Multiannual Cycles in Field Vole Populations: Spatial Data and Spatiotemporal Models

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Introduction: Field Voles in Kielder Forest
Why Do Field Vole Populations Cycle in Kielder?
Spatiotemporal Field Data
Mathematical Modelling of Periodic Travelling Waves

Collaborators

Matthew Smith

Andy White

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Mike Begon
Outline

1. Introduction: Field Voles in Kielder Forest
2. Why Do Field Vole Populations Cycle in Kielder?
3. Spatiotemporal Field Data
4. Mathematical Modelling of Periodic Travelling Waves
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1. Introduction: Field Voles in Kielder Forest
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Cyclic rodent populations are one of the most studied systems in ecology.

The multiannual fluctuations in abundance are not driven by the environment.

Despite more than 100 years of study, the underlying mechanisms remain unclear.
Introduction: Field Voles in Kielder Forest

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Multiannual Rodent Cycles

Field Voles in Kielder Forest

Field vole (Microtus agrestis)
Kielder Forest is a large commercial forest plantation (613 km$^2$). Vole habitat is forest clear cuts (5-100 Ha) that last 12-15 years.
Field voles in Kielder Forest are cyclic (period 4 years)
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4. Mathematical Modelling of Periodic Travelling Waves
Hypothesis I: Predation by Weasels

Weasels (*Mustela nivalis*) are the main terrestrial predator of voles in Kielder.
Hypothesis I: Predation by Weasels

- Weasels (*Mustela nivalis*) are the main terrestrial predator of voles in Kielder.
- In Finland, weasels drive multiannual vole cycles. *(Evidence: live-trapping and removal of weasels changes the vole dynamics to annual cycles).*
Hypothesis I: Predation by Weasels

Weasels (Mustela nivalis) are the main terrestrial predator of voles in Kielder.

In Finland, weasels drive multiannual vole cycles. (Evidence: live-trapping and removal of weasels changes the vole dynamics to annual cycles).
Hypothesis I: Predation by Weasels

- Weasels (*Mustela nivalis*) are the main terrestrial predator of voles in Kielder.
- In Finland, weasels drive multiannual vole cycles. (*Evidence*: live-trapping and removal of weasels changes the vole dynamics to annual cycles).
- However, in Kielder, live-trapping and removal of weasels does not stop multiannual vole cycles.
Some rodent parasites affect host fecundity e.g. cowpox in female bank voles and wood mice delays reproduction until the following breeding season (recent data from Manor Wood, UK)
Hypothesis II: Disease Effects on Reproduction

- Some rodent parasites affect host fecundity, e.g., cowpox in female bank voles and wood mice delays reproduction until the following breeding season (recent data from Manor Wood, UK).

- In Kielder, prevalences of field vole cowpox is significantly correlated with past population densities (also for TB).
Hypothesis II: Disease Effects on Reproduction

- Some rodent parasites affect host fecundity. e.g. cowpox in female bank voles and wood mice delays reproduction until the following breeding season (recent data from Manor Wood, UK)
- In Kielder, prevalences of field vole cowpox is significantly correlated with past population densities (also for TB)
- Therefore cowpox and other diseases may alter reproductive timing in a delayed density dependent manner – this could in turn lead to multiannual cycles
Hypothesis II: Schematic Illustration of the Model

- **Birth (seasonal)**
  - Susceptible
    - Death
    - Death (higher rate due to disease)
    - Death
    - Infected
      - Recovered, immune & non-reproductive
        - Birth (seasonal) at reduced rate (fraction f of susceptible birth rate)
      - Recovered, immune & reproductive
        - Rate \( \tau \)

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Multiannual Cycles in Field Vole Populations: Spatial Data and Spatiotemporal Models
Hypothesis II: Examples of Model Solutions

- 1/τ=22 days
- 1/τ=36 days
- 1/τ=189 days
- 1/τ=564 days

Graphs showing the number of voles per hectare (Voles ha\(^{-1}\)) over time (Years) for different time periods.
Hypothesis II: Examples of Model Solutions

Basic dynamics: population crash in non-breeding season, recovery in breeding season.
Hypothesis II: Examples of Model Solutions

1/τ = 22 days
1/τ = 36 days
1/τ = 189 days
1/τ = 564 days

**Large τ**: recovery is fast enough for annual cycles.
Hypothesis II: Examples of Model Solutions

\[ \frac{1}{\tau} = 22 \text{ days} \]
\[ \frac{1}{\tau} = 36 \text{ days} \]
\[ \frac{1}{\tau} = 189 \text{ days} \]
\[ \frac{1}{\tau} = 564 \text{ days} \]

**Smaller \( \tau \):** recovery is too slow for annual cycles.
Hypothesis II: Seasonal Forcing is Important

Multiannual cycles do not occur if the reproductive season is either too short or too long.

- **low** disease prevalence
- voles die out

breeding season length as a fraction of the year

- disease absent
- insufficient time for population crash

multiannual cycles

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Hypothesis II: When are Disease-Induced Cycles Expected?

(Other param estimates for field voles in Kielder forest and cowpox)
Hypothesis II: Conclusions

- Multiannual cycles can be caused by the combination of:
  1. delayed reproduction following infection
  2. reduced fecundity after recovery
  3. annual forcing (seasonal reproduction)

- For cowpox in field voles in Kielder forest, the key requirement is a greatly reduced fecundity after infection (no data currently available)
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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
What is a Periodic Travelling Wave?

A useful analogy is the “Mexican Wave”

![Image of a crowd at a stadium performing the Mexican Wave]

- Population Density
- Space
What is a Periodic Travelling Wave?

A useful analogy is the “Mexican Wave”
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![Mexican Wave Image]

![Population Density Wave](image-url)
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[Graph of Population Density vs. Space]

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![Image of a crowd performing the Mexican Wave](image_url)

**Graph**

Population Density vs. Space
What is a Periodic Travelling Wave?

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Population Density

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[Graph showing population density over space]

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![Image of a crowd with a Mexican Wave]

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![Population Density Diagram]

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Population Density

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- **What is a Periodic Travelling Wave?**
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[Diagram of a sine wave over space]
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![Mexican Wave](image_url)

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[Diagram showing a periodic travelling wave with population density varying across space]
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![Image of a crowd with aMexican Wave pattern](image-url)
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![Population Density Chart]

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[Image of a Mexican Wave]

[Graph showing population density over space]

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Detection of a Periodic Wave from Field Data

**Step 1:** At each sampling site $i$, calculate a time series of growth rates $G^i_t = \log N^i_t - \log N^i_{t-1}$

**Step 2:** Calculate the cross-correlation coefficient of the growth rates for each pair of sites

$$\rho_{i,j} = \frac{\text{cov}(G^i_t, G^j_t)}{\sqrt{\text{var}(G^i_t), \text{var}(G^j_t)}}$$
Detection of a Periodic Wave from Field Data

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$$

**Step 3:** Plot the $\rho_{i,j}$’s against “projected distance” between sites $i$ and $j$, for different directions. This gives a “Mantel correlogram” for each direction considered.
Detection of a Periodic Wave from Field Data

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Step 4: For each direction $\theta$, use the Mantel correlogram to calculate the Mantel correlation, and plot this vs $\theta$. A significant reduction in correlation in one direction suggests a travelling wave.
Detection of a Periodic Wave from Field Data

**Step 4:** For each direction $\theta$, use the Mantel correlogram to calculate the Mantel correlation, and plot this vs $\theta$. A significant reduction in correlation in one direction suggests a travelling wave.

**Step 5:** Detailed fitting of statistical models, using projected distances, gives robust parameter estimates and significance levels. This implies a wave speed of 19 km/year.
What Causes the Spatial Component of the Oscillations?

Hypothesis: the periodic travelling waves are caused by the large central reservoir
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Predator-Prey Equations

\[
\frac{\partial p}{\partial t} = D_p \nabla^2 p + \frac{akph}{1 + kh} - bp
\]

\[
\text{predators (dispersal)}
\]

\[
\text{benefit from predation}
\]

\[
\text{death}
\]

\[
\frac{\partial h}{\partial t} = D_h \nabla^2 h + rh(1 - h/h_0) - \frac{ckph}{1 + kh}
\]

\[
\text{prey (dispersal)}
\]

\[
\text{intrinsic birth & death}
\]

\[
\text{predation}
\]

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Multiannual Cycles in Field Vole Populations: Spatial Data and Spatiotemporal Models
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 Condition 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.
- Therefore we expect very high vole loss at the reservoir edge, implying a Robin boundary condition:

\[
\frac{d}{dx} \left( \text{vole density} \right) = - \left( \text{large constant} \right) \cdot \left( \text{vole density} \right)
\]
Boundary Condition at the Reservoir Edge

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\]

- To a first approximation, this boundary condition is just:

\[
\left( \begin{array}{c} \text{vole density} \\ \end{array} \right) = 0
\]
Field Vole Wave Generation Question

Question
Could the boundary condition at the reservoir edge play a role in generating the periodic travelling waves?
Typical Model Solution
Typical Model Solution
Typical Model Solution
Typical Model Solution

[Image of a typical model solution, likely a graphical representation of field vole population dynamics in Kielder Forest.]

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Multiannual Cycles in Field Vole Populations: Spatial Data and Spatiotemporal Models
Typical Model Solution

![Image of field vole population model solution]

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Typical Model Solution
Click here to play the movie
The periodic waves are driven by the reservoir. This is most easily demonstrated by simulating removal of the reservoir.
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Conclusion of Periodic Travelling Wave Study

The expected behaviour at the edge of Kielder Water provides a possible explanation for the observed periodic travelling waves.
Future Work

- Spatiotemporal dynamics of the disease model
- More realistic modelling of the Kielder Forest habitat
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Spatiotemporal Field Data

Mathematical Modelling of Periodic Travelling Waves

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   - Hypothesis I: Predation by Weasels
   - Hypothesis II: Disease Effects on Reproduction
   - Hypothesis II: Seasonal Forcing is Important
   - Hypothesis II: When are Disease-Induced Cycles Expected?

3. Spatiotemporal Field Data
   - Field Voles in Kielder Forest
   - What is a Periodic Travelling Wave?
   - Detection of a Periodic Wave from Field Data
   - What Causes the Spatial Component of the Oscillations?

4. Mathematical Modelling of Periodic Travelling Waves
   - Predator-Prey Equations
   - Boundary Condition at the Reservoir Edge
   - Typical Model Solution
   - Removing the Reservoir
   - Conclusion of Periodic Travelling Wave Study