How Does Seasonal Forcing Affect Vole Population Cycles?

Jonathan A. Sherratt

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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

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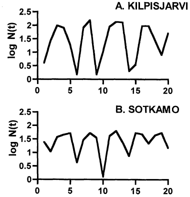
Fennoscandian voles



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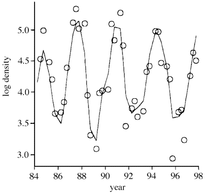

Outline

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Predation by Weasels

Voles in Fennoscandia are subject to predation by weasels.

Vole

Weasel

Predation by Weasels

Voles in Fennoscandia are subject to predation by weasels.

Vole

Weasel

Removal of weasels ⇒ loss of multi-year cycles

Implication: vole cycles are caused by predation by weasels

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:

predators

$$dp/dt = \underbrace{sp}_{\text{birth}} - \underbrace{sp^2/h}_{\text{death}}$$

prey

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

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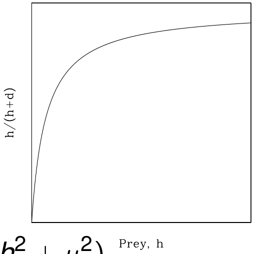

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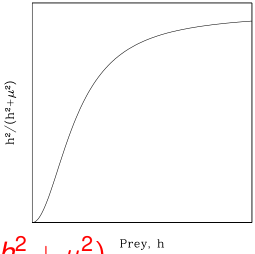

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The parameter g

determines the extent of generalist predation

prey

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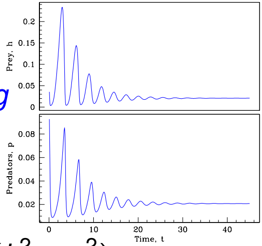
Large g



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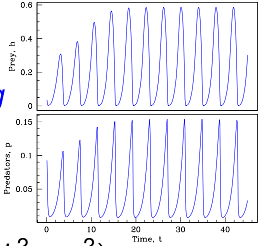

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Population Dynamics in Northern and Southern Fennoscandia

North
Few generalist predators
Multi-year vole cycles

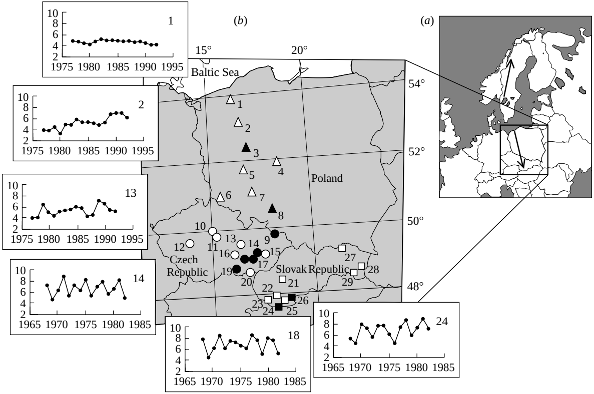
South
Many generalist predators
No multi-year vole cycles

Traditional Explanation for Fennoscandian Gradient

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

Vole Cycles in Central Europe

BUT: in Central Europe there is an opposing geographical gradient (E. Tkadlec & N.C. Stenseth, Proc. R. Soc. Lond. B 268: 1547-1552, 2001)



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

$$dp/dt = \underbrace{F(t)sp}_{\text{birth}} - \underbrace{sp^2/h}_{\text{death}}$$

$$dh/dt = \underbrace{F(t)rh(1-h)}_{\substack{\text{intrinsic} \\ \text{birth \& death}}} - \underbrace{ahp/(h+d)}_{\substack{\text{specialist} \\ \text{predation}}} - \underbrace{h^2/(h^2+\mu^2)}_{\substack{\text{generalist} \\ \text{predation}}}$$

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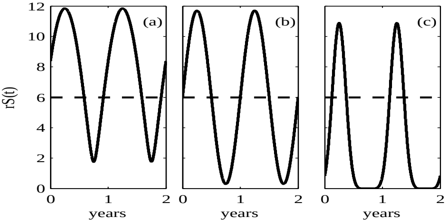
$$F(t) = 2\left[\frac{1}{2}(1+0.95\sin(2\pi t))\right]^{l}$$

A Model with Seasonal Forcing

Smaller $l \leftrightarrow$ longer breeding season



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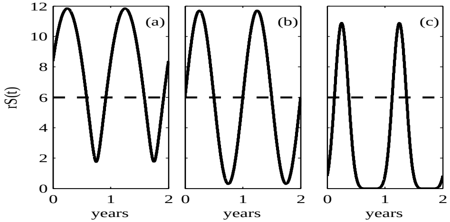
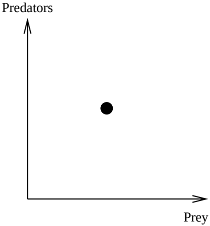


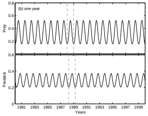
We will consider the population dynamics predicted by the model as a function of g and l.

Seasonal Forcing: Poincaré Map

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



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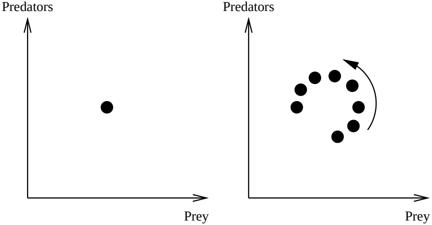

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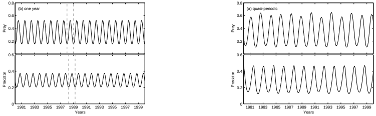

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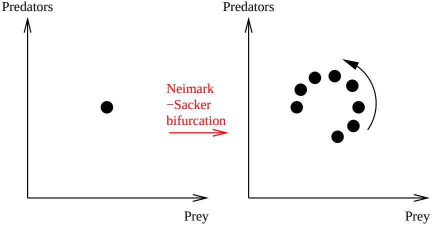

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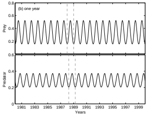

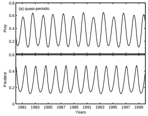

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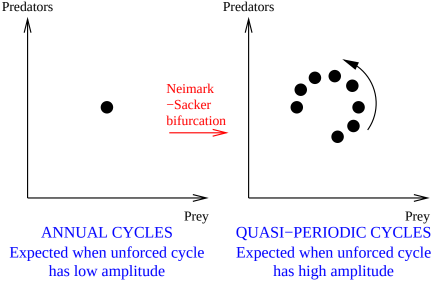

It is possible to track the location of the Neimark-Sacker bifurcation in the l–g plane.

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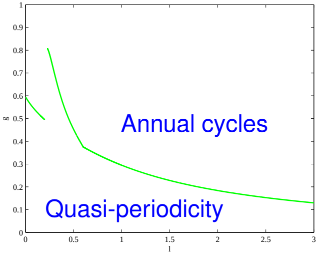
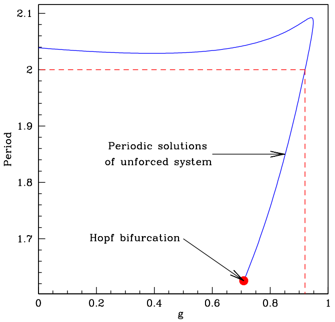


Rachel Taylor

It is possible to track the location of the Neimark-Sacker bifurcation in the *l*–*g* plane.

Resonance and Arnold Tongues

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.



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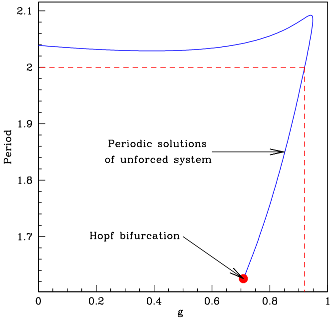
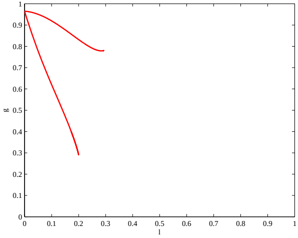
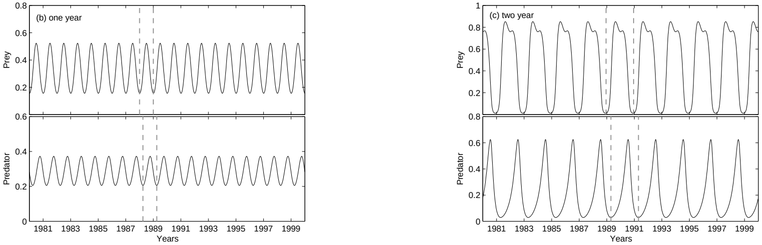




Period Doubling

A further complication is that the annual cycles can undergo period doubling as the forcing is increased.



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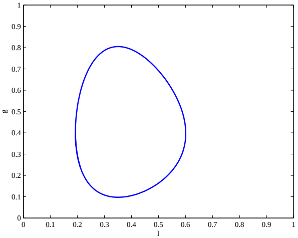
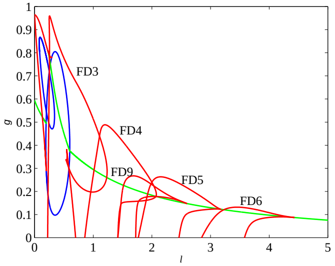
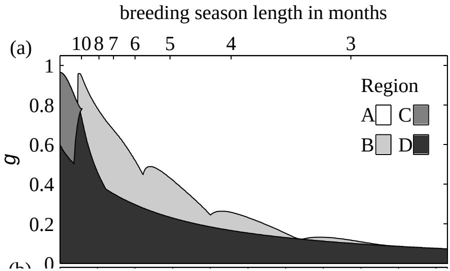


Bifurcation and Simulation Diagrams

Combining these and other similar curves gives a complete bifurcation diagram





A: annual cycles
B: annual and multi-year cycles
C: annual, multi-year and quasi-periodic cycles
D: multi-year and quasi-periodic cycles

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The bifurcation diagram gives information about the possible solutions, but not their frequency. For this we use simulations.

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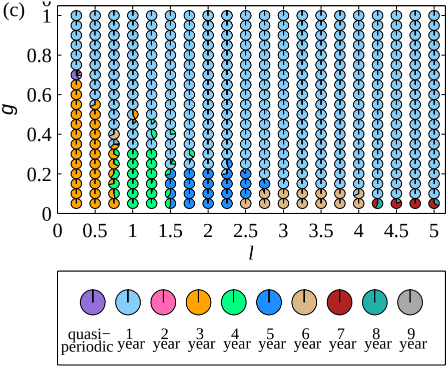
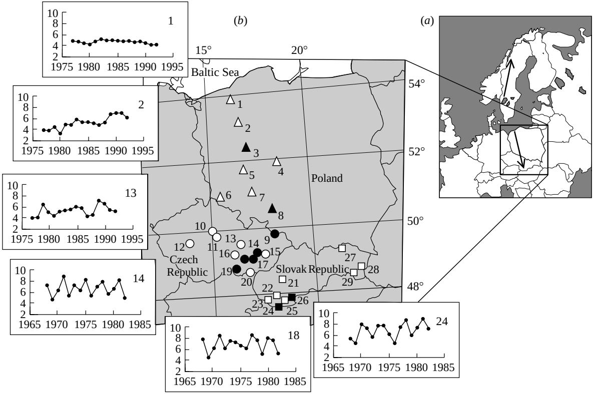


Conclusions So Far

- 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.

Vole Cycles in Central Europe

A gradient in breeding season length but not in generalist predators would explain the Central European data.



Outline

Predator Exclusion Experiments in UK

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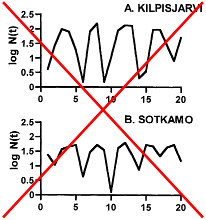

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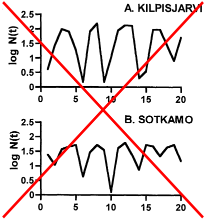

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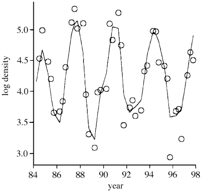

Predator Exclusion Experiments in UK

Implication: vole cycles are not caused by predation

Possible alternative cause: vole–grass interaction

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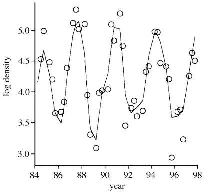

Predator Exclusion Experiments in UK

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Possible alternative cause: vole–grass interaction

Food quantity is not (usually) a consideration, but cycles could be caused by changes in food quality

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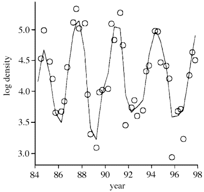

NERC Consortium Grant

Vole ecologists (Univ Aberdeen)

Xavier Lambin

Jane Degabriel

Plant ecologists (Univ York)

Sue Hartley

Stefan Reidinger

Mathematical biologists (Heriot-Watt U)

Jonathan Sherratt

Andy White

Jennifer Reynolds

Grass Can Bite Back

Deschampsia caespitosa

After grazing, grass regrows with higher levels of silica

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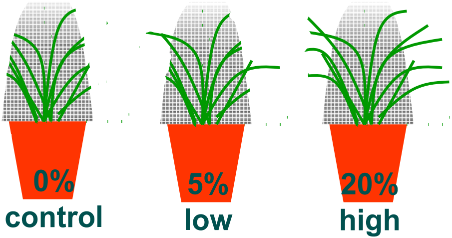
Silica affects vole growth rate

Silica Induction: Greenhouse Experiment

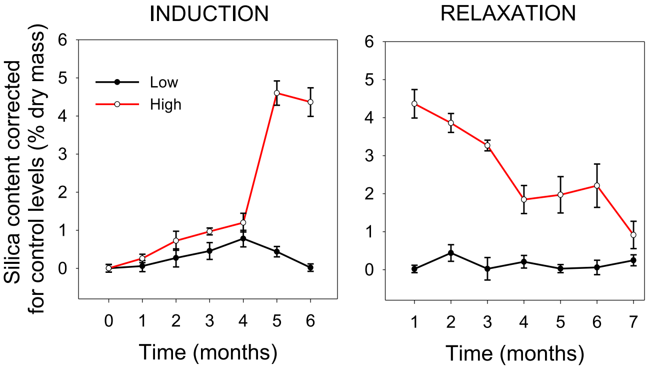


Every 4weeks

Damage (induction) – 6 months

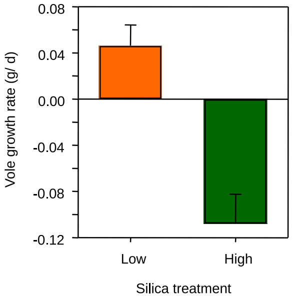
Relaxation – 7 months

Silica Induction: Greenhouse Experiment



Data on Vole Response to Silica

Captive voles fed high-silica grasses showed reduced growth

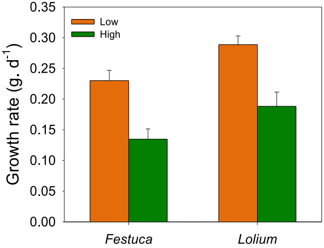


Massey *et al.* 2007, *Biology Letters*

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

Data on Vole Response to Silica

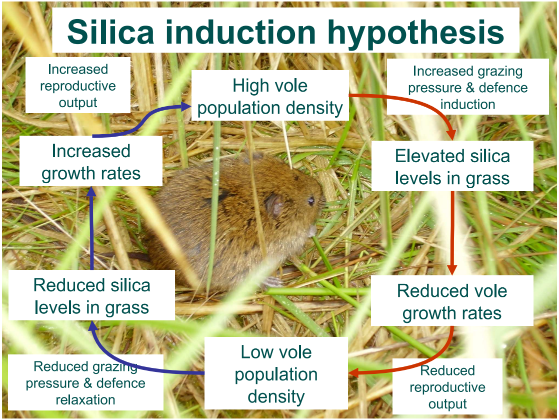
Juvenile voles also grew poorly on high-silica grasses



Massey & Hartley 2006, *Proc. Roy. Soc. B*

Silica prevents voles from breaking plant cell walls and absorbing nitrogen

Silica Induction Hypothesis

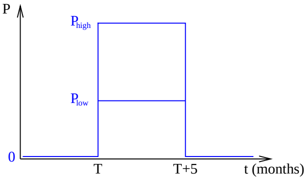


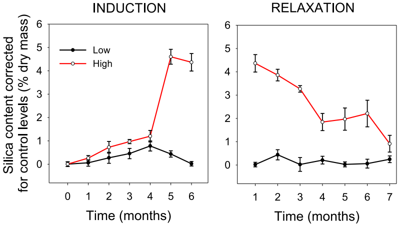
Outline

Stage 1: Modelling the Greenhouse Experiment

$S(t)$=silica concentration in grass

$$\begin{aligned} dS/dt &= -c\cdot(S(t)-S_{\text{control}}) \\ &\quad +P(t-T) \end{aligned}$$





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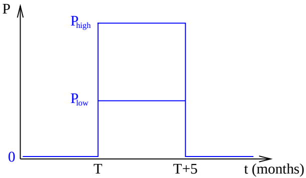
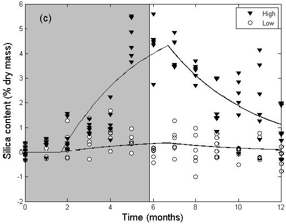


We estimate c, T, $S_{control}$, P_{low} and P_{high} using the data from the greenhouse experiment



Stage 2: Including Vole Dynamics

$V(t)$=vole density

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

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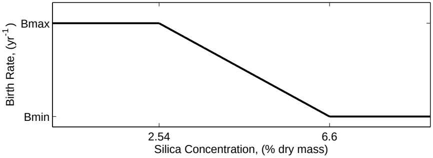

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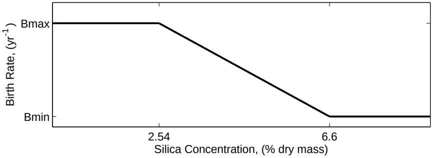
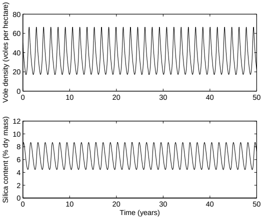
Vole birth/death: $dV/dt = \underbrace{F(S(t))V(t)}_{\text{birth}} - \underbrace{\delta V(t)}_{\text{death}}$

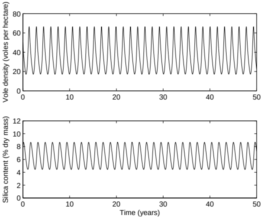


B_{min} and B_{max} are estimated using data from experiments on caged voles

Model Solution

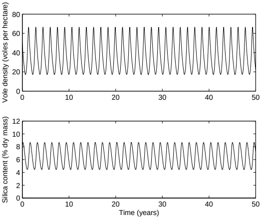


Model Solution



The model predicts population cycles, but only for unrealistically high values of vole birth rate, and the period of the cycles is too short.

Model Solution

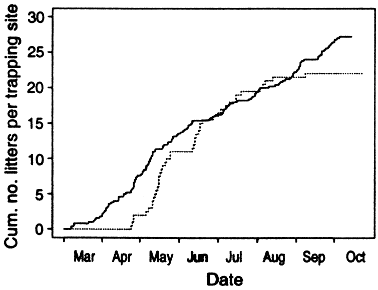


The model predicts population cycles, but only for unrealistically high values of vole birth rate, and the period of the cycles is too short.

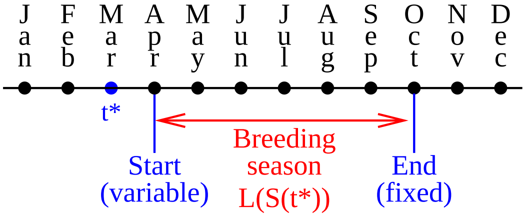
Remedy: include seasonal forcing

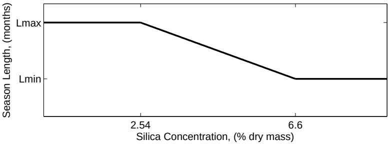
Seasonal Forcing in Kielder Forest, UK

- 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

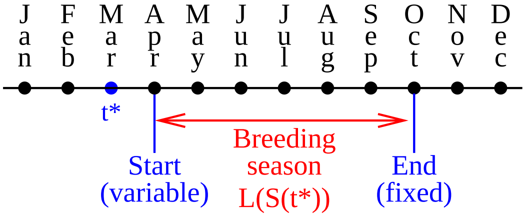


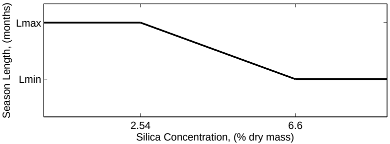
A Model including Seasonal Forcing





A Model including Seasonal Forcing





L_{min} and L_{max} are estimated using field data from Kielder Forest

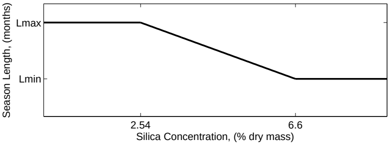
A Model including Seasonal Forcing

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

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

Seasonal model:

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



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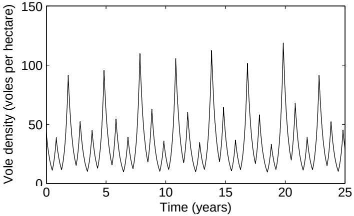
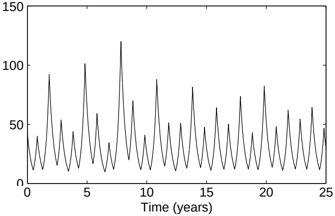
A Model including Seasonal Forcing





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

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- 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_{length} and p_{birth} between 0 and 1:

$p_{length} = 0$: breeding season length fixed
$p_{length} = 1$: breeding season length highly variable

$p_{birth} = 0$: birth rate fixed
$p_{birth} = 1$: birth rate highly variable

Comparison of Different Effects of Silica

$$\begin{aligned} B_{min} &= (1 - p_{birth})B_{max} \\ L_{min} &= (1 - p_{length})L_{max} \end{aligned}$$

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$p_{length} = 1$: breeding season length highly variable

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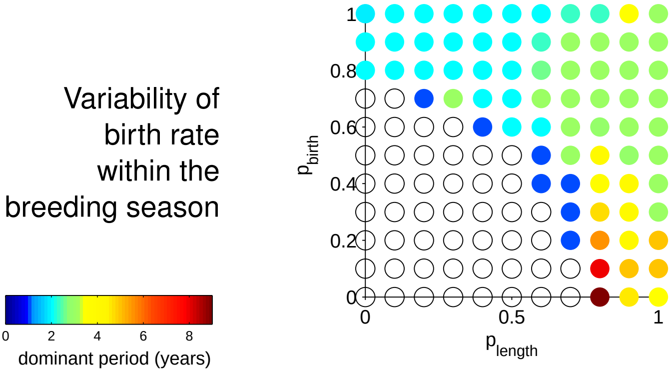
Comparison of Different Effects of Silica

Variability of birth rate within the breeding season



Variability of breeding season length

Outline

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

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

University of York:
Sue Hartley, Stefan Reidinger

Microsoft Research, Cambridge:
Matthew Smith

References

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