Numerical Study of Periodic Traveling Wave Solutions for the Predator–Prey Model with Landscape Features

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We numerically investigate periodic traveling wave solutions for a diffusive predator–prey system with landscape features. The landscape features are modeled through the homogeneous Dirichlet boundary condition which is imposed at the edge of the obstacle domain. To effectively treat the Dirichlet boundary condition, we employ a robust and accurate numerical technique by using a boundary control function. We also propose a robust algorithm for calculating the numerical periodicity of the traveling wave solution. In numerical experiments, we show that periodic traveling waves which move out and away from the obstacle are effectively generated. We explain the formation of the traveling waves by comparing the wavelengths. The spatial asynchrony has been shown in quantitative detail for various obstacles. Furthermore, we apply our numerical technique to the complicated real landscape features.

Keywords: Dirichlet boundary; periodic traveling waves; predator–prey model; landscape features; numerical periodicity.

1. Introduction

The spatial behavior of species has been considered as a central problem in the ecological field [Cross & Hohenberg, 1993]. For the interactions of species, predator and prey equations have been mathematically studied after Lotka’s [Lotka, 1925] and Volterra’s [Volterra, 1926] models. These studies are usually considered on the homogeneous domain. However, the realistic domain is a large-scale domain with heterogeneity [Benson et al., 1993]. In experimental results [Ims & Andreassen, 2000; Lambin et al., 1998; Mackin-Rogalska & Nabaşko,
2. The Governing System

The governing system for the ratio-dependent predator–prey model having prey-dependent functional response [Sherratt et al., 2002; Banerjee & Banerjee, 2012] with the diffusion is:

\[
\frac{\partial U}{\partial t} = rU \left(1 - \frac{U}{U_0}\right) - \frac{abVU}{1 + cU} + D_1 \Delta U, \quad (1)
\]

\[
\frac{\partial V}{\partial t} = -bV + \frac{abUV}{1 + kU} + D_2 \Delta V, \quad (2)
\]

where \(U(x, t)\) and \(V(x, t)\) are the population densities of prey and predators, respectively. \(\Delta\) is the Laplacian operator, \(D_1, D_2\) are prey and predator diffusion coefficients, respectively. Here \(r\) is a growth factor of the prey, \(b\) is a death rate of the predator in the absence of the prey, \(U_0\) is the maximal carrying capacity of the prey, and \(c, r\) are interaction parameters between the prey and the predator, and \(k\) measures the satiation effect [Dunbar, 1986]. By introducing dimensionless variables

\[
\tilde{t} = rt, \quad \tilde{u} = \frac{U}{U_0}, \quad \tilde{v} = \frac{V}{V_0}, \quad \tilde{x} = \frac{x}{D_1},
\]

we have the nondimensional system after omitting tilde notation:

\[
u_1 = u(1 - u) - \frac{\gamma uv}{1 + \gamma u} + \Delta u, \quad (3)
\]

\[
u_1 = \frac{\gamma uv}{\beta(1 + \gamma u)} - \frac{v}{\alpha^2} + \sigma \Delta v. \quad (4)
\]

Here \(u\) and \(v\) are non-negative. The governing system has the equilibrium points at \((0, 0), (1, 0), \) and at least one point having positive values \((\bar{u}, \bar{v})\) where \(\bar{u}\) and \(\bar{v}\) are defined as \(\bar{u} = 1/\gamma(a - 1)\) and \(\bar{v} = (1 - \bar{u}^2)/(1 + \beta \bar{v})\), respectively. For positiveness, \(a > 1\). The domain \(\Omega\) is constituted as \(\Omega = \Omega_0 \cup \partial \Omega_0 \cup \partial \Omega \subset \mathbb{R}^d, d = 1, 2,\) where \(\Omega_0\) is an obstacle domain, \(\partial \Omega_0\) is an obstacle boundary, and \(\Omega\) is a physical domain as shown in Fig. 1. The boundary condition, \(\partial \Omega\), is imposed as the no-flux boundary condition:

\[
\mathbf{n} \cdot \nabla u = \mathbf{n} \cdot \nabla v = 0, \quad (5)
\]

where \(\mathbf{n}\) is the unit vector normal to the domain boundary \(\partial \Omega\). Moreover, the homogeneous Dirichlet
boundary condition is assumed for the obstacle domain \( \partial \Omega_b \) which means both the predator and prey die at the obstacle boundary.

3. Numerical Solution

In this section, we present a robust numerical scheme for the discretized governing system and an accurate algorithm for calculating numerical periodicity is proposed. The governing systems (3) and (4) are solved by using an operator splitting method: For the first step, we solve the system of nonlinear ordinary differential equations:

\[
F_1(u, v) := u(1-u) - \frac{\gamma uv}{1+\gamma v},
\]

\[
F_2(u, v) := \frac{\beta v}{\alpha \beta} - \frac{u}{c},
\]

Here, we solve them by using the fourth-order Runge–Kutta method [Zhong, 1996]. The second step is solving the system of diffusion equations:

\[
\frac{u_{i,j}^{n+1} - u_{i,j}^n}{\Delta t} = G_{ij}, \quad \frac{v_{i,j}^{n+1} - v_{i,j}^n}{\Delta t} = \sigma G_{ij},
\]

where the discrete Laplacian for the Cartesian domain is defined as:

\[
\Delta(c) = \frac{u_{i+1,j}^{n+1} + u_{i-1,j}^{n+1} + u_{i,j+1}^{n+1} + u_{i,j-1}^{n+1} - 4u_{i,j}^{n+1}}{h^2}.
\]

To have efficient numerical solutions for Step 2, we use a multigrid method [Briggs, 1987]. For the multigrid method, detailed description is summarized in [Li et al., 2013]. Note that the dimensional case and the radially symmetric domain can be similarly defined.

Periodic Traveling Wave Solutions for the Predator–Prey Model
Then the velocity $u$ is a traveling wave solution. Especially, this solution is space-periodic for some integers $p$ and $i$, we call $u_0^i$ is a traveling wave solution. Especially, this solution is space-periodic with period of $hp$ for a space step size $h$. For some integer $\tau$, if $u_0^i$ satisfies $u_0^{i+\tau} = u_0^i$, the solution $u_0^i$ is time-periodic with period of $\tau \Delta t$ for the time step $\Delta t$. Let us define the velocity $l$ as $u_l^{i+1} = u_l^{i+\tau}$. Then the velocity $l/k$ satisfies $u_l^{i+k} = u_l^{i+\tau}$.

**Definition 3.1.** The solution $u_0^i$ satisfying $u_0^{i+k} = u_0^{i+\tau}$ is called the periodic traveling wave solution [Zhang et al., 2007].

That is, the periodic traveling wave solution is the space and time periodic solution. Then we propose an algorithm on the one-dimensional space to detect the numerical periodicity in the following:

Algorithm 1. The numerical periodicity is obtained by calculating the smallest velocity $T_p$ with following steps:

**Step 1.** Initial conditions for $u$ and $v$ are given as small random perturbations from the stationary solutions $\pi$ and $\pi$, respectively.

**Step 2.** Let $u_{\text{ref}}$ and $v_{\text{ref}}$ be solutions at the reference time.

**Step 3.** Calculate the local maximum and local minimum errors.

If $e^{m-2} - e^{m-1} < 0$ and $e^{m-1} - e^m > 0$, the temporal error has the local maximum. While $e^{l-2} - e^{l-1} > 0$ and $e^{l-1} - e^l < 0$ where $l > m$, the error has the local minimum. When the error reaches the local minimum and $|e^{m} - e^{l}| < \text{tol}$, we define the numerical periodicity as $T_p = l - m$. Therefore, we have one-period from $n_{\text{ref}}$ to $n_{\text{ref}} + T_p$.

If $e^{m} - e^{l} > \text{tol}$, return to Step 2.

**Step 4.** To confirm the obtained numerical periodicity $T_p$, we calculate the error between $n_{\text{ref}} + T_p$ to $n_{\text{ref}} + 2T_p$.

The discrete $l_2$-norm error is defined as

$$e^n = \left( \frac{1}{N_x} \sum_{i=1}^{N_x} \left( (u_0^i - u_{\text{ref}}^i)^2 + (u_0^i - v_{\text{ref}}^i)^2 \right) \right)^{1/2},$$

for $n > n_{\text{ref}}$.

Figure 3(a) shows the description for the one-period of predator with a space-time plot. Figure 3(b) shows the temporal plot of $e$ with the first one-period Step 3 (marked as circles) and the second one-period Step 4 (solid line) of the traveling wave solution. The result suggests that our method performs well to get the period of predator. Moreover, we can use the algorithm Step 3 to find the one-period of the space traveling wave solution when we analyze the spatial amplitude and wavelength.
4. Numerical Experiments

In this section, we perform various numerical experiments to systematically demonstrate various aspects of the formation of the traveling wave solutions in one-dimensional space, radially symmetric domain, and two-dimensional space. Our numerical experiments confirm the formation of the traveling wave solution in a complicated two-dimensional space. Moreover, the existence of the traveling wave solution and the convergence test are included. In numerical tests, following the field experiments, nondimensionalized values \( \alpha = 1.8, \beta = 1.2, \gamma = 4.9 \) [Sherratt et al., 2002] are used, unless otherwise specified. The diffusion effect is governed as \( \sigma = 25 \). Unless otherwise specified, we use a tol = 0.001, a temporal step size \( \Delta t = 0.5 \) and a spatial step size \( h = 1 \). In two-dimensional space, we set initial conditions \( u(x, y, 0) = v(x, y, 0) = 0 \) in the domain \( \Omega_0 \) and \( u(x, y, 0) = 1.1\varpi + 0.05\text{rand}(x, y) \) and \( v(x, y, 0) = 1.1\varpi + 0.05\text{rand}(x, y) \) in domain \( \Omega_0 \). Here, \( \text{rand}(x, y) \in [-1, 1] \) is a random generated number.

4.1. Existence of traveling wave solution

When the kinetic system has a stable limit cycle, there exists traveling wave solution [Kopell & Howard, 1973]. In the kinetic system, the prey and predator systems have complex eigenvalues with given parameter values. After some calculation, the equilibrium solution \( (\varpi, \varpi) \) is an unstable node when \( \gamma > (\alpha + 1)/(\alpha - 1) \) and the kinetic system shows oscillatory behavior [Sherratt et al., 2002]. To examine the existence of the traveling wave solution numerically, we illustrate the phase portraits with velocity fields (arrows) for the prey and predator in the kinetic system (without diffusion terms). Figure 4 shows two phase portraits arising from different initial points with given parameter sets, i.e. \( (u, v) = (\varpi + 0.05\varpi, \varpi) \) (marked as a star) and \( (u, v) = (\varpi + 0.7\varpi, \varpi) \) (marked as a circle) where the square marker represents \( (\varpi, \varpi) \) and the solid line represents the stable limit cycle.

Fig. 4. Phase portraits starting from two points \( (u, v) = (\varpi + 0.05, \varpi) \) (marked as a star) and \( (u, v) = (\varpi + 0.7, \varpi) \) (marked as a circle) associated with velocity fields (arrows). Here, the square marker represents \( (\varpi, \varpi) \) and the solid line represents the stable limit cycle.
represents the stable limit cycle. Hence, $\Delta t = 0.11$ and $T = 50$ are used for the computation. The temporal evolutions of the phase portraits converge to the limit cycle with two different initial conditions. Hence, the limit cycle is stable and the traveling wave solution for the system exists.

### 4.2. Parameter studies

We calculate the formation of traveling wave solutions having an obstacle with varying parameter values. It is sufficient to show in one-dimensional space. The given parameter set $\alpha = 1.8$, $\beta = 1.2$, and $\gamma = 4.9$ shows oscillatory behavior in the kinetic system, as described in Sec. 4.1. With obstacle at $x = 0$, numerical solutions are obtained with $h = 0.1$ on the domain $(0, 204)$. We terminate the numerical calculation when the solution shows periodicity (see Sec. 3.2). First, we consider different values of $\gamma = 2.1$, 4.9, and 6 [Sherratt et al., 2002]. As shown in Fig. 5, the kinetic solution is stable, if $\gamma = 2.1 < (\alpha + 1)/(\alpha - 1)$, and the kinetic solution shows oscillatory behavior, when $\gamma$ is larger than $(\alpha + 1)/(\alpha - 1)$. Furthermore, when the governing system is stable, it does not generate traveling wave solution in spite of the presence of obstacle. When the system has a limit cycle, it generates traveling wave solution with obstacle.

Then we consider the effect of $\beta$. As $\alpha$ and $r$ are positive in governing systems (1) and (2), $\beta$ is positive. Here we numerically examine different values of $\beta = 0.4, 1.2$, and 2 as shown in Fig. 6. When the
values of $\beta$ increases, the amplitude of prey solution gets bigger and the amplitude of predator solution gets smaller.

Finally, we consider the effect of $\sigma$, which is the ratio of diffusion coefficient, with different values of $\sigma = 1.5, 2.5$, and $3.5$. Observing the results in Fig. 7, we can find that as the values of $\sigma$ are increasing, the wavelength of the numerical solutions gets larger.

4.3. Convergence test

We perform numerical calculations to obtain the spatial convergence rate with increasingly finer grids $h = 1/2^n$ for $n = 8, 9, 10$, and $11$ on the one-dimensional domain $(0, 256)$. The initial conditions are given as

\[
\begin{align*}
    u(x, 0) &= \alpha \sin \left( \frac{\pi x}{256} \right) \quad \text{and} \\
    v(x, 0) &= \beta \sin \left( \frac{\pi x}{256} \right).
\end{align*}
\]

Numerical solutions are computed up to time $T = 250$ with a small time step size $\Delta t = h^2$. Since no analytical solutions are available, we use the relative error. We define the error as the discrete $l_2$-norm of the difference between the grid and the average of the neighboring solutions as follows:

\[
e_i^h := \frac{h}{2} \left( \frac{u_{i+1}^h - u_{i-1}^h}{2} + u_i^h \right).
\]

The rate of convergence is defined as the ratio of successive errors: $\log_2(\|e_i^h\|_2/\|e_l^h\|_2)$. The obtained errors and rates of convergence using these definitions are given in Table 1. For $u$ and $v$, the second-order accuracy with respect to the space is observed as expected from the discretization.

To obtain the convergence rate for the temporal discretization, we fix the spatial grid as $512$ and choose a set of decreasing time steps $\Delta t = 1, 0.5, 0.25$, and $0.125$. We also run the computation up to time $T = 250$. Note that we define the temporal discrete $l_2$-norm error as $e_i^{\Delta t} := u_i^h - u_i^{\Delta t}$. The obtained errors and rates of convergence are given in Table 2. For both $u$ and $v$, the first-order accuracy with respect to the time is observed.

4.4. Numerical solutions in one-dimensional domain

We examine numerical solutions with an obstacle given at $x = 0$ in the one-dimensional space. The numerical solutions are calculated on the domain $(0, 512)$ with the spatial step size $h = 2$ and temporal step size $\Delta t = 0.5$. The initial conditions are

The obtained errors and rates of convergence are given in Table 2. For both $u$ and $v$, the first-order accuracy with respect to the time is observed.

Table 1. Error and convergence results with various mesh grids.

<table>
<thead>
<tr>
<th>Case</th>
<th>256-512</th>
<th>Rate 512-1024</th>
<th>Rate 1024-2048</th>
</tr>
</thead>
<tbody>
<tr>
<td>$u$: $l_2$-error</td>
<td>5.623e-3</td>
<td>2.15</td>
<td>1.264e-3</td>
</tr>
<tr>
<td>$v$: $l_2$-error</td>
<td>1.238e-3</td>
<td>2.03</td>
<td>3.025e-4</td>
</tr>
</tbody>
</table>

Table 2. Error and convergence results with various time steps.

<table>
<thead>
<tr>
<th>Case</th>
<th>1</th>
<th>0.5</th>
<th>0.25</th>
<th>Rate 0.25-0.12</th>
</tr>
</thead>
<tbody>
<tr>
<td>$u$: $l_2$-error</td>
<td>1.718e-3</td>
<td>1.05</td>
<td>8.301e-4</td>
<td>1.02</td>
</tr>
<tr>
<td>$v$: $l_2$-error</td>
<td>3.981e-4</td>
<td>0.99</td>
<td>2.005e-4</td>
<td>1.00</td>
</tr>
</tbody>
</table>
Fig. 8. Space-time plots of the one-period of the periodic traveling wave solutions of (a) the prey and (b) the predator with the obstacle at $x = 0$.

In this test, we set the domain as $(0, 163.84)$ with 16384 spatial grid points. The effect of the Dirichlet boundary to the local region is observed around the zero Dirichlet boundary. In the local region, numerical solutions show one bounded fluctuation for each calculation. The region far from the boundary, the maximum and minimum densities constitute the amplitude of the traveling wave solutions.

4.5. Numerical solutions in radially symmetric domain

The governing Eqs. (3) and (4) are rewritten on a radially symmetric domain with respect to $r$-axis $\Omega = (0, L)$ as follows:

$$u_t = \Delta r u + u(1 - u) - \frac{\gamma uv}{1 + \gamma u},$$  \quad (11)

$$v_t = \sigma \Delta r v + \frac{\gamma uv}{\beta(1 + \gamma u)} - \frac{v}{\alpha^2}.$$  \quad (12)

Here, we consider the obstacle size defined as $r_b$ then it is sufficient to calculate the numerical solutions on the domain $(r_b, L)$ [see Fig. 10(a)]. For $h = (L - r_b)/(N_r + 0.5)$, a number of node points $N_r$, the discretized system for the radially symmetric case is written as:

$$\frac{u_i^{n+1} - u_i^n}{\Delta t} = F_1(u^n, v^n) + G_i \Delta_t u_i^{n+1},$$  \quad (13)

$$\frac{v_i^{n+1} - v_i^n}{\Delta t} = F_2(u^n, v^n) + \sigma G_i \Delta_t v_i^{n+1},$$  \quad (14)
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for $F_1(u^n, v^n) = u^n(1 - u^n) - \gamma u^n v^n / (1 + \gamma u^n)$ and $F_2(u^n, v^n) = \gamma u^n v^n / (\beta(1 + \gamma u^n)) - v^n / (\alpha \beta)$.

The Laplacian operator in the radially symmetric domain is defined as:

$$\Delta_r u_{i+1}^{n+1} = \frac{1}{h^2} \left[ \frac{1}{r_i} \left( u_{i+1}^{n+1} - u_i^{n+1} \right) - \frac{1}{r_i} \left( u_{i+1}^{n+1} - u_{i-1}^{n+1} \right) \right],$$

where $r_i = i h$, $r_{i+\frac{1}{2}} = (r_i + r_{i+1})/2$, and $r_{i-\frac{1}{2}} = (r_i + r_{i-1})/2$. We illustrate the numerical result with $r_b = 40$ and $L = 284.5$ for $h = 1$ in Fig. 10(b).

Then we perform numerical calculation to show the effect of the obstacle radius using our scheme following the results in Smith et al.'s work [2008]. With varying sizes of an obstacle, the formulation of the traveling wave solution is obtained for an obstacle size $r_b$. The initial configurations are set as $u(r, 0) = \Phi + 0.1 \text{rand}(r)$, $v(r, 0) = \Phi + 0.1 \text{rand}(r)$ if $r > r_b$ and $u(r_b, 0) = v(r_b, 0) = 0$ otherwise.

In the first test, we calculate amplitudes and wavelengths in radially symmetric domain. The calculations are computed on the domain $(r_b, 512)$ with 2048 mesh grids. The amplitude is defined as half of the average of difference between the maximum and minimum values of each density. Figure 11(a) shows the amplitudes of the prey (marked as circles) and predator (marked as stars) with increasing obstacle sizes $r_b$, respectively. Likewise, Fig. 11(b) shows the wavelengths of the prey (marked as circles) and predator (marked as stars). The obtained values are drawn with solid lines using a line interpolation and the dashed lines are results obtained

![Figure 10](image1.png)

![Figure 11](image2.png)
from the one-dimensional space. These results suggest that the amplitudes decrease as the obstacle radius \( r_b \) increases, which approaches dashed lines (results from 1D) for both prey and predator numerical solutions. From Fig. 11(b), we deduce that the formations of the periodic traveling wave solutions have similar pattern between the prey and predator.

Figure 12 shows the convergence of the range of the predator solution with increasing obstacle radius. The star (\( r_b = 10 \)), circle (\( r_b = 50 \)), and plus sign (\( r_b = 400 \)) symbols denote the spatial plots for each obstacle size. Solid lines indicate the maximum (upper side) and the minimum (lower side) of the numerical solution. From these graphs, we attain that the range of increasing obstacle radius converges to the one-dimensional case.

4.6. Numerical solutions in two-dimensional domain

The numerical solutions are calculated to show the generation of the wave in the two-dimensional domain. The zero Dirichlet boundary condition at \( x = 2 \) is imposed on the domain \( (0, 128) \times (0, 32) \). In Fig. 13, we display the temporal evolutions of the predator. By the effect of Dirichlet boundary condition, the propagation of waves starting from the left \( (x = 2) \) generates the traveling wave solution.

For the circular obstacle with a radius of 18, the temporal evolutions of the predator are drawn in Fig. 14. As can be seen that the periodic traveling wave solutions around the obstacle are generated. Moreover, as we impose the zero-flux boundary, the waves are orthogonal to the boundary at the edge of the domain boundary.

4.7. Numerical experiments for convex obstacles

In this section, we examine some numerical experiments to describe the formation of the periodic traveling wave solutions with convex obstacles.

![Fig. 13. Temporal evolution of the predator in two-dimensional space with obstacle (0, 2).](image-url)
4.7.1. Comparison of circular obstacles

We compare the radially symmetric domain and 2D with the same obstacle radius. For detailed comparison, Fig. 15(a) is the solution on the radially symmetric domain which is represented in two-dimensional space as shown in Fig. 10(a) (dashed arrow). Here, the obstacle radius $r_b = 25.6$ is imposed. And the predator solution is calculated at time $T = 1420$ on $(r_b, 256.5)$ with a spatial mesh size $h = 1$. Figures 15(a) and 15(b) show the contour plots of the predator solutions obtained from the radially symmetric domain and the two-dimensional space, respectively. Figure 15(c) is the overlapped spatial plots on the radially symmetric and two-dimensional domains. The spatial plots suggest that the generation of traveling wave occurs similarly for all directions surrounding the circle.

4.7.2. Comparison of rectangular obstacles

The generation of the traveling wave solutions are observed by rectangular obstacles. On the domain $\Omega = (0, 256) \times (0, 256)$, the obstacle domains $\Omega_o = (0, 10) \times (0, 10)$ (upper row) and $\Omega_o = (0, 50) \times (0, 2)$ (lower row) are considered. The calculations are computed with a spatial mesh size $h = 1$. The contour of the predator solution in the two-dimensional space is overlapped with the stem plot as shown in Fig. 16(a). The $x$-axis ($x = 1$, marked as circle), axial side ($x = y$, marked as triangle, upper row), and $y$-axis ($y = 1$, marked as star) are illustrated with stem plots. Figure 16(b) shows overlapped spatial plots at the $x$-axis ($x = 1$, marked as circle), axial side ($x = y$, marked as triangle, upper row), and $y$-axis ($y = 1$, marked as star). Observing the results in Fig. 16(b), we can see that the wavelengths are different due to the size of the obstacle. When far from the obstacle, the effect of the obstacle will be much reduced.

4.7.3. Range of the wavelengths

The range of the class of wavelengths is examined based on the wavelength. Let us define $u(m)$ as the wavelength of the obstacle for obstacle radius $r_b$.

$$u(m) = \frac{2\pi}{\lambda}$$

where $\lambda$ is the wavelength of the obstacle. The range of the wavelengths is given by

$$u(m)_{\text{min}} < u(m) < u(m)_{\text{max}}$$

The results show that the range of the wavelengths is

$$0.75 < u(m) < 0.25$$

Fig. 14. Temporal evolution with a circular obstacle at $t = 1505, 1512.5, 1520, and 1525$ (from left to right).

Fig. 15. Traveling wave solutions for predator with obstacle for (a) radially symmetric domain, (b) two-dimensional space and (c) comparison between radially symmetric and 2D.
\( r_k = m, \ m \in N. \) And we define \( w_c \) and \( w_i \) as the radius of sectors of circumscribed and inscribed circles of the obstacle with origin as \( O \), respectively. The obstacle domains are given as \( \Omega_{\text{1o},k} = (0,10) \times (0,kf) \) \( \text{for} \ k = 1, 2, \ldots, 10. \) Table 3 shows the relationship between \( \Omega_{\text{1o},k} \) and \( w(n). \) Figure 17(a) shows the overlapped spatial plots for obstacle domains \( \Omega_{\text{1o},1} \) (marked with circles) and the corresponding result from radially symmetric domain with \( w(7) \) (marked with solid line). Likewise, Fig. 17(b) illustrates \( \Omega_{\text{1o},10} \) (marked with circles) at \( y = 1 \) and corresponding \( w(12) \) (marked with solid line), respectively. In this test, we shifted spatial plots and the results are completely matched. Figure 17(c) describes obstacle domains \( \Omega_{\text{1o},1} \) (marked with circles) and \( \Omega_{\text{1o},10} \) (marked with triangles) with \( w_c \) and \( w_i \) for \( \Omega_{\text{1o},1} \) (marked with stars) and for \( \Omega_{\text{1o},10} \) (dashed lines). As we have \( w(7) \) and \( w(12), \) we deduce that \( R \) lies between \( w_c \) and \( w_i. \)

For the second test, we investigate the circular obstacles with obstacle domains defined as \( \Omega_{\text{2o},a,b} \) where \( a \) and \( b \) are one-half of the ellipse’s major and minor axes. Table 4 shows the relationship between \( \Omega_{\text{2o},a,b} \) and corresponding \( w(n). \) Based on Table 4, corresponding values of \( w(n) \) are \( w(6) \) and \( w(10), \) \( w \) lies between \( w_c \) and \( w_i. \)

Figure 18 shows temporal evolutions of the predator with triangle and rectangle shaped obstacles. The calculations are obtained for one-period.
at $t = 1500, 1750, 2250$, and $2750$ (upper row) and $t = 1500, 1625, 1750$, and $1875$ (lower row).

4.8. **Numerical experiments for formation of traveling wave solutions with nonconvex obstacle**

For the nonconvex obstacles, we observe the characteristics based on the wavelength as in the previous section. In $(0,256) \times (0,256)$, complex nonconvex obstacles with $\Omega^{10}_{4,1} = ((0,5) \times (0,10)) \cup ((0,10) \times (0,1))$ and $\Omega^{12}_{4,9} = ((0,5) \times (0,10)) \cup ((0,10) \times (0,9))$ are considered. Wavelengths are matched for $\Omega^{10}_{4,1}$ as $w(10)$ and $\Omega^{12}_{4,9}$ as $w(12)$. Figure 19(a) shows $w_c$ and $w_i$ for $\Omega^{5,10}_{4,1}$ (marked with circles) and $\Omega^{10,9}_{4,9}$ (marked with stars) in Fig. 19(b). For the nonconvex obstacle, we have similar results as convex obstacles.

To observe more cases, Fig. 20 shows the non-convex obstacles such as a polygon and a star with $w(10)$ and $w(12)$, respectively. The spatial plots for corresponding waves $w$ are overlapped with (b) a polygon (dashed line) and (c) a star (dashed dots). We observe that the wavelengths are also between $w_c$ and $w_i$.  

**Table 4.** Comparison between circular obstacles and $\omega$.

<table>
<thead>
<tr>
<th>Case</th>
<th>$\Omega^{10,2}_{5,10}$</th>
<th>$\Omega^{10,4}_{5,10}$</th>
<th>$\Omega^{10,8}_{5,10}$</th>
<th>$\Omega^{10,10}_{5,10}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$w$</td>
<td>$w(6)$</td>
<td>$w(7)$</td>
<td>$w(8)$</td>
<td>$w(9)$</td>
</tr>
</tbody>
</table>

Fig. 17. (a) Overlapped spatial plots for $\Omega^{1,1}_{1,1}$ (marked with circles) at $y = 1$ corresponding to $w(7)$ (marked with solid line), (b) overlapped spatial plots for $\Omega^{1,10}_{1,1}$ (marked with circles) at $y = 1$ corresponding to $w(12)$ (marked with solid line) and (c) obstacle domains $\Omega^{1,1}_{1,1}$ (marked with circles) and $\Omega^{1,10}_{1,1}$ (marked with triangles) with $w_i$ and $w_c$ for $\Omega^{1,1}_{1,1}$ (marked with stars) and for $\Omega^{1,10}_{1,1}$ (dashed lines), respectively.
Figure 18. Temporal evolutions of the predator with various convex obstacle domains. From left to right, $t = 1500$, 1750, 2250, and 2750 (upper row), $t = 1500$, 1625, 1750, and 1875 (lower row).

Figure 21 illustrates temporal evolutions for the predator with two shapes of obstacles. Compared to the nonconvex cases, the formation of the periodic traveling waves is different from the convex obstacles.

4.9. Geometric landscape features

In this section, we consider the traveling wave solutions around the geometric landscape features, which are obtained by using the image segmentation. The first geometric landscape is the large domain with an obstacle as the Kielder Water in northern Britain. Note that the regular periodic population dynamics for the predator is experimentally performed in [Lambin et al., 1998]. Figures 22(a) and 22(b) show a whole view and a closed view of the predator at $t = 7000$. As can be seen that our numerical simulation indeed demonstrates the traveling wave solutions with complicated obstacles.

For the second example, the traveling wave solutions for the Inari region in Fennoscandia are considered. The population dynamics on islands in
Fig. 20. (a) Stars and dots depict the range of $R$ for a polygon (marked with circles) and a star (marked with triangles), (b) corresponding wavelengths with $w(10)$ (dashed line) and (c) corresponding wavelengths with $w(12)$ (marked with dashed dots).

Fig. 21. Temporal evolution of the predator with various nonconvex obstacle domains. From left to right: (a) $t = 1625, 1750, 1875,$ and $2125$ and (b) $t = 2200, 2800, 3400,$ and $3900.$
Fig. 21. (Continued)

Fig. 22. Traveling wave solutions with obstacle (Kielder Water) for the predator at: (a) $t = 7000$ and (b) closed up view of dashed region in (a).

Fig. 23. Traveling wave solutions having obstacle (the Lake Inari) for the predator at: (a) $t = 7000$ and (b) closed up view of dashed region in (a).
the Lake Inari for the regional synchrony was also experimentally studied by [Heikkilä et al., 1994] in a small domain. The predator solution is illustrated in Fig. 23(a) at \( t = 7000 \). And a closed up view of dashed region in (a) is shown in Fig. 23(b). In a large domain, which has not been studied experimentally, numerical simulation can perform well to simulate the regular traveling wave.

5. Discussion

The periodic traveling wave solutions for the predator–prey model with landscape features have been studied after the work of Sherratt et al. [2002] who imposed homogeneous Dirichlet boundary at the edge of the obstacles. We have analyzed the numerical traveling wave solutions with robust and accurate numerical methods. For the regular periodic traveling wave solutions in spatiotemporal oscillations, we proposed a numerical algorithm for numerical periodicity to detect one-period of traveling wave solutions. Based on the assumption of the homogeneous Dirichlet boundary condition at the edge of the domain, we systematically investigate numerical solutions in one-, radially symmetric, and two-dimensional domains where the asynchrony behaviors are almost similar. Then we measured wavelengths to evaluate the spatial asynchrony around the two-dimensional obstacles, convex and nonconvex shapes where wavelengths are bounded. By adapting this method, we expect to have more general description for a generation of traveling wave solutions.

By the numerical simulations with realistic landscape features such as the Kielder Water and Lake Inari, the generation of traveling wave solutions was able to be observed which takes a long time in field studies. Our investigation clearly reflected the regular periodicity and the geometric assumption with a larger domain including the Lake Inari suggesting movement of predator and prey. We expect that our numerical approach could give a good tool to investigate the ecological features, as well as provide a mathematical analysis.

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