Spatiotemporal Dynamics of Field Voles

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This talk can be downloaded from my web site
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In collaboration with:

Matthew Smith

Xavier Lambin

Outline

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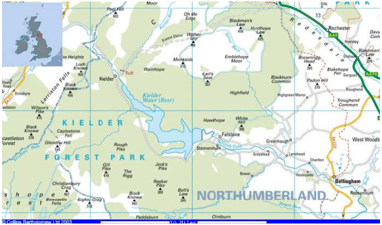
Field Voles in Kielder Forest



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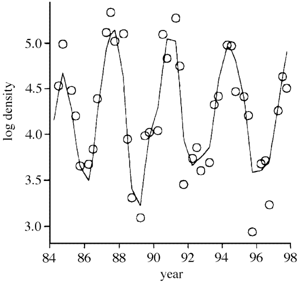

Field voles in Kielder Forest are cyclic (period 4 years).

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We assume that vole cycles are caused by predation by weasels, and study using a predator-prey model.

A Standard Predator-Prey Model

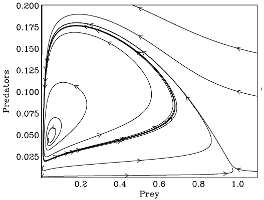
predators

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

prey

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

Phase plane of local dynamics:



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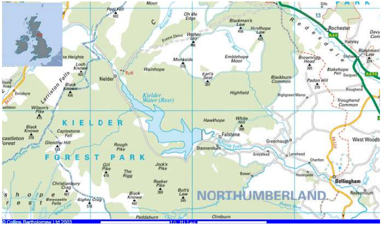

Spatiotemporal field data shows that the cycles are spatially organised into a periodic travelling wave,
speed 19km/year, direction 72° from N.

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Everyday example: Mexican wave

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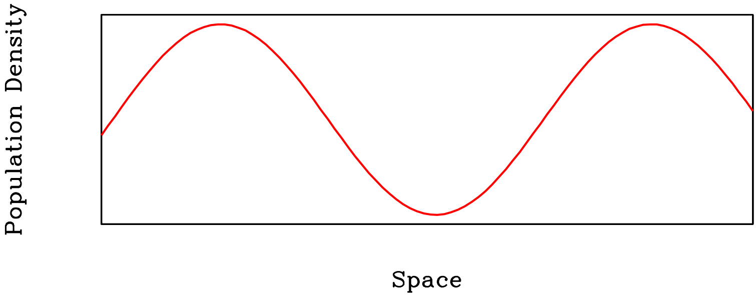

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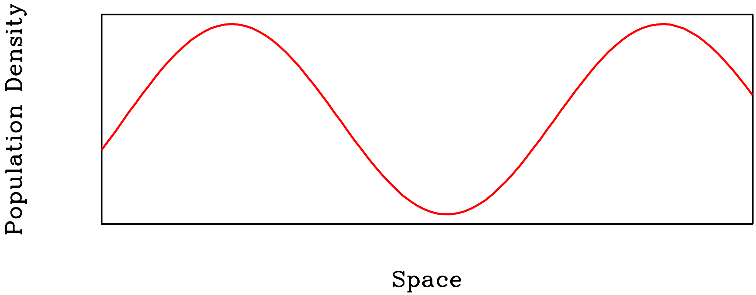

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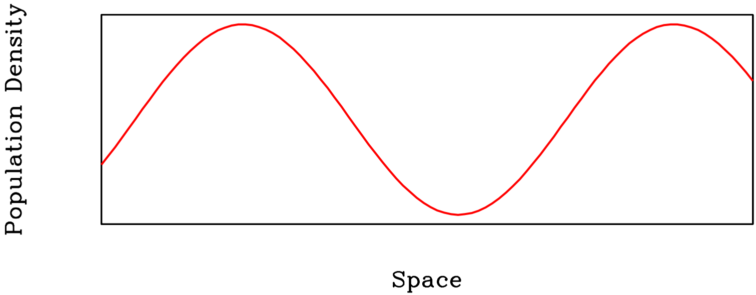

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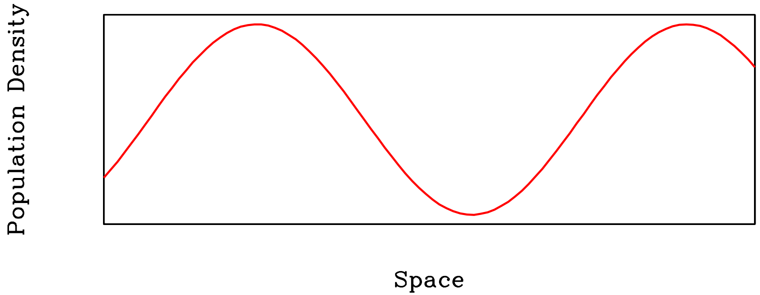

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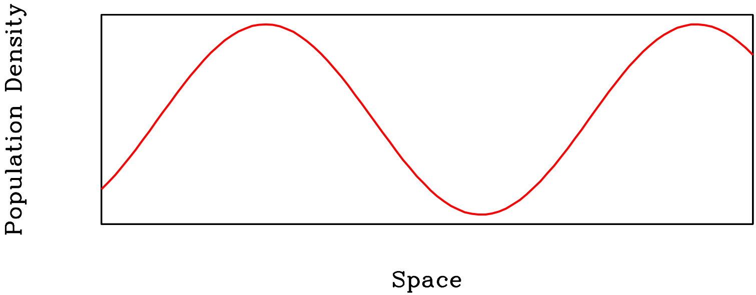

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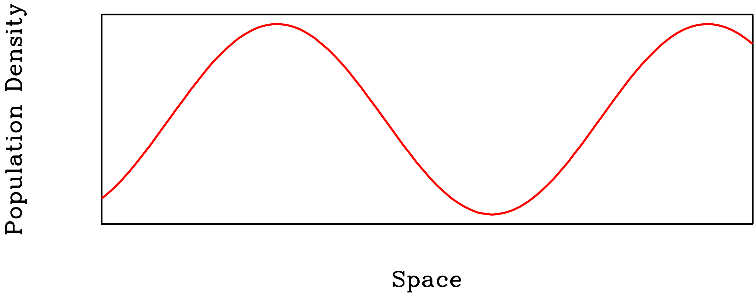

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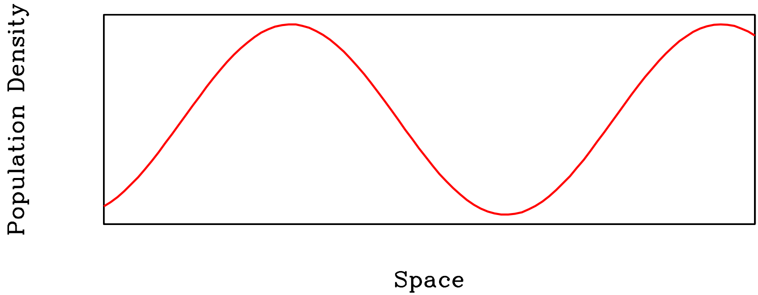

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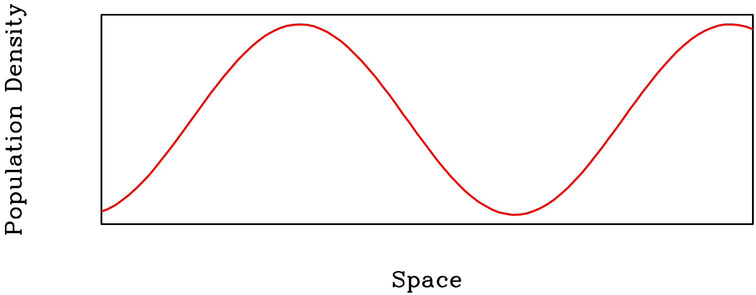

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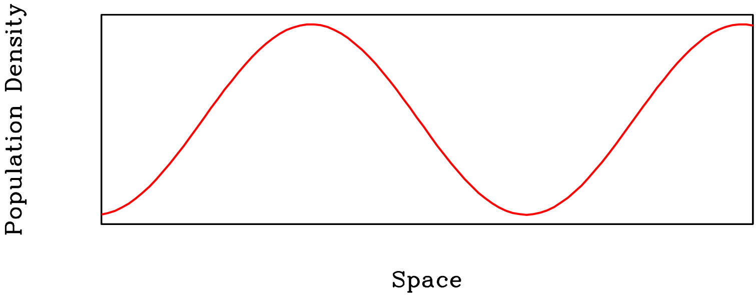

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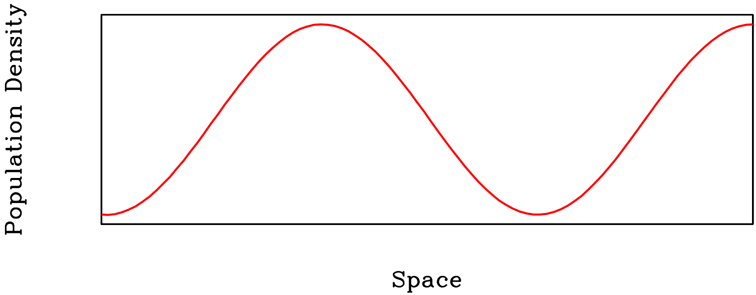

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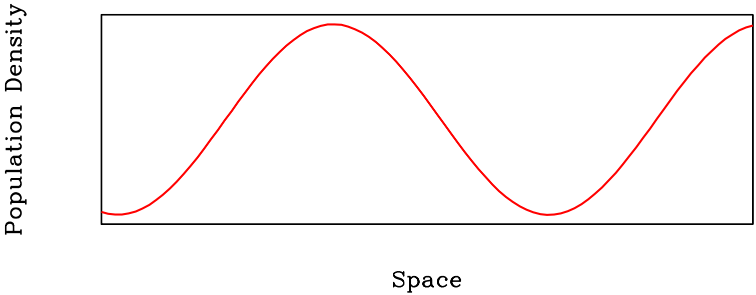

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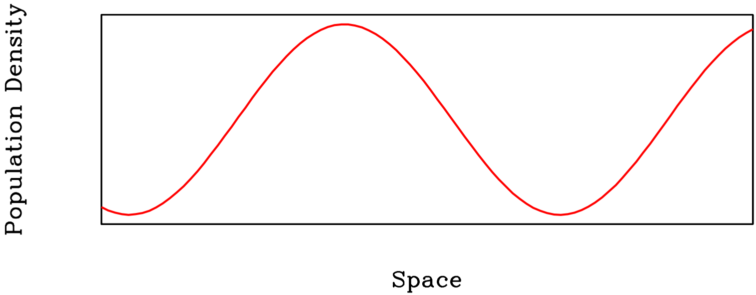

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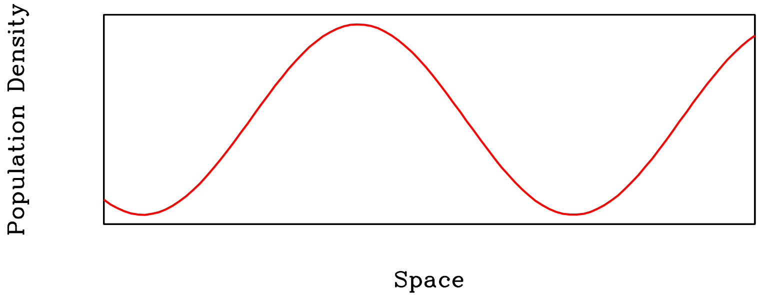

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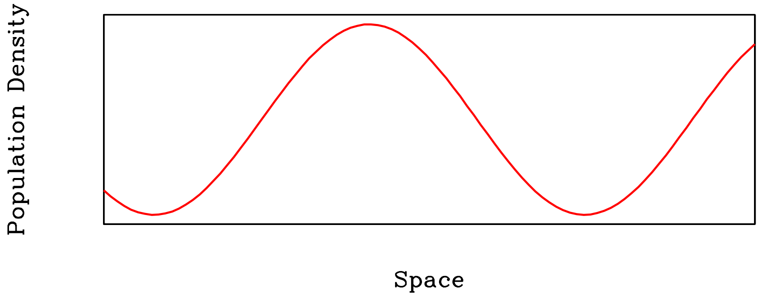

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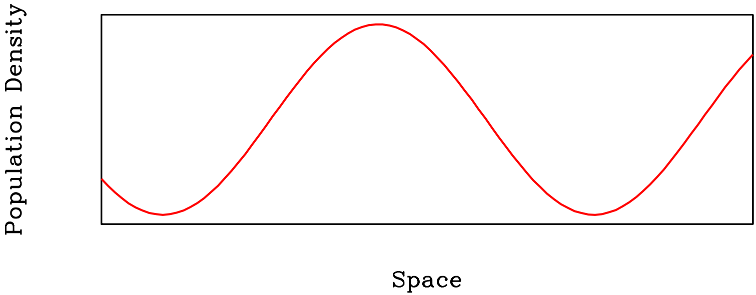

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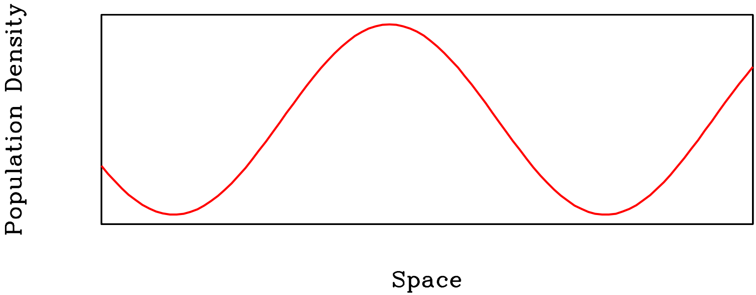

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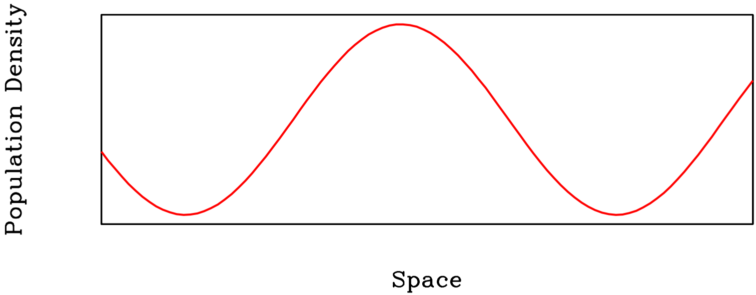

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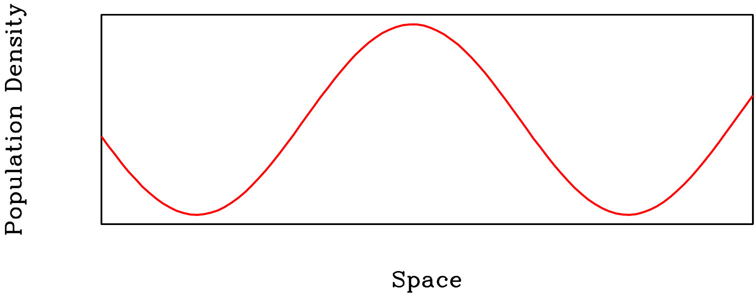

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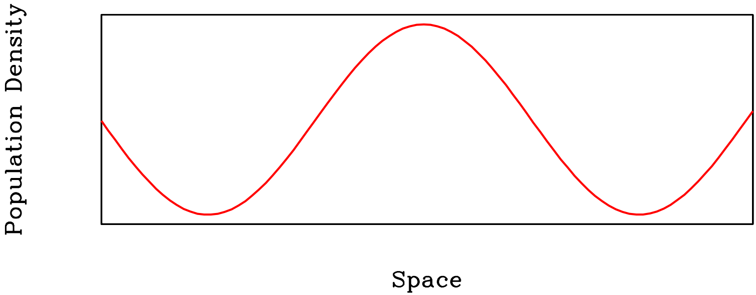

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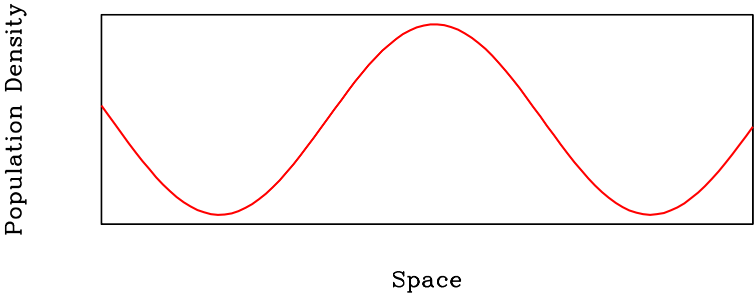

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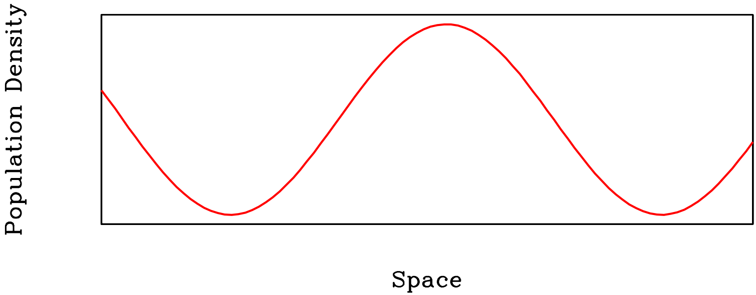

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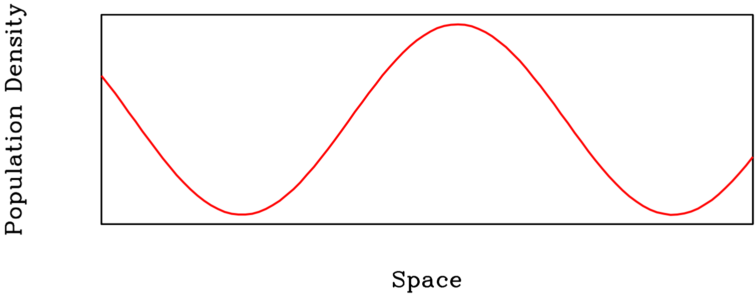

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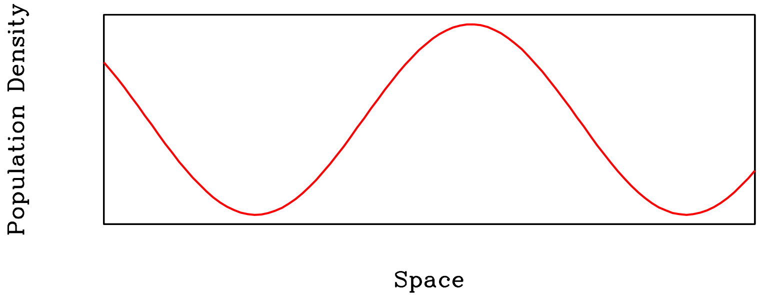

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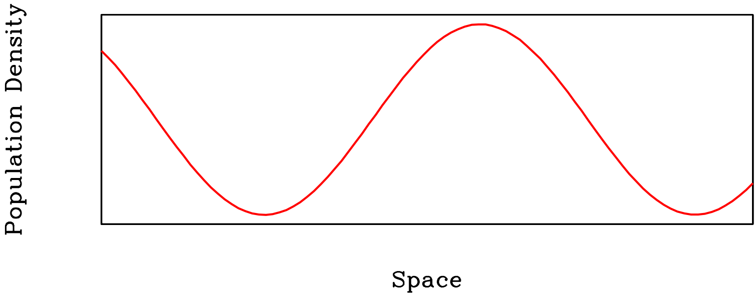

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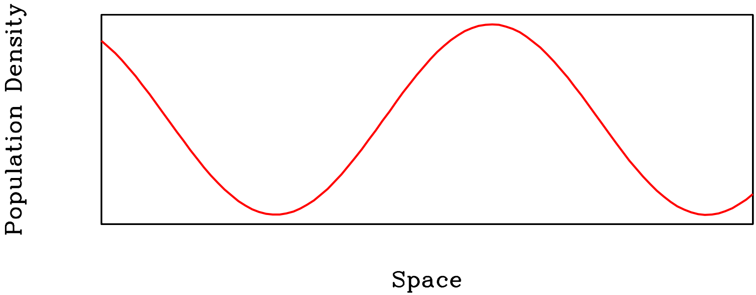

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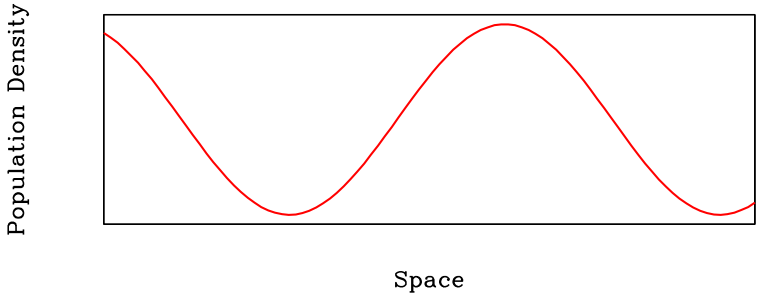

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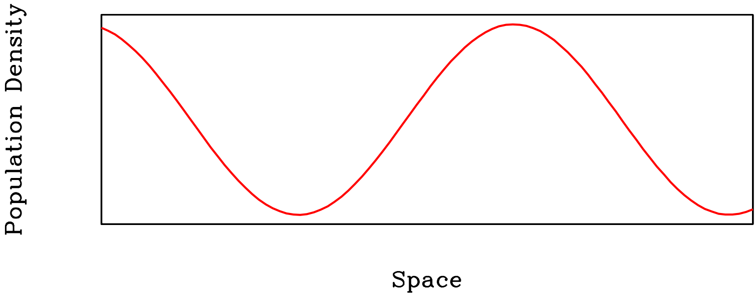

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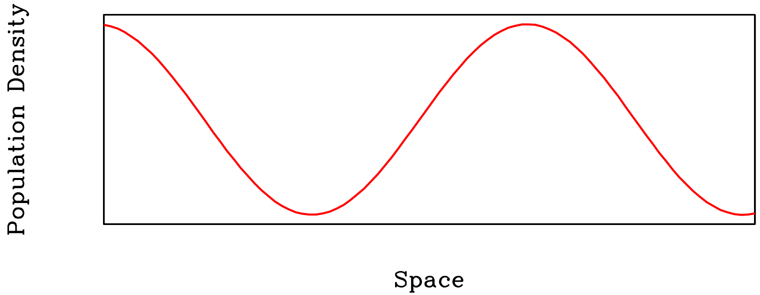

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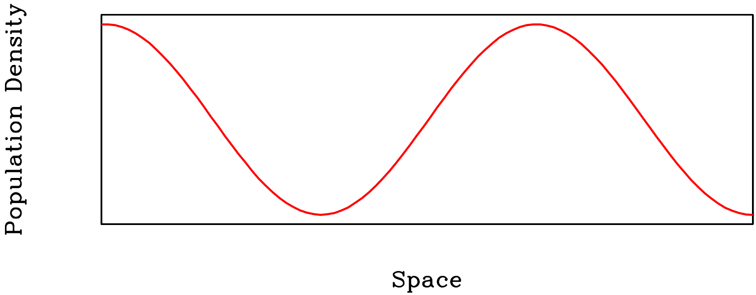

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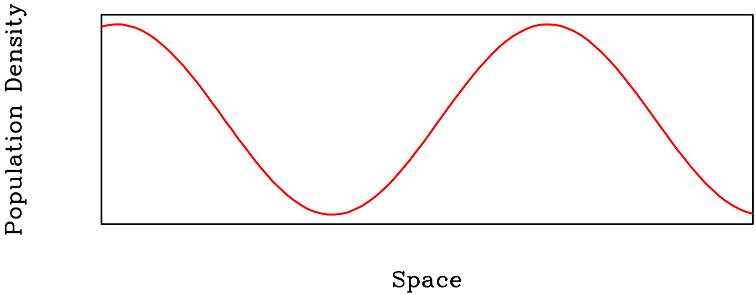

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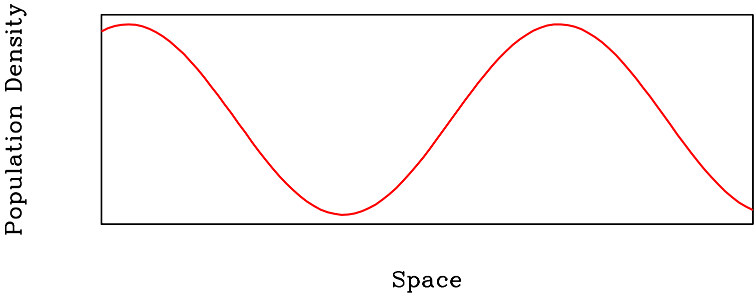

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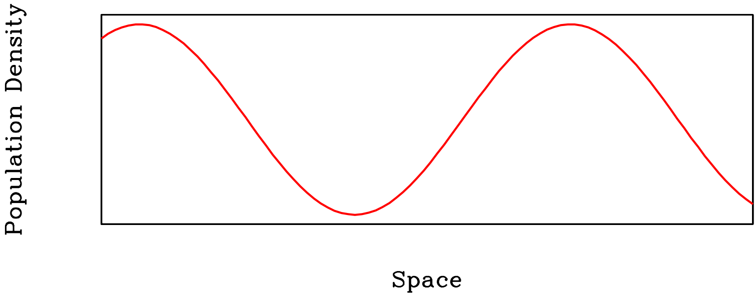

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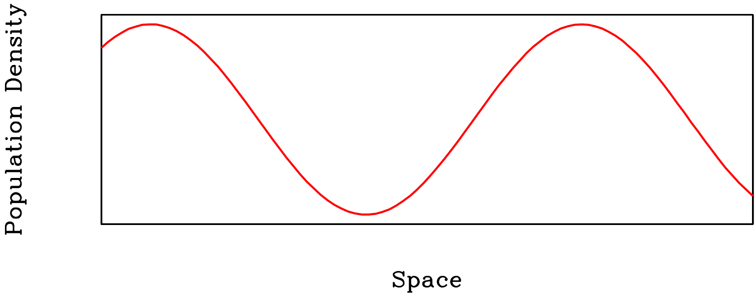

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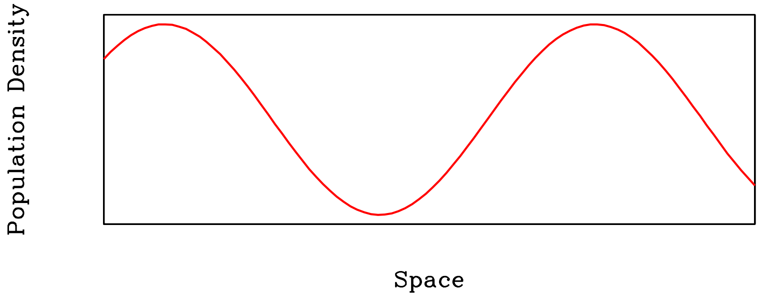

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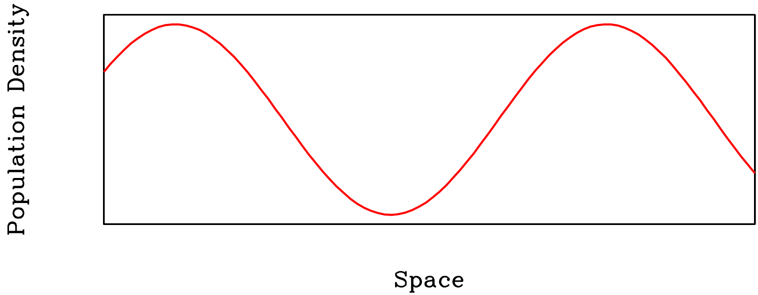

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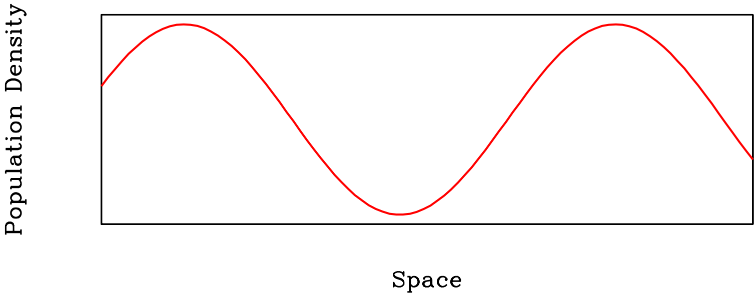

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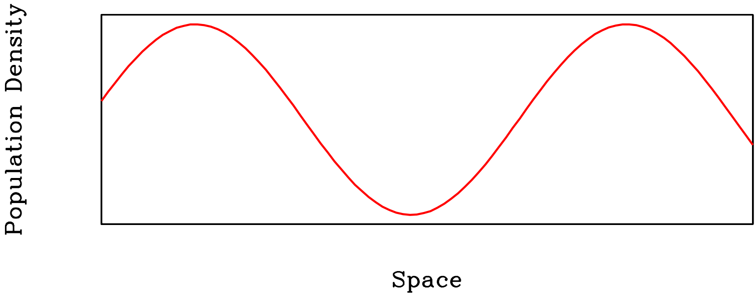

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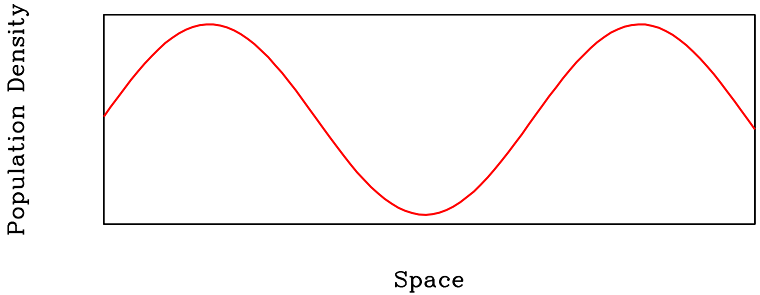

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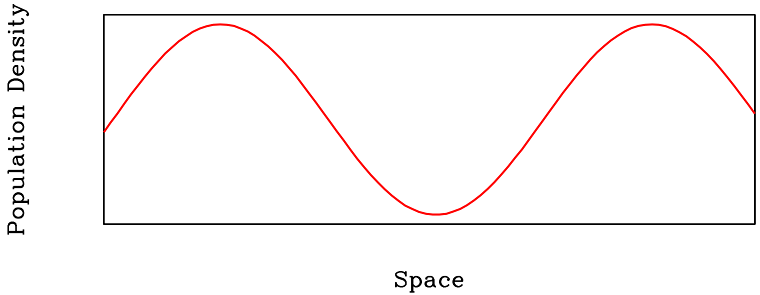

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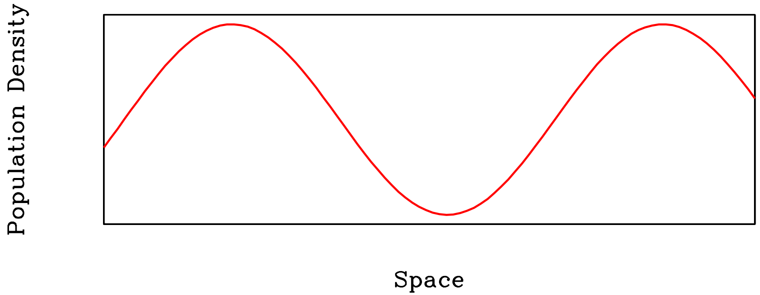

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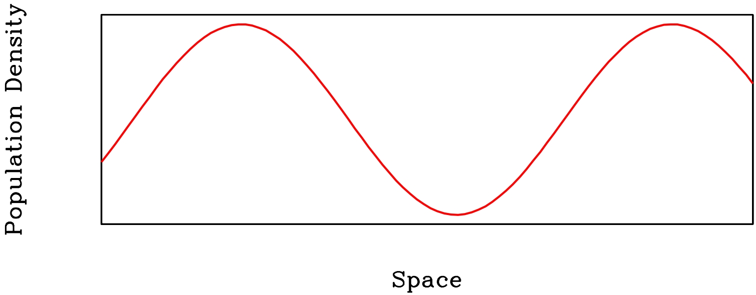

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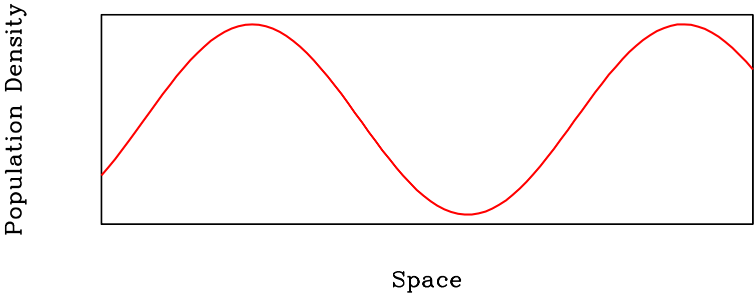

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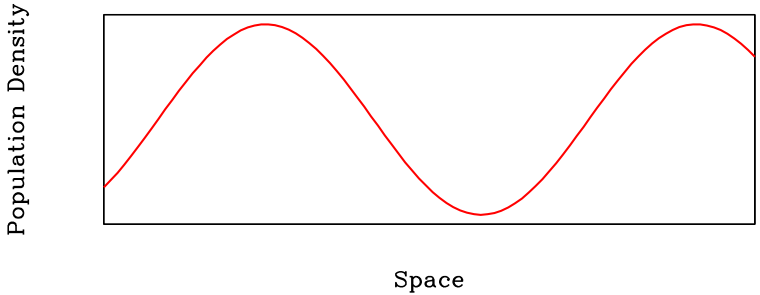

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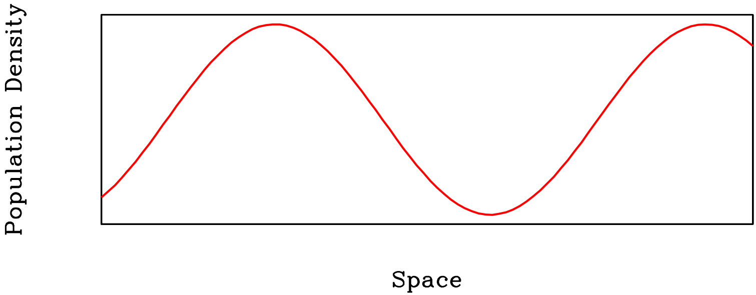

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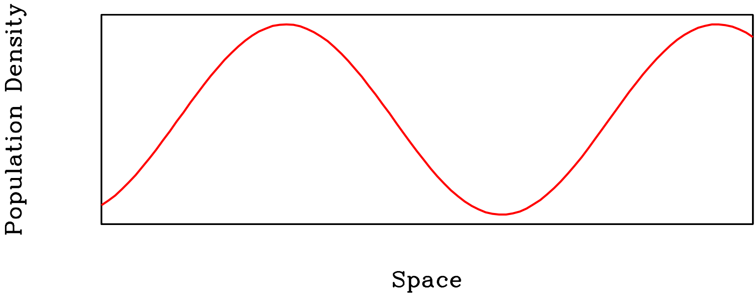

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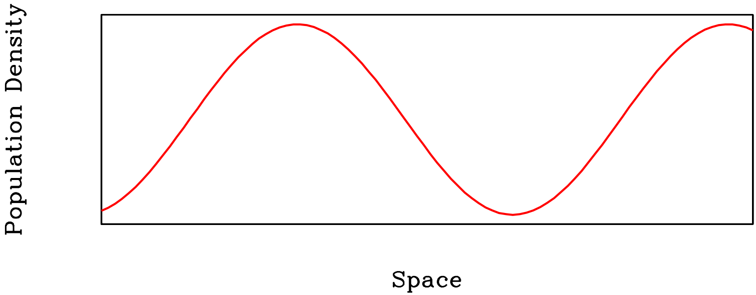

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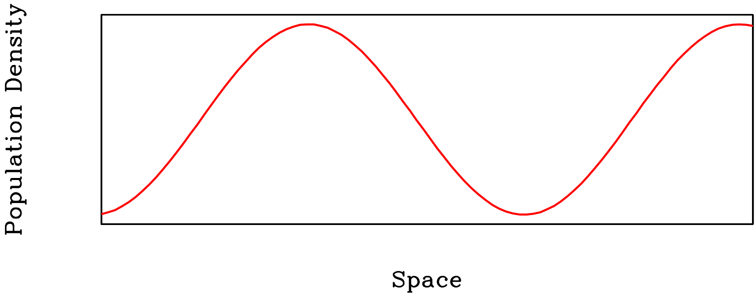

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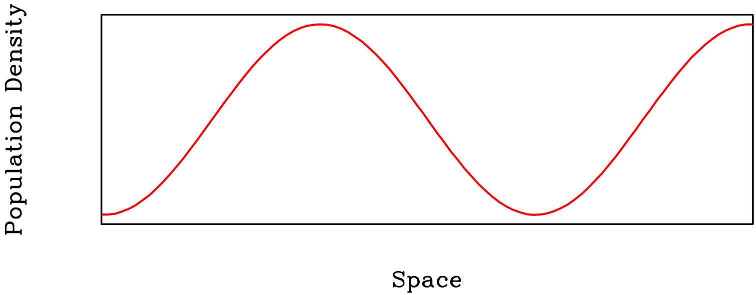

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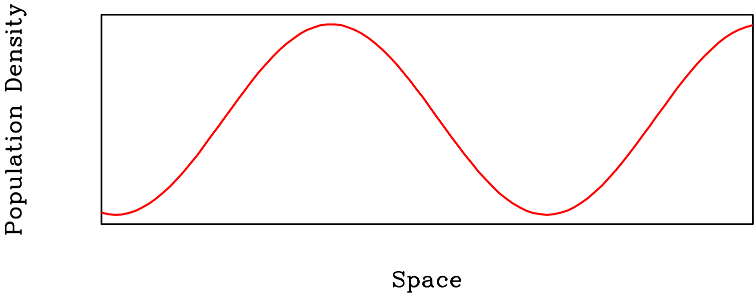

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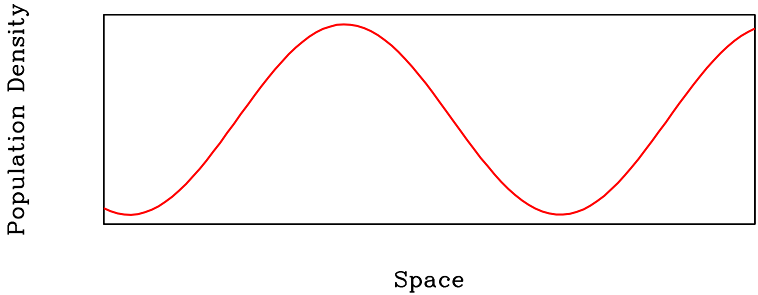

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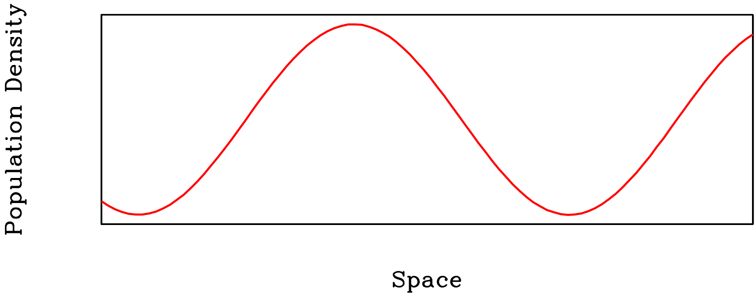

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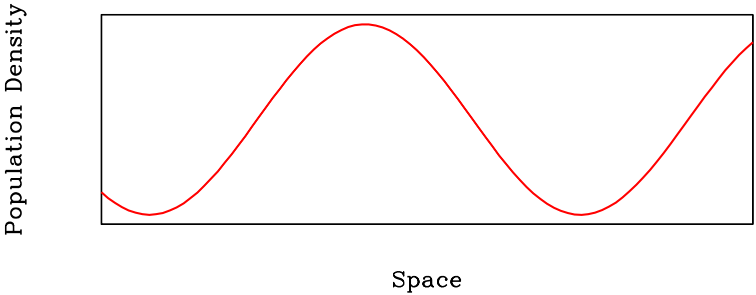

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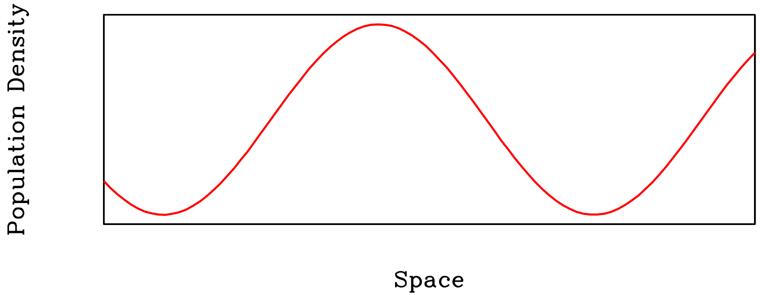

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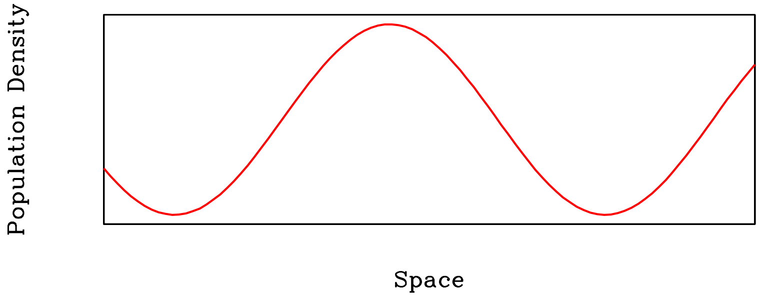

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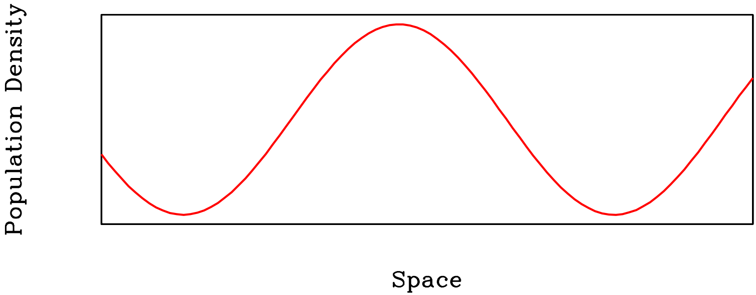

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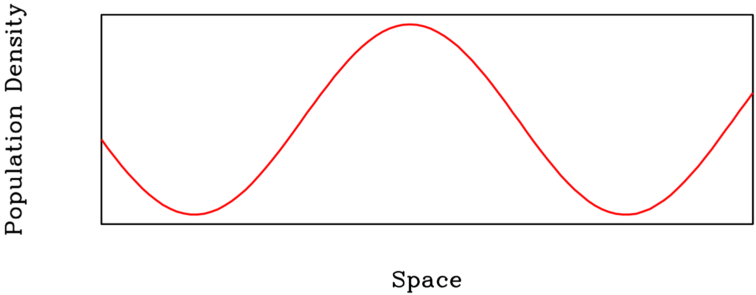

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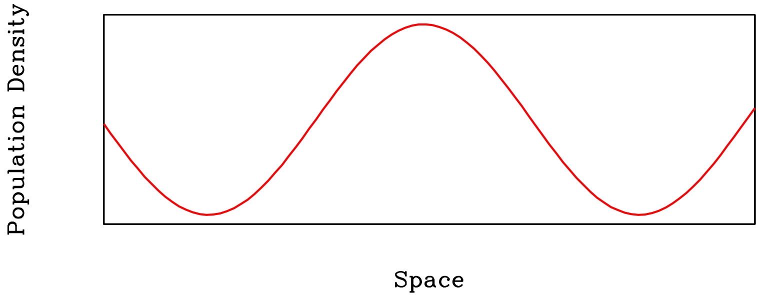

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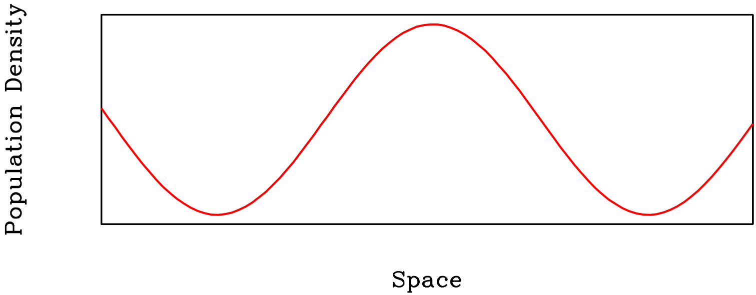

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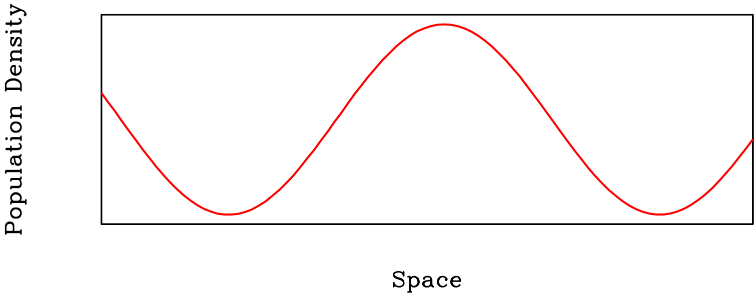

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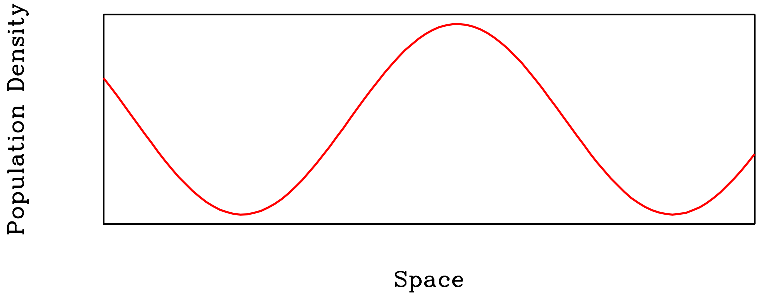

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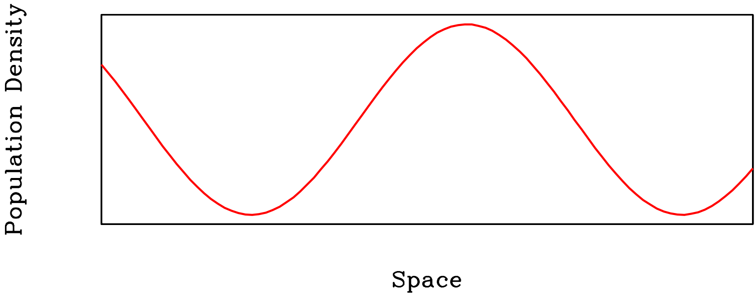

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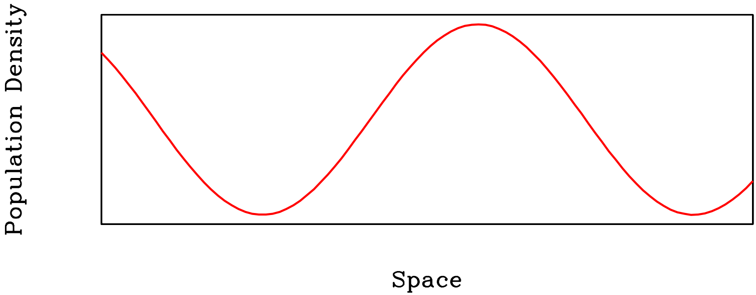

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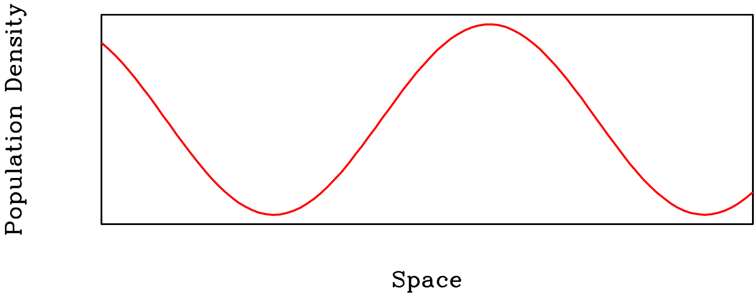

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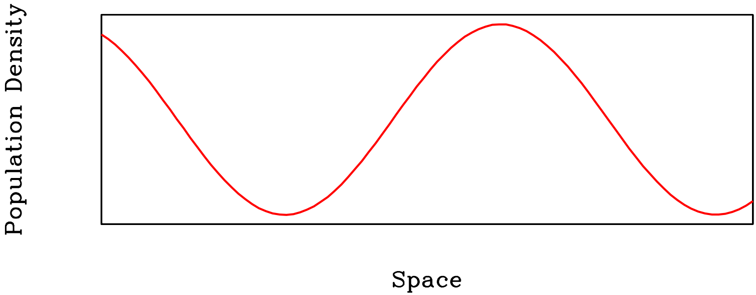

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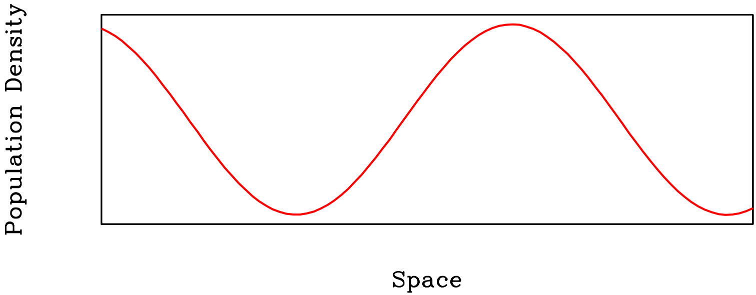

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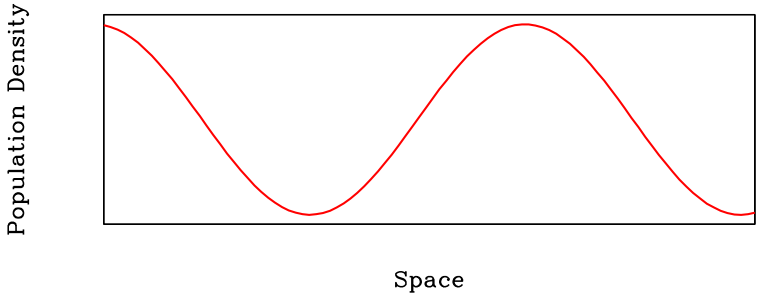

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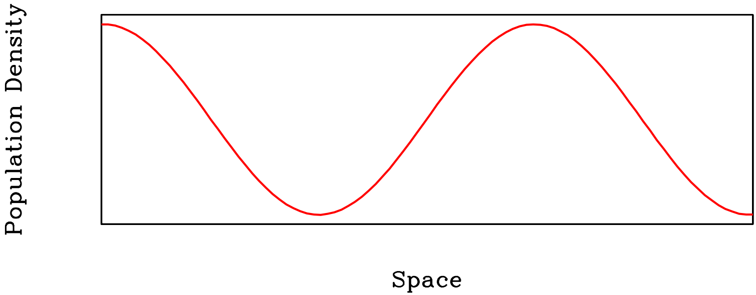

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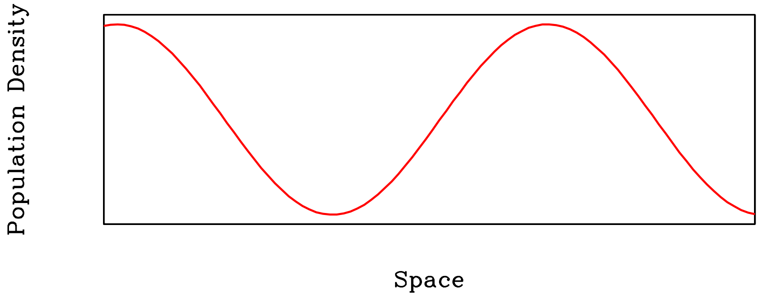

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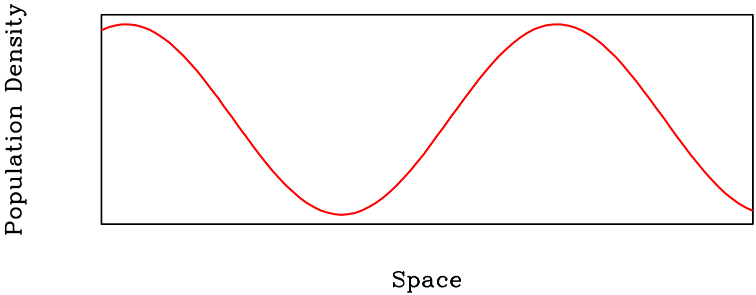

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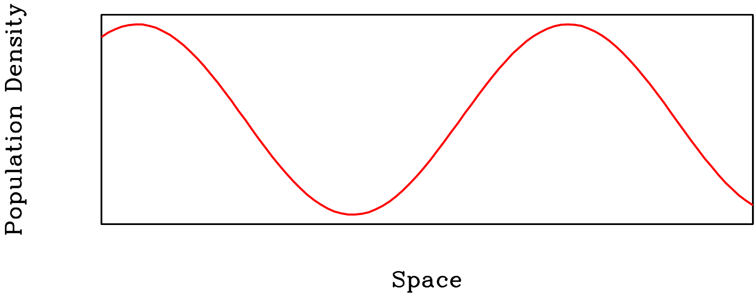

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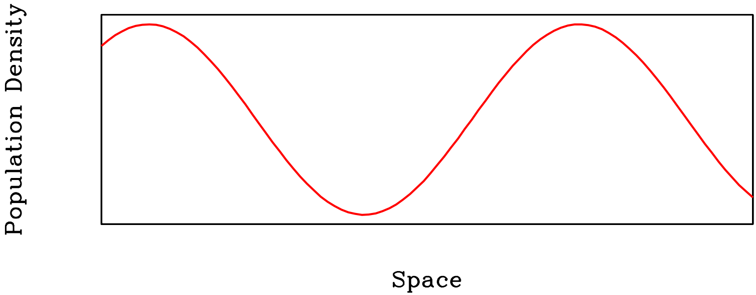

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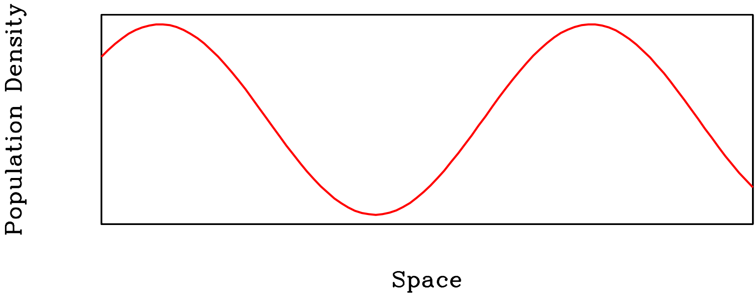

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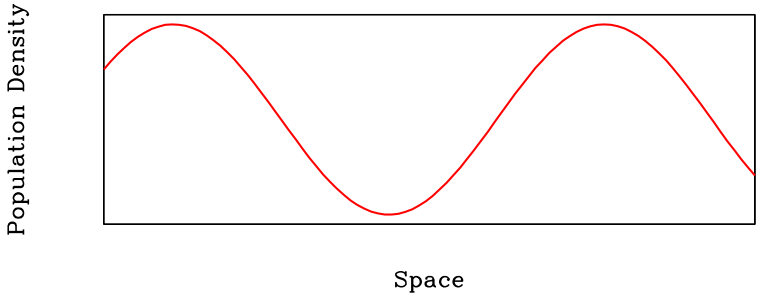

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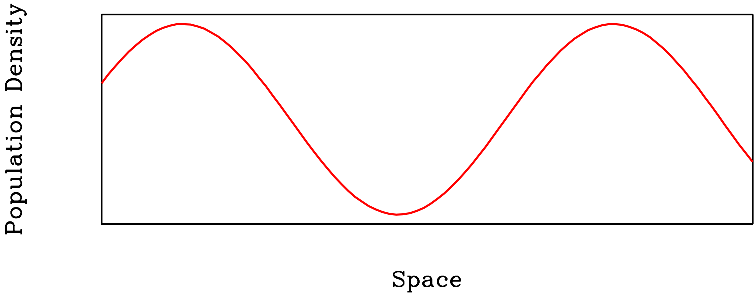

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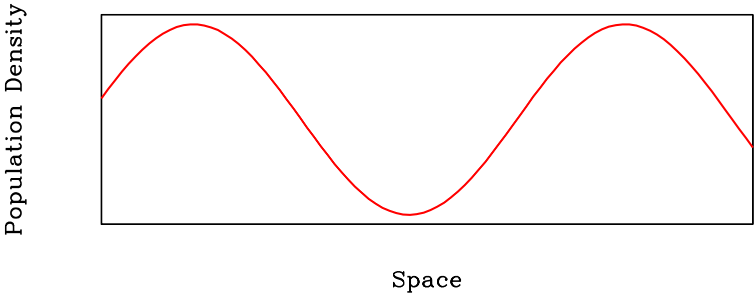

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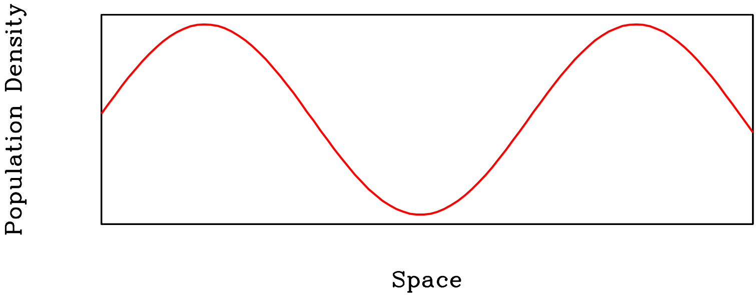

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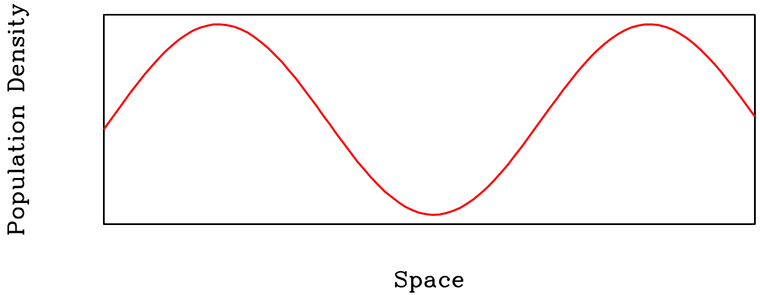

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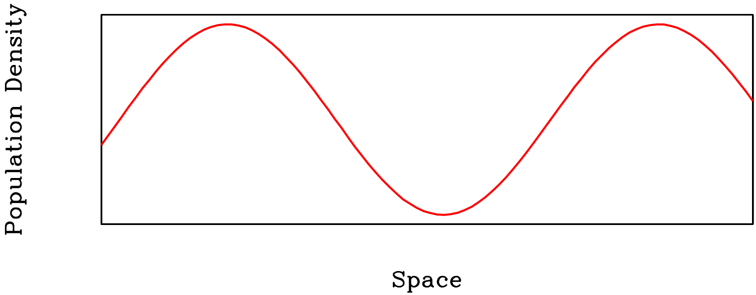

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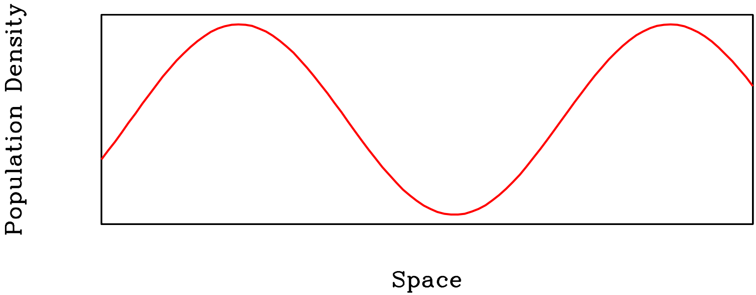


What is a Periodic Travelling Wave?

Everyday example: Mexican wave

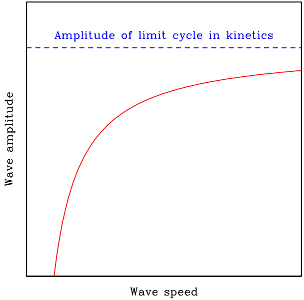
There is an extensive literature on periodic travelling waves in oscillatory reaction-diffusion equations

$$\begin{aligned} \partial u/\partial t &= D_u\, \partial^2 u/\partial x^2 + f(u,v) \\ \partial v/\partial t &= D_v\, \partial^2 v/\partial x^2 + \underbrace{g(u,v)}_{\text{kinetics have a stable limit cycle}} \end{aligned}$$

What is a Periodic Travelling Wave?

Everyday example: Mexican wave

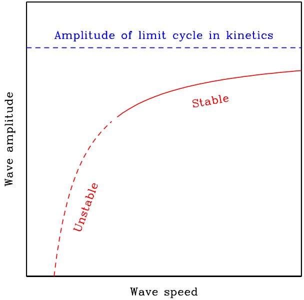
Theorem (Kopell & Howard, 1973):
An oscillatory reaction-diffusion system has a one-parameter family of periodic travelling wave solutions if the diffusion coefficients are sufficiently close to one another.



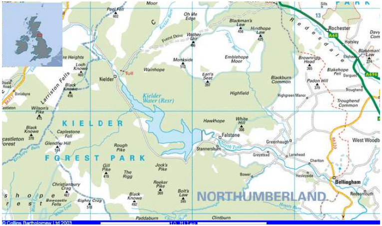
What is a Periodic Travelling Wave?

Everyday example: Mexican wave

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



What Causes the Spatial Component of the Oscillations?



Hypothesis: the periodic travelling waves are caused by the large central reservoir.

Outline

Boundary Conditions in the Field Vole Example

- 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

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- Therefore we expect very high vole loss at the reservoir edge, implying a Robin boundary condition

$$\frac{\partial}{\partial n}\left(\begin{array}{c}\text{vole}\\ \text{density}\end{array}\right) = -\left(\begin{array}{c}\text{large}\\ \text{constant}\end{array}\right)\cdot\left(\begin{array}{c}\text{vole}\\ \text{density}\end{array}\right)$$

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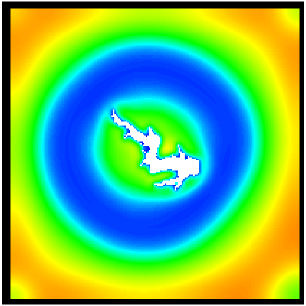
- To a good approx, vole density $=0$ at the reservoir edge
- At the edge of the forest, a zero flux boundary condition is a natural assumption

Typical Model Solution



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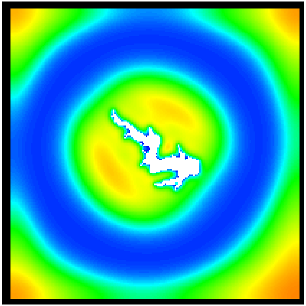

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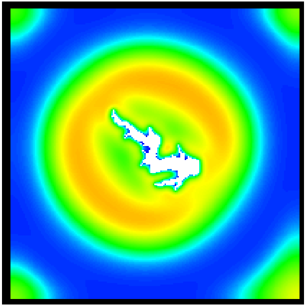

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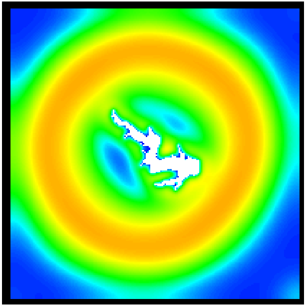

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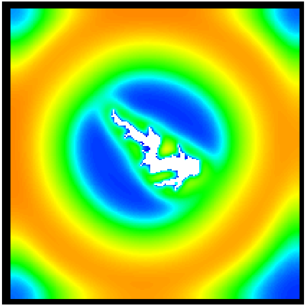

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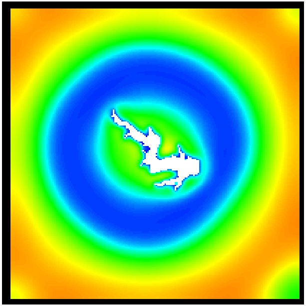
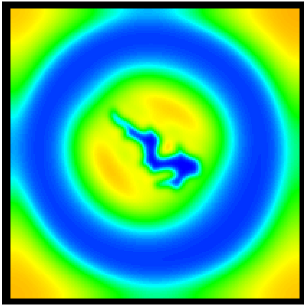


Removing the Reservoir

The periodic waves are driven by the reservoir. This is most easily demonstrated by simulating removal of the reservoir.



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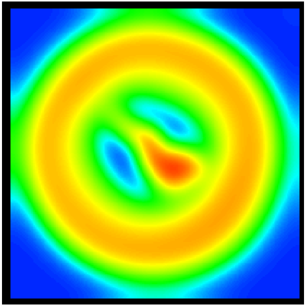

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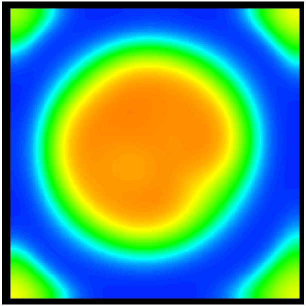

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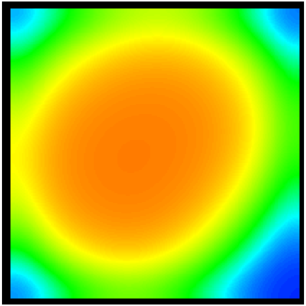

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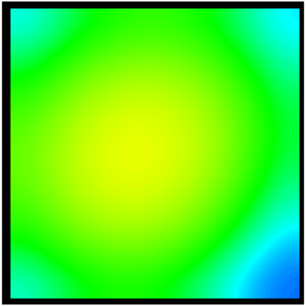

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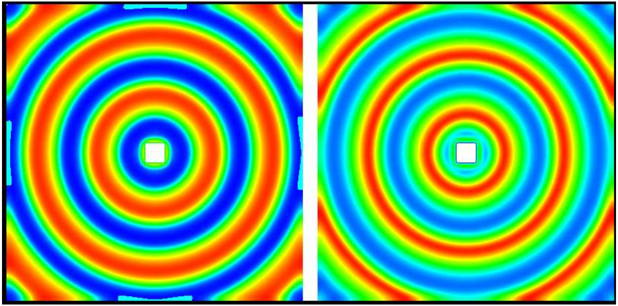
Periodic Wave Generation on a Large Domain

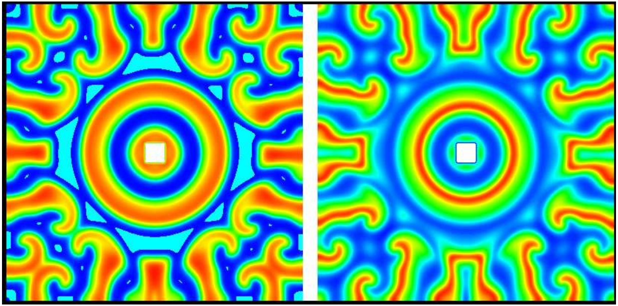


Movie of Wave Generation on a Large Domain

Click here to
play the movie

An Example of Irregular Pattern Generation

For some parameter values, obstacles with Dirichlet boundary conditions generate irregular spatiotemporal patterns.



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Mathematical Goal

Mathematical goal: predict which parameter sets will give periodic travelling waves, and which will give spatiotemporal irregularity.

Outline

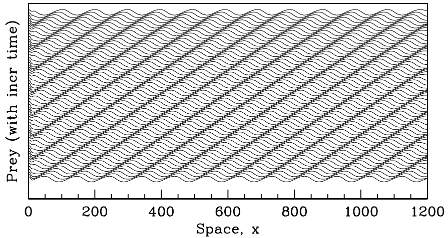
One-Dimensional Problem

To simplify, solve on $0 < x < x_{max}$ with

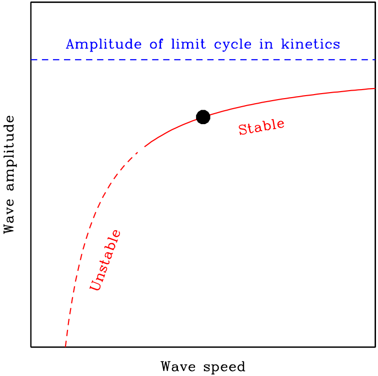
$$\begin{aligned} h = p = 0 \quad &\text{at} \quad x = 0 \qquad &\leftrightarrow \text{edge of reservoir} \\ h_x = p_x = 0 \quad &\text{at} \quad x = x_{max} \qquad &\leftrightarrow \text{edge of forest.} \end{aligned}$$

In fact the condition at $x = x_{max}$ plays no significant role, and we can consider the equations on $0 < x < \infty$.

Wave Selection Problem



The boundary condition at $x = 0$ selects a particular member of the periodic travelling wave family.



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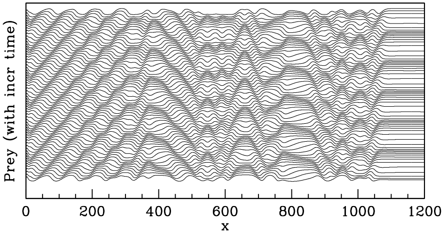
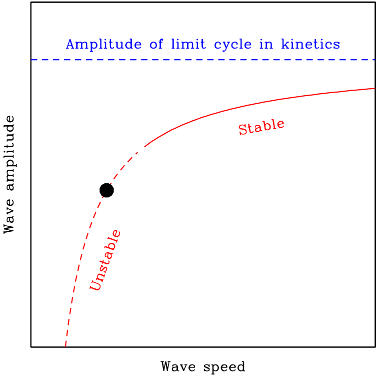


The boundary condition at $x = 0$ selects a particular member of the periodic travelling wave family.

Irregular patterns occur when the selected wave is unstable.



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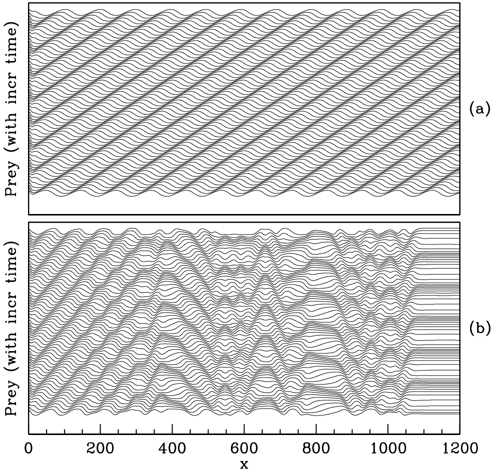
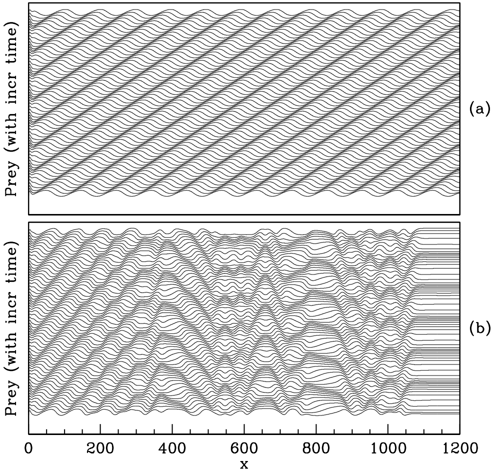
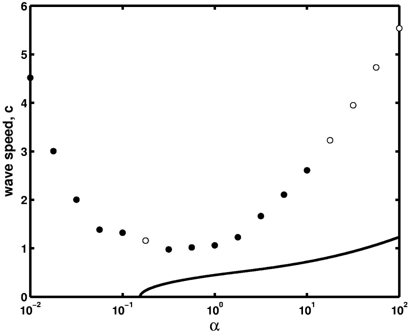


Therefore we must investigate wave stability in detail.

Wave Selection Problem





The Eigenvalue Problem

Reaction-diffusion eqns:
$$u_t = D_u u_{zz} + c u_z + f(u,v)$$
$$v_t = D_v v_{zz} + c v_z + g(u,v)$$

Periodic wave satisfies:
$$0 = D_u U_{zz} + c U_z + f(U,V)$$
$$0 = D_v V_{zz} + c V_z + g(U,V)$$

Consider
$$u(z,t) = U(z) + e^{\lambda t}\overline{u}(z) \quad \text{with } |\overline{u}| \ll |U|$$
$$v(z,t) = V(z) + e^{\lambda t}\overline{v}(z) \quad \text{with } |\overline{v}| \ll |V|$$

$\Rightarrow$ Eigenfunction eqn:
$$\lambda\overline{u} = D_u \overline{u}_{zz} + c\overline{u}_z + f_u(U,V)\overline{u} + f_v(U,V)\overline{v}$$
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Boundary conditions:
$$\overline{u}(0) = \overline{u}(L)e^{i\gamma} \quad (0 \le \gamma < 2\pi)$$
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$$\lambda\overline{u} = D_u \overline{u}_{zz} + c\overline{u}_z + f_u(U,V)\overline{u} + f_v(U,V)\overline{v}$$
$$\lambda\overline{v} = D_v \overline{v}_{zz} + c\overline{v}_z + g_u(U,V)\overline{u} + g_v(U,V)\overline{v}$$

Boundary conditions:
$$\overline{u}(0) = \overline{u}(L)e^{i\gamma} \quad (0 \le \gamma < 2\pi)$$
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The Eigenvalue Problem

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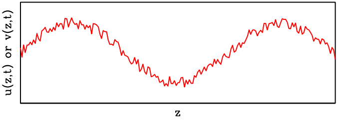
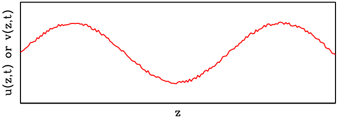
Here $0 < z < L$, with $(\overline{u},\overline{v})(0) = (\overline{u},\overline{v})(L)e^{i\gamma}$ $(0 \le \gamma < 2\pi)$



$\text{Re}(\lambda) < 0$ $\longrightarrow$



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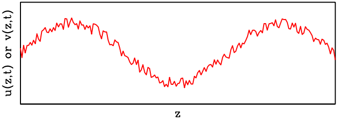

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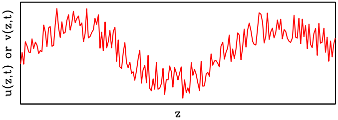

Numerical Calculation of Eigenvalue Spectrum

(based on Jens Rademacher, Bjorn Sandstede, Arnd Scheel Physica D 229 166-183, 2007)

1. solve numerically for the periodic wave by continuation in c from a Hopf bifn point in the travelling wave eqns

$$\begin{aligned} 0 &= U_{zz} + cU_z + f(U,W) \\ 0 &= W_{zz} + cW_z + g(U,W) \quad (z = x - ct) \end{aligned}$$

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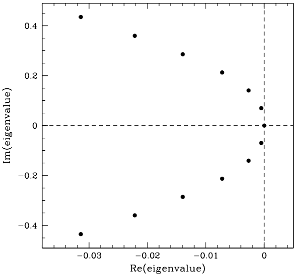

$$\begin{aligned} \lambda\overline{u} &= \overline{u}_{zz} + c\overline{u}_z + f_u(U,W)\overline{u} + f_w(U,W)\overline{w}, \quad \overline{u}(0) = \overline{u}(L)e^{i\gamma} \\ \lambda\overline{w} &= \overline{w}_{zz} + c\overline{w}_z + g_u(U,W)\overline{u} + g_w(U,W)\overline{w}, \quad \overline{w}(0) = \overline{w}(L)e^{i\gamma} \end{aligned}$$

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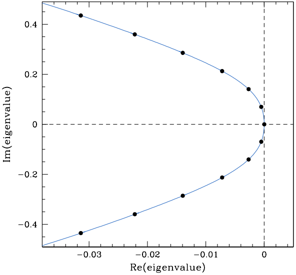

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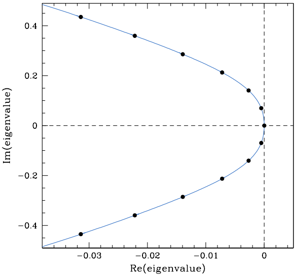

This gives the eigenvalue spectrum, and hence (in)stability

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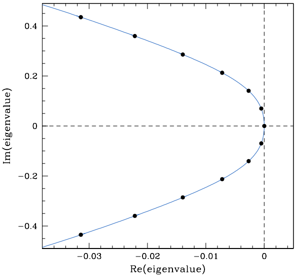
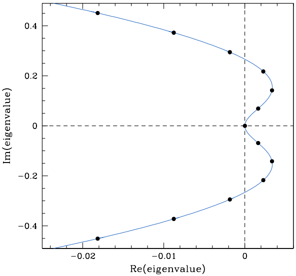


STABLE

Eckhaus instability

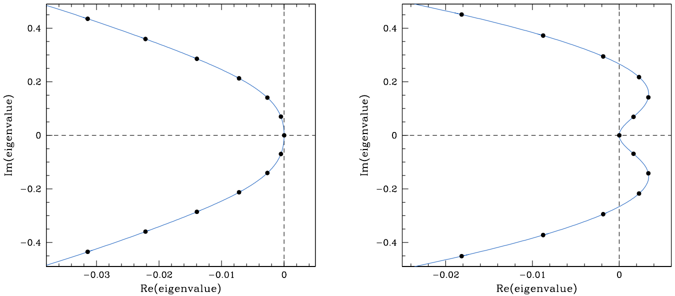


UNSTABLE

This gives the eigenvalue spectrum, and hence (in)stability

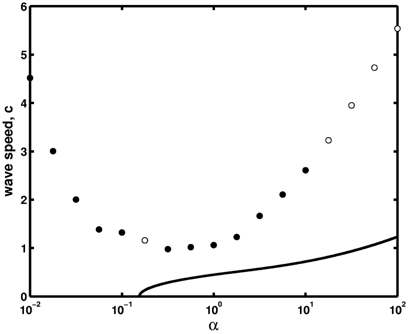
Pattern Stability: Numerical Approach

The boundary between stable and unstable patterns can also be calculated by numerical continuation.



Calculations of this type can be performed using the software package WAVETRAIN (`www.ma.hw.ac.uk/wavetrain`).

Periodic Wave Generation in 1-D Simulations



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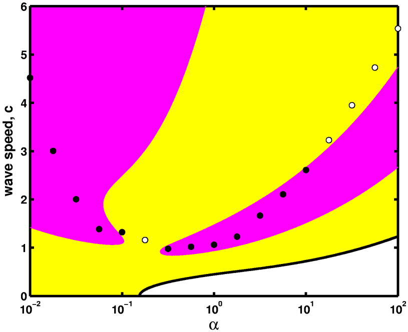
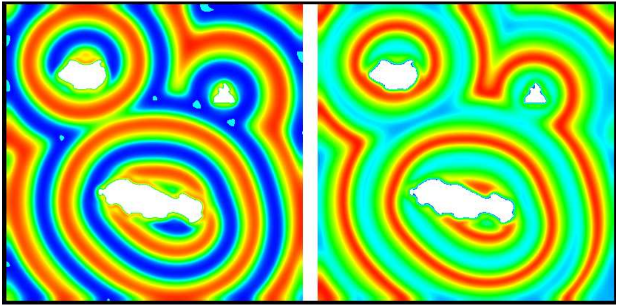


Our stability calculations explain the surprising results from simulations of periodic wave generation.

Outline

Typical Predator-Prey Solution with Multiple Obstacles



Movie of Solution with Multiple Obstacles

Click here to
play the movie

Competition between Obstacles

Question: How do the waves generated by different obstacles interact?

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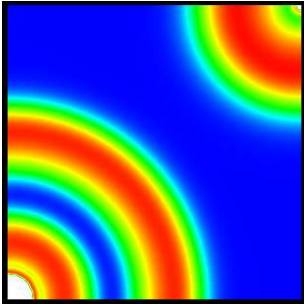

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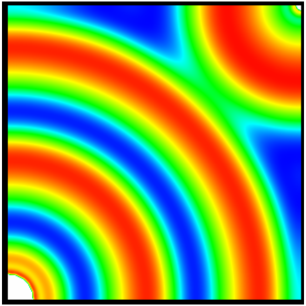

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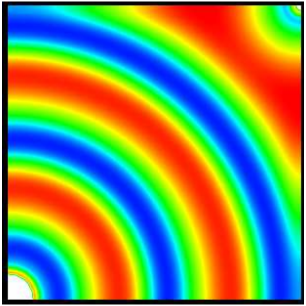

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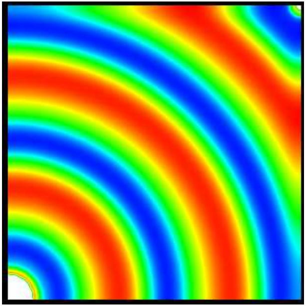


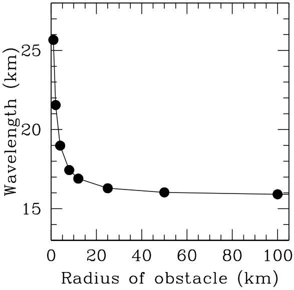
Competition between Obstacles

Question: How do the waves generated by different obstacles interact?

Answer: the wave generated by a larger obstacle dominates that generated by a smaller obstacle

Wavelength vs Obstacle Radius

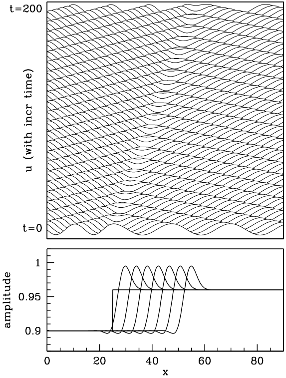
Numerical solutions for circular obstacles indicate that wavelength far from the obstacle varies with obstacle radius.



Larger obstacle $\Rightarrow$ Shorter wavelength $\Rightarrow$ Lower amplitude wave

Explanation of Competition between Obstacles

Consider an interface between periodic waves in 1-D



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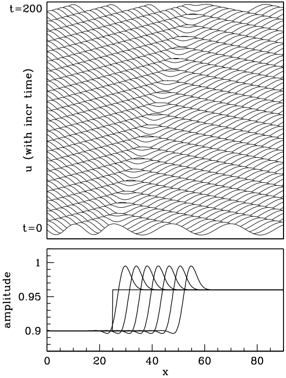

Analytical study of transition fronts in periodic wave amplitude shows that these move from a lower to a higher amplitude wave.

Therefore the wave generated by a larger obstacle will replace that generated by a smaller obstacle.

Outline

Conclusions

- The expected behaviour at the edge of Kielder Water provides a possible explanation for the periodic travelling waves that are observed in field vole density.
- For other parameter sets, the same mechanism generates spatiotemporal irregularity. A detailed explanation of this is possible via numerical calculation of wave stability.
- Results on obstacle size and multiple obstacles are consistent with intuitive expectations, and explain why very large obstacles are required to give detectable periodic waves.

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Future Work

The major outstanding issues are:

- Analytical prediction of wave stability away from Hopf bifurcation.
- Detailed study of how obstacle shape affects periodic travelling wave selection.

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List of Frames