Periodic Travelling Waves in Field Vole Populations

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Department of Mathematics
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This talk can be downloaded from my web site
www.ma.hw.ac.uk/~jas
Ecological Background
Spatiotemporal Patterns Generated by Obstacles
Predicting Regular vs Irregular Patterns
Multiple Obstacles
Conclusions and Future Work

Periodic Travelling Waves in Field Vole Populations
In collaboration with:

Matthew Smith                             Xavier Lambin
Outline

1. Ecological Background
2. Spatiotemporal Patterns Generated by Obstacles
3. Predicting Regular vs Irregular Patterns
4. Multiple Obstacles
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Field Voles in Kielder Forest

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Field Voles in Kielder Forest
A Standard Predator-Prey Model
What is a Periodic Travelling Wave?
What Causes the Spatial Component of the Oscillations?
Field voles in Kielder Forest are cyclic (period 4 years).
Field voles in Kielder Forest are cyclic (period 4 years). We assume that vole cycles are caused by predation by weasels, and study using a predator-prey model.
A Standard Predator-Prey Model

\[
\begin{align*}
\frac{\partial p}{\partial t} &= D_p \nabla^2 p + \frac{akph}{1 + kh} - bp \\
\frac{\partial h}{\partial t} &= D_h \nabla^2 h + rh(1 - h/h_0) - \frac{ckph}{1 + kh}
\end{align*}
\]

Phase plane of local dynamics:
Spatiotemporal field data shows that the cycles are spatially organised into a periodic travelling wave, speed 19km/year, direction 72° from N.
What is a Periodic Travelling Wave?

Everyday example: Mexican wave
What is a Periodic Travelling Wave?

Everyday example: Mexican wave

Population Density vs Space
What is a Periodic Travelling Wave?

Everyday example: Mexican wave

![Periodic Travelling Wave](image-url)
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![Population Density vs Space](image_url)
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![Graph showing a periodic travelling wave](image)

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![Graph showing a periodic travelling wave in population density over space](image)
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[Graph showing a periodic travelling wave with population density on the y-axis and space on the x-axis]
What is a Periodic Travelling Wave?

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![Graph showing a periodic travelling wave in space and population density.](chart.png)
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![Population Density](image)

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There is an extensive literature on periodic travelling waves in oscillatory reaction-diffusion equations

\[
\begin{align*}
\frac{\partial u}{\partial t} &= D_u \frac{\partial^2 u}{\partial x^2} + f(u, v) \\
\frac{\partial v}{\partial t} &= D_v \frac{\partial^2 v}{\partial x^2} + g(u, v)
\end{align*}
\]

kinetics have a stable limit cycle
What is a Periodic Travelling Wave?

Everyday example: Mexican wave

Theorem (Kopell & Howard, 1973):
An oscillatory reaction-diffusion system has a one-parameter family of periodic travelling wave solutions if the diffusion coefficients are sufficiently close to one another.

![Graph showing wave amplitude vs wave speed with the Amplitude of limit cycle in kinetics as a dashed line.](image-url)
What is a Periodic Travelling Wave?

Everyday example: Mexican wave

Some members of the periodic travelling wave family are stable as solutions of the partial differential equations, while others are unstable.
What Causes the Spatial Component of the Oscillations?

Hypothesis: the periodic travelling waves are caused by the large central reservoir.
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Boundary Conditions in the Field Vole Example

- Voles are an important prey species for owls and kestrels
- The open expanse of Kielder Water will greatly facilitate hunting at its edge

Short eared owl

Common kestrel
Voles are an important prey species for owls and kestrels

The open expanse of Kielder Water will greatly facilitate hunting at its edge

Therefore we expect very high vole loss at the reservoir edge, implying a Robin boundary condition

\[
\frac{\partial}{\partial n} \left( \begin{array}{c}
vole \\
density 
\end{array} \right) = - \left( \begin{array}{c}
large \\
constant 
\end{array} \right) \cdot \left( \begin{array}{c}
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Voles are an important prey species for owls and kestrels. The open expanse of Kielder Water will greatly facilitate hunting at its edge. Therefore we expect very high vole loss at the reservoir edge, implying a Robin boundary condition:

$$\frac{\partial}{\partial n} \begin{pmatrix} \text{vole density} \\ \end{pmatrix} = - \begin{pmatrix} \text{large constant} \\ \end{pmatrix} \cdot \begin{pmatrix} \text{vole density} \\ \end{pmatrix}$$

To a good approx, vole density = 0 at the reservoir edge.
Voles are an important prey species for owls and kestrels.

The open expanse of Kielder Water will greatly facilitate hunting at its edge.

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To a good approx, vole density = 0 at the reservoir edge.

At the edge of the forest, a zero flux boundary condition is a natural assumption.
Typical Model Solution
Typical Model Solution
Typical Model Solution
Typical Model Solution
Movie of Typical Model Solution

Click here to play the movie
Removing the Reservoir

The periodic waves are driven by the reservoir. This is most easily demonstrated by simulating removal of the reservoir.
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Periodic Wave Generation on a Large Domain
Movie of Wave Generation on a Large Domain

Click here to play the movie
An Example of Irregular Pattern Generation

For some parameter values, obstacles with Dirichlet boundary conditions generate irregular spatiotemporal patterns.
Movie of Irregular Pattern Generation

Click here to play the movie
Mathematical goal: predict which parameter sets will give periodic travelling waves, and which will give spatiotemporal irregularity.
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To simplify, solve on $0 < x < x_{\text{max}}$ with

\[
\begin{align*}
  h &= p = 0 \quad \text{at} \quad x = 0 \quad \leftrightarrow \text{edge of reservoir} \\
  h_x &= p_x = 0 \quad \text{at} \quad x = x_{\text{max}} \quad \leftrightarrow \text{edge of forest}.
\end{align*}
\]

In fact the condition at $x = x_{\text{max}}$ plays no significant role, and we can consider the equations on $0 < x < \infty$. 
Periodic Wave Generation in 1-D Simulations

Example of periodic wave generation by Dirichlet boundary conditions in the predator-prey model:
Example of periodic wave generation by Dirichlet boundary conditions in the predator-prey model:

Conclusion: irregular patterns occur when the Dirichlet boundary condition at $x = 0$ generates a periodic travelling wave that is unstable.
Example of periodic wave generation by Dirichlet boundary conditions in the predator-prey model:

Conclusion: irregular patterns occur when the Dirichlet boundary condition at \( x = 0 \) generates a periodic travelling wave that is unstable.

Therefore we must investigate wave stability in detail.
Periodic Wave Generation in 1-D Simulations

Example of periodic wave generation by Dirichlet boundary conditions in the predator-prey model:
Model Equations in a Moving Frame

Model eqns: \( \frac{\partial u}{\partial t} = D_u \frac{\partial^2 u}{\partial x^2} + f(u, v) \)
\( \frac{\partial v}{\partial t} = D_v \frac{\partial^2 v}{\partial x^2} + g(u, v) \)
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Population Density

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Use “travelling wave” coordinate \( z = x - ct \)

\[ \Rightarrow \frac{\partial u}{\partial t} = D_u \frac{\partial^2 u}{\partial z^2} + c \frac{\partial u}{\partial z} + f(u, v) \]
\[ \frac{\partial v}{\partial t} = D_v \frac{\partial^2 v}{\partial z^2} + c \frac{\partial v}{\partial z} + g(u, v) \]
The Eigenvalue Problem

Model eqns: \[ u_t = D_u u_{zz} + cu_z + f(u,v) \]
\[ v_t = D_v v_{zz} + cv_z + g(u,v) \quad (z = x - ct) \]

Periodic wave satisfies: \[ 0 = D_u U_{zz} + cU_z + f(U,V) \]
\[ 0 = D_v V_{zz} + cV_z + g(U,V) \quad \text{period}=L \]

Consider \[ u(z,t) = U(z) + \tilde{u}(z,t) \quad \text{with} \quad |\tilde{u}| \ll |U| \]
\[ v(z,t) = V(z) + \tilde{v}(z,t) \quad \text{with} \quad |\tilde{v}| \ll |V| \]

For linear stability: \[ \tilde{u}_t = D_u \tilde{u}_{zz} + c\tilde{u}_z + f_u(U,V)\tilde{u} + f_v(U,V)\tilde{v} \]
\[ \tilde{v}_t = D_v \tilde{v}_{zz} + c\tilde{v}_z + g_u(U,V)\tilde{u} + g_v(U,V)\tilde{v} \]
The Eigenvalue Problem

Model eqns: \[ u_t = D_u u_{zz} + c u_z + f(u, v) \]
\[ v_t = D_v v_{zz} + c v_z + g(u, v) \quad (z = x - ct) \]

Periodic wave satisfies: \[ 0 = D_u U_{zz} + c U_z + f(U, V) \]
\[ 0 = D_v V_{zz} + c V_z + g(U, V) \quad \text{period} = L \]

Consider \[ u(z, t) = U(z) + \tilde{u}(z, t) \quad \text{with } |\tilde{u}| \ll |U| \]
\[ v(z, t) = V(z) + \tilde{v}(z, t) \quad \text{with } |\tilde{v}| \ll |V| \]

For linear stability: \[ \tilde{u}_t = D_u \tilde{u}_{zz} + c \tilde{u}_z + f_u(U, V)\tilde{u} + f_v(U, V)\tilde{v} \]
\[ \tilde{v}_t = D_v \tilde{v}_{zz} + c \tilde{v}_z + g_u(U, V)\tilde{u} + g_v(U, V)\tilde{v} \]
The Eigenvalue Problem

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Consider \( u(z, t) = U(z) + \tilde{u}(z, t) \) with \(|\tilde{u}| \ll |U|\)
\( v(z, t) = V(z) + \tilde{v}(z, t) \) with \(|\tilde{v}| \ll |V|\)

For linear stability: \( \tilde{u}_t = D_u \tilde{u}_{zz} + c \tilde{u}_z + f_u(U, V)\tilde{u} + f_v(U, V)\tilde{v} \)
\( \tilde{v}_t = D_v \tilde{v}_{zz} + c \tilde{v}_z + g_u(U, V)\tilde{u} + g_v(U, V)\tilde{v} \)
The Eigenvalue Problem

Model eqns: \( u_t = D_u u_{zz} + cu_z + f(u, v) \)
\[
\begin{align*}
\nu_t &= D_v \nu_{zz} + cv_z + g(u, v) \\
(\text{period}=L)
\end{align*}
\]

Periodic wave satisfies: \( 0 = D_u U_{zz} + cU_z + f(U, V) \)
\[
\begin{align*}
0 &= D_v V_{zz} + cV_z + g(U, V)
\end{align*}
\]

Consider \( u(z, t) = U(z) + \tilde{u}(z, t) \) with \|\tilde{u}\| \ll \|U\|
\[
\begin{align*}
\nu(z, t) &= V(z) + \tilde{\nu}(z, t) \quad \text{with} \quad \|\tilde{\nu}\| \ll \|V\|
\end{align*}
\]

For linear stability: \( \tilde{u}_t = D_u \tilde{u}_{zz} + c\tilde{u}_z + f_u(U, V)\tilde{u} + f_v(U, V)\tilde{\nu} \)
\[
\begin{align*}
\tilde{\nu}_t &= D_v \tilde{\nu}_{zz} + c\tilde{\nu}_z + g_u(U, V)\tilde{u} + g_v(U, V)\tilde{\nu}
\end{align*}
\]
The Eigenvalue Problem

For linear stability:

\[ \tilde{u}_t = D_u \tilde{u}_{zz} + c \tilde{u}_z + f_u(U, V) \tilde{u} + f_v(U, V) \tilde{v} \]

\[ \tilde{v}_t = D_v \tilde{v}_{zz} + c \tilde{v}_z + g_u(U, V) \tilde{u} + g_v(U, V) \tilde{v} \]

Solution form is:

\[ \tilde{u}(z, t) = e^{\lambda t} \bar{u}(z) \quad \text{with} \quad |\bar{u}| \ll |U| \]

\[ \tilde{v}(z, t) = e^{\lambda t} \bar{v}(z) \quad \text{with} \quad |\bar{v}| \ll |V| \]

Note that \( \lambda, \bar{u}, \bar{v} \) are complex-valued.
The Eigenvalue Problem

For linear stability:

\[ \begin{align*}
\ddot{u}_t &= D_u \ddot{u}_{zz} + c \ddot{u}_z + f_u(U, V)\ddot{u} + f_v(U, V)\ddot{v} \\
\ddot{v}_t &= D_v \ddot{v}_{zz} + c \ddot{v}_z + g_u(U, V)\ddot{u} + g_v(U, V)\ddot{v}
\end{align*} \]

Soln form is:

\[ \begin{align*}
\ddot{u}(z, t) &= e^{\lambda t} \ddot{u}(z) \quad \text{with } |\ddot{u}| \ll |U| \\
\ddot{v}(z, t) &= e^{\lambda t} \ddot{v}(z) \quad \text{with } |\ddot{v}| \ll |V|
\end{align*} \]

Note that \( \lambda, \ddot{u}, \ddot{v} \) are complex-valued.
The Eigenvalue Problem

For linear stability:

\[
\begin{align*}
\tilde{u}_t &= D_u \tilde{u}_{zz} + c \tilde{u}_z + f_u(U, V)\tilde{u} + f_v(U, V)\tilde{v} \\
\tilde{v}_t &= D_v \tilde{v}_{zz} + c \tilde{v}_z + g_u(U, V)\tilde{u} + g_v(U, V)\tilde{v}
\end{align*}
\]

Soln form is:

\[
\begin{align*}
\tilde{u}(z, t) &= e^{\lambda t} \tilde{u}(z) \quad \text{with} \quad |\tilde{u}| \ll |U| \\
\tilde{v}(z, t) &= e^{\lambda t} \tilde{v}(z) \quad \text{with} \quad |\tilde{v}| \ll |V|
\end{align*}
\]

Note that \(\lambda, \tilde{u}, \tilde{v}\) are complex-valued

\[\text{Re}(\lambda) < 0\]
The Eigenvalue Problem

For linear stability:

\[ \tilde{u}_t = D_u \tilde{u}_{zz} + c \tilde{u}_z + f_u(U, V) \tilde{u} + f_v(U, V) \tilde{v} \]
\[ \tilde{v}_t = D_v \tilde{v}_{zz} + c \tilde{v}_z + g_u(U, V) \tilde{u} + g_v(U, V) \tilde{v} \]

Solution form is:

\[ \tilde{u}(z, t) = e^{\lambda t} \tilde{u}(z) \quad \text{with} \quad |\tilde{u}| \ll |U| \]
\[ \tilde{v}(z, t) = e^{\lambda t} \tilde{v}(z) \quad \text{with} \quad |\tilde{v}| \ll |V| \]

Note that \( \lambda, \tilde{u}, \tilde{v} \) are complex-valued

\[ \text{Re}(\lambda) > 0 \]
The Eigenvalue Problem

For linear stability:
\[ \begin{align*}
\tilde{u}_t &= D_u \tilde{u}_{zz} + c \tilde{u}_z + f_u(U, V) \tilde{u} + f_v(U, V) \tilde{v} \\
\tilde{v}_t &= D_v \tilde{v}_{zz} + c \tilde{v}_z + g_u(U, V) \tilde{u} + g_v(U, V) \tilde{v}
\end{align*} \]

Soln form is:
\[ \begin{align*}
\tilde{u}(z, t) &= e^{\lambda t} \bar{u}(z) \quad \text{with} \quad |\bar{u}| \ll |U| \\
\tilde{v}(z, t) &= e^{\lambda t} \bar{v}(z) \quad \text{with} \quad |\bar{v}| \ll |V|
\end{align*} \]

Note that \( \lambda, \bar{u}, \bar{v} \) are complex-valued

\[ \text{Re}(\lambda) > 0 \]

Periodic wave is stable \( \iff \text{Re}(\lambda) < 0 \) for all possible values of \( \lambda \).
The Eigenvalue Problem

⇒ Eigenfunction eqn: \[ \lambda \bar{u} = D_u \bar{u}_{zz} + c \bar{u}_z + f_u(U, V)\bar{u} + f_v(U, V)\bar{v} \]
\[ \lambda \bar{v} = D_v \bar{v}_{zz} + c \bar{v}_z + g_u(U, V)\bar{u} + g_v(U, V)\bar{v} \]

We solve on \( 0 < z < L \); need to consider boundary conditions.
The Eigenvalue Problem

⇒ Eigenfunction eqn: \( \lambda \overline{u} = D_u \overline{u}_{zz} + c \overline{u}_z + f_u(U, V)\overline{u} + f_v(U, V)\overline{v} \)
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We solve on \( 0 < z < L \); need to consider boundary conditions.

\[ |\overline{u}(L)| > |\overline{u}(0)| \Rightarrow \]

\[
\begin{align*}
\text{u(z,t)} & \\
\text{\[ L \quad \cdots \quad z \]}
\end{align*}
\]
The Eigenvalue Problem

⇒ Eigenfunction eqn: \( \lambda \overline{u} = D_u \overline{u}_{zz} + c \overline{u}_z + f_u(U, V) \overline{u} + f_v(U, V) \overline{v} \)

\( \lambda \overline{v} = D_v \overline{v}_{zz} + c \overline{v}_z + g_u(U, V) \overline{u} + g_v(U, V) \overline{v} \)

We solve on \( 0 < z < L \); need to consider boundary conditions.

\[ |\overline{u}(L)| < |\overline{u}(0)| \Rightarrow \]
The Eigenvalue Problem

⇒ Eigenfunction eqn: \[ \lambda \overline{u} = D_u \overline{u}_{zz} + c \overline{u}_z + f_u(U, V)\overline{u} + f_v(U, V)\overline{v} \]
\[ \lambda \overline{v} = D_v \overline{v}_{zz} + c \overline{v}_z + g_u(U, V)\overline{u} + g_v(U, V)\overline{v} \]

We solve on \( 0 < z < L \); need to consider boundary conditions.

However there can be a phase difference between \( \overline{u}(0) \) and \( \overline{u}(L) \)
(and similarly for \( \overline{v} \)).
The Eigenvalue Problem

⇒ Eigenfunction eqn: \[ \lambda \bar{u} = D_u \bar{u}_{zz} + c \bar{u}_z + f_u(U, V) \bar{u} + f_v(U, V) \bar{v} \]
\[ \lambda \bar{v} = D_v \bar{v}_{zz} + c \bar{v}_z + g_u(U, V) \bar{u} + g_v(U, V) \bar{v} \]

We solve on \(0 < z < L\); need to consider boundary conditions.

However there can be a phase difference between \(\bar{u}(0)\) and \(\bar{u}(L)\) (and similarly for \(\bar{v}\)).

⇒ Boundary conditions: \(\bar{u}(0) = \bar{u}(L)e^{i\gamma}\) (\(0 \leq \gamma < 2\pi\))
\(\bar{v}(0) = \bar{v}(L)e^{i\gamma}\) (\(0 \leq \gamma < 2\pi\))
Numerical Calculation of Eigenvalue Spectrum

(based on Jens Rademacher, Bjorn Sandstede, Arnd Scheel Physica D 229 166-183, 2007)

Step 1: solve numerically for the periodic wave by continuation in $c$ from a Hopf bifurcation point in the periodic wave eqns

\[
0 = D_u U_{zz} + c U_z + f(U, V)
\]
\[
0 = D_v V_{zz} + c V_z + g(U, V)
\]
Step 1: solve numerically for the periodic wave by continuation in \(c\) from a Hopf bifurcation point in the periodic wave eqns

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Step 1: solve numerically for the periodic wave by continuation in $c$ from a Hopf bifurcation point in the periodic wave eqns

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\end{align*}
\]
Step 1: solve numerically for the periodic wave by continuation in $c$ from a Hopf bifurcation point in the periodic wave eqns

\[
0 = D_u U_{zz} + cU_z + f(U, V) \\
0 = D_v V_{zz} + cV_z + g(U, V)
\]

Repeat until the required wave speed is reached.
Numerical Calculation of Eigenvalue Spectrum

(based on Jens Rademacher, Bjorn Sandstede, Arnd Scheel Physica D 229 166-183, 2007)

\[
\lambda \overline{u} = D_u \overline{u}_{zz} + c \overline{u}_z + f_u(U, V)\overline{u} + f_v(U, V)\overline{v}, \quad \overline{u}(0) = \overline{u}(L)e^{i\gamma}
\]

\[
\lambda \overline{v} = D_v \overline{v}_{zz} + c \overline{v}_z + g_u(U, V)\overline{u} + g_v(U, V)\overline{v}, \quad \overline{v}(0) = \overline{v}(L)e^{i\gamma}
\]

**Step 2:** For \( \gamma = 0 \), discretise these equations in space.

- \( z \quad \mapsto \quad 0 = z_1, z_2, \ldots, z_N = L \)
- \( \overline{u} \quad \mapsto \quad \overline{u}_1, \overline{u}_2, \ldots, \overline{u}_N \)
- \( d\overline{u}/dz \quad \mapsto \quad (\overline{u}_{i+1} - \overline{u}_{i-1})/(z_{i+1} - z_{i-1}) \)
- \( \gamma = 0 \quad \Rightarrow \quad \overline{u}(0) = \overline{u}(L) \mapsto \overline{u}_1 = \overline{u}_N \)
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\begin{align*}
\lambda \overline{u} &= D_u \overline{u}_{zz} + c \overline{u}_z + f_u(U, V) \overline{u} + f_v(U, V) \overline{v}, \quad \overline{u}(0) = \overline{u}(L) e^{i \gamma} \\
\lambda \overline{v} &= D_v \overline{v}_{zz} + c \overline{v}_z + g_u(U, V) \overline{u} + g_v(U, V) \overline{v}, \quad \overline{v}(0) = \overline{v}(L) e^{i \gamma}
\end{align*}
\]

Step 2: For $\gamma = 0$, discretise these equations in space.

\[
\begin{align*}
z &\mapsto 0 = z_1, z_2, \ldots, z_N = L \\
\overline{u} &\mapsto \overline{u}_1, \overline{u}_2, \ldots, \overline{u}_N \\
\frac{d \overline{u}}{dz} &\mapsto (\overline{u}_{i+1} - \overline{u}_{i-1})/(z_{i+1} - z_{i-1}) \\
\gamma = 0 &\Rightarrow \overline{u}(0) = \overline{u}(L) \leftrightarrow \overline{u}_1 = \overline{u}_N
\end{align*}
\]

This gives a (large) matrix eigenvalue problem.
Numerical Calculation of Eigenvalue Spectrum

(based on Jens Rademacher, Bjorn Sandstede, Arnd Scheel Physica D 229 166-183, 2007)

\[
\begin{align*}
\lambda \overline{u} & = D_u \overline{u}_{zz} + c \overline{u}_z + f_u(U, V) \overline{u} + f_v(U, V) \overline{v}, \quad \overline{u}(0) = \overline{u}(L) e^{i \gamma} \\
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\end{align*}
\]

**Step 2:** For \( \gamma = 0 \), discretise these equations in space.

\[
\begin{align*}
z & \mapsto 0 = z_1, z_2, \ldots, z_N = L \\
\overline{u} & \mapsto \overline{u}_1, \overline{u}_2, \ldots, \overline{u}_N \\
\frac{d \overline{u}}{dz} & \mapsto \frac{(\overline{u}_{i+1} - \overline{u}_{i-1})}{(z_{i+1} - z_{i-1})} \\
\gamma = 0 \Rightarrow \overline{u}(0) & = \overline{u}(L) \mapsto \overline{u}_1 = \overline{u}_N
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\[
\lambda \bar{u} = D_u \bar{u}_{zz} + c \bar{u}_z + f_u(U, V) \bar{u} + f_v(U, V) \bar{v}, \quad \bar{u}(0) = \bar{u}(L) e^{i \gamma} \\
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\]

**Step 3:** continue the eigenfunction equations numerically in \( \gamma \), starting from each of the \( \gamma = 0 \) solutions.
Numerical Calculation of Eigenvalue Spectrum

(based on Jens Rademacher, Bjorn Sandstede, Arnd Scheel Physica D 229 166-183, 2007)

\[
\begin{align*}
\lambda \bar{u} &= D_u \bar{u}_{zz} + c \bar{u}_z + f_u(U, V)\bar{u} + f_v(U, V)\bar{v}, \quad \bar{u}(0) = \bar{u}(L)e^{i\gamma} \\
\lambda \bar{v} &= D_v \bar{v}_{zz} + c \bar{v}_z + g_u(U, V)\bar{u} + g_v(U, V)\bar{v}, \quad \bar{v}(0) = \bar{v}(L)e^{i\gamma}
\end{align*}
\]

Step 3: continue the eigenfunction equations numerically in $\gamma$, starting from each of the $\gamma = 0$ solutions.
Numerical Calculation of Eigenvalue Spectrum

(based on Jens Rademacher, Bjorn Sandstede, Arnd Scheel Physica D 229 166-183, 2007)

This gives the eigenvalue spectrum, and hence (in)stability

(Eckhaus instability)

\[ \text{STABLE} \quad \text{UNSTABLE} \]
Periodic Wave Families with Stability

\[ \alpha = \frac{D_{\text{prey}}}{D_{\text{predator}}} \]
Stability in a Parameter Plane

By following this procedure at each point on a grid in parameter space, regions of stability/instability can be determined.

In fact, stable/unstable boundaries can be computed accurately by numerical continuation of Eckhaus instability points.
Periodic Wave Generation in 1-D Simulations

Example of periodic wave generation by Dirichlet boundary conditions in the predator-prey model:
Periodic Wave Generation in 1-D Simulations

Example of periodic wave generation by Dirichlet boundary conditions in the predator-prey model:
Periodic Wave Generation in 1-D Simulations

Example of periodic wave generation by Dirichlet boundary conditions in the predator-prey model:

Our stability calculations explain the surprising results from simulations of periodic wave generation.
Outline

1. Ecological Background
2. Spatiotemporal Patterns Generated by Obstacles
3. Predicting Regular vs Irregular Patterns
4. Multiple Obstacles
5. Conclusions and Future Work
Typical Predator-Prey Solution with Multiple Obstacles
Question: How do the waves generated by different obstacles interact?
Question: How do the waves generated by different obstacles interact?
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**Question:** How do the waves generated by different obstacles interact?
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**Question:** How do the waves generated by different obstacles interact?

**Answer:** the wave generated by a larger obstacle dominates that generated by a smaller obstacle.
Movie of Competition between Obstacles

Click here to play the movie
Numerical solutions for circular obstacles indicate that wavelength far from the obstacle varies with obstacle radius.

![Graph showing the relationship between wavelength and obstacle radius](chart.png)
Consider an interface between periodic waves in 1-D.
Consider an interface between periodic waves in 1-D

Analytical study of transition fronts in periodic wave amplitude shows that these move from a lower to a higher amplitude wave.

Therefore the wave generated by a larger obstacle will replace that generated by a smaller obstacle.
The expected behaviour at the edge of Kielder Water provides a possible explanation for the periodic travelling waves that are observed in field vole density.

For other parameter sets, the same mechanism generates spatiotemporal irregularity. A detailed explanation of this is possible via numerical calculation of wave stability.

Results on obstacle size and multiple obstacles are consistent with intuitive expectations, and explain why very large obstacles are required to give detectable periodic waves.
Conclusions

- The expected behaviour at the edge of Kielder Water provides a possible explanation for the periodic travelling waves that are observed in field vole density.
- For other parameter sets, the same mechanism generates spatiotemporal irregularity. A detailed explanation of this is possible via numerical calculation of wave stability.
- Results on obstacle size and multiple obstacles are consistent with intuitive expectations, and explain why very large obstacles are required to give detectable periodic waves.
Conclusions

- The expected behaviour at the edge of Kielder Water provides a possible explanation for the periodic travelling waves that are observed in field vole density.
- For other parameter sets, the same mechanism generates spatiotemporal irregularity. A detailed explanation of this is possible via numerical calculation of wave stability.
- Results on obstacle size and multiple obstacles are consistent with intuitive expectations, and explain why very large obstacles are required to give detectable periodic waves.
The major outstanding issues are:

- Analytical prediction of wave stability away from Hopf bifurcation.
- Detailed study of how obstacle shape affects periodic travelling wave selection.

This paper is a review of periodic travelling waves in ecological field data and in mathematical models of cyclic populations. The associated online material contains a detailed tutorial on numerical calculation of periodic travelling wave stability, including computer code (in Fortran).

The paper and the online material are freely available from my web site: [www.ma.hw.ac.uk/~jas](http://www.ma.hw.ac.uk/~jas)
Ecological Background
Field Voles in Kielder Forest
A Standard Predator-Prey Model
What is a Periodic Travelling Wave?
What Causes the Spatial Component of the Oscillations?

Spatiotemporal Patterns Generated by Obstacles
Boundary Conditions in the Field Vole Example
Typical Model Solution
Removing the Reservoir
Examples of Regular and Irregular Pattern Generation
Mathematical Goal

Predicting Regular vs Irregular Patterns
One-Dimensional Problem
Model Equations in a Moving Frame
The Eigenvalue Problem
Numerical Calculation of Eigenvalue Spectrum
Stability in a Parameter Plane

Multiple Obstacles
Typical Predator-Prey Solution with Multiple Obstacles
Competition between Obstacles
Wavelength vs Obstacle Radius
Explanation of Competition between Obstacles

Conclusions and Future Work
Conclusions
Future Work
Review Paper and Software