Periodic Travelling Waves in Ecology: A Users Guide

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This talk can be downloaded from my web site
www.ma.hw.ac.uk/~jas
An Ecological Case Study
Stage I: Modelling and Numerical Simulation
Stage II: Predicting Regular vs Irregular Patterns
Stage III: Predicting Wave Properties
Conclusions and Limitations

In collaboration with:

Matthew Smith

Xavier Lambin
Outline

1. An Ecological Case Study
2. Stage I: Modelling and Numerical Simulation
3. Stage II: Predicting Regular vs Irregular Patterns
4. Stage III: Predicting Wave Properties
5. Conclusions and Limitations
An Ecological Case Study
Stage I: Modelling and Numerical Simulation
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Field Voles in Kielder Forest
What is a Periodic Travelling Wave?
What Causes the Spatial Component of the Oscillations?
Field Voles in Kielder Forest

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). 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?

Population density is periodic in space, with peaks and troughs moving across the domain at a constant speed.

Mathematically: a soln of form $U(x \pm ct)$, with $U(.)$ periodic.
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![Graph showing a periodic travelling wave](image-url)
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![Graph showing periodic travelling wave with population density on the y-axis and space on the x-axis.](image)
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What Causes the Spatial Component of the Oscillations?

Hypothesis: the periodic travelling waves are caused by the large central reservoir.
An Ecological Case Study

Stage I: Modelling and Numerical Simulation
Stage II: Predicting Regular vs Irregular Patterns
Stage III: Predicting Wave Properties

Conclusions and Limitations

Outline

1. An Ecological Case Study
2. Stage I: Modelling and Numerical Simulation
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For modelling, we need an assumption on the cause of the population cycles.
Field Voles in Kielder Forest

For modelling, we need an assumption on the cause of the population cycles.

We assume that vole cycles are caused by predation by weasels, and study using a standard predator-prey model.
A Standard Predator-Prey Model

\[
\begin{align*}
\frac{\partial p}{\partial t} &= D_p \nabla^2 p + \frac{akph}{1 + kh} - bp \\
\text{dispersal} & \quad \text{benefit from predation} & \quad \text{death} \\
\frac{\partial h}{\partial t} &= D_h \nabla^2 h + rh(1 - h/h_0) - \frac{ckph}{1 + kh} \\
\text{dispersal} & \quad \text{intrinsic birth & death} & \quad \text{predation}
\end{align*}
\]

Phase plane of kinetics:

Periodic travelling waves in ecology: a users guide
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
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.
- Therefore we expect very high vole loss at the reservoir edge, implying a Robin boundary condition:

\[
\frac{\partial}{\partial n}\left( \text{vole density} \right) = -\left( \text{large constant} \right) \cdot \left( \text{vole density} \right)
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  \[
  \frac{\partial}{\partial n} \begin{pmatrix} \text{vole density} \\ \text{large constant} \end{pmatrix} \cdot \begin{pmatrix} \text{vole density} \end{pmatrix} = - \begin{pmatrix} \text{vole density} \end{pmatrix}
  \]
- To a good approx, vole density = 0 at the reservoir edge.
Boundary Conditions in the Field Vole Example

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\[
\frac{\partial}{\partial n} \left( \begin{array}{c} \text{vole density} \\ \text{vole density} \end{array} \right) = - \left( \begin{array}{c} \text{large constant} \\ \text{vole density} \end{array} \right) \cdot \left( \begin{array}{c} \text{vole density} \end{array} \right)
\]

- 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
An Example of Irregular Pattern Generation

For some parameter values, obstacles with Dirichlet boundary conditions generate irregular spatiotemporal patterns.
An Ecological Case Study
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Field Voles in Kielder Forest
A Standard Predator-Prey Model
Boundary Conditions in the Field Vole Example
Typical Model Solution

Movie of Irregular Pattern Generation

Click here to play the movie
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Regular and Irregular Patterns: the Goal
Standard Theory of Periodic Travelling Wave
One-Dimensional Problem
The Eigenvalue Spectrum
Back to Wave Generation in 1-D Simulations

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Regular and Irregular Patterns: the Goal

Goal: to predict which parameter sets will give periodic travelling waves, and which will give spatiotemporal irregularity.
Standard Theory of Periodic Travelling Wave

Mathematically, a periodic travelling wave is a solution of form $U(x \pm ct)$, with $U(.)$ periodic.

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

\[
\begin{align*}
\frac{\partial u}{\partial t} &= D_u \frac{\partial^2 u}{\partial x^2} + f(u, v) \\
\frac{\partial v}{\partial t} &= D_v \frac{\partial^2 v}{\partial x^2} + \underbrace{g(u, v)}_{\text{kinetics have a stable limit cycle}}
\end{align*}
\]
Mathematically, a periodic travelling wave is a soln of form $U(x \pm ct)$, with $U(\cdot)$ periodic.

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.
Mathematically, a periodic travelling wave is a solution of form $U(x \pm ct)$, with $U(.)$ periodic.

Some members of the periodic travelling wave family are stable as solutions of the partial differential equations, while others are unstable.
To simplify the field vole problem, solve on $0 < x < x_{max}$ with

\[ h = p = 0 \quad \text{at} \quad x = 0 \quad \leftrightarrow \text{edge of reservoir} \]
\[ h_x = p_x = 0 \quad \text{at} \quad x = x_{max} \quad \leftrightarrow \text{edge of forest} \]

In fact the condition at $x = x_{max}$ plays no significant role, and we can consider the equations on $0 < x < \infty$. 

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Periodic Wave Generation in 1-D Simulations

Example of periodic wave generation by boundary conditions corresponding to the reservoir edge in 1-D:
Example of periodic wave generation by boundary conditions corresponding to the reservoir edge in 1-D:

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 boundary conditions corresponding to the reservoir edge in 1-D:
Wave stability depends on the eigenvalue spectrum.

Eckhaus instability

STABLE

Recently methods have been developed that enable the spectrum to be calculated using numerical continuation.

( Jens Rademacher, Björn Sandstede, Arnd Scheel. Physica D 229 166-183, 2007)
Example of periodic wave generation by Dirichlet boundary conditions in the predator-prey model:
From such simulations, we can easily calculate wave speed vs parameters.
From such simulations, we can easily calculate wave speed vs parameters.

Our stability calculations explain the surprising results from simulations of periodic wave generation.
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An oscillatory reaction-diffusion system has a one-parameter family of periodic travelling waves.
The Wave Selection Problem

An oscillatory reaction-diffusion system has a one-parameter family of periodic travelling waves.

Key Question:
which member of the wave family is selected by the boundary condition at the reservoir edge?

Amplitude of limit cycle in kinetics

Wave amplitude

Wave speed

SELECTED WAVE
An oscillatory reaction-diffusion system has a one-parameter family of periodic travelling waves.

Key Question:
which member of the wave family is selected by the boundary condition at the reservoir edge?

This question can be answered analytically when $D_p = D_h$, close to Hopf bifurcation in the kinetics.
Step 1: Reduction to Normal Form

Consider the case of $D_p = D_h$ close to Hopf bifurcation in the kinetics. Then standard normal form analysis reduces the predator-prey model to

$$
\begin{align*}
    u_t &= u_{xx} + \lambda(r)u - \omega(r)v \\
    v_t &= v_{xx} + \omega(r)u + \lambda(r)v
\end{align*}
$$

where

$$
\begin{align*}
    \lambda(r) &= 1 - r^2 \\
    \omega(r) &= \omega_0 - \omega_1 r^2.
\end{align*}
$$

Here

$$
\begin{align*}
    \omega_0 &= \frac{2}{C(A-1)-(A+1)} \left[ \frac{A(A^2-1)}{B} \right]^{1/2} + \left[ \frac{A-1}{A(A+1)B} \right]^{1/2} \\
    \omega_1 &= \frac{4A^2B^2+(A^2-1)(A^2+5)AB+(A^2-1)^2}{6A^{5/2}(A^2-1)^{1/2}B^{3/2}}
\end{align*}
$$
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"\(\lambda-\omega\) system"
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\end{align*}
\]

where $\lambda(r) = 1 - r^2$ and $\omega(r) = \omega_0 - \omega_1 r^2$.

The periodic travelling wave family is

\[
\begin{align*}
    u &= r^* \cos \left[ \omega(r^*) t \pm \sqrt{\lambda(r^*)} x \right] \\
    v &= r^* \sin \left[ \omega(r^*) t \pm \sqrt{\lambda(r^*)} x \right]
\end{align*}
\]
For the $\lambda-\omega$ equations, the long term solution is

$$r(x, t) \equiv \sqrt{u^2 + v^2} = R(x)$$

independent of time.
For the $\lambda-\omega$ equations, the long term solution is

$$r(x, t) \equiv \sqrt{u^2 + v^2} = R(x)$$

independent of time, where

$$R(x) = r_{ptw} \tanh \left( \frac{x}{\sqrt{2}} \right) \quad \text{with} \quad r_{ptw} = \left\{ \frac{1}{2} \left[ 1 + \sqrt{1 + \frac{8}{9} \omega_1^2} \right] \right\}^{-1/2}$$
Step 3: Deduce Wave Properties from Amplitude

The periodic travelling wave amplitude is
\[ r_{ptw} = \left\{ \frac{1}{2} \left[ 1 + \sqrt{1 + \frac{8}{9} \omega^2} \right] \right\}^{-1/2} . \]

The wave solution is
\[
\begin{align*}
  u &= r_{ptw} \cos[\omega(r_{ptw}) t \pm \lambda(r_{ptw})^{1/2} x] \\
  v &= r_{ptw} \sin[\omega(r_{ptw}) t \pm \lambda(r_{ptw})^{1/2} x]
\end{align*}
\]

\((\lambda(r) = 1 - r^2, \omega(r) = \omega_0 - \omega_1 r^2)\).

Therefore:

- Wavelength: \( 2\pi / \sqrt{1 - r_{ptw}^2} \)
- Time period: \( 2\pi / (\omega_0 - \omega_1 r_{ptw}^2) \)
- Speed: \( (\omega_0 - \omega_1 r_{ptw}^2) / \sqrt{1 - r_{ptw}^2} \)
Outline

1. An Ecological Case Study
2. Stage I: Modelling and Numerical Simulation
3. Stage II: Predicting Regular vs Irregular Patterns
4. Stage III: Predicting Wave Properties
5. Conclusions and Limitations
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.

Analytical periodiction of periodic travelling wave properties is possible close to Hopf bifurcation in the kinetics, by solving the wave selection problem.
Conclusions (continued)

Since $\lambda - \omega$ equations are the normal form of any oscillatory reaction-diffusion system close to Hopf bifurcation, and since boundaries with Dirichlet conditions are common in applications, we expect both periodic travelling waves and spatiotemporal irregularity to be a general feature of such systems.
Mathematically, the major limitations are:

- Analytical prediction of wave stability away from Hopf bifurcation is not currently possible.
- There is not currently a solution of the wave selection problem away from Hopf bifurcation (either analytical or numerical).

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)

This paper concerns ecological applications of periodic travelling wave generation by obstacles. The associated online material contains a detailed tutorial on the reduction of an oscillatory reaction-diffusion system to normal form close to Hopf bifurcation, including computer code (in Maple).

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)
An Ecological Case Study

Stage I: Modelling and Numerical Simulation

Field Voles in Kielder Forest
A Standard Predator-Prey Model
Boundary Conditions in the Field Vole Example
Typical Model Solution

Stage II: Predicting Regular vs Irregular Patterns

Regular and Irregular Patterns: the Goal
Standard Theory of Periodic Travelling Wave
One-Dimensional Problem
The Eigenvalue Spectrum
Back to Wave Generation in 1-D Simulations

Stage III: Predicting Wave Properties

The Wave Selection Problem
Step 1: Reduction to Normal Form
Step 2: Exact Solution for the Wave Amplitude
Step 3: Deduce Wave Properties from Amplitude

Conclusions and Limitations

Conclusions
Mathematical limitations
Relevant Papers and Software

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Periodic travelling waves in ecology: a users guide