Periodic Travelling Waves in Ecology

Jonathan A. Sherratt

Department of Mathematics and Maxwell Institute for Mathematical Sciences
Heriot-Watt University

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This talk can be downloaded from my web site
`www.ma.hw.ac.uk/~jas`

In collaboration with:

Matthew Smith

Xavier Lambin

Outline

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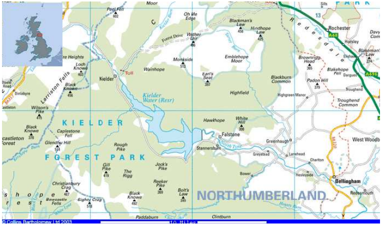
Field Voles in Kielder Forest



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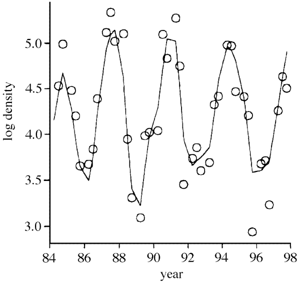

Field voles in Kielder Forest are cyclic (period 4 years).

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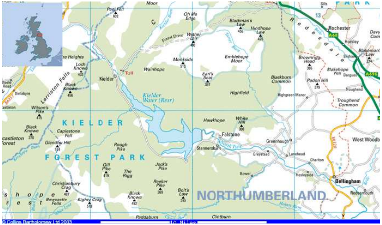

Field voles in Kielder Forest are cyclic (period 4 years).

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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Population density is periodic in space, with peaks and troughs moving across the domain at a constant speed.

Mathematically: a soln of form $U(x \pm ct)$, with $U(.)$ periodic.

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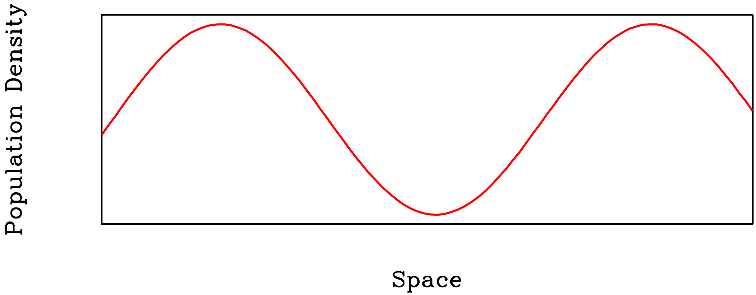

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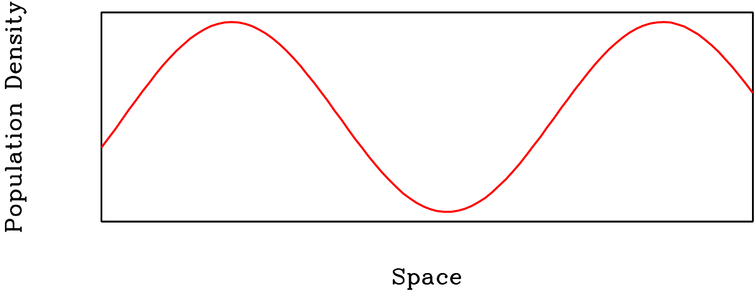

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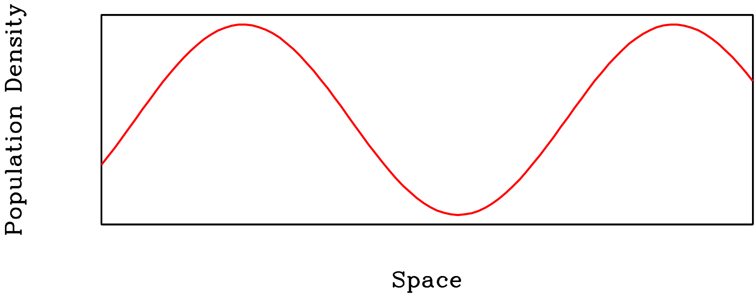

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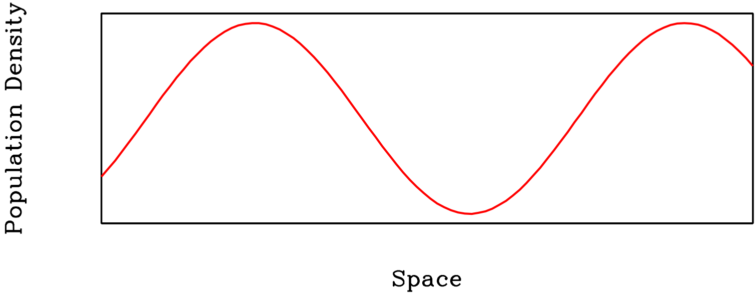

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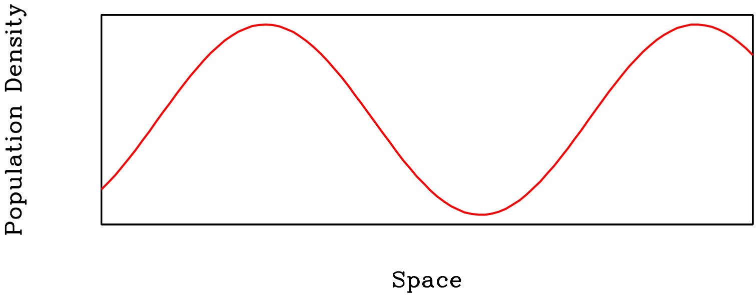

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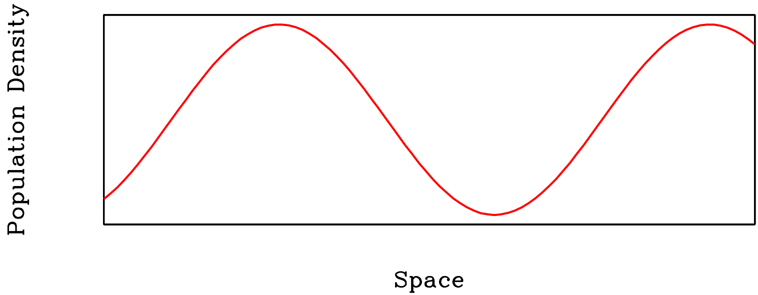

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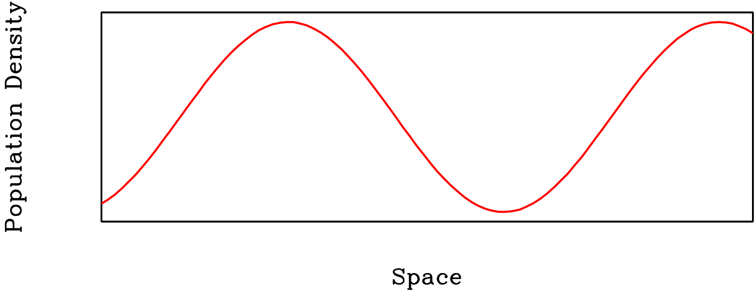

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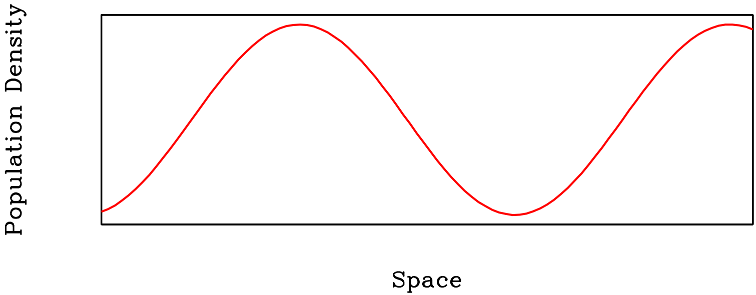

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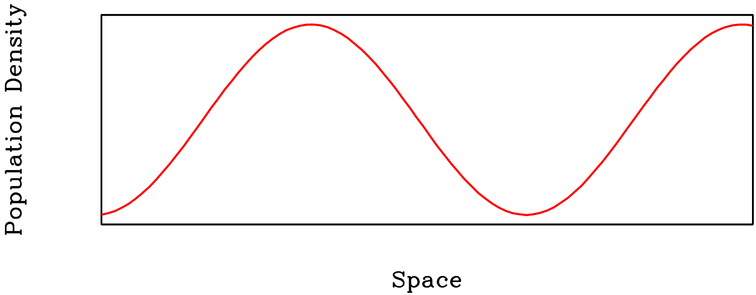

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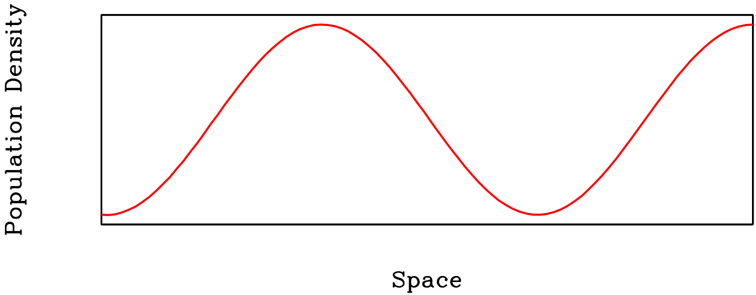

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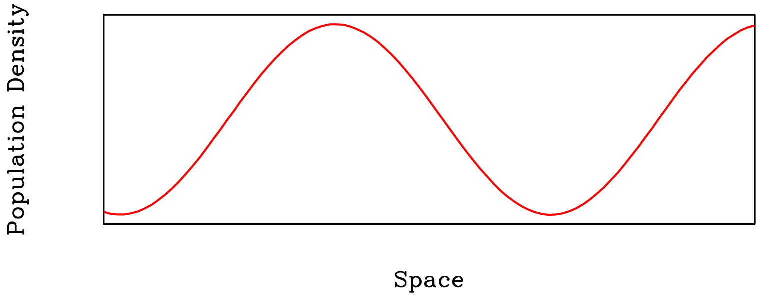

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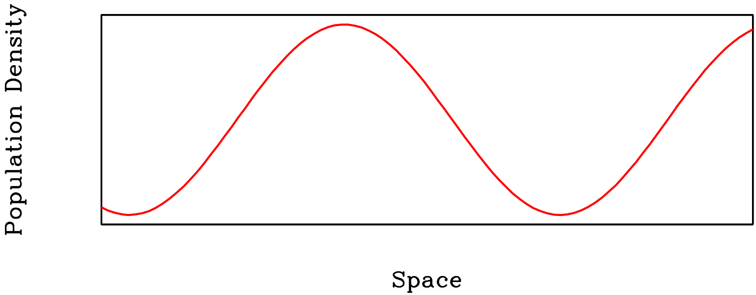

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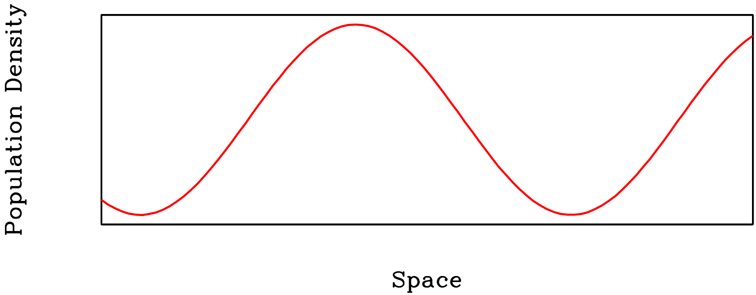

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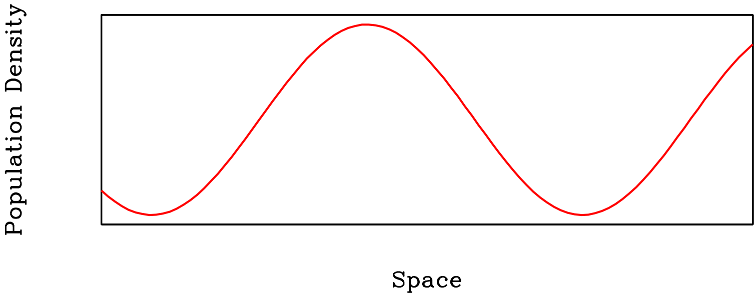

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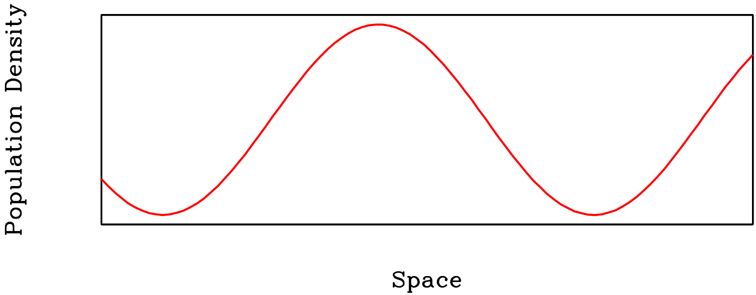

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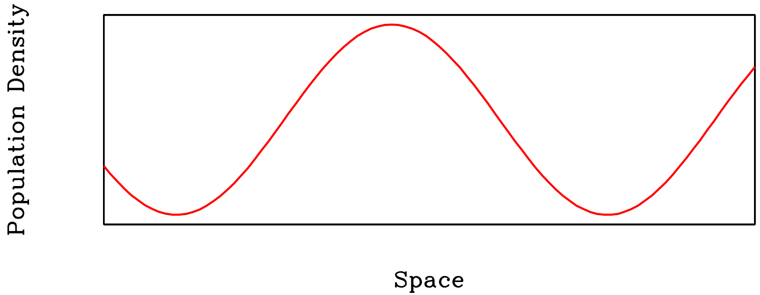

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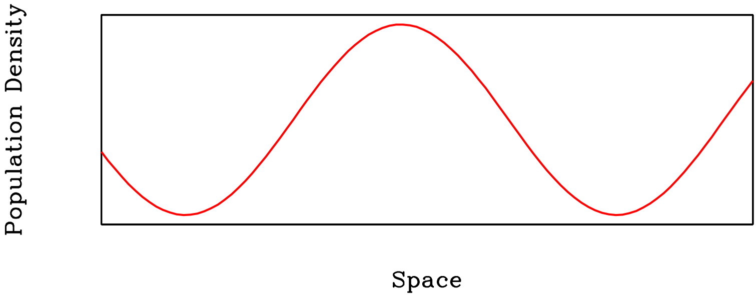

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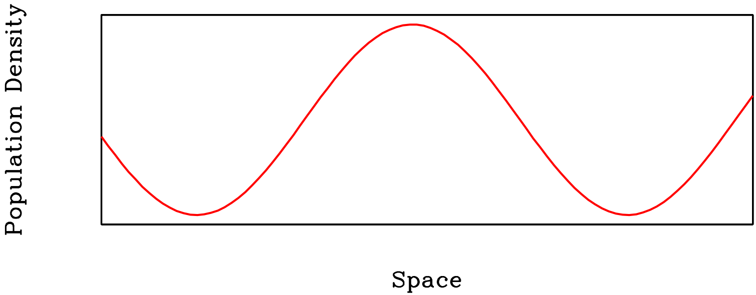

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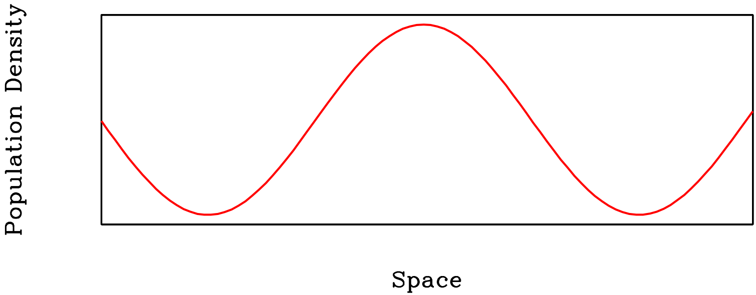

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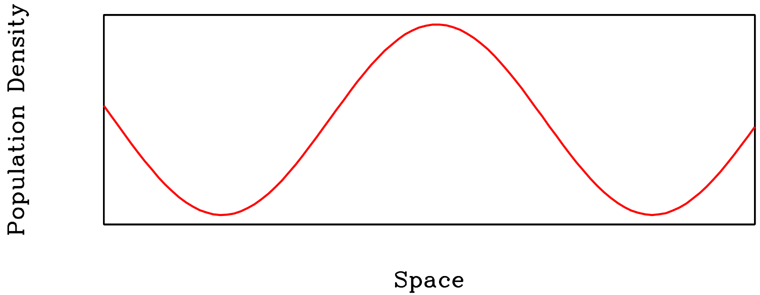

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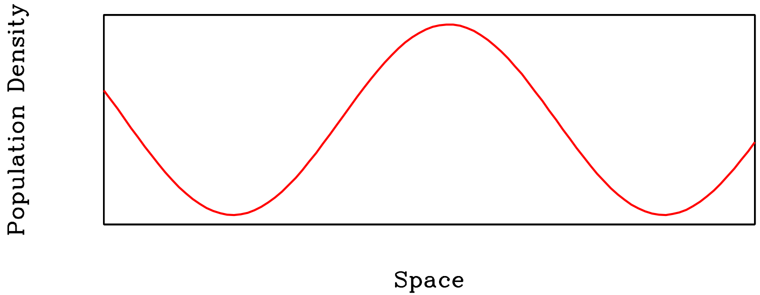

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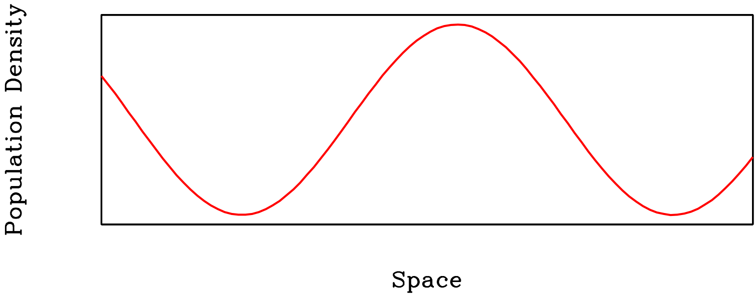

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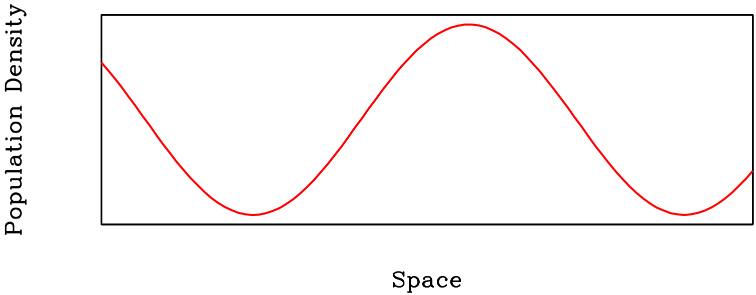

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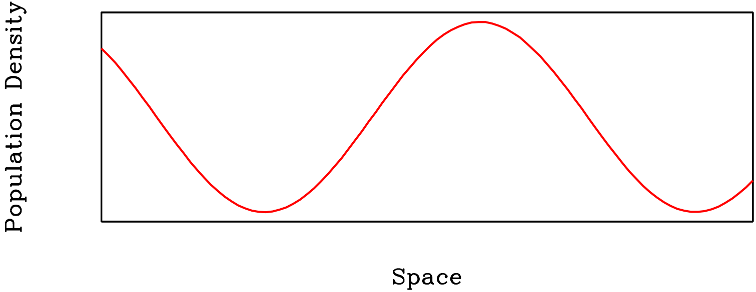

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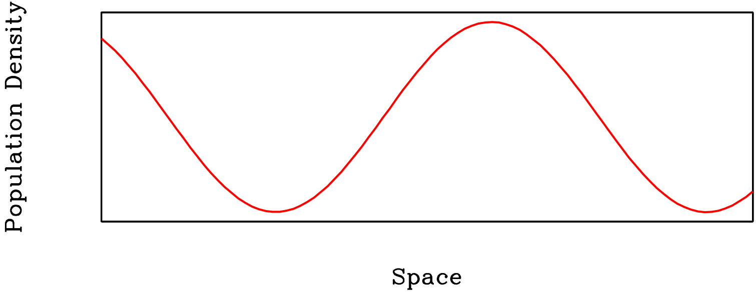

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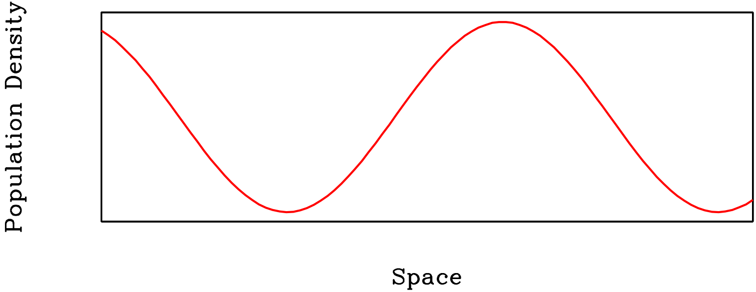

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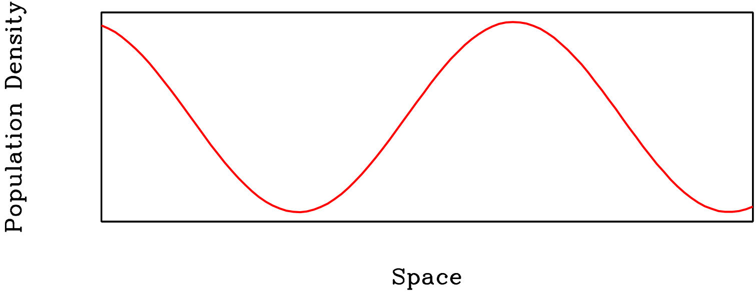

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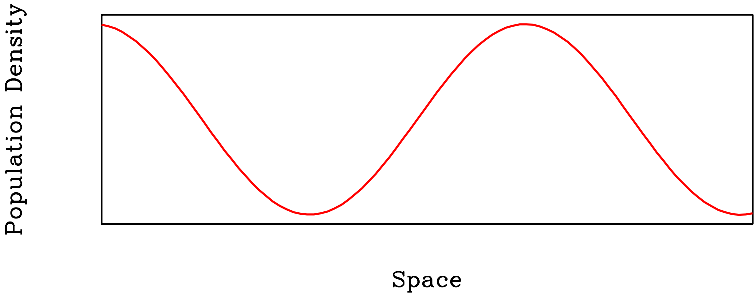

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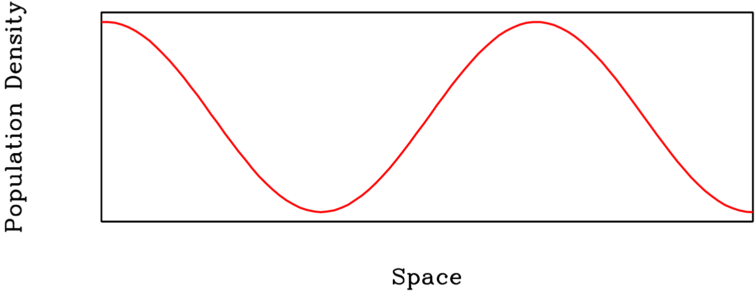

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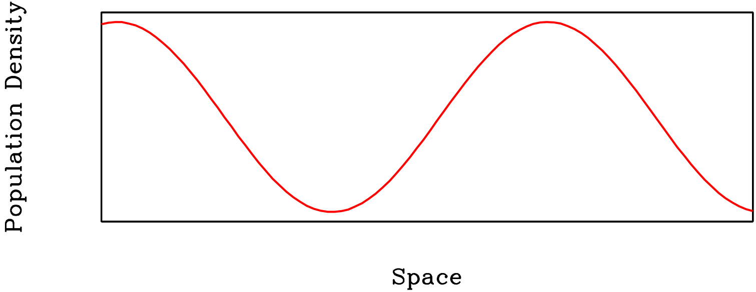

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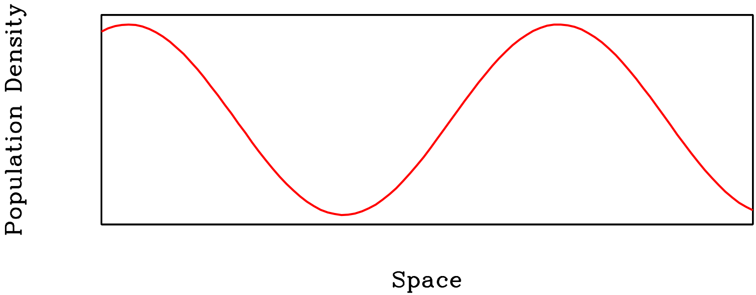

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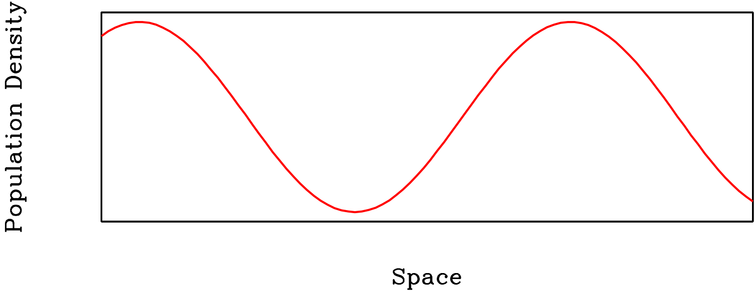

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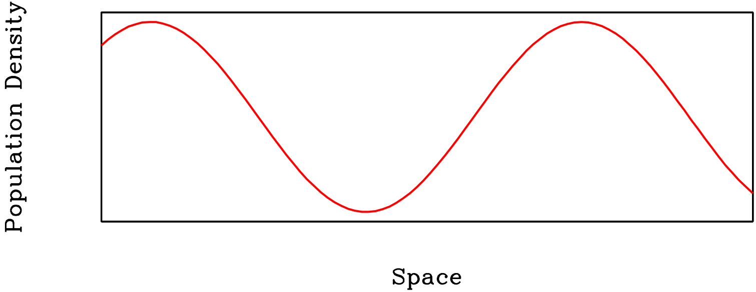

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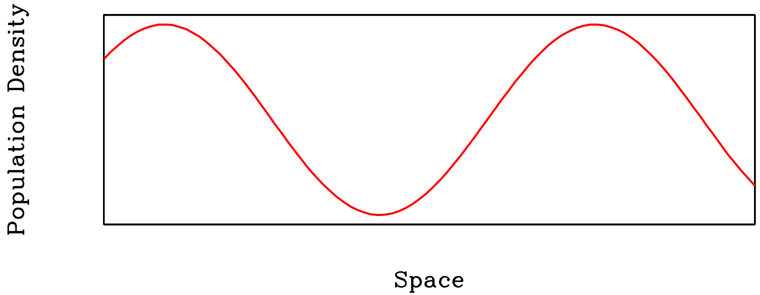

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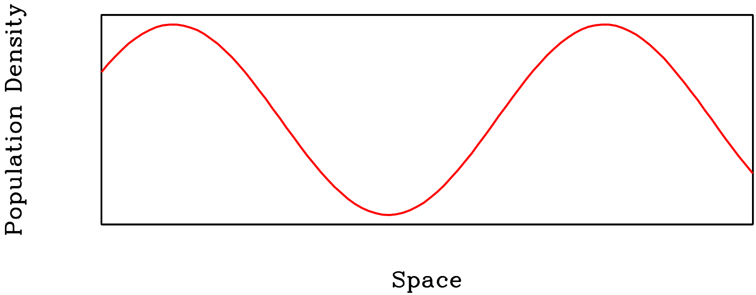

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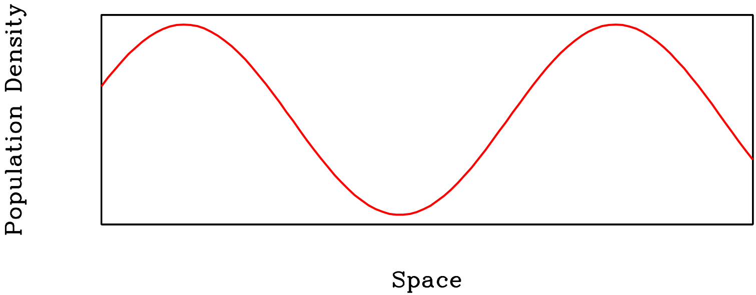

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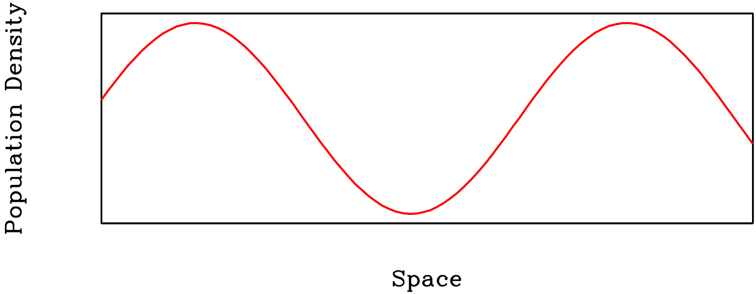

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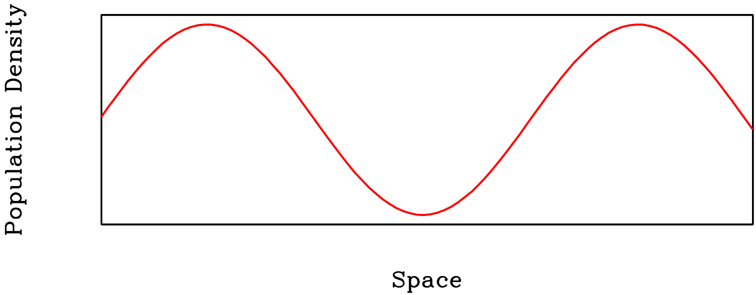

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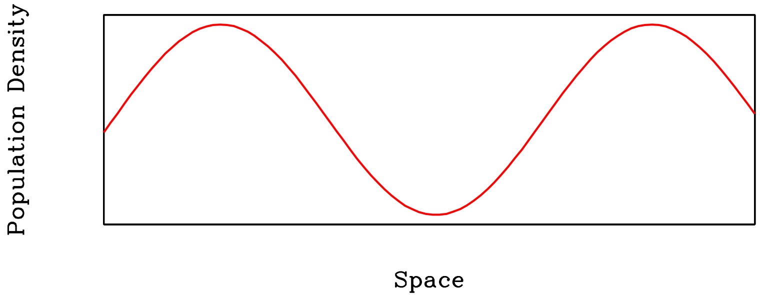

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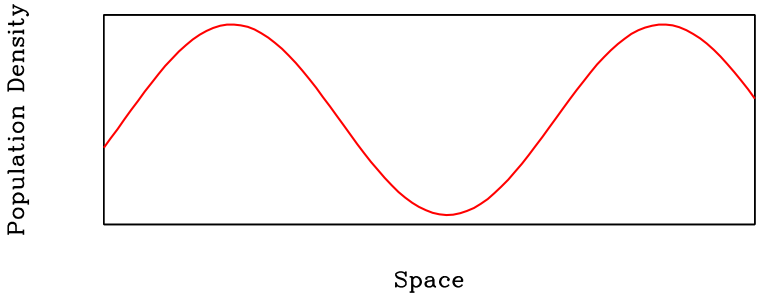

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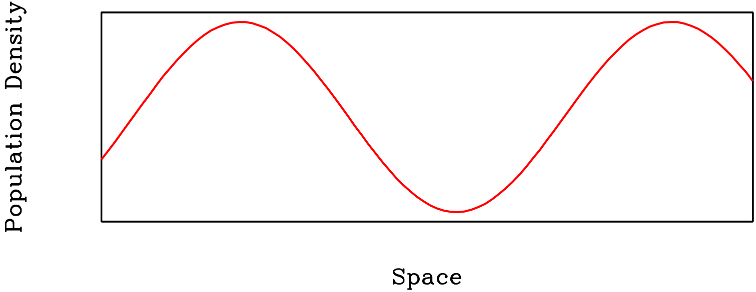

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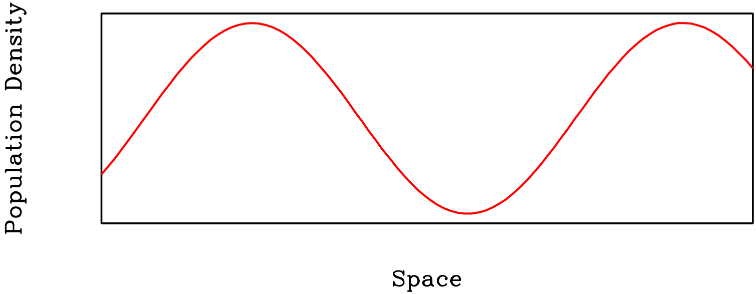

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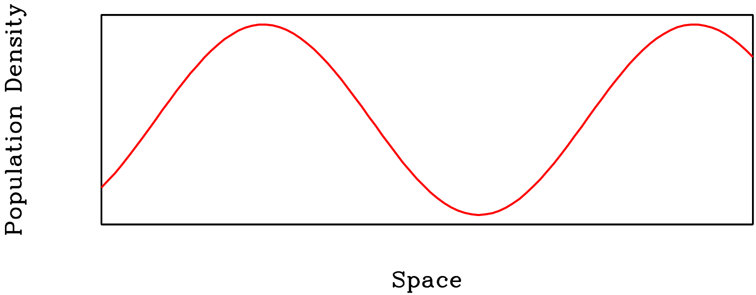

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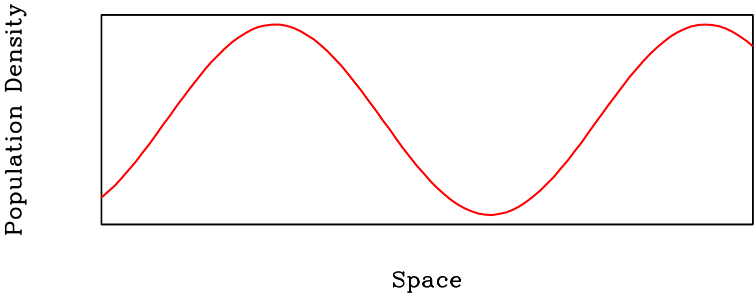

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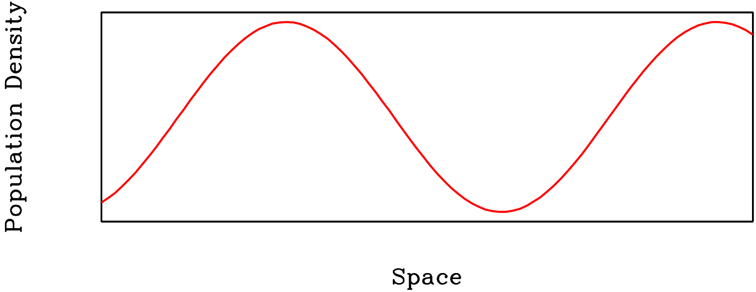

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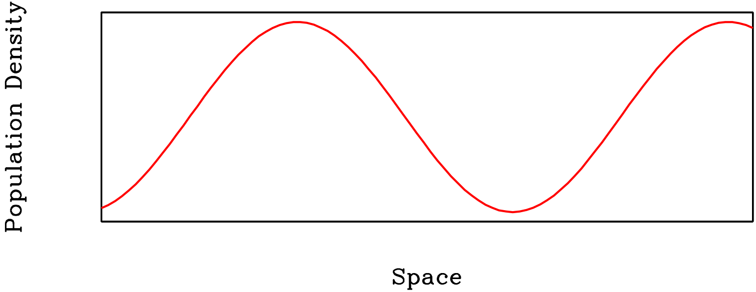

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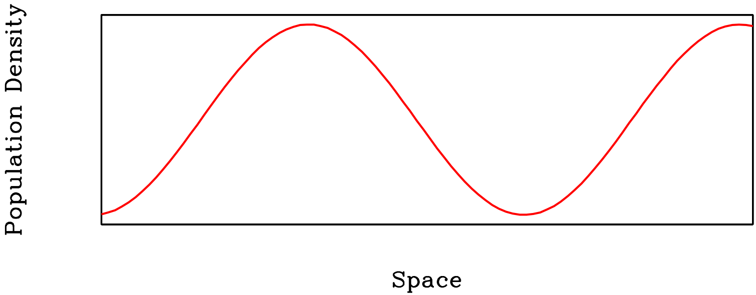

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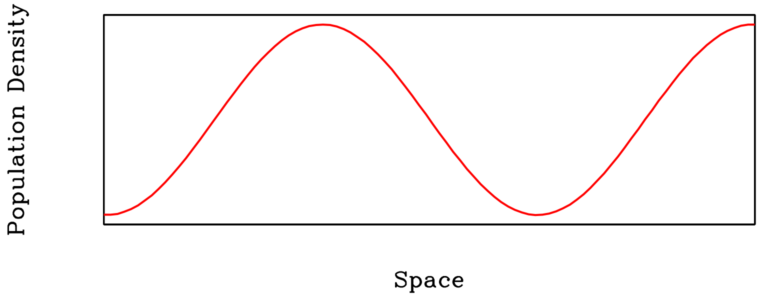

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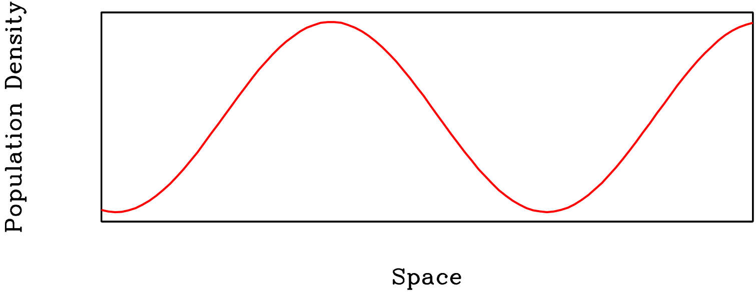

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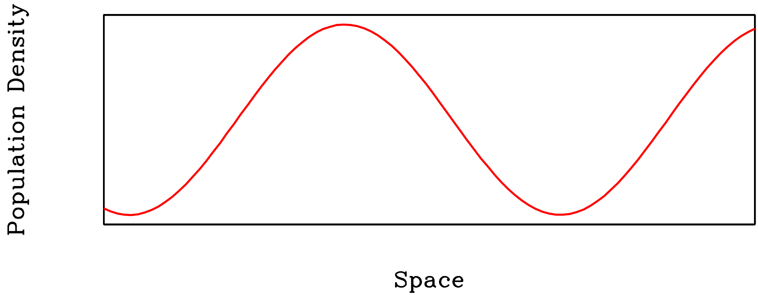

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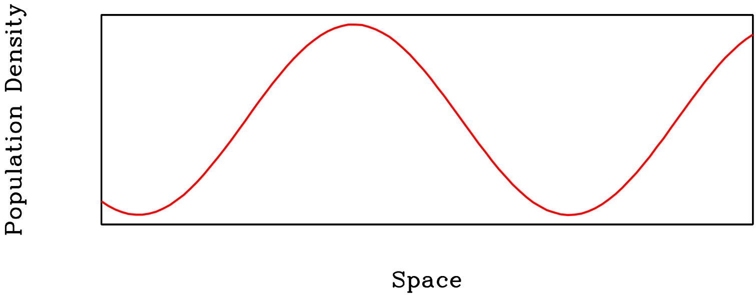

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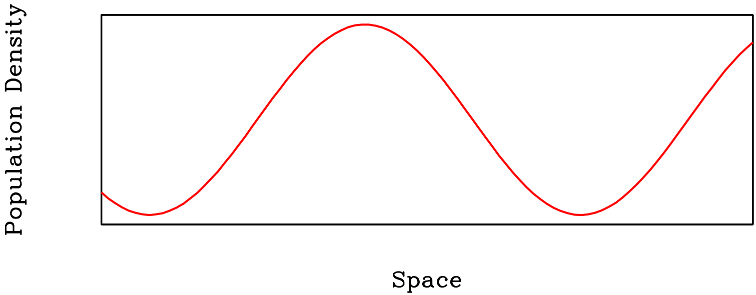

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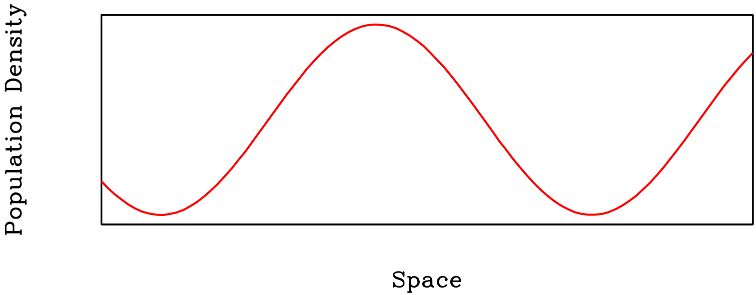

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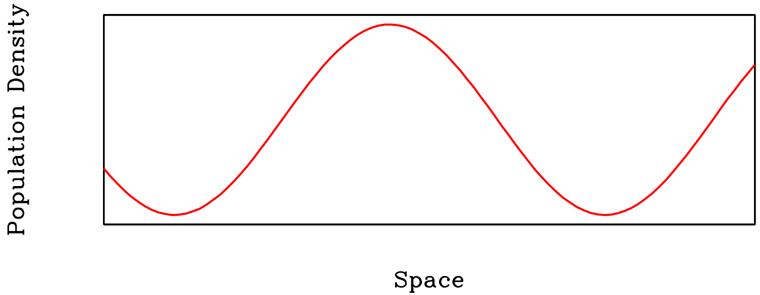

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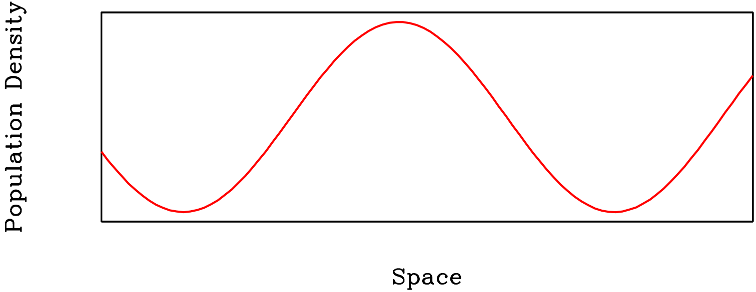

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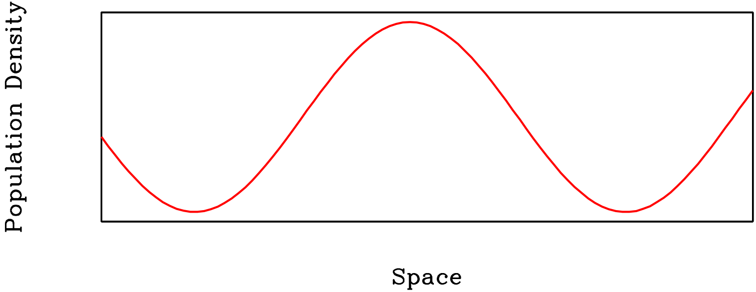

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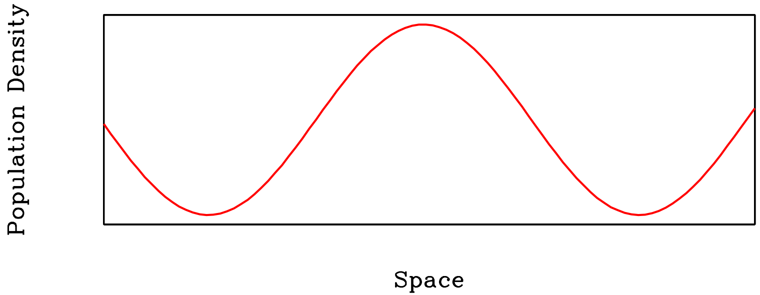

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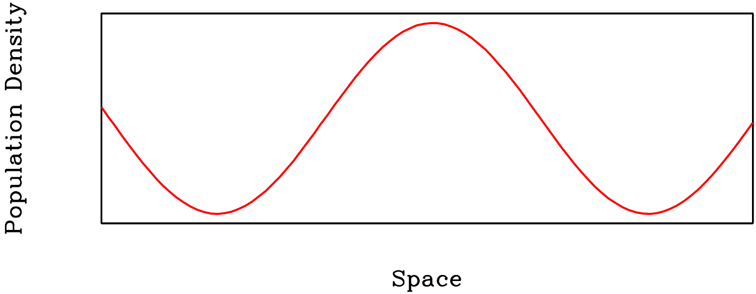

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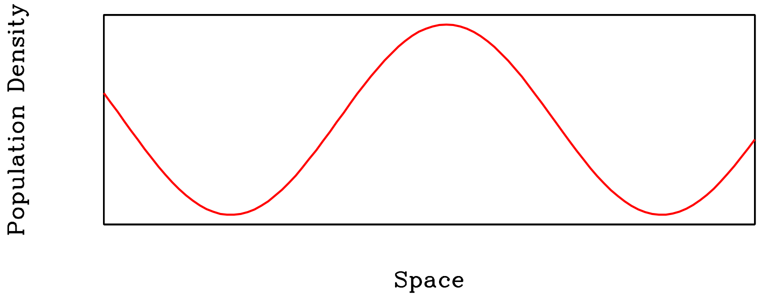

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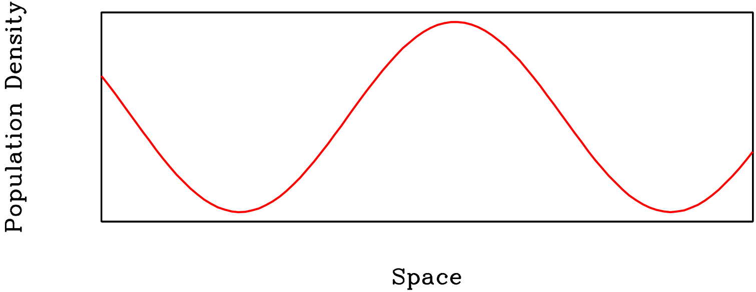

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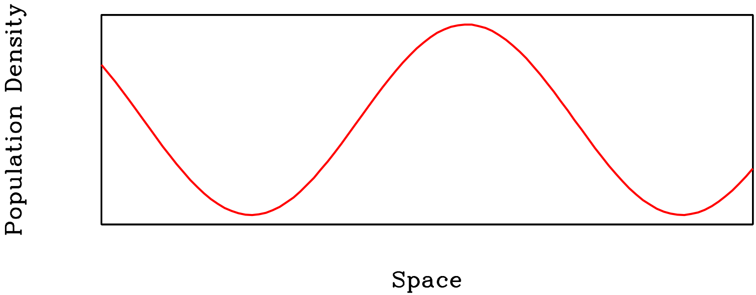

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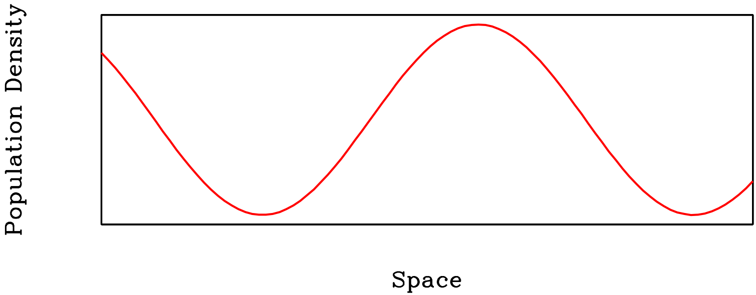

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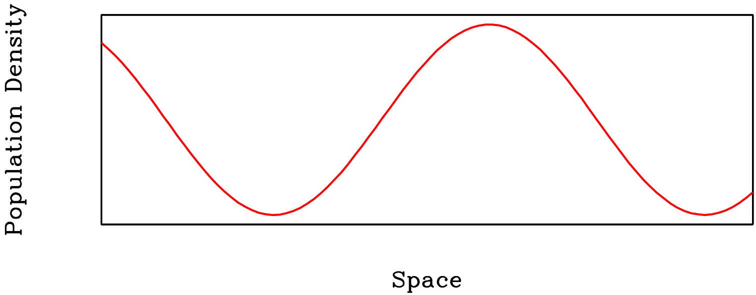

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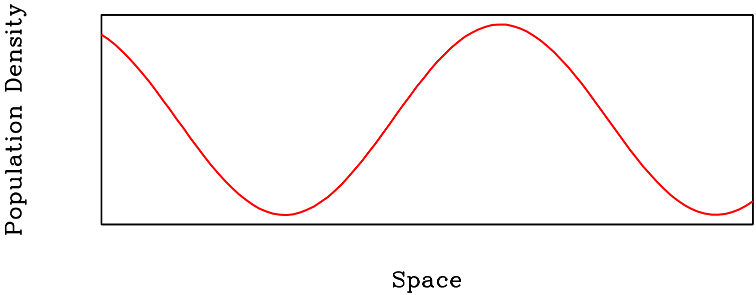

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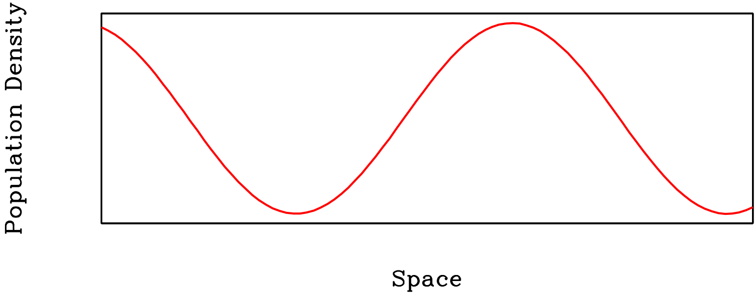

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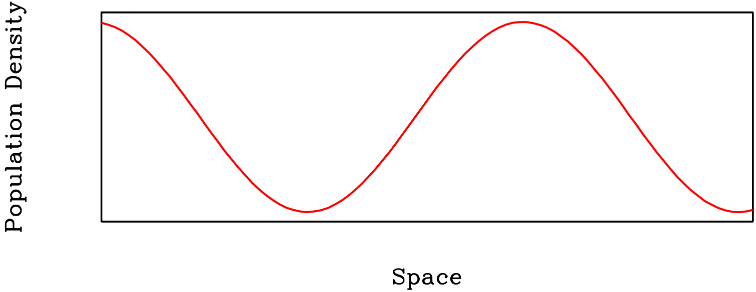

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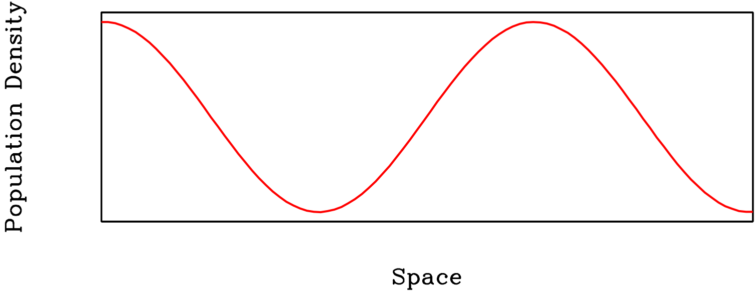

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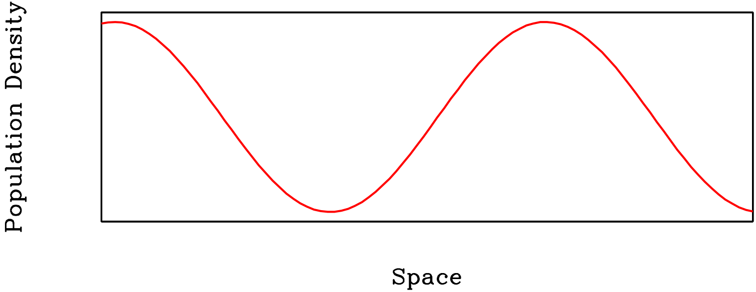

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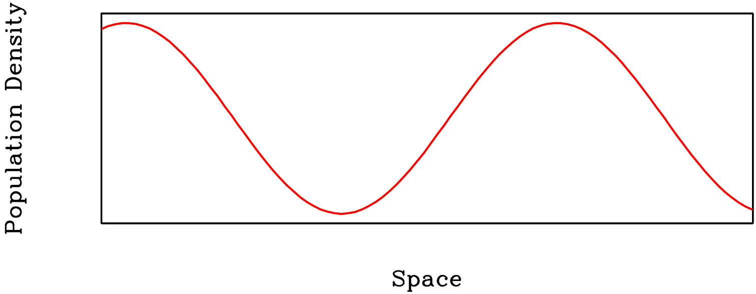

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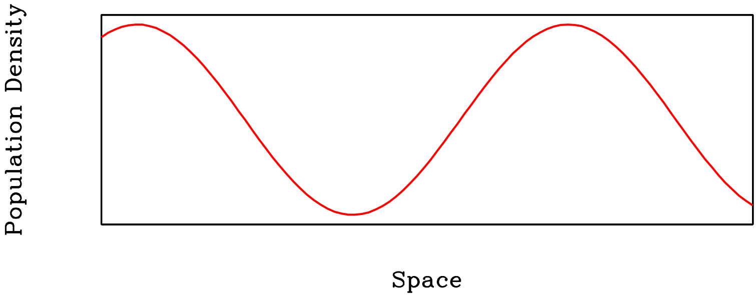

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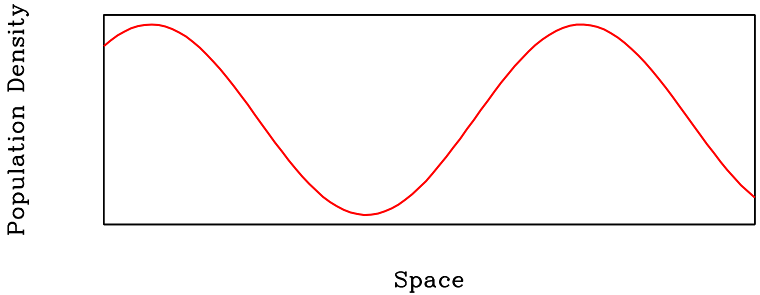

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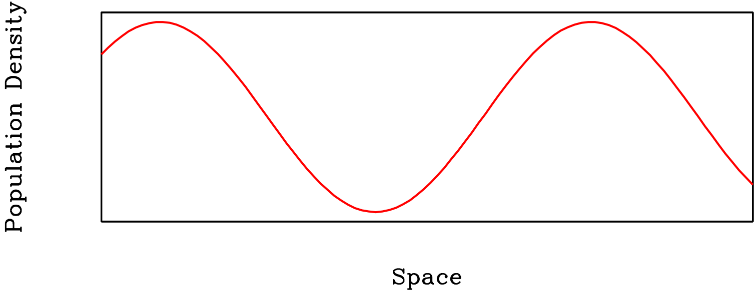

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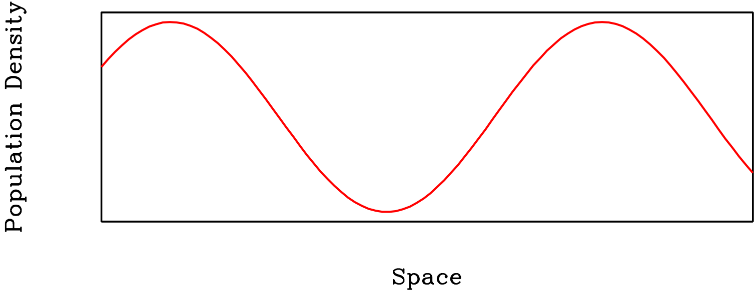

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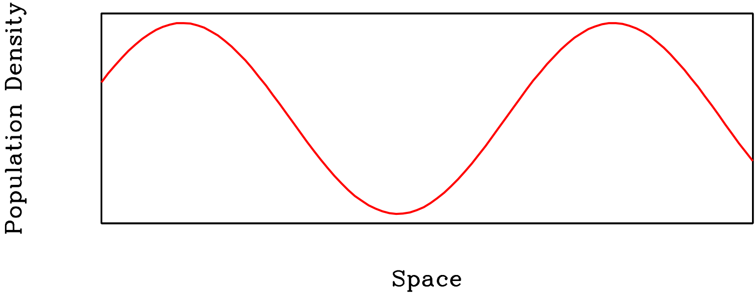

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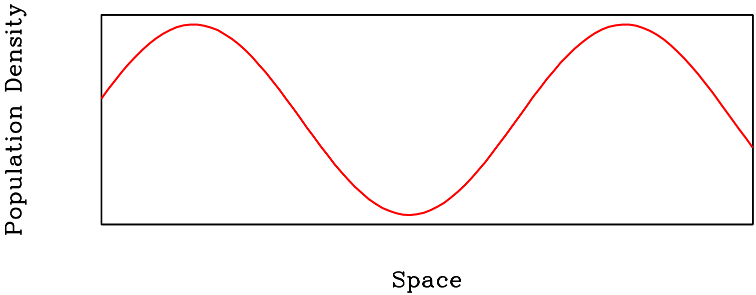

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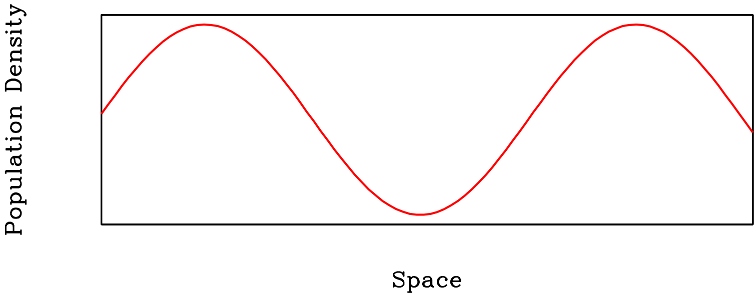

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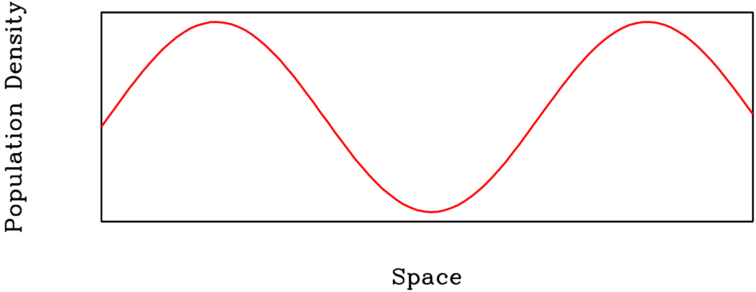

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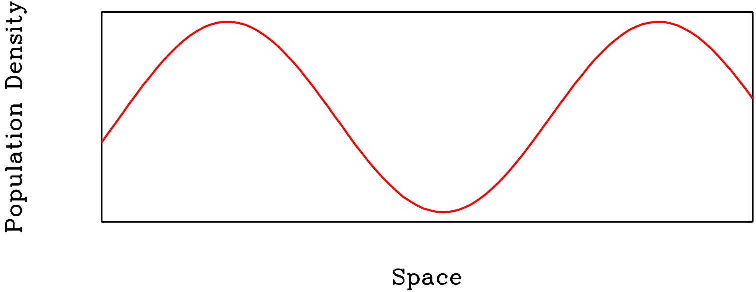

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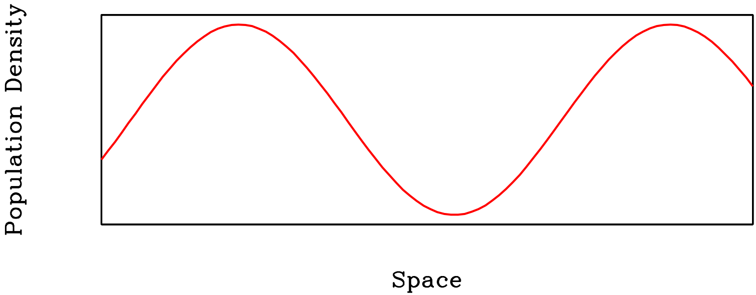
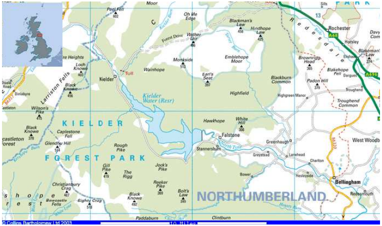


What Causes the Spatial Component of the Oscillations?



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

Outline

Field Voles in Kielder Forest

For modelling, we need an assumption on the cause of the population cycles.

Field Voles in Kielder Forest

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

A Standard Predator-Prey Model

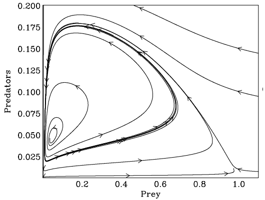
predators

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

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 kinetics:



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

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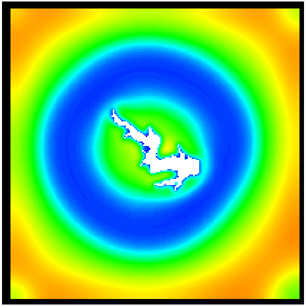
- To a good approx, vole density $=0$ at the reservoir edge
- At the edge of the forest, a zero flux boundary condition is a natural assumption

Typical Model Solution



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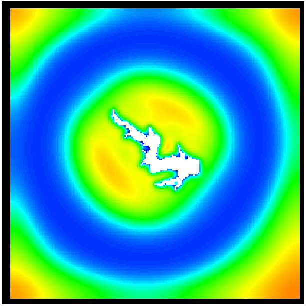

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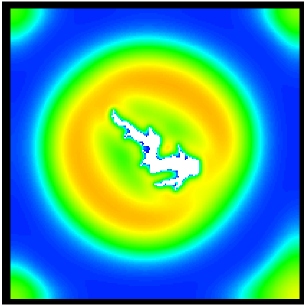

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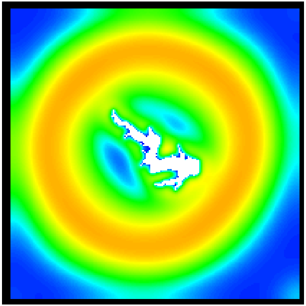

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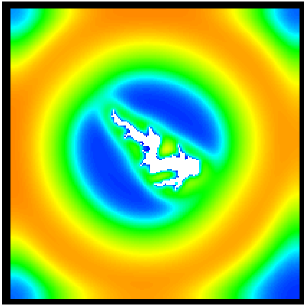

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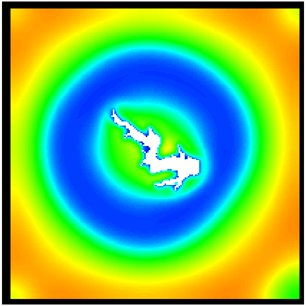
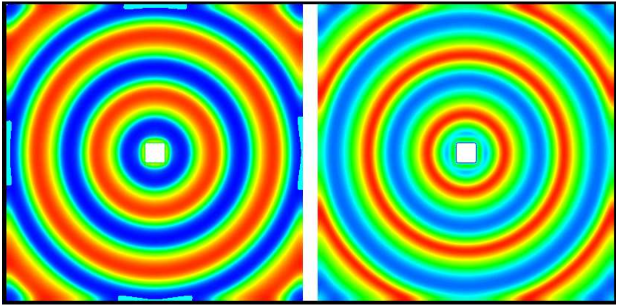


Periodic Wave Generation on a Large Domain

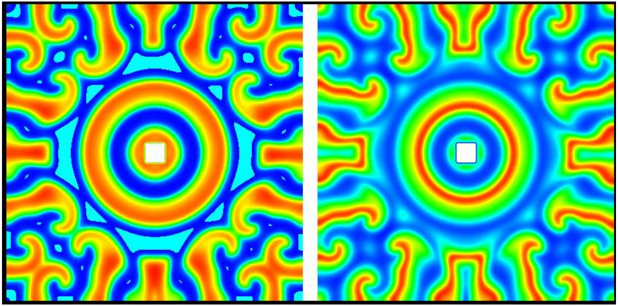


Movie of Wave Generation on a Large Domain

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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Outline

Regular and Irregular Patterns: the Goal

Goal: to predict which parameter sets will give periodic travelling waves, and which will give spatiotemporal irregularity.

Standard Theory of Periodic Travelling Wave

Mathematically, a periodic travelling wave is a soln of form $U(x \pm ct)$, with $U(.)$ periodic.

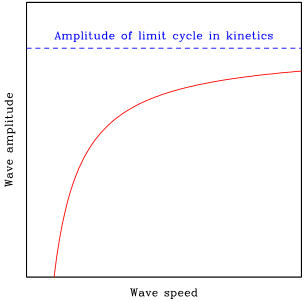
There is an extensive literature on periodic travelling waves in oscillatory reaction-diffusion equations

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

Standard Theory of Periodic Travelling Wave

Mathematically, a periodic travelling wave is a soln of form $U(x \pm ct)$, with $U(.)$ periodic.

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.



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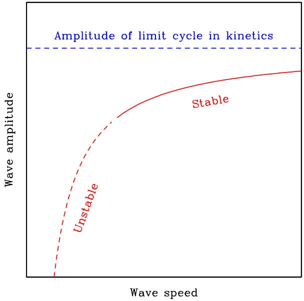
Some members of the periodic travelling wave family are stable as solutions of the partial differential equations, while others are unstable.



One-Dimensional Problem

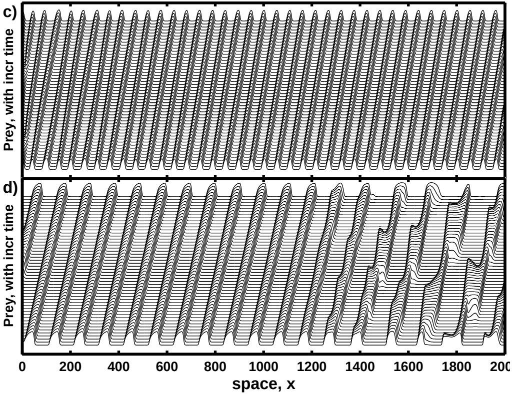
To simplify the field vole problem, solve on $0 < x < x_{max}$ with

$$\begin{array}{cccl} h = p = 0 & \text{at} & x = 0 & \leftrightarrow \text{edge of reservoir} \\ h_x = p_x = 0 & \text{at} & x = x_{max} & \leftrightarrow \text{edge of forest} \end{array}$$

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

Periodic Wave Generation in 1-D Simulations

Example of periodic wave generation by boundary conditions corresponding to the reservoir edge in 1-D:



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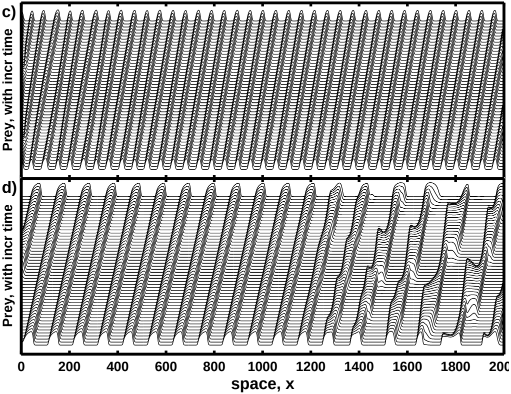

Conclusion: irregular patterns occur when the (Dirichlet) boundary condition at $x = 0$ generates a periodic travelling wave that is unstable.

Therefore we must investigate wave stability in detail.

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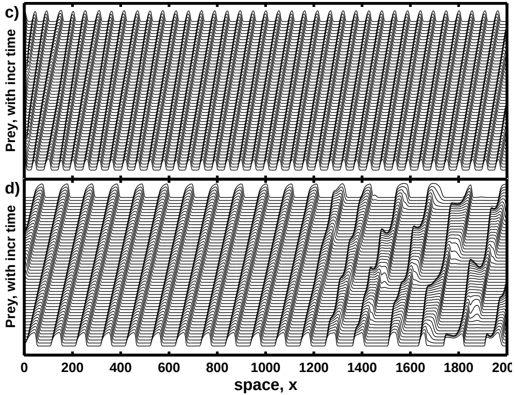

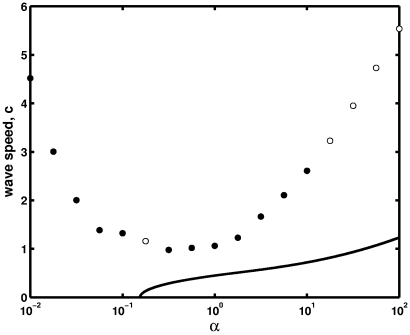

The Eigenvalue Problem

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

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

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

$\Rightarrow$ Eigenfunction eqn:
$$\begin{aligned} \lambda\overline{u} &= D_u \overline{u}_{zz} + c\overline{u}_z + f_u(U,V)\overline{u} + f_v(U,V)\overline{v} \\ \lambda\overline{v} &= D_v \overline{v}_{zz} + c\overline{v}_z + g_u(U,V)\overline{u} + g_v(U,V)\overline{v} \end{aligned}$$

Boundary conditions:
$$\begin{aligned} \overline{u}(0) &= \overline{u}(L)e^{i\gamma} \quad (0 \le \gamma < 2\pi) \\ \overline{v}(0) &= \overline{v}(L)e^{i\gamma} \quad (0 \le \gamma < 2\pi) \end{aligned}$$

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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 periodic wave eqns

$$
\begin{aligned}
0 &= D_u U_{zz} + cU_z + f(U,V) \\
0 &= D_v V_{zz} + cV_z + g(U,V) \quad (z = x - ct)
\end{aligned}
$$

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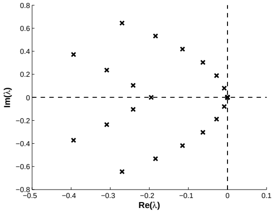

$$\begin{aligned}\lambda\overline{u} &= D_u\overline{u}_{zz} + c\overline{u}_z + f_u(U,V)\overline{u} + f_v(U,V)\overline{v}, \quad \overline{u}(0)=\overline{u}(L)\\ \lambda\overline{v} &= D_v\overline{v}_{zz} + c\overline{v}_z + g_u(U,V)\overline{u} + g_v(U,V)\overline{v}, \quad \overline{v}(0)=\overline{v}(L)\end{aligned}$$

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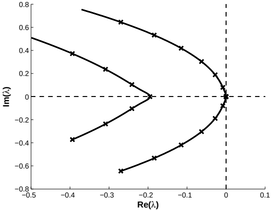

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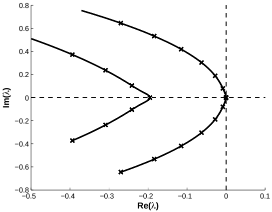

This gives the eigenvalue spectrum, and hence (in)stability

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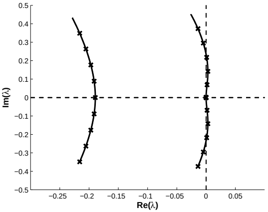
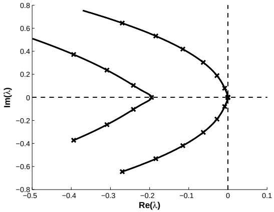


UNSTABLE

Eckhaus instability



STABLE

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

Stability in a Parameter Plane

By following this procedure at each point on a grid in parameter space, regions of stability/instability can be determined.

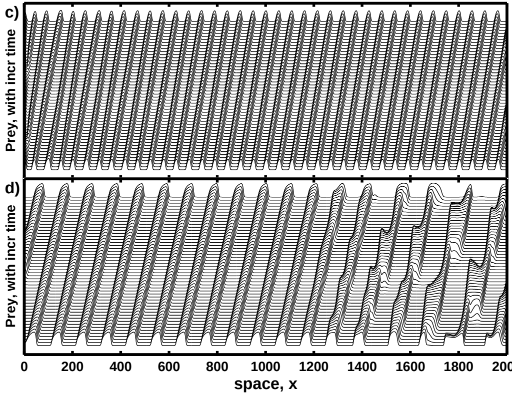
In fact, stable/unstable boundaries can be computed accurately by numerical continuation of the point at which

$$\mathrm{Re}\lambda = \mathrm{Im}\lambda = \gamma = \partial^2 \mathrm{Re}\lambda / \partial\gamma^2 = 0$$

(Eckhaus instability point)

Back to Wave Generation in 1-D Simulations

Example of periodic wave generation by Dirichlet boundary conditions in the predator-prey model:



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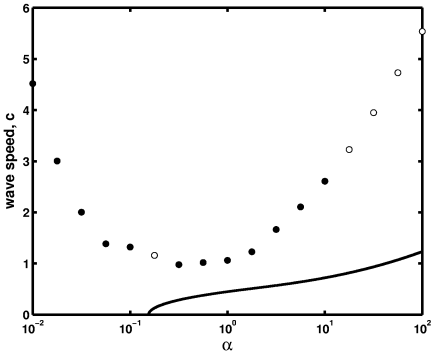
From such simulations, we can easily calculate wave speed vs parameters



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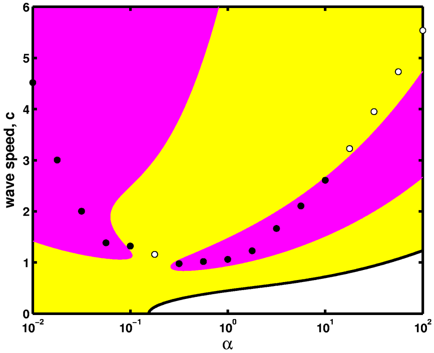
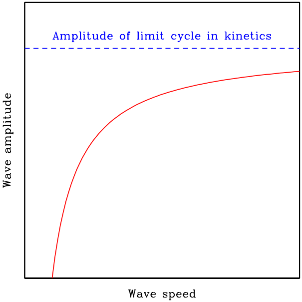


Our stability calculations explain the surprising results from simulations of periodic wave generation

Outline

The Wave Selection Problem

An oscillatory reaction-diffusion system has a one-parameter family of periodic travelling waves.



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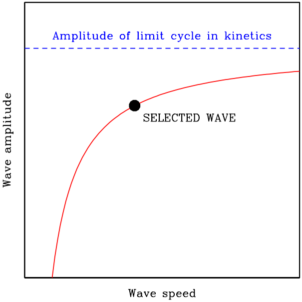

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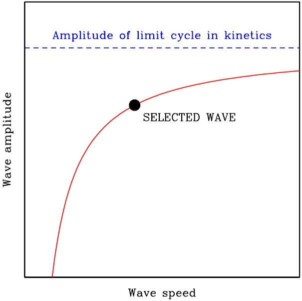

Key Question:
which member of the wave family is selected by the boundary condition at the reservoir edge?

This question can be answered analytically when $D_p = D_h$, close to Hopf bifurcation in the kinetics.

Step 1: Reduction to Normal Form

Consider the case of $D_p = D_h$ close to Hopf bifurcation in the kinetics. Then standard normal form analysis reduces the predator-prey model to

$$\begin{aligned} u_t &= u_{xx} + \lambda(r)u - \omega(r)v \\ v_t &= v_{xx} + \omega(r)u + \lambda(r)v \end{aligned} \qquad \text{where} \quad \begin{aligned} \lambda(r) &= 1 - r^2 \\ \omega(r) &= \omega_0 - \omega_1 r^2. \end{aligned}$$

$$\text{Here} \quad \begin{aligned} \omega_0 &= \frac{2}{C(A-1)-(A+1)}\left[\frac{A(A^2-1)}{B}\right]^{1/2} + \left[\frac{A-1}{A(A+1)B}\right]^{1/2} \\ \omega_1 &= \frac{4A^2B^2+(A^2-1)(A^2+5)AB+(A^2-1)^2}{6A^{5/2}(A^2-1)^{1/2}B^{3/2}} \end{aligned}$$

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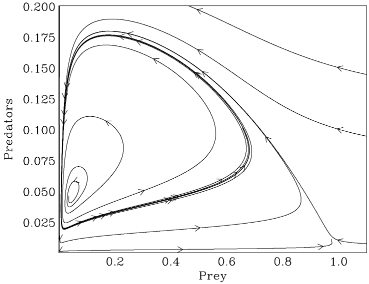

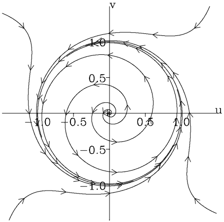

"λ–ω system"

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The periodic travelling wave family is

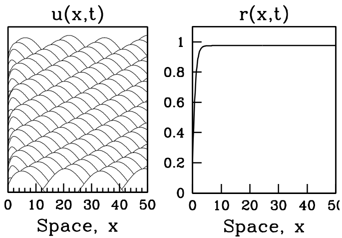
$$\begin{aligned} u &= r^* \cos\left[\omega(r^*)t \pm \sqrt{\lambda(r^*)}x\right] \\ v &= r^* \sin\left[\omega(r^*)t \pm \sqrt{\lambda(r^*)}x\right] \end{aligned}$$

Step 2: Exact Solution for the Wave Amplitude

For the λ–ω equations, the long term solution is

$$r(x,t) \equiv \sqrt{u^2+v^2} = R(x)$$

independent of time



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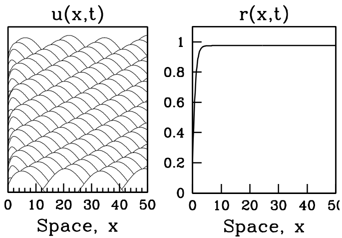


$$R(x) = r_{ptw} \tanh\left(x/\sqrt{2}\right) \qquad \text{with } r_{ptw} = \left\{\tfrac{1}{2}\left[1+\sqrt{1+\tfrac{8}{9}\omega_1^2}\right]\right\}^{-1/2}$$

Step 3: Deduce Wave Properties from Amplitude

The periodic travelling wave amplitude is $r_{ptw} = \left\{ \frac{1}{2}\left[1+\sqrt{1+\frac{8}{9}\omega_1^2}\right]\right\}^{-1/2}$.

The wave solution is

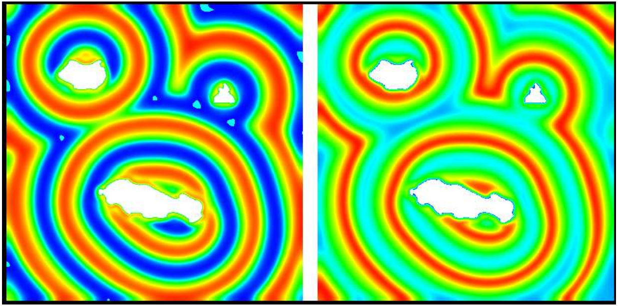
$$\begin{aligned} u &= r_{ptw} \cos[\omega(r_{ptw})t \pm \lambda(r_{ptw})^{1/2}x] \\ v &= r_{ptw} \sin[\omega(r_{ptw})t \pm \lambda(r_{ptw})^{1/2}x] \\ & \quad (\lambda(r) = 1 - r^2, \omega(r) = \omega_0 - \omega_1 r^2). \end{aligned}$$

Therefore:

$$\begin{aligned} \text{wavelength} &= 2\pi/\sqrt{1 - r_{ptw}^2} \\ \text{time period} &= 2\pi/(\omega_0 - \omega_1 r_{ptw}^2) \\ \text{speed} &= (\omega_0 - \omega_1 r_{ptw}^2)/\sqrt{1 - r_{ptw}^2} \end{aligned}$$

Outline

Typical Predator-Prey Solution with Multiple Obstacles



Competition between Obstacles

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

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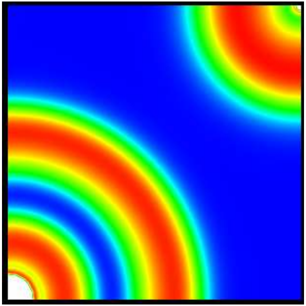

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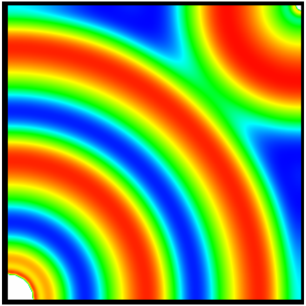

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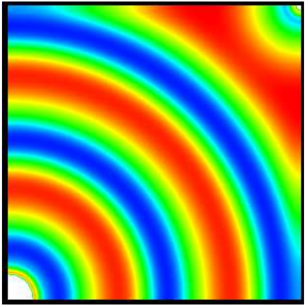

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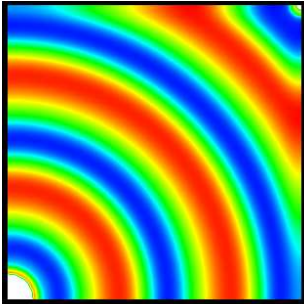


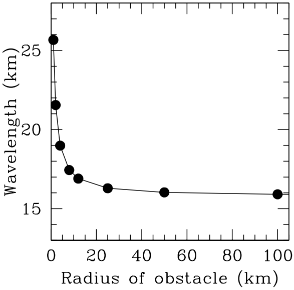
Competition between Obstacles

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

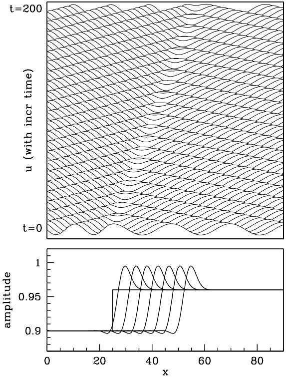
Numerical solutions for circular obstacles indicate that wavelength far from the obstacle varies with obstacle radius.



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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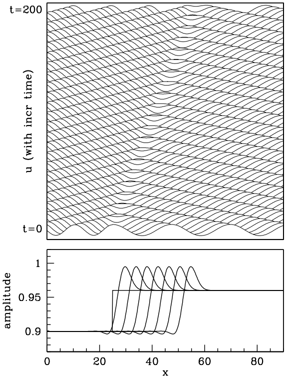

Analytical study of transition fronts in periodic wave amplitude shows that these move from a lower to a higher amplitude wave.

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

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.
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Conclusions (continued)

- Analytical periodiction of periodic travelling wave properties is possible close to Hopf bifurcation in the kinetics, by solving the wave selection problem.
- Since λ–ω equations are the normal form of *any* oscillatory reaction-diffusion system close to Hopf bifurcation, and since boundaries with Dirichlet conditions are common in applications, we expect both periodic travelling waves and spatiotemporal irregularity to be a general feature of such systems.

Conclusions (continued)

- Analytical periodiction of periodic travelling wave properties is possible close to Hopf bifurcation in the kinetics, by solving the wave selection problem.
- Since λ–ω equations are the normal form of *any* oscillatory reaction-diffusion system close to Hopf bifurcation, and since boundaries with Dirichlet conditions are common in applications, we expect both periodic travelling waves and spatiotemporal irregularity to be a general feature of such systems.

Mathematical Limitations

Mathematically, the major limitations are:

- Analytical prediction of wave stability away from Hopf bifurcation is not currently possible.
- There is not currently a solution of the wave selection problem away from Hopf bifurcation (either analytical or numerical).

Relevant Papers and Software

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

This paper is a review of periodic travelling waves in ecological field data and in mathematical models of cyclic populations. The associated online material contains a detailed tutorial on numerical calculation of periodic travelling wave stability, including computer code (in Fortran).

The paper and the online material are freely available from my web site: `www.ma.hw.ac.uk/~jas`

Relevant Papers and Software

J.A. Sherratt, X. Lambin, T.N. Sherratt (2003) The effects of the size and shape of landscape features on the formation of travelling waves in cyclic populations. *Am. Nat.* 162, 503-513.

This paper concerns ecological applications of periodic travelling wave generation by obstacles. The associated online material contains a detailed tutorial on the reduction of an oscillatory reaction-diffusion system to normal form close to Hopf bifurcation, including computer code (in Maple).

The paper and the online material are freely available from my web site: `www.ma.hw.ac.uk/~jas`

List of Frames