

# Spatiotemporal Dynamics in Ecology: Insights from Physics

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*This talk can be downloaded from my web site*

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

## Voles



## Voles



## Climate change



## Voles



## Climate change



**ABSOLUTE  
STABILITY**

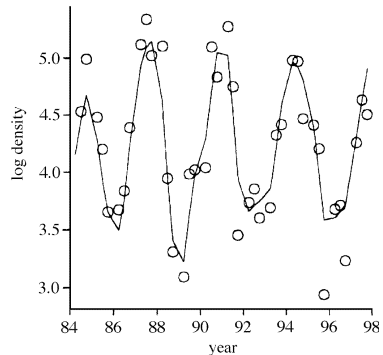
# Outline

- 1 Spatiotemporal Dynamics of Voles
- 2 Stable and Unstable Plane Waves
- 3 Calculating the Width of the Plane Wave Band
- 4 Band Width Sensitivity and Ecological Implications

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# Vole Population Cycles



Voles

*Clethrionomys glareolus*

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Voles

*Clethrionomys glareolus*



Fennoscandia



# Vole Population Cycles



Voles

*Clethrionomys glareolus*



Weasel

*Mustela nivalis*

# Cyclic Predator-Prey Systems

The interaction between a predator population and its prey can cause population cycles.

This has been modelled extensively using systems of two coupled ODEs.

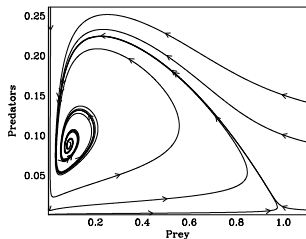
$$\boxed{\text{predators}} \quad \frac{dp}{dt} = \underbrace{akph/(1+kh)}_{\text{benefit from predation}} - \underbrace{bp}_{\text{death}}$$

$$\boxed{\text{prey}} \quad \frac{dh}{dt} = \underbrace{rh(1-h/h_0)}_{\text{intrinsic birth \& death}} - \underbrace{ckph/(1+kh)}_{\text{predation}}$$

# Cyclic Predator-Prey Systems

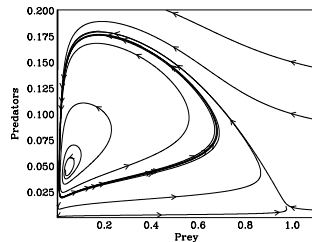
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This has been modelled extensively using systems of two coupled ODEs.



constant coexistence

change  
→  
parameters



cycles

# Spatiotemporal Data



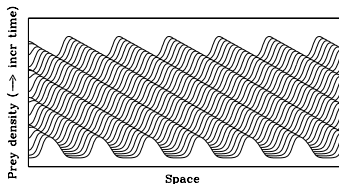
Field data from different sites  
⇒ vole cycles are not  
spatially homogeneous.

Rather they are organised into a  
plane wave.

Voles

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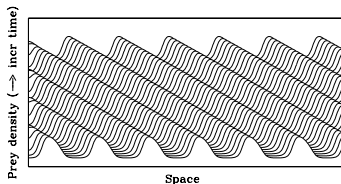
# Spatiotemporal Data



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⇒ vole cycles are not  
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Rather they are organised into a  
plane wave.

# Spatiotemporal Data



**Plane wave:** periodic as a function of space (1-D) and time.

**Mathematically:** a solution of the form  $f(x \pm ct)$ , with the function  $f(\cdot)$  periodic.

**Terminology:** the terms  
*plane wave,*  
*wavetrain,*  
*periodic travelling wave*  
 are equivalent.

# Modelling Predator-Prey Invasion

To study spatiotemporal dynamics, we add diffusion terms to represent local dispersal.

predators

$$\frac{\partial p}{\partial t} = \underbrace{D_p \frac{\partial^2 p}{\partial x^2}}_{\text{dispersal}} + \underbrace{akph/(1 + kh)}_{\text{benefit from predation}} - \underbrace{bp}_{\text{death}}$$

prey

$$\frac{\partial h}{\partial t} = \underbrace{D_h \frac{\partial^2 h}{\partial x^2}}_{\text{dispersal}} + \underbrace{rh(1 - h/h_0)}_{\text{intrinsic birth \& death}} - \underbrace{ckph/(1 + kh)}_{\text{predation}}$$

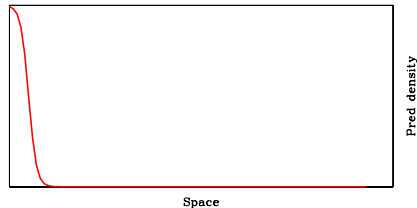
# Modelling Predator-Prey Invasion

To study spatiotemporal dynamics, we add diffusion terms to represent local dispersal.

The most natural initial conditions correspond to invasion.



Initially we set the prey to the prey-only equilibrium throughout the domain.



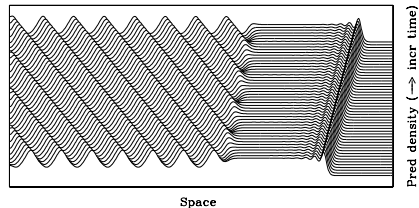
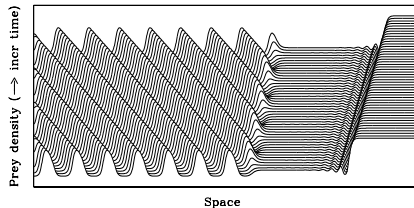
Initially we set the predators to zero except near the left hand boundary.



# Modelling Predator-Prey Invasion

To study spatiotemporal dynamics, we add diffusion terms to represent local dispersal.

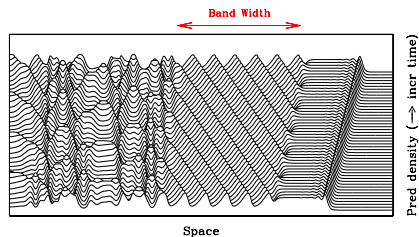
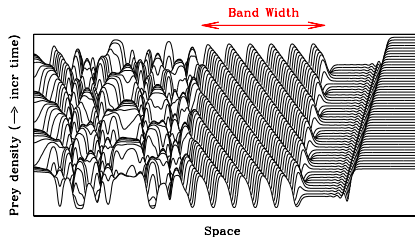
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# Modelling Predator-Prey Invasion

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# Outline

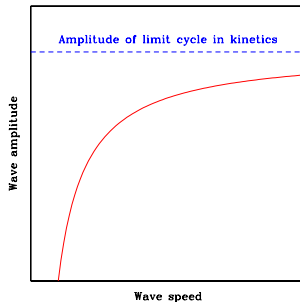
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- 2 **Stable and Unstable Plane Waves**
- 3 Calculating the Width of the Plane Wave Band
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# Plane Wave Stability

An oscillatory reaction-diffusion system has a one-parameter family of plane wave solutions

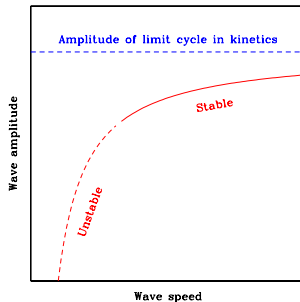
(if the diffusion coefficients are sufficiently close to one another)

(Kopell, Howard (1973) *Stud Appl Math* 52:291)



# Plane Wave Stability

Some members of the plane wave family are stable as solutions of the partial differential equations, while others are unstable.



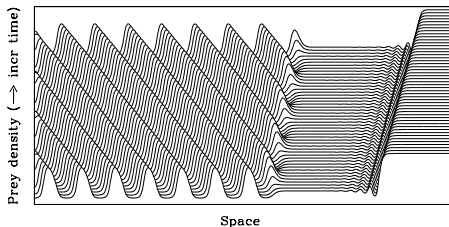
# Plane Wave Stability

The invasion process selects a particular member of the plane wave family (Sherratt (1998) *Physica D* 117:145).

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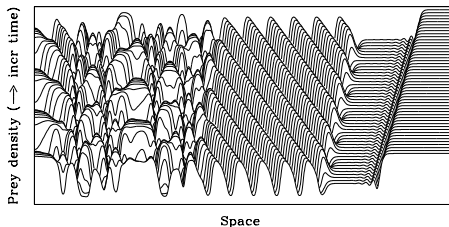
For these parameters,  
the selected plane  
wave is stable.



# Plane Wave Stability

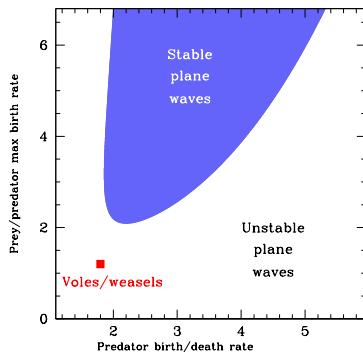
The invasion process selects a particular member of the plane wave family (Sherratt (1998) *Physica D* 117:145).

A “plane wave band” occurs when the selected plane wave is unstable.



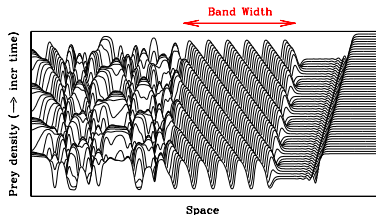


# Back to Voles and Weasels



For vole–weasel parameters, the selected plane wave is **unstable**.

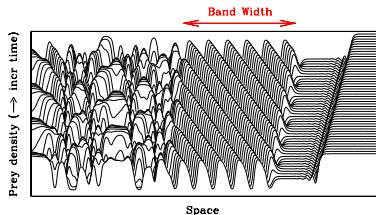
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**Conclusion:** we expect to observe plane waves of field voles only if the band width is large compared to the domain length.

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**Conclusion:** we expect to observe plane waves of field voles only if the band width is large compared to the domain length.

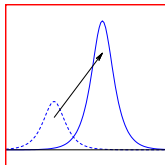
**Question:** how can we calculate the band width?

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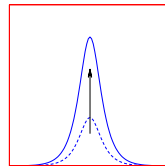
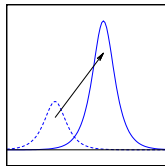
# Convective and Absolute Stability

- In spatially extended systems, a solution can be unstable, but with any perturbation that grows also moving. This is “**convective instability**”.



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- In spatially extended systems, a solution can be unstable, but with any perturbation that grows also moving. This is “convective instability”.
- Alternatively, a solution can be unstable with perturbations growing without moving. This is “absolute instability”.



# Absolute Stability in a Moving Frame of Reference

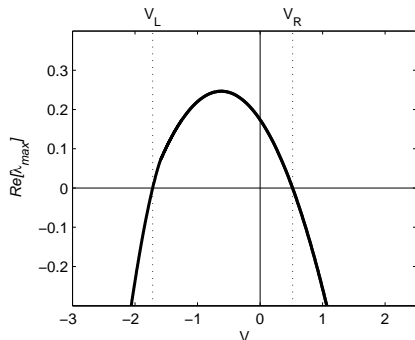
Absolute stability refers to the growth/decay of **stationary** perturbations.

We must consider the growth/decay of perturbations **moving** with a specified velocity  $V$ , i.e. absolute stability in a frame of reference moving with velocity  $V$ .

Define  $\lambda_{max}(V)$  = temporal eigenvalue of the most unstable linear mode

$\nu_{max}(V)$  = the corresponding spatial eigenvalue

# Absolute Stability in a Moving Frame of Reference

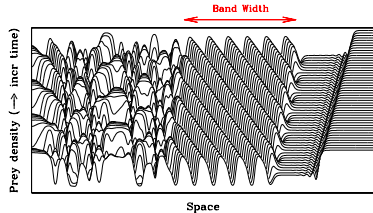


A tutorial guide to calculating absolute stability is freely available at

<http://research.microsoft.com/en-us/projects/loptw/tutorial.aspx>

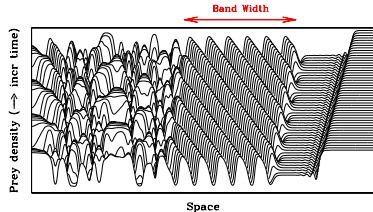


# Defining the Width of the Plane Wave Band



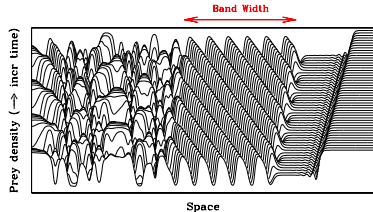
- We define the left-hand edge of the plane wave band as where unstable linear modes first become amplified by an arbitrary factor  $\mathcal{F}$ .

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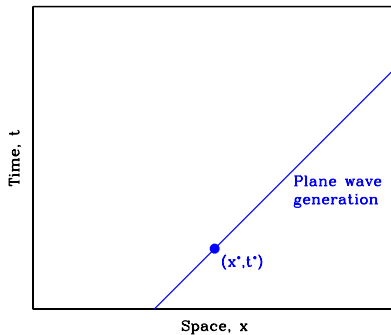
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- Our calculations  $\Rightarrow$  band width =  $\underbrace{\log(\mathcal{F})}_{\text{arbitrary}} \cdot \underbrace{W}_{\text{"band width coefficient"}}$

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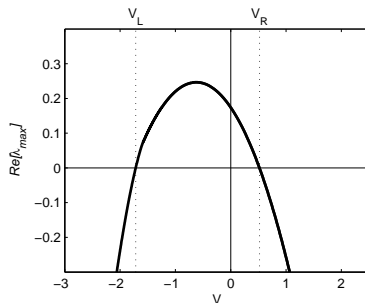
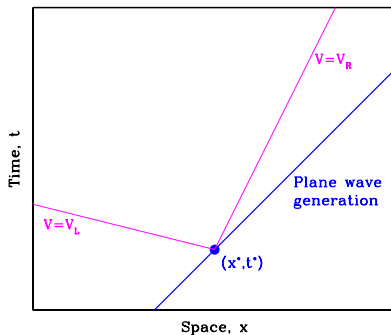


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- The dependence on ecological parameters is via  $\mathcal{W}$ .

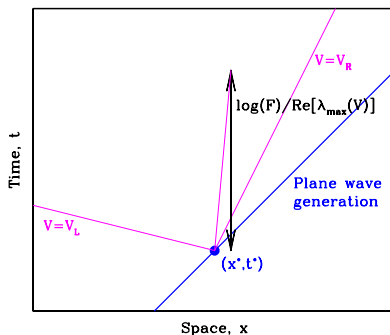
# The Band Width Formula



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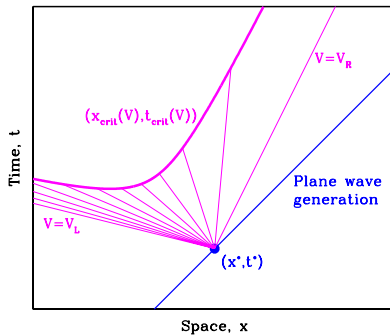
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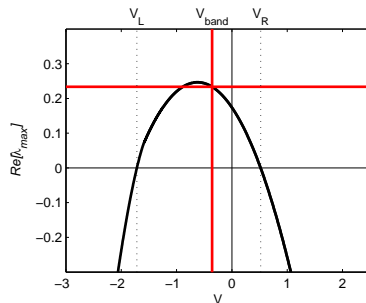
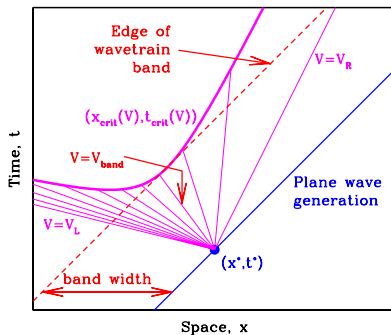
Perturbations moving with velocity  $V$  grow as  $\exp[\text{Re}(\lambda_{\max}(V)) \cdot t]$

$\Rightarrow$  amplified by the factor  $\mathcal{F}$  after time  $= \log(\mathcal{F})/\text{Re}(\lambda_{\max}(V))$

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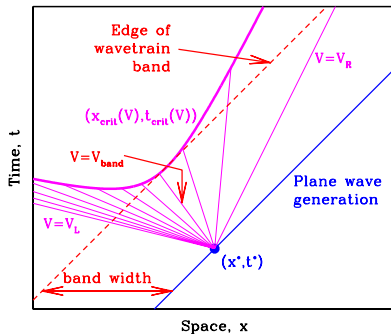


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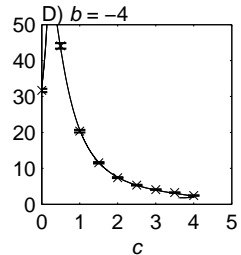
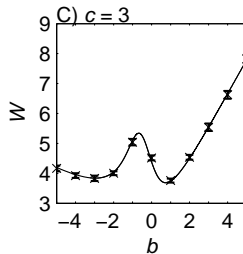
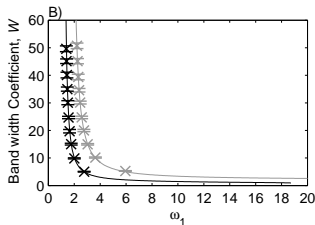
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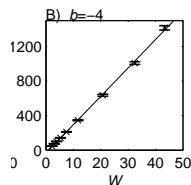
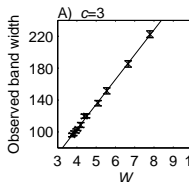
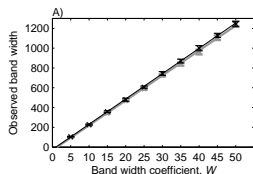
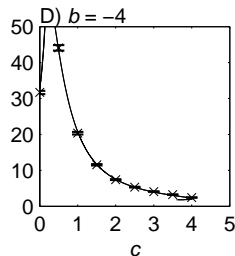
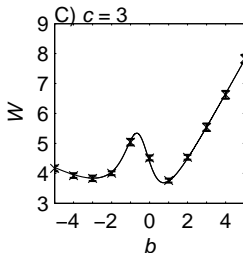
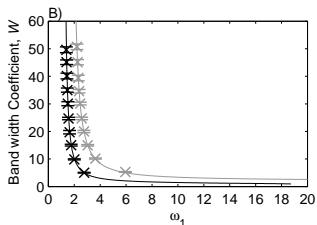
$$\mathcal{W} = 1/\text{Re} [\nu_{\max}(V_{\text{band}})]$$

$$\text{where } (V_{\text{band}} - c_{\text{inv}})\text{Re} [\nu_{\max}(V_{\text{band}})] = \text{Re} [\lambda_{\max}(V_{\text{band}})]$$

# The Form of $W$



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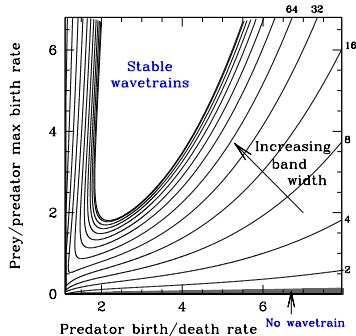


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# Band Width Sensitivity

Our formula gives band width vs ecological parameters.



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What does this imply for the vole – weasel interaction?



voles

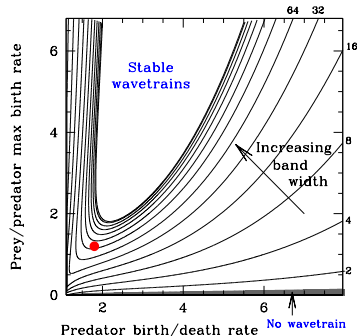


weasel



# Band Width Sensitivity

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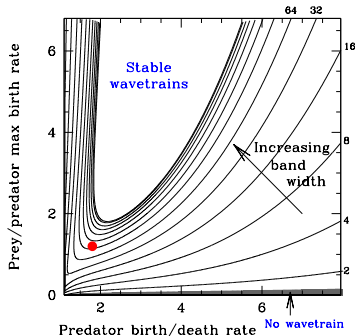


● = weasel–vole  
parameters.

The plane wave band  
is very wide:  
about 300 wavelengths.

# Band Width Sensitivity

Our formula gives band width vs ecological parameters.



● = weasel–vole  
parameters.

5%↑ in vole birth rate  
⇒ 22%↑ in band width.



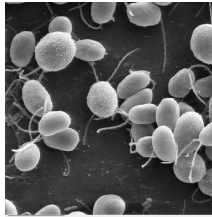
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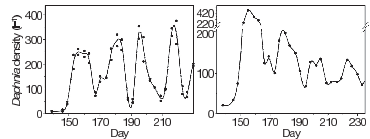
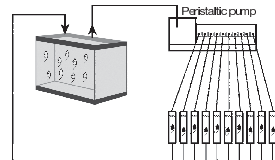
Example: *Daphnia pulex*–*Chlamydomonas reinhardtii* interaction



*Daphnia pulex*



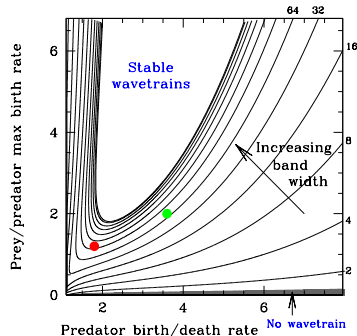
*Chlamydomonas  
reinhardtii*



(from McCauley *et al* (2008), *Nature* 455:1240, 2008)

# Band Width Sensitivity

Our formula gives band width vs ecological parameters.



● = plankton parameters  
 (*Daphnia pulex*–*Chlamydomonas reinhardtii*).

5.2%↓ in *Daphnia*  
 birth rate  
 ⇒ doubling of band width.

## Ecological Implications

- It is known that climate change is significantly affecting the parameters of oscillatory ecological systems (e.g. Ims *et al* (2008) *TREE* 23:79).
- Also, climate change  $\Rightarrow$  more frequent invasions.
- The width of the plane wave band determines whether one sees spatiotemporal chaos or periodic homogeneous oscillations behind the invasion.
- We have shown that band width depends sensitively on ecological parameters.

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- The width of the plane wave band determines whether one sees spatiotemporal chaos or periodic homogeneous oscillations behind the invasion.
- We have shown that band width depends sensitively on ecological parameters.
- This suggests that the implications of climate change for *spatio*temporal dynamics may be even more dramatic than for purely temporal behaviour.

This work is in collaboration with:

Matthew Smith

(Microsoft Research  
Cambridge)



Jens Rademacher

(CWI, Amsterdam)



Xavier Lambin

(University of Aberdeen)



# References

J.A. Sherratt, M.J. Smith: Periodic travelling waves in cyclic populations: field studies and reaction-diffusion models.  
*J. R. Soc. Interface* **5**, 483-505 (2008).

J.A. Sherratt, M.J. Smith, J.D.M. Rademacher: Locating the transition from periodic oscillations to spatiotemporal chaos in the wake of invasion.  
*Proc. Natl. Acad. Sci. USA*, published online (open access).

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- Vole Population Cycles
- Cyclic Predator-Prey Systems
- Spatiotemporal Data
- Modelling Predator-Prey Invasion

## 2 Stable and Unstable Plane Waves

- Plane Wave Stability
- Back to Voles and Weasels

## 3 Calculating the Width of the Plane Wave Band

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- Absolute Stability in a Moving Frame of Reference
- Defining the Width of the Plane Wave Band
- The Band Width Formula
- The Form of W

## 4 Band Width Sensitivity and Ecological Implications

- Band Width Sensitivity
- Ecological Implications
- References

## The Form of $V_{band}$

