \phi = (\phi_1, \phi_2, \ldots, \phi_9) \in \mathcal{L} \), there exists a sequence \( n_k \to \infty \) such that \( \Psi^{n_k}_\omega(v) \to \phi \) as \( k \to \infty \). Since \( m(n_k \omega, x) \leq M(n_k \omega, x) \) for all \( x \in \bar{\omega} \), letting \( n_k \to \infty \), we obtain \( 0 \leq \phi_6(x) \leq \phi_1(x) \equiv Q \) for all \( x \in \bar{\omega} \). It then follows that \( \mathcal{L}_1 \subset Y \). It is easy to see that

\[
\Psi_\omega|_{L}(Q, L^*(0), V^*(0), N^*(0), A^*(0), \phi_6, \phi_7, \phi_8, \phi_9) = \{(Q, L^*(0), V^*(0), N^*(0), A^*(0))\} \times Y_{\omega}|_{\mathcal{L}_1}(\phi_6, \phi_7, \phi_8, \phi_9),
\]

where \( \{T_{\epsilon}\}_{\epsilon \geq 0} \) is the solution semiflow associated with system (2.7) on \( Y \). Since \( \mathcal{L} \) is an internally chain transitive set for \( \Psi_\omega \), it follows that \( \mathcal{L}_1 \) is an internally chain transitive set for \( Y_\omega \).

In the case where \( R_0 \leq 1 \), it follows from Theorem 2.4(i) that \( (0, 0, 0, 0) \) is globally asymptotically stable. By [7, Theorem 3.1] (see also [23, Theorem 1.2.1]), we have \( \mathcal{L}_1 = \{(0, 0, 0, 0)\} \), and hence \( \mathcal{L} = \{(Q, L^*(0), V^*(0), N^*(0), A^*(0), 0, 0, 0, 0, 0)\} \). This implies that statement (i) is valid.

In the case where \( R_0 > 1 \), by Theorem 2.4(ii) and [7, Theorem 3.2] (see also [23, Theorem 1.2.2]), it follows that

\[
\text{either } \mathcal{L}_1 = \{(0, 0, 0, 0)\} \text{ or } \mathcal{L}_1 = \{(m^*(0), v^*(0), n^*(0), a^*(0))\}.
\]

We further claim that \( \mathcal{L}_1 \neq \{(0, 0, 0, 0)\} \). Suppose, by contradiction, that \( \mathcal{L}_1 = \{(0, 0, 0, 0)\} \). Then we have \( \mathcal{L} = \{(Q, L^*(0), V^*(0), N^*(0), A^*(0), 0, 0, 0, 0, 0, 0)\} \). Thus, \( \lim_{t \to \infty} (m(t, x), v(t, x), n(t, x)) = 0 \) uniformly for \( x \in \Omega \), and for any \( \epsilon > 0 \), there exists \( T_\epsilon > 0 \) such that

\[
|\{M(t, x), L(t, x), \mathcal{V}(t, x), \mathcal{N}(t, x), \mathcal{A}(t, x)\} - (Q, L^*(t), V^*(t), N^*(t), A^*(t))| < \epsilon
\]

for all \( t \geq T_\epsilon \) and \( x \in \bar{\Omega} \). Hence, for any \( t \geq T_\epsilon \), we have

\[
\begin{align*}
\frac{dm}{dt} & \geq D_M \Delta m + \alpha_2(t)\beta(Q - \epsilon - m)n - \mu_M m, \\
\frac{dv}{dt} & \geq D_M \Delta v + \alpha_1(t)m(L^*(t) - \epsilon) - v(\sigma(t) + \mu_V) - \delta_V(V^*(t) + \epsilon)v, \\
\frac{dn}{dt} & \geq \beta_T\sigma(t)v - n[\gamma + \alpha_2(t)(Q + \epsilon) + \mu_N].
\end{align*}
\]

By the assumption on \( \psi \) in statement (ii), we further have \( (m(0, \cdot), v(0, \cdot), n(0, \cdot)) \in C(\Omega, \mathbb{R}_+^4 \setminus \{0\}) \). Let \( r_3 \) be the principal Floquet multiplier of the periodic linear system

\[
\begin{align*}
\frac{dm}{dt} & = \alpha_2(t)\beta(Q - \epsilon)n - \mu_M m, \\
\frac{dv}{dt} & = \alpha_1(t)m(L^*(t) - \epsilon) - v(\sigma(t) + \mu_V) - \delta_V(V^*(t) + \epsilon)v, \\
\frac{dn}{dt} & = \beta_T\sigma(t)v - n[\gamma + \alpha_2(t)(Q + \epsilon) + \mu_N].
\end{align*}
\]

Since \( r_3 > 1 \), we can fix \( 0 < \epsilon < \min(Q, \min_{0 \leq t \leq \omega} L^*(t)) \) small enough such that \( r_\epsilon > 1 \). By a result similar to Theorem 2.4(ii), we see that the Poincaré map of

\[
\begin{align*}
\frac{dm}{dt} & = D_M \Delta m + \alpha_2(t)\beta(Q - \epsilon - m)n - \mu_M m, \\
\frac{dv}{dt} & = D_M \Delta v + \alpha_1(t)m(L^*(t) - \epsilon) - v(\sigma(t) + \mu_V) - \delta_V(V^*(t) + \epsilon)v, \\
\frac{dn}{dt} & = \beta_T\sigma(t)v - n[\gamma + \alpha_2(t)(Q + \epsilon) + \mu_N]
\end{align*}
\]
admits a globally attractive fixed point \((\bar{m}_e(0), \bar{e}_r(0), \bar{e}_s(0)) \gg 0\). In view of (2.13) and (2.15), the comparison principle implies that
\[
\liminf_{n \to \infty} \left( m(n \omega, x), n(n \omega, x), v(n \omega, x) \right) \geq \left( \bar{m}_e(0), \bar{e}_r(0), \bar{e}_s(0) \right) \gg 0,
\]
which contradicts \(\lim_{t \to \infty} \left( m(t, x), v(t, x), n(t, x) \right) = 0\). It then follows that
\[
\mathcal{L}_1 = \{(m^*(0), v^*(0), n^*(0), a^*(0))\},
\]
and hence \(\mathcal{L} = \{(Q, L^*(0), V^*(0), A^*(0), m^*(0), v^*(0), n^*(0), a^*(0))\}\). This implies that statement (ii) is valid.

3. Spreading speed and traveling waves. In this section, we consider the spreading speed and traveling waves for system (2.7) in an unbounded spatial habitat \(\Omega\). Since all coefficients in (2.7) are spatially homogeneous, it suffices to study the spreading speed and traveling waves for system (2.7) in an unbounded spatial habitat \(\Omega\). Periodic evolution systems to study the spreading speed and monotone traveling waves appeal to the theory of spreading speeds and traveling waves developed in [8] for periodic evolution systems to study the spreading speed and monotone traveling waves connecting 0 and \(u^*(t)\) for system (2.7).

Let \(C := BC(\mathbb{R}, \mathbb{R}^3)\) be the set of all bounded and continuous functions from \(\mathbb{R}\) to \(\mathbb{R}^3\) equipped with the compact open topology; that is, a sequence \(\psi_n\) converges to \(\psi\) in \(C\) if and only if \(\psi_n(x)\) converges to \(\psi(x)\) in \(\mathbb{R}^3\) uniformly for \(x\) in any compact subset of \(\mathbb{R}\). For any \(\psi = (\psi_1, \psi_2, \psi_3) \in C\), we denote \(\psi^2 \geq \psi^1\) if \(\psi_i^2 \geq \psi_i^1\) for all \(1 \leq i \leq 3, x \in \mathbb{R}\), and \(\psi^2 > \psi^1\) if \(\psi^2 \geq \psi^1\) but \(\psi^2 \neq \psi^1\). For any vectors \(a, b \in \mathbb{R}^3\), we can define \(a \geq (\geq, \geq, \geq)\) similarly. For any \(\beta \gg 0\) in \(\mathbb{R}^3\), we define \([0, \beta] := \{\psi \in \mathbb{R}^3 : \beta \geq \psi \geq 0\}\) and \(C_\beta := \{\psi \in C : \beta \geq \psi \geq 0\}\). Define the reflection operator \(R\) by \(R[\psi](x) = \psi(-x)\), and the translation operator \(T_\beta\) by \(T_\beta[\psi](x) = \psi(x - \beta)\) for any \(\beta \in \mathbb{R}^3\).

Let \(Q\) be an operator from \(C_\beta\) to \(C_\beta\). In order to use the results in [8, 10], we need the following assumptions on \(Q\):

- (A1) \(Q[R[\phi]] = R[Q[\phi]], T_\beta \circ Q[\phi] = Q \circ T_\beta[\phi]\) for all \(\phi \in C_\beta, y \in \mathbb{R}\).
- (A2) \(Q : C_\beta \to C_\beta\) is continuous with respect to the compact open topology.
- (A3) \(Q\) is order preserving in the sense that \(Q[\phi] \geq Q[\psi]\) whenever \(\phi \geq \psi\) in \(C_\beta\).
- (A4) \(Q : [0, \beta] \to [0, \beta]\) admits exactly two fixed points 0 and \(\beta\), and \(\lim_{n \to \infty} Q^n[\alpha] = \beta\) for any \(\alpha \in [0, \beta]\) with \(0 < \alpha \leq \beta\).

Given a function \(\phi \in C_\beta\) and a bounded interval \(I = [a, b] \subset \mathbb{R}\), we define a function \(\phi_I \in C(I, \mathbb{R}^3)\) by \(\phi_I(x) = \phi(x)\). Moreover, for any subset \(D\) of \(C_\beta\), we define \(D_I = \{\phi_I \in C(I, \mathbb{R}^3) : \phi \in D\}\). In order to obtain the existence of traveling waves, we need the following weak compactness assumption:

- (A5) For any \(\delta > 0\), there exists \(l = l(\delta) \in [0, 1]\) such that for any \(D \subset C_\beta\) and any interval \(I = [a, b]\) of the length \(\delta\), we have \(\alpha(Q[D_I]) \leq \alpha(D_I)\), where \(\alpha\) is the Kuratowski measure of noncompactness on the Banach space \(C(I, \mathbb{R}^3)\).

Let \(\{Q_t\}_{t \geq 0}\) be the solution semiflow associated with system (2.12) on \(C_{\hat{w}^*(0)}\), that is,
\[
Q_t(\phi)(x) = \hat{w}(t, x, \phi) \quad \forall \phi \in C_{\hat{w}^*(0)}, \quad x \in \mathbb{R}, t \geq 0.
\]
It then follows that \( \{Q_t\}_{t \geq 0} \) is a monotone periodic semiflow and each map \( Q_t \) is subhomogeneous in the sense that \( Q_t(s\phi) \geq sQ_t(\phi) \) for all \( \phi \in C_{\omega^+}(0) \) and \( s \in [0,1] \). Moreover, we have the following observation.

**Lemma 3.1.** The Poincaré map \( Q_{\omega} \) satisfies conditions (A1)–(A5) with \( \beta = \dot{w}^*(0) \).

**Proof.** It is easy to verify that \( Q_{\omega} \) admits conditions (A1)–(A3). By statement (b) in the proof of Lemma 2.3, we see that condition (A4) holds for \( Q_{\omega} \). Furthermore, by a decomposition argument similar to that in the proof of [24, Lemma 3.1], it follows that (A5) holds for \( Q_{\omega} \).

Note that the results of spreading speeds and traveling waves in [8] are still valid provided that the assumption (A5) in [8] is replaced by the standing assumption (A4) (see [10]). By [8, Theorem 2.1], it then follows that the map \( Q_{\omega} : C_{\omega^+}(0) \rightarrow C_{\omega^+}(0) \) admits a spreading speed \( c_{\omega}^* \). In order to estimate \( c_{\omega}^* \), we consider the following linear system:

\[
\begin{align*}
\frac{\partial m}{\partial t} &= D_M \Delta m + \alpha_2(t)\beta Qn - \mu MMm, \\
\frac{\partial v}{\partial t} &= D_M \Delta v + \alpha_1(t)mL^*(t) - v(\sigma(t) + \mu V + \delta V^*(t)), \\
\frac{\partial n}{\partial t} &= \beta_T \sigma(t)v - n[\gamma + \alpha_2(t)Q + \mu N].
\end{align*}
\]

(3.1)

Let \( (u_1(t,x), u_2(t,x), u_3(t,x)) = e^{-\mu t}(\bar{u}_1(t), \bar{u}_2(t), \bar{u}_3(t)) \) be a solution of (3.1). Then \( (\bar{u}_1(t), \bar{u}_2(t), \bar{u}_3(t)) \) satisfies the following ODE system with the initial data \( \bar{u}(0) \in \mathbb{R}^3 \):

\[
\begin{align*}
\frac{d\bar{u}_1(t)}{dt} &= \mu^2 D_M \bar{u}_1(t) + \alpha_2(t)\beta Q\bar{u}_3(t) - \mu M\bar{u}_2(t), \\
\frac{d\bar{u}_2(t)}{dt} &= \mu^2 D_M \bar{u}_2(t) + \alpha_1(t)L^*(t)\bar{u}_1(t) - (\sigma(t) + \mu V + \delta V^*(t))\bar{u}_2(t), \\
\frac{d\bar{u}_3(t)}{dt} &= \beta_T \sigma(t)\bar{u}_2(t) - [\gamma + \alpha_2(t)Q + \mu N]\bar{u}_3(t).
\end{align*}
\]

(3.2)

Let \( \{M_t\}_{t \geq 0} \) be the solution map associated with (3.1). Define \( B^t_{\mu} : \mathbb{R}^3 \rightarrow \mathbb{R}^3 \) as

\[
B^t_{\mu}(z) := M_t(ze^{-\mu t})(0) = (\bar{u}_1(t,z), \bar{u}_2(t,z), \bar{u}_3(t,z)).
\]

Thus, \( B^t_{\mu}(\cdot) \) is the solution map of the linear system (3.2) on \( \mathbb{R}^3 \). Let \( r(\mu) \) be the spectral radius of the Poincaré map \( B^t_{\mu} \). It is easy to verify that \( r(\mu) \) is even on \( \mathbb{R} \) and \( B^t_{\mu} = (B^t_{\mu})^2 \) is a compact and strongly positive operator (actually, \( B^t_{\mu} \) is strongly positive for all \( t \geq 2\omega \)). By [9, Lemma 3.1], it follows that \( r(\mu) > 0 \), and it is a simple eigenvalue of \( B^\omega_{\mu} \) with a strongly positive eigenvector \( w^* \gg 0 \). Moreover, it follows from [9, Lemma 3.7] that \( r(\mu) \) is log convex on \( \mathbb{R} \). Using an argument similar to that in the proof of [22, Lemma 2.1], we see that there exists a positive \( \omega \)-periodic function \( w(t) \) such that \( v(t) = e^{\lambda(\mu)t}w(t) \) is a solution of (3.2), where \( \lambda(\mu) = \frac{1}{\mu} \ln r(\mu) \) and \( w(0) = w^* \). That is, \( B^t_{\mu}(w(0)) = e^{\lambda(\mu)t}w(t) \). Letting \( \omega = \omega \), we have \( B^\omega_{\mu}(w(0)) = e^{\lambda(\mu)\omega}w(0) \), which implies that \( e^{\lambda(\mu)\omega} \) is the principal eigenvalue of \( B^\omega_{\mu} \) with strongly positive eigenvector \( w(0) \). Following [9], we define

\[
\Phi(\mu) := \frac{1}{\mu} \ln(e^{\lambda(\mu)\omega}) = \frac{\lambda(\mu)\omega}{\mu} = \frac{\ln r(\mu)}{\mu} \quad \forall \mu > 0.
\]

When \( \mu = 0 \), system (3.2) reduces to the linear system (2.11). Since \( R_0 > 1 \), we have \( r(\mu) = r_3 > 1 \). Thus, \( \lim_{\mu \rightarrow 0^+} \Phi(\mu) = \infty \). Note that \( \lambda(\mu) = \frac{1}{\mu} \ln r(\mu) \) is even and

\[
\Phi(\mu) := \frac{1}{\mu} \ln(e^{\lambda(\mu)\omega}) = \frac{\lambda(\mu)\omega}{\mu} = \frac{\ln r(\mu)}{\mu} \quad \forall \mu > 0.
\]

When \( \mu = 0 \), system (3.2) reduces to the linear system (2.11). Since \( R_0 > 1 \), we have \( r(\mu) = r_3 > 1 \). Thus, \( \lim_{\mu \rightarrow 0^+} \Phi(\mu) = \infty \). Note that \( \lambda(\mu) = \frac{1}{\mu} \ln r(\mu) \) is even and
convex; then \( \lambda(\mu) \geq \lambda(0) > 0 \) on \( \mathbb{R} \). Since \( v(t) = e^{\lambda(\mu)t}w(t) \) is a solution of (3.2), we see that

\[
\frac{dv_2(t)}{dt} \geq [\mu^2D_M - (\sigma(t) + \mu_V + \delta_V\nu^*(t))]v_2(t).
\]

It follows that

\[
\frac{w_2'(t)}{w_2(t)} \geq \mu^2D_M - \mu_V - \sigma(t) - \lambda(\mu) - \delta_V\nu^*(t).
\]

Integrating the above inequality from 0 to \( \omega \), we get

\[
0 = \int_0^\omega \frac{w_2'(t)}{w_2(t)} dt \geq \mu^2D_M\omega - \mu_V\omega - \lambda(\mu)\omega - \int_0^\omega (\sigma(t) + \delta_V\nu^*(t))dt.
\]

Then we have

\[
\Phi(\mu) = \frac{\lambda(\mu)\omega}{\mu} \geq \mu D_M\omega - \frac{\mu V\omega}{\mu} - \frac{\int_0^\omega (\sigma(t) + \delta_V\nu^*(t))dt}{\mu} \to \infty
\]

as \( \mu \to \infty \). Therefore, \( \Phi(\mu) \) attains its positive minimum at some finite value \( \mu^\ast \).

Then we have the following result.

**Lemma 3.2.** Let \( c^\ast_\omega \) be the spreading speed of map \( Q_\omega \) on \( C_{\bar{w}^\ast(0)} \). Then \( c^\ast_\omega = \inf_{\mu > 0} \Phi(\mu) \), and hence \( c^\ast_\omega > 0 \).

**Proof.** It is easy to verify that the map \( M_t \) satisfies all conditions (C1)–(C7) in [9] for all \( t > 0 \). Comparing systems (2.12) and (3.1), we see that \( Q_t \) is a lower solution of linear system (3.1) for all \( t \geq 0 \). Then we have

\[
Q_t(\phi) \leq M_t(\phi) \quad \forall \phi \in C_{\bar{w}^\ast(0)}, \forall t \geq 0.
\]

Fix \( t = \omega \). It follows from [9, Theorem 3.1] that \( c^\ast_\omega \leq \inf_{\mu > 0} \Phi(\mu) \).

By the continuity of the solution on the initial data, we know that for any \( \epsilon \in (0, Q) \), there exists \( \eta > 0 \) such that the solution \( \bar{w}(t, \eta) \) of system (2.10) with \( \bar{w}(0, \eta) = \eta \) satisfies \( \bar{w}(t, \eta) < \bar{c} \) for all \( t \in [0, \omega] \), where \( \bar{c} = (\epsilon, \epsilon, \epsilon, \bar{\eta} = (\eta, \eta, \eta) \). Then the comparison principle implies that

\[
\bar{w}(t, x, \phi) \leq \bar{w}(t, \bar{\eta}) \leq \bar{c} \quad \forall x \in \mathbb{R}, \phi \in C_{\bar{\eta}}, \, t \in [0, \omega].
\]

Thus, for any \( x \in \mathbb{R}, \, t \in [0, \omega], \) and \( \phi \in C_{\bar{\eta}} \), \( \bar{w}(t, x, \phi) \) satisfies

\[
\begin{aligned}
\frac{\partial \bar{w}_1}{\partial t} & \geq D_M \Delta \bar{w}_1 - \mu_M \bar{w}_1 + \alpha_2(t)\beta(Q - \epsilon)\bar{w}_3, \\
\frac{\partial \bar{w}_2}{\partial t} & = D_M \Delta \bar{w}_2 + \alpha_1(t)L^*(t)\bar{w}_1 - \sigma(t) + \mu_V + \delta_V\nu^*(t)\bar{w}_2, \\
\frac{\partial \bar{w}_3}{\partial t} & = \beta_T\sigma(t)\bar{w}_2 - [\gamma + \alpha_2(t)Q + \mu_N]\bar{w}_3.
\end{aligned}
\]

Let \( \{M_t^\prime \}_{t \geq 0} \) be the solution semiflow associated with the linear system

\[
\begin{aligned}
\frac{\partial \bar{w}_1}{\partial t} & = D_M \Delta \bar{w}_1 - \mu_M \bar{w}_1 + \alpha_2(t)\beta(Q - \epsilon)\bar{w}_3, \\
\frac{\partial \bar{w}_2}{\partial t} & = D_M \Delta \bar{w}_2 + \alpha_1(t)L^*(t)\bar{w}_1 - \sigma(t) + \mu_V + \delta_V\nu^*(t)\bar{w}_2, \\
\frac{\partial \bar{w}_3}{\partial t} & = \beta_T\sigma(t)\bar{w}_2 - [\gamma + \alpha_2(t)Q + \mu_N]\bar{w}_3.
\end{aligned}
\]
By the comparison principle, we have
\[ M^*_t(\phi) \leq \mathcal{Q}_t(\phi) \quad \forall \phi \in \mathcal{C}_b, \ t \in [0, \omega]. \]

Letting \( t = \omega \) and \( 0 < \epsilon < Q \) small enough, we can perform an analysis on \( \{M^*_t\}_{t \geq 0} \) similar to that for \( \{M_t\}_{t \geq 0} \). It follows from [9, Theorem 3.10] that
\[ \inf_{\mu > 0} \Phi_\epsilon(\mu) \leq c^*_\omega \leq \inf_{\mu > 0} \Phi(\mu) \]
for all sufficiently small \( \epsilon \). Letting \( \epsilon \to 0 \), we obtain \( c^*_\omega = \inf_{\mu > 0} \Phi(\mu) \).  

Let \( c^* := c^*_\omega / \omega \). Then the following result shows that \( c^* \) is the spreading speed for system (2.12).

**Theorem 3.3.** Assume \( R_0 > 1 \). Let \( \hat{w}(t, x, \phi) \) be the solution of system (2.12) with \( \hat{w}(0, \cdot, \phi) = \phi \in \mathcal{C}_{\hat{\omega}^*(0)} \). Then the following statements hold:

(i) For any \( c > c^* \), if \( \phi \in \mathcal{C}_{\hat{\omega}^*(0)} \) with \( 0 \leq \phi < \hat{w}^*(0) \), and \( \phi = 0 \) outside a bounded interval, then \( \lim_{t \to \infty, |x| \leq ct} \hat{w}(t, x, \phi) = (0, 0, 0) \).

(ii) For any \( c \in (0, c^*) \), if \( \phi \in \mathcal{C}_{\hat{\omega}^*(0)} \) with \( \phi \neq 0 \), then \( \lim_{t \to \infty, |x| \leq ct} (\hat{w}(t, x, \phi) - \hat{w}^*(t)) = 0 \).

Proof. In view of Lemma 3.1, statement (i) is a straightforward consequence of [8, Theorem 2.1] and [10, Theorem 3.4(ii)]. For statement (ii), since \( \mathcal{Q}_t \) is subhomogeneous, \( \hat{r}_\sigma \) in [8, Theorem 2.1] can be chosen to be independent of \( \sigma \gg 0 \). Denote \( r_\sigma \). For any \( \phi \in \mathcal{C}_{\hat{\omega}^*(0)} \) with \( \phi > 0 \), from the strong positivity of \( \mathcal{Q}_t \), we know that \( \mathcal{Q}_{2\omega}(\hat{\phi}) > 0 \). Then there exists a \( \sigma \gg 0 \) in \( \mathbb{R}^3 \) such that \( \mathcal{Q}_{2\omega}(\phi) \gg \sigma \) for \( \phi \) on an interval \( I \) of length \( 2\sigma \). Taking \( \hat{w}(2\omega, x, \phi) \) as new initial data, we see from [8, Theorem 2.1(iii)] that statement (ii) is valid.

Recall that \( U(t, x - ct) \) is said to be an \( \omega \)-periodic traveling wave of (2.12) provided that \( U(t, z) \) is \( \omega \)-periodic in \( t \) and \( \hat{w}(t, x) = U(t, x - ct) \) satisfies (2.12), and we say \( U(t, x - ct) \) connects \( \hat{w}^*(t) \) to \( 0 \) if \( U(t, -\infty) = \hat{w}^*(t) \) and \( U(t, \infty) = 0 \) uniformly for \( t \in [0, \omega] \).

The existence and nonexistence of traveling waves are straightforward consequences of Lemma 3.1; see [8, Theorems 2.2 and 2.3] and [10, Theorems 4.1 and 4.2].

**Theorem 3.4.** Assume that \( R_0 > 1 \). Then the following statements are valid:

(i) For any \( c \in (0, c^*) \), system (2.12) has no \( \omega \)-periodic traveling wave \( U(t, x - ct) \) connecting \( \hat{w}^*(t) \) to \( 0 \).

(ii) For any \( c > c^* \), system (2.12) has an \( \omega \)-periodic traveling wave \( U(t, x - ct) \) connecting \( \hat{w}^*(t) \) to \( 0 \), and \( U(t, z) \) is continuous and nonincreasing in \( z \in \mathbb{R} \).

Note that we can regard the fourth equation in system (2.7) as the following nonhomogeneous reaction-diffusion equation:
\[
\frac{\partial a}{\partial t} = D_H \Delta a - (\mu_A + \delta_A A^*(t) a(t, x) + \alpha_2(t)[Qn(t, x) + \beta_T m(t, x)](N^*(t) - n(t, x))].
\]

By an argument similar to that in the proof of [6, Theorems 3.1 and 3.2], it follows that similar results in Theorems 3.3 and 3.4 are also valid for \( a(t, x) \). Thus, \( c^* \) is the spreading speed and the minimal wave speed for monotone periodic traveling waves of system (2.7).

**4. A case study.** In this section, we do a case study for Lyme disease in Port Dover, Ontario, and present some numerical simulations.

According to [15], the duration of development and the questing activity of ticks can be explained largely by temperature effects alone. Thus, we focus on the discussion
of the temperature effects on the transmission of Lyme disease. Using the published data in [13, 15, 16, 17] and mean monthly temperature normals at Port Dover from the Canadian meteorological website [19], we can evaluate the temperature-dependent coefficients \( r(t) \), \( \alpha_1(t) \), \( \sigma(t) \), and \( \alpha_2(t) \) and other constant coefficients in our model. In this study, we let the period \( \omega = 12 \) months.

First, we estimate the constant coefficients in our model. Note that in [13, 15, 16, 17], the authors determined some realistically feasible constant coefficients in Lyme disease models based on the valuable data from laboratory study and field observation. We refer the reader to their work and list values of constants coefficients for the Lyme disease models (1.1) in Table 4.1. According to Table 2 in [13], we know that the maximum number of ticks of a given life stage that a mouse and a deer can feed in one year is 595.35 and 521.12, respectively. We suppose that the number of mice and deer is \( Q \) and 42, respectively, in the region. Then we estimate

\[
\delta_V = \frac{Q}{595.35/12}, \quad \delta_A = \frac{42}{521.12/12}.
\]

Next, we use the monthly mean temperatures at Port Dover, temperature-dependent questing activity rate for immature ticks, and the relationship between the temperature and the development rate to estimate the periodic coefficients \( r(t) \), \( \alpha_1(t) \), \( \sigma(t) \), and \( \alpha_2(t) \). In this case study, we take January to be the starting point and assume that tick development is zero for all stages when the air temperature is \( 0^\circ C \) or below [16].

We list the monthly mean temperature for Port Dover in Table 4.2 according to the temperature statistics in [19].

It follows from Figure 1 in [15] that the preoviposition period of female adults, preclosion period for egg masses, and premolt period of larvae are given in days,

\[
\begin{align*}
\delta_V &= \frac{Q}{595.35/12}, \\
\delta_A &= \frac{42}{521.12/12}.
\end{align*}
\]
respectively, by

\[ Y = 1300C^{-1.42}, \quad Y = 34234C^{-2.27}, \quad Y = 101181C^{-2.55}, \]

where \( C > 0 \) is the temperature in °C. We assume that five percent of adult ticks are pregnant females, and per-capital egg production by pregnant females is 3000 [17]. Then the temperature-dependent developmental rates for larvae and nymphs per month can be expressed as

\[
30.4 \times \frac{1}{20} \times \frac{3000}{1300C^{-1.42} + 34234C^{-2.27}} \quad \text{and} \quad 30.4 \times \frac{1}{101181C^{-2.55}}.
\]

Using the temperature data in Table 4.2 and the curve fitting tool (CFTOOL) in MATLAB, we can fit the time-dependent individual birth rate of tick \( r(t) \) and the individual development rate of nymph \( \sigma(t) \) (see Table 1.1) as

\[
r(t) = 31.87 - 37.77 \cos(\pi t/6) - 25.75 \sin(\pi t/6) + 5.815 \cos(\pi t/3) + 12.38 \sin(\pi t/3)
\]

and

\[
\sigma(t) = 0.2325 - 0.2896 \cos(\pi t/6) - 0.1951 \sin(\pi t/6) + 0.05472 \cos(\pi t/3) \\
+ 0.1181 \sin(\pi t/3) - 0.00855 \cos(\pi t/6) - 0.00345 \sin(\pi t/2) \\
+ 0.01085 \cos(2\pi t/3) - 0.00433 \sin(2\pi t/3).
\]

According to [16, 17], the biting rate of larvae and nymphs to mice are dependent on the mice-finding probability (see Table 1 in [17]) and the activity proportion, where the activity proportion is temperature-dependent (see Figure 3 in [16]). In [17], the daily mice-finding probability of questing larvae and nymphs is expressed as

\[
\lambda_{ql} = 0.0013m^{0.515} \quad \text{and} \quad \lambda_{qm} = 0.002m^{0.515},
\]

where \( m \) is the total number of mice. The relationship between the temperature and the activity proportion of immature ticks is given in Figure 3 of [16]. Combining the temperature data in Table 4.2, we fit the temperature-dependent activity proportion of immature ticks as

\[
\theta(t) = 0.08292 - 0.1158 \cos(\pi t/6) - 0.07253 \sin(\pi t/6) + 0.02833 \cos(\pi t/3) \\
+ 0.06495 \sin(\pi t/3) + 0.008333 \cos(3\pi t/6) - 0.0125 \sin(3\pi t/6).
\]

Thus, in this case study, the monthly biting rate of larvae and nymphs to one mouse (see Table 1.1) can be given by

\[
\alpha_1(t) = 30.4 \times \frac{0.0013Q^{0.515}}{Q} \times \theta(t), \quad \alpha_2(t) = 30.4 \times \frac{0.002Q^{0.515}}{Q} \times \theta(t).
\]

With the above temperature-dependent coefficients and constants parameters in Table 4.1, we numerically calculate the principal Floquet multiplier of system (2.5) \( r_1 = 3870.6 > 1 \). Then we use solver ODE45 and the CFTOOL package in MATLAB to find the periodic solution \( (\mathbf{X}^*(t), \mathbf{V}^*(t), \mathbf{N}^*(t), \mathbf{A}^*(t)) \) for system (2.4). Thanks to [21, Theorem 2.1], we can further numerically compute the basic reproduction ratio \( R_0 \) for system (2.7). Since all coefficients in our model are spatially homogeneous, without loss of generality, we assume the spatial domain \( \Omega = [-I, I] \subset \mathbb{R} \) when \( \Omega \) is bounded and truncate the infinite domain \( \mathbb{R} \) to be \([-I, I]\).
In order to simulate the global dynamics of system (2.1) in a bounded domain, we apply the difference method to the system with the Neumann boundary condition and \( I = 10 \), and choose the initial data as

\[
\begin{align*}
M(0, x) &= L(0, x) = 100 \times \cos \left( \frac{\pi x}{2T} \right), \quad V(0, x) = \frac{4}{5} \times L(0, x), \\
N(0, x) &= \frac{3}{5} \times L(0, x), \quad A(0, x) = \frac{1}{2} \times L(0, x), \\
m(0, x) &= \frac{1}{5} \times L(0, x), \quad v(0, x) = \frac{3}{10} \times L(0, x), \\
n(0, x) &= \frac{1}{4} \times L(0, x), \quad a(0, x) = \frac{1}{3} \times L(0, x).
\end{align*}
\]

Using the parameter values in Table 4.1 and the periodic coefficients, we numerically calculate the basic reproduction ratio \( R_0 = 3.625 > 1 \). Figure 4.1 shows the evolution of \( v(t) \) and \( n(t) \) in system (2.1). If the susceptibility to infection in mice and ticks is, respectively, reduced to \( \beta = 0.2 \) and \( \beta_T = 0.22 \) due to some preventive measures, we numerically get \( R_0 = 0.825 < 1 \). In this situation, Figure 4.2 shows that \( v(t) \) and \( n(t) \) will eventually approach zero. The simulation results for \( m(t) \) and \( a(t) \) are also consistent with our analytic result in Theorem 2.5.

In the case of unbounded domain, using the given parameters such that \( R_0 = 3.625 > 1 \), we numerically estimate the spreading speed \( c_0^*/\omega = 0.2644 \). To simulate
the spatial spread of the disease, we choose $I = 40$. Figure 4.3 shows the numerical plots of the solution of system (2.7) with the initial data given by

$$m(0, x) = \begin{cases} 
0, & |x| \geq 20, \\
10 \times (20 - |x|), & 10 \leq |x| \leq 20, \\
100, & |x| \leq 10,
\end{cases}$$

Fig. 4.2. The evolution of $v$ and $n$ with $R_0 = 0.825 < 1$.

Fig. 4.3. The spread of $v$ and $n$, and the densities of $v$ and $n$ at $t = n\omega$ with $n = 0, 1, 2, 3, 4, 5$, respectively.
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(a) The evolution of $v$.

(b) The evolution of $n$.

FIG. 4.4. The time-periodic traveling waves observed for $v$ and $n$.

and

$$v(0, x) = 10 \times m(0, x), \quad n(0, x) = 8 \times m(0, x), \quad a(0, x) = 6 \times m(0, x).$$

To observe traveling waves, we choose the initial data as

$$m(0, x) = \begin{cases} 
1200, & -40 \leq x \leq -20, \\
30 \times (20 - x), & |x| \leq 20, \\
0, & 20 \leq x \leq 40,
\end{cases}$$

and

$$v(0, x) = 30 \times m(0, x), \quad n(0, x) = \frac{110}{3} \times m(0, x), \quad a(0, x) = \frac{3}{4} \times m(0, x).$$

Then the evolution of the solution is as shown in Figure 4.4.

5. Discussion. In this paper, we incorporated seasonal forcing into a reaction-diffusion Lyme disease model. Since seasonal variations are critical for the development of ticks and their activities, we assume that the developmental rate of ticks and their biting rates are time-periodic. We investigated the global dynamics of this model in a bounded and an unbounded habitat. In the case of a bounded habitat, we introduced the basic reproduction ratio $R_0$ for Lyme disease, and further proved that $R_0$ can serve as the threshold parameter for the global stability of either disease-free or positive periodic solution. Biologically, this means that the disease will die out when $R_0 < 1$, and the disease will stabilizes at a positive periodic solution when $R_0 > 1$. In the case of an unbounded habitat, we consider the spatial spread of the disease and the existence of time-periodic traveling waves. We established the existence of the spreading speed of infection and its coincidence with the minimal wave speed for limiting system (2.7). Moreover, we got an implicit formula for the spreading speed in Lemma 3.2, which may be used to compute the spreading speed numerically.

For our model, we picked some feasible coefficients and estimated the time-periodic coefficients using some published data. We numerically calculated the basic reproduction ratio $R_0$. Since $R_0 = 3.625 > 1$, we can see from Figure 4.1 that the disease stabilizes at a positive periodic state. If the infection susceptibilities $\beta$ and $\beta_T$ decrease such that the basic reproduction ratio $R_0 = 0.825 < 1$, then Figure 4.2 shows that the disease will die out eventually. In order to consider the spatial propagation of
the disease in an unbounded domain, we calculated the spreading speed numerically. Figure 4.3 shows that the disease spreads at a certain speed. To control the disease, we may use some strategies to reduce the spreading speed. For example, we may use some chemical methods to reduce the infection susceptibilities or the total number of hosts. Our analytic results and the numerical values of the basic reproduction ratio and the spreading speed may provide some helpful suggestions for disease control.

When the spatial domain Ω is bounded, we can also study the global dynamics of model (1.1) under the Robin-type or Dirichlet boundary conditions. In such a case, we can show that solution maps of reaction-diffusion systems (2.2) and (2.12) and their linearizations at zero are α-contractions by a decomposition argument similar to that in [24, Lemma 3.1]. Thus, the abstract threshold type result for monotone and subhomogeneous systems (see [23, Theorem 2.3.4]), together with the generalized Krein–Rutman theorem, can be applied directly to (2.2) and (2.12), respectively. It then follows that the analogues of Theorems 2.2–2.5 still hold true. In these results, however, two numbers $r_1$ and $R_0$ should be replaced by the spectral radii of the Poincaré (period) maps of the linearized systems of (2.2) and (2.12) at zero solution, respectively.

We should point out that our model ignores the time delays between tick life stages. It would be more interesting to incorporate time delays into the model. Another challenging problem is to study the spreading speeds and traveling waves in the case where some parameters are spatially dependent. We leave these problems for future investigation.

**Acknowledgments.** We are very grateful to Yijun Lou for his valuable comments and discussions on the Lyme disease modeling and numerical simulations. Our sincere thanks also go to two anonymous referees for their careful reading and helpful comments which led to an improvement of the original manuscript.

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