Jonathan A. Sherratt

Department of Mathematics
Heriot-Watt University

University of Dundee, 27 January 2014

*This talk can be downloaded from my web site*

www.ma.hw.ac.uk/~jas
Voles in Fennoscandia and UK

**Fennoscandian voles**

**Kielder forest vole**

How does seasonal forcing affect vole population cycles?
Voles in Fennoscandia and UK

Fennoscandian voles

Kielder forest vole

How does seasonal forcing affect vole population cycles?
Voles in Fennoscandia and UK

Fennoscandian voles

Kielder forest vole

How does seasonal forcing affect vole population cycles?
How does seasonal forcing affect vole population cycles?
Introduction

1. How does seasonal forcing affect vole population cycles?
Voles in Fennoscandia are subject to predation by weasels.

Vole

Weasel

How does seasonal forcing affect vole population cycles?
Voles in Fennoscandia are subject to predation by weasels.

Removal of weasels $\Rightarrow$ loss of multi-year cycles

*Implication: vole cycles are caused by predation by weasels*
In Fennoscandia voles are subject to predation from weasels (a vole specialist) and also birds, badgers and foxes (generalists). Turchin & Hanski (Am. Nat. 149: 842-874, 1997) proposed the model:

\[
\frac{dp}{dt} = \underbrace{sp} - \underbrace{sp^2/h} \\
\text{birth} \quad \text{death}
\]

\[
\frac{dh}{dt} = \underbrace{rh(1 - h)} - \underbrace{ahp/(h + d)} - \underbrace{gh^2/(h^2 + \mu^2)} \\
\text{intrinsic birth & death} \quad \text{specialist predation} \quad \text{generalist predation}
\]

Jonathan A. Sherratt  
www.ma.hw.ac.uk/~jas  
How does seasonal forcing affect vole population cycles?
In Fennoscandia voles are subject to predation from weasels (a vole specialist) and also birds, badgers and foxes (generalists). Turchin & Hanski (Am. Nat. 149: 842-874, 1997) proposed the model:

\[
\begin{align*}
\frac{dp}{dt} &= sp - \frac{sp^2}{h} \\
\frac{dh}{dt} &= rh(1-h) - \frac{ahp}{h+d} - \frac{gh^2}{h^2 + \mu^2}
\end{align*}
\]

How does seasonal forcing affect vole population cycles?
A Predator-Prey Model

In Fennoscandia voles are subject to predation from weasels (a vole specialist) and also birds, badgers and foxes (generalists). Turchin & Hanski (Am. Nat. 149: 842-874, 1997) proposed the model:

\[
\begin{align*}
\frac{dp}{dt} &= sp - \frac{sp^2}{h} \\
\frac{dh}{dt} &= r h (1 - h) - \frac{ahp}{h + d} - \frac{gh^2}{h^2 + \mu^2}
\end{align*}
\]

where:
- \( p \) is the population of predators
- \( h \) is the population of prey
- \( sp \) is the intrinsic growth rate of predators
- \( sp^2/h \) is the density-dependent mortality of predators
- \( rh(1-h) \) is the intrinsic growth rate of prey
- \( ahp/(h+d) \) is the predation rate by specialists
- \( gh^2/(h^2 + \mu^2) \) is the predation rate by generalists

How does seasonal forcing affect vole population cycles?
A Predator-Prey Model

In Fennoscandia voles are subject to predation from weasels (a vole specialist) and also birds, badgers and foxes (generalists). Turchin & Hanski (Am. Nat. 149: 842-874, 1997) proposed the model:

\[
\begin{align*}
\frac{dp}{dt} &= sp - \frac{sp^2}{h} \\
\frac{dh}{dt} &= rh(1 - h) - \frac{ahp}{h + d} - \frac{gh^2}{(h^2 + \mu^2)}
\end{align*}
\]

The parameter \( g \) determines the extent of generalist predation.

How does seasonal forcing affect vole population cycles?
In Fennoscandia voles are subject to predation from weasels (a vole specialist) and also birds, badgers and foxes (generalists). Turchin & Hanski (Am. Nat. 149: 842-874, 1997) proposed the model:

\[
\frac{dp}{dt} = sp - \frac{sp^2}{h} \\
\frac{dh}{dt} = rh(1 - h) - \frac{ahp}{h + d} - \frac{gh^2}{h^2 + \mu^2}
\]

**Predators**

Birth and death

**Prey**

Intrinsic birth and death, specialist predation, generalist predation

How does seasonal forcing affect vole population cycles?
A Predator-Prey Model

In Fennoscandia voles are subject to predation from weasels (a vole specialist) and also birds, badgers and foxes (generalists). Turchin & Hanski (Am. Nat. 149: 842-874, 1997) proposed the model:

\[
\frac{dp}{dt} = sp - \frac{sp^2}{h}, \\
\frac{dh}{dt} = rh(1 - h) - \frac{ahp}{h + d} - \frac{gh^2}{h^2 + \mu^2}
\]

How does seasonal forcing affect vole population cycles?
Population Dynamics in Northern and Southern Fennoscandia

North
Few generalist predators
Multi-year vole cycles

South
Many generalist predators
No multi-year vole cycles

Jonathan A. Sherratt
www.ma.hw.ac.uk/~jas

How does seasonal forcing affect vole population cycles?
Traditional explanation for Fennoscandian gradient: specialist predators (weasels) cause multi-year vole cycles when there are few generalist predators.
BUT: in Central Europe there is an opposing geographical gradient
A Gradient of Seasonality

Traditional explanation for Fennoscandian gradient: specialist predators (weasels) cause multi-year vole cycles when there are few generalist predators.

Question: can the inclusion of seasonality reconcile the Fennoscandian and Central European data sets? Note that the breeding season varies between 3 and 8 months across Fennoscandia.
A Model with Seasonal Forcing

\[
\frac{dp}{dt} = \frac{F(t)sp - sp^2/h}{\text{birth death}}
\]

\[
\frac{dh}{dt} = \frac{F(t)rh(1 - h) - ahp/(h + d) - h^2/(h^2 + \mu^2)}{\text{intrinsic birth & death specialist predation generalist predation}}
\]
A Model with Seasonal Forcing

\[
\frac{dp}{dt} = F(t)sp - \frac{sp^2}{h} \\
\text{birth} \quad \text{death}
\]

\[
\frac{dh}{dt} = F(t)rh(1 - h) - \frac{ahp}{(h + d)} - \frac{h^2}{(h^2 + \mu^2)} \\
\text{intrinsic birth & death} \quad \text{specialist predation} \quad \text{generalist predation}
\]

\[
F(t) = 2 \left[ \frac{1}{2} (1 + 0.95 \sin(2\pi t)) \right]^l
\]

How does seasonal forcing affect vole population cycles?
How does seasonal forcing affect vole population cycles?

\[ F(t) = 2 \left[ \frac{1}{2} (1 + 0.95 \sin(2\pi t)) \right]' \]
A Model with Seasonal Forcing

Smaller $l \leftrightarrow$ longer breeding season

We will consider the population dynamics predicted by the model as a function of $g$ and $l$. 

Jonathan A. Sherratt  
www.ma.hw.ac.uk/~jas

How does seasonal forcing affect vole population cycles?
To study dynamics with seasonal forcing, fix a census date and consider population densities on that date in successive years.
To study dynamics with seasonal forcing, fix a census date and consider population densities on that date in successive years.

- **ANNUAL CYCLES**
  - Expected when unforced cycle has low amplitude

- **QUASI–PERIODIC CYCLES**
  - Expected when unforced cycle has high amplitude

How does seasonal forcing affect vole population cycles?
To study dynamics with seasonal forcing, fix a census date and consider population densities on that date in successive years.

**Annual Cycles**
Expected when unforced cycle has low amplitude

**Quasi-Periodic Cycles**
Expected when unforced cycle has high amplitude

How does seasonal forcing affect vole population cycles?
Seasonal Forcing: Poincaré Map

To study dynamics with seasonal forcing, fix a census date and consider population densities on that date in successive years.

It is possible to track the location of the Neimark-Sacker bifurcation in the $l$–$g$ plane.
To study dynamics with seasonal forcing, fix a census date and consider population densities on that date in successive years.

It is possible to track the location of the Neimark-Sacker bifurcation in the $l-g$ plane.
Setting \( I = 0 \) gives an unforced system (always breeding season). When this has a limit cycle with a rational period (in number of years), there is resonance. These points are the cusps of “Arnold tongues”, in which there are multi-year cycles.
Setting $I = 0$ gives an unforced system (always breeding season). When this has a limit cycle with a rational period (in number of years), there is resonance. These points are the cusps of “Arnold tongues”, in which there are multi-year cycles.
A further complication is that the annual cycles can undergo period doubling as the forcing is increased.
A further complication is that the annual cycles can undergo period doubling as the forcing is increased.

---

**How does seasonal forcing affect vole population cycles?**
Bifurcation and Simulation Diagrams

Combining these and other similar curves gives a complete bifurcation diagram.

How does seasonal forcing affect vole population cycles?
Bifurcation and Simulation Diagrams

Combining these and other similar curves gives a complete bifurcation diagram.

The bifurcation diagram gives information about the possible solutions, but not their frequency. For this we use simulations.
How does seasonal forcing affect vole population cycles?
Vole cycles in Fennoscandia are driven by predation by weasels.

The differences between North and South Fennoscandia involve a complex interplay between gradients in generalist predation and breeding season length.
A gradient in breeding season length but not in generalist predators would explain the Central European data.
How does seasonal forcing affect vole population cycles?
How does seasonal forcing affect vole population cycles?
How does seasonal forcing affect vole population cycles?
Implication: vole cycles are not caused by predation

Possible alternative cause: vole–grass interaction
Implication: vole cycles are not caused by predation

Possible alternative cause: vole–grass interaction

Food quantity is not (usually) a consideration, but cycles could be caused by changes in food quality
How does seasonal forcing affect vole population cycles?
Grass Can Bite Back

Deschampsia caespitosa

After grazing, grass regrows with higher levels of silica
Grass Can Bite Back

After grazing, grass regrows with higher levels of silica

*Deschampsia caespitosa*

Silica affects vole growth rate
Silica Induction: Greenhouse Experiment

Damage (induction) – 6 months
Relaxation – 7 months

How does seasonal forcing affect vole population cycles?
How does seasonal forcing affect vole population cycles?
Data on Vole Response to Silica

Captive voles fed high-silica grasses showed reduced growth

- Grasses grown in greenhouse in low and high silica soils
- No-choice feeding experiment

Massey et al. 2007, Biology Letters
Juvenile voles also grew poorly on high-silica grasses

Silica prevents voles from breaking plant cell walls and absorbing nitrogen

Silica Induction Hypothesis

Silica induction hypothesis

- Increased reproductive output
- Increased growth rates
- Reduced silica levels in grass
- Reduced grazing pressure & defence relaxation
- Low vole population density
- Reduced vole growth rates

- Increased grazing pressure & defence induction
- Elevated silica levels in grass
- High vole population density

Jonathan A. Sherratt  
www.ma.hw.ac.uk/~jas

How does seasonal forcing affect vole population cycles?
Introduction

Vole Cycles in Fennoscandia: Predation

Vole Cycles in UK: Killer Grass

Modelling the Vole-Grass Interaction

Summary and Conclusions

Stage 1: Modelling the Greenhouse Experiment

Stage 2: Including Vole Dynamics

Seasonal Forcing in Kielder Forest, UK

A Model including Seasonal Forcing

Comparison of Different Effects of Silica

Outline

1. Introduction

2. Vole Cycles in Fennoscandia: Predation

3. Vole Cycles in UK: Killer Grass

4. Modelling the Vole-Grass Interaction

5. Summary and Conclusions

How does seasonal forcing affect vole population cycles?
Stage 1: Modelling the Greenhouse Experiment

\[ S(t) = \text{silica concentration in grass} \]

\[ \frac{dS}{dt} = -c \cdot (S(t) - S_{\text{control}}) + P(t - T) \]

How does seasonal forcing affect vole population cycles?
Stage 1: Modelling the Greenhouse Experiment

$S(t) =$ silica concentration in grass

$$\frac{dS}{dt} = -c \cdot (S(t) - S_{control}) + P(t - T)$$

We estimate $c$, $T$, $S_{control}$, $P_{low}$ and $P_{high}$ using the data from the greenhouse experiment.
Stage 2: Including Vole Dynamics

$V(t) =$ vole density

Silica production: $P(t) = K V(t)^n / \left[ V_0^n + V(t)^n \right]$
Stage 2: Including Vole Dynamics

$V(t) =$ vole density

Silica production: $P(t) = K V(t)^n / \left[ V_0^n + V(t)^n \right]$

Vole birth/death: $\frac{dV}{dt} = F(S(t)) V(t) - \delta V(t)$

- Birth
- Death

How does seasonal forcing affect vole population cycles?
Stage 2: Including Vole Dynamics

\[ V(t) = \text{vole density} \]

Silica production:  
\[ P(t) = K V(t)^n / \left[ V_0^n + V(t)^n \right] \]

Vole birth/death: \[ \frac{dV}{dt} = F(S(t)) V(t) - \delta V(t) \]

\[ \text{birth} \quad \text{death} \]

\[ B_{\text{min}} \quad B_{\text{max}} \]

\[ B_{\text{min}} \] and \[ B_{\text{max}} \] are estimated using data from experiments on caged voles.

How does seasonal forcing affect vole population cycles?
Model Solution

How does seasonal forcing affect vole population cycles?
The model predicts population cycles, but only for unrealistically high values of vole birth rate, and the period of the cycles is too short.
The model predicts population cycles, but only for unrealistically high values of vole birth rate, and the period of the cycles is too short.

**Remedy:** include seasonal forcing
Voles in Kielder Forest have a well-defined breeding season.

The breeding season length is variable, mainly due to a variable start.

We assume that the start date depends on the silica level in grass in the early part of the year.
How does seasonal forcing affect vole population cycles?
How does seasonal forcing affect vole population cycles?

$L_{\text{min}}$ and $L_{\text{max}}$ are estimated using field data from Kielder Forest.
A Model including Seasonal Forcing

\[
dS/dt = KV(t)^n / \left[ V_0^n + V(t)^n \right] - c \cdot (S(t) - S_{\text{control}})
\]

Non-seasonal model: \( dV/dt = F(S(t)) V(t) - \delta V(t) \)

Seasonal model:

\[
dV/dt = \begin{cases} B_{\text{max}} V(t) - \delta V(t) & \text{in breeding season} \\ -\delta V(t) & \text{otherwise} \end{cases}
\]

\( L_{\text{min}} \) and \( L_{\text{max}} \) are estimated using field data from Kielder Forest

Jonathan A. Sherratt  
www.ma.hw.ac.uk/~jas

How does seasonal forcing affect vole population cycles?
The model now predicts realistic population cycles for appropriate parameter values.
Comparison of Different Effects of Silica

- Non-seasonal model: silica affects vole birth rate
- Seasonal model: silica affects breeding season length
- In reality silica has both of these effects
- Which is the most important?
Comparison of Different Effects of Silica

- Non-seasonal model: silica affects vole birth rate
- Seasonal model: silica affects breeding season length
- In reality silica has both of these effects
- Which is the most important?

To study this we set up a model with both dependences, with parameters $p_{\text{length}}$ and $p_{\text{birth}}$ between 0 and 1:

- $p_{\text{length}} = 0$: breeding season length fixed
- $p_{\text{length}} = 1$: breeding season length highly variable
- $p_{\text{birth}} = 0$: birth rate fixed
- $p_{\text{birth}} = 1$: birth rate highly variable
Comparison of Different Effects of Silica

\[ B_{\text{min}} = (1 - p_{\text{birth}})B_{\text{max}} \]
\[ L_{\text{min}} = (1 - p_{\text{length}})L_{\text{max}} \]

To study this we set up a model with both dependences, with parameters \( p_{\text{length}} \) and \( p_{\text{birth}} \) between 0 and 1:

- \( p_{\text{length}} = 0 \): breeding season length fixed
- \( p_{\text{length}} = 1 \): breeding season length highly variable
- \( p_{\text{birth}} = 0 \): birth rate fixed
- \( p_{\text{birth}} = 1 \): birth rate highly variable
Comparison of Different Effects of Silica

Variability of birth rate within the breeding season

Variability of breeding season length

How does seasonal forcing affect vole population cycles?
How does seasonal forcing affect vole population cycles?
Conclusions

- Vole cycles in Fennoscandia are driven by predation.
- Seasonal forcing is a key ingredient of the cyclic dynamics.
- The vole-grass interaction has the potential to generate population cycles.
- The effect of silica on breeding season length is more important than its effect on birth rate.
- This is a plausible mechanism for the population cycles observed in Kielder Forest, UK: field tests are ongoing.

Jonathan A. Sherratt

www.ma.hw.ac.uk/~jas

How does seasonal forcing affect vole population cycles?
Ongoing Field Tests: Vole Enclosures

- 81 4m×4m cells
- Add 0, 1, 2, 4, 6 or 8 voles per cell, for 3 days each month
- Monitor silica levels
Collaborators

This work is in collaboration with:

**Heriot-Watt University:**
Jennifer Reynolds, Rachel Taylor, Andy White

**University of Aberdeen:**
Xavier Lambin, Jane Degabriel, Fergus Massey

**University of York:**
Sue Hartley, Stefan Reidinger

**Microsoft Research, Cambridge:**
Matthew Smith


How does seasonal forcing affect vole population cycles?