Population Cycles in Voles: Predators, Seasonality and Killer Grass

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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

田鼠=VOLE

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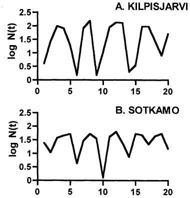
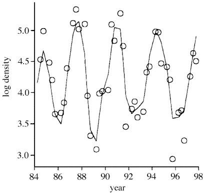
Voles in Fennoscandia and UK

Fennoscandian voles



Kielder forest vole



Outline

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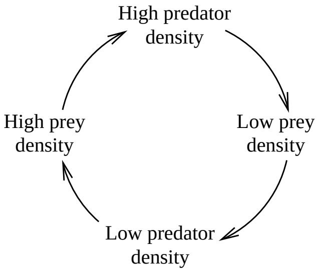
Cycles in Predator-Prey Models

Population cycles in predator-prey systems is a long-standing prediction from mathematical models.



Predation by Weasels

Voles in Fennoscandia are subject to predation by weasels.

Vole

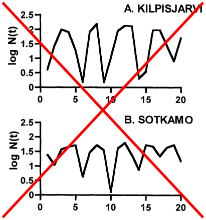
Weasel

田鼠=VOLE

鼬屬（黃鼠狼）=WEASEL

Predator Exclusion Experiments in Fennoscandia

$\Rightarrow$



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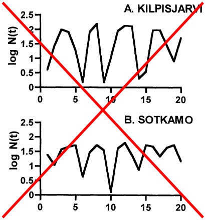
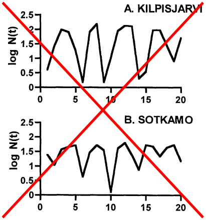


Implication: vole cycles are caused by predation

Outline

Predator Exclusion Experiments in UK

$\Rightarrow$



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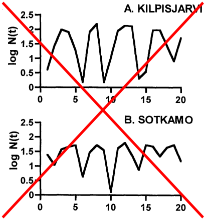

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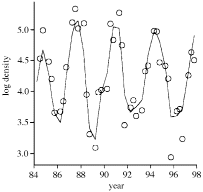
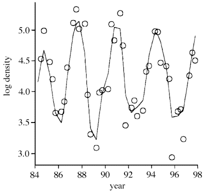


Predator Exclusion Experiments in UK

Implication: vole cycles are not caused by predation

Possible alternative cause: vole–grass interaction 草=GRASS

⇒



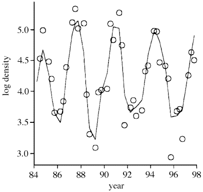
Predator Exclusion Experiments in UK

Implication: vole cycles are not caused by predation

Possible alternative cause: vole–grass interaction 草=GRASS

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

$\Rightarrow$



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

二氧化硅=silica

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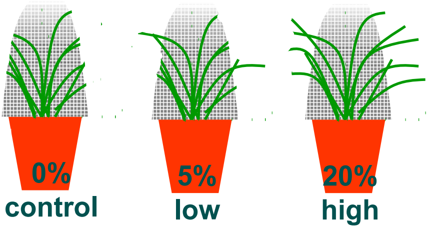
Silica affects vole growth rate

Silica Induction: Greenhouse Experiment



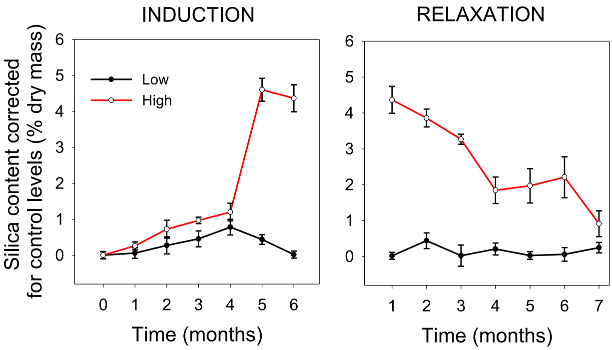
Every 4weeks

Damage (induction) – 6 months

Relaxation – 7 months

温室 = greenhouse

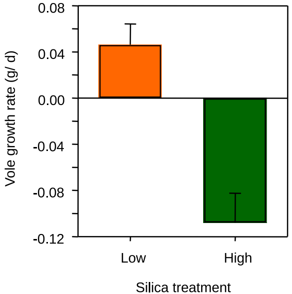
Silica Induction: Greenhouse Experiment



温室 = greenhouse

Data on Vole Response to Silica

Captive voles fed high-silica grasses showed reduced growth

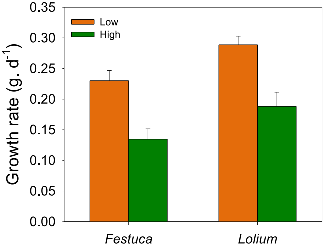


Massey *et al.* 2007, *Biology Letters*

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

Data on Vole Response to Silica

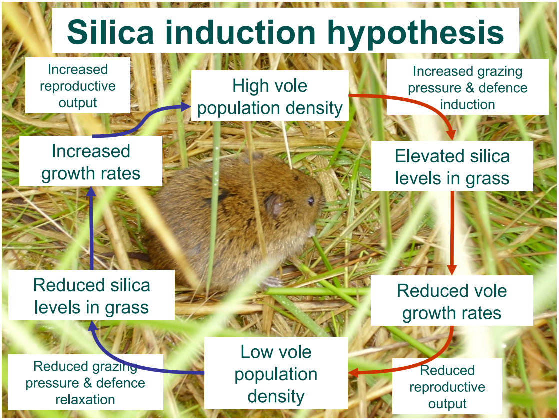
Juvenile voles also grew poorly on high-silica grasses



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

Silica prevents voles from breaking plant cell walls and absorbing nitrogen

Silica Induction Hypothesis

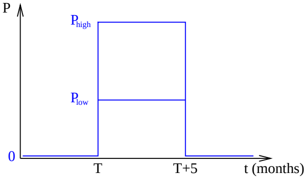


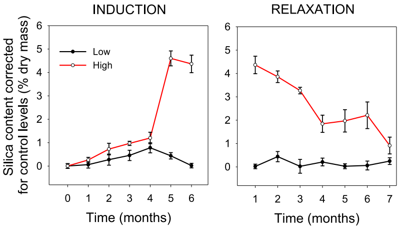
Outline

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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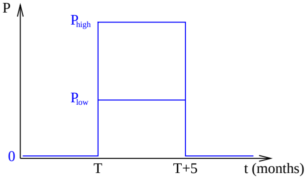
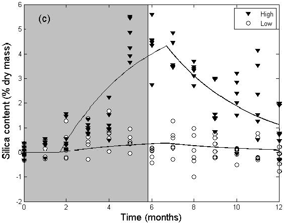


We estimate c, T, $S_{control}$, P_{low} and P_{high} using the data from the greenhouse experiment



Stage 2: Including Vole Dynamics

$V(t)$=vole density

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

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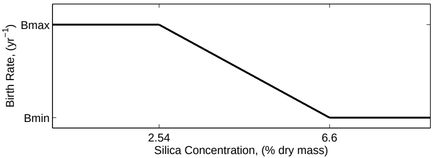

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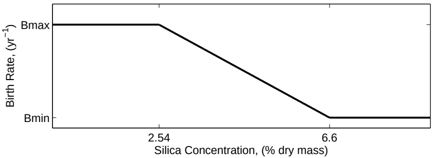
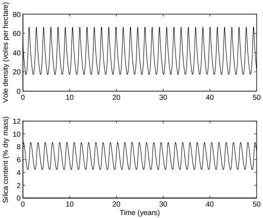


B_{min} and B_{max} are estimated using data from experiments on caged voles

Model Solution



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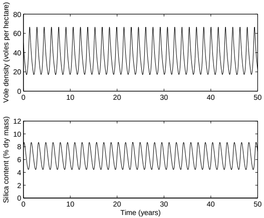
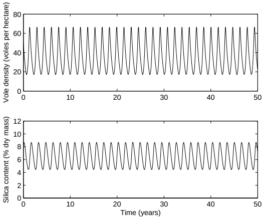


The model predicts population cycles, but only for unrealistically high values of vole birth rate, and the period of the cycles is too short.

Model Solution



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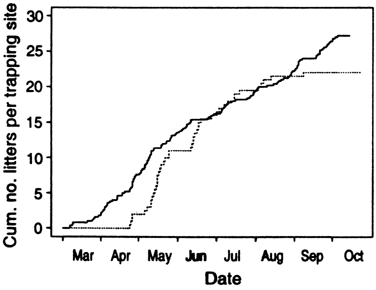
Remedy: include seasonal forcing

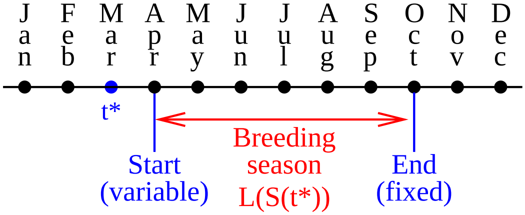
Outline

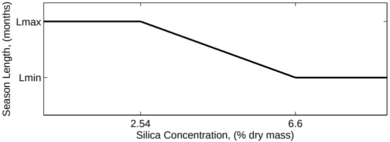
Seasonal Forcing in Kielder Forest, UK

- 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





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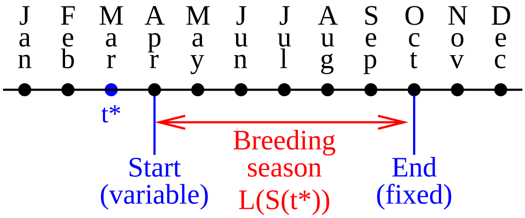
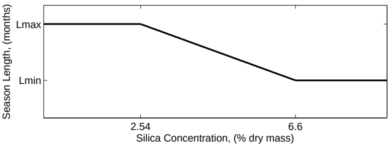




L_{min} and L_{max} are estimated using field data from Kielder Forest

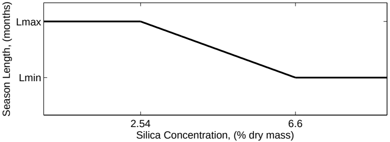
A Model including Seasonal Forcing

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

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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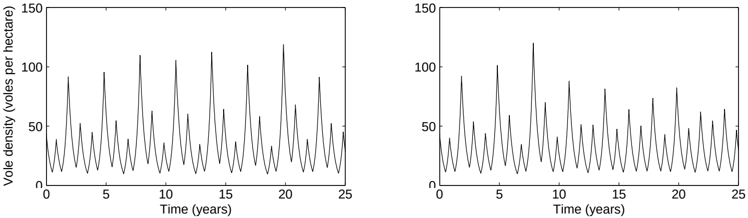
A Model including Seasonal Forcing



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?

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- 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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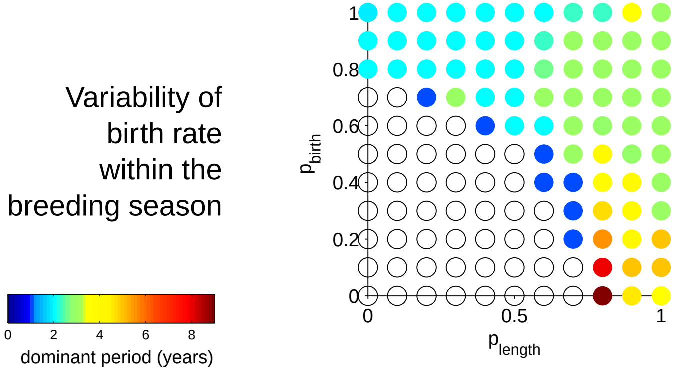
Comparison of Different Effects of Silica

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$\times$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, Andy White

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

University of York:
Sue Hartley, Stefan Reidinger

Microsoft Research, Cambridge:
Matthew Smith

References

J.J.H. Reynolds, F.P. Massey, X. Lambin, S. Reidinger, J.A. Sherratt, M.J. Smith, A. White, S.E. Hartley: Delayed induced silica defences in grasses and their potential for destabilising herbivore population dynamics. Oecologia, in press.

J.J.H. Reynolds, J.A. Sherratt, A. White, X. Lambin: A comparison of the dynamical impact of seasonal mechanisms in a herbivore-plant defence system. Submitted.

List of Frames