How to Generate an Unstable Wavetrain, and Why it Matters for Voles

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In collaboration with:

Matthew Smith

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Outline

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What is a Periodic Travelling Wave?

Mathematically: a soln of form $f(x \pm ct)$, with $f(.)$ periodic
Everyday example: Mexican wave

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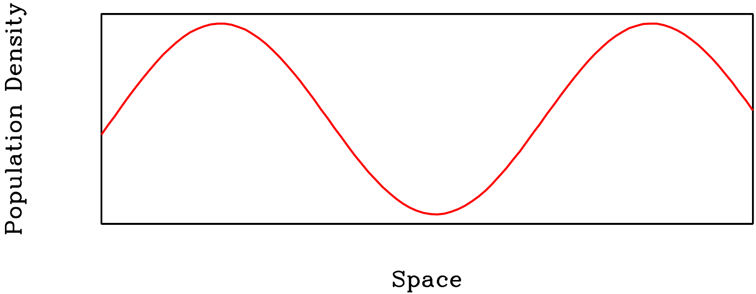

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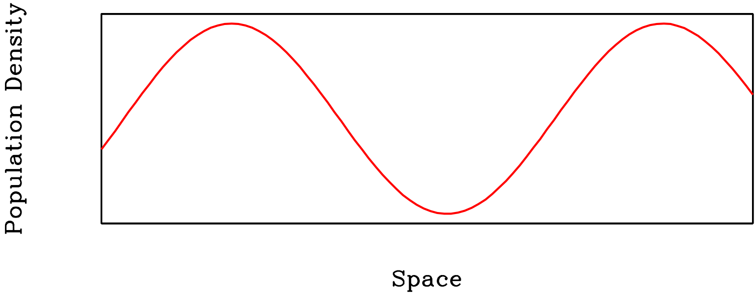

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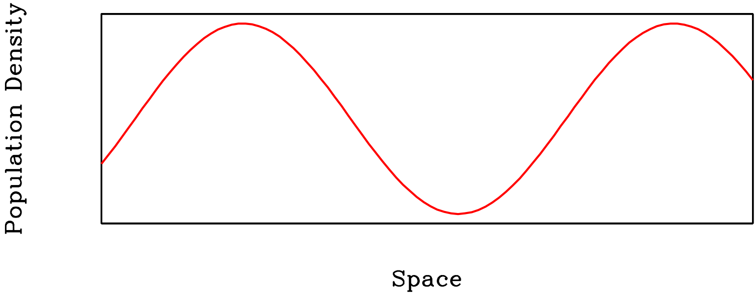

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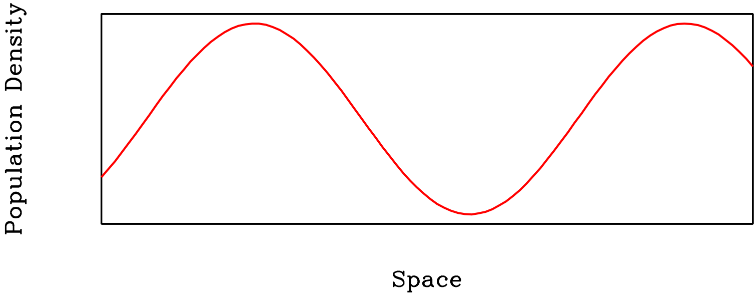

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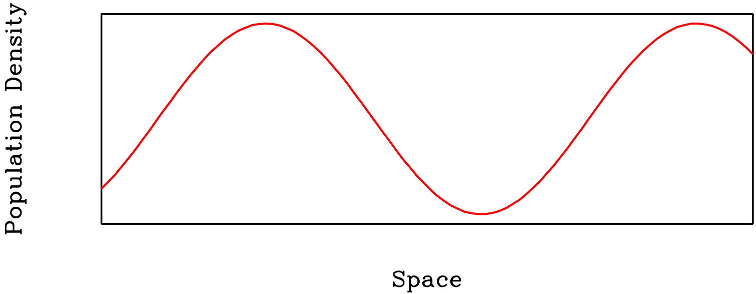

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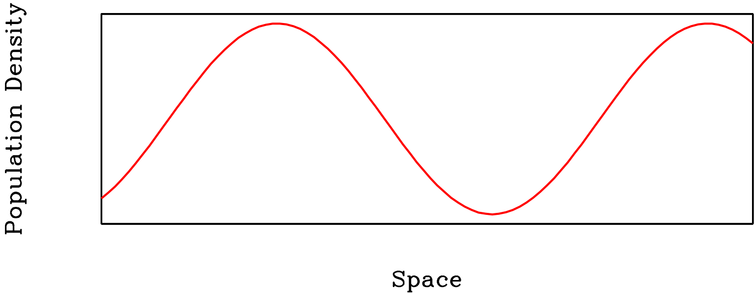

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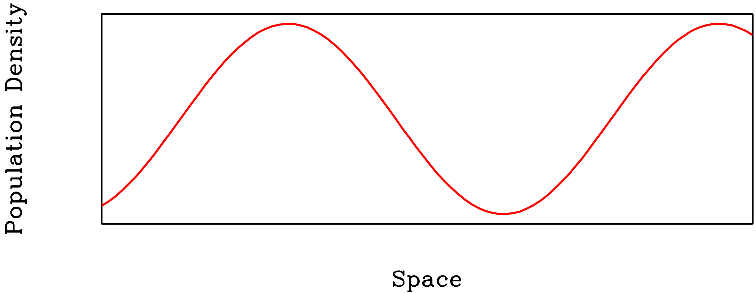

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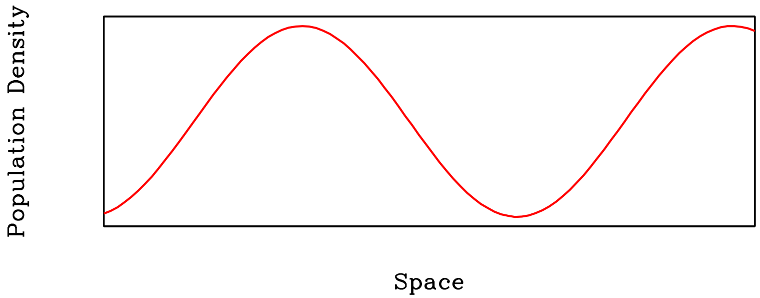

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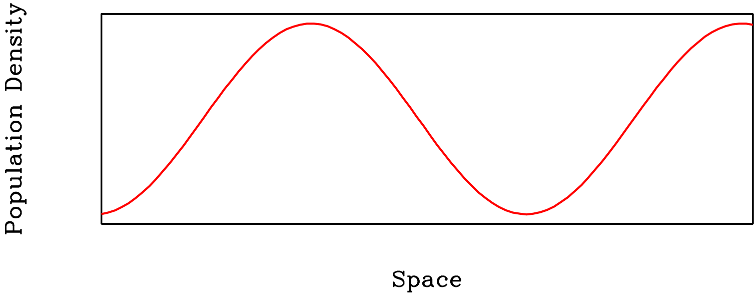

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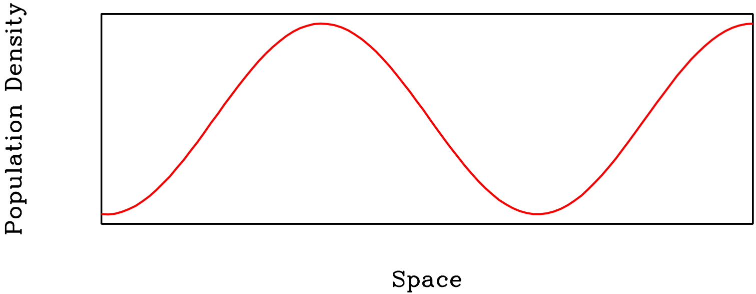

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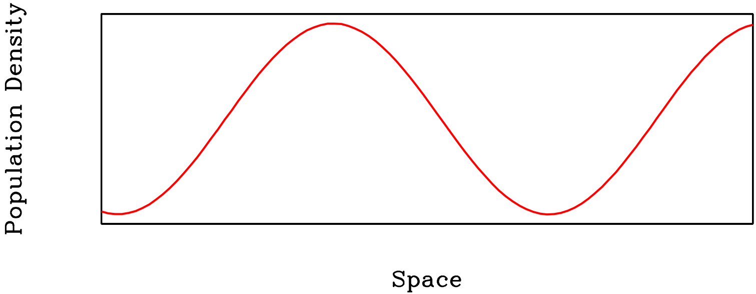

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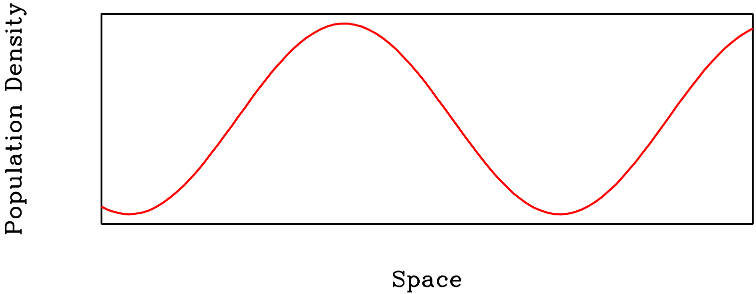

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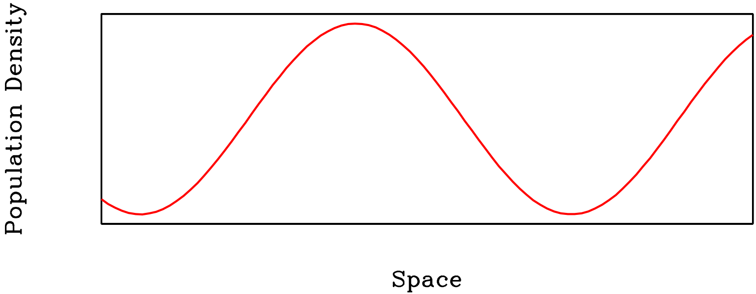

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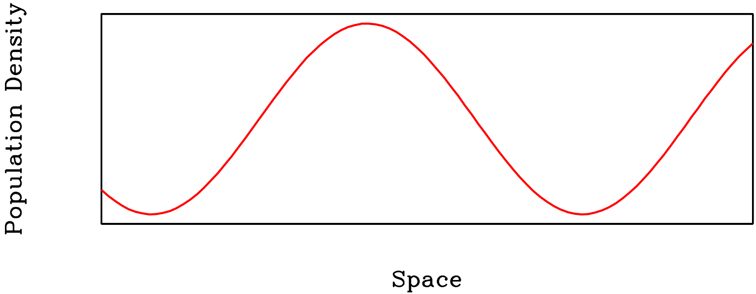

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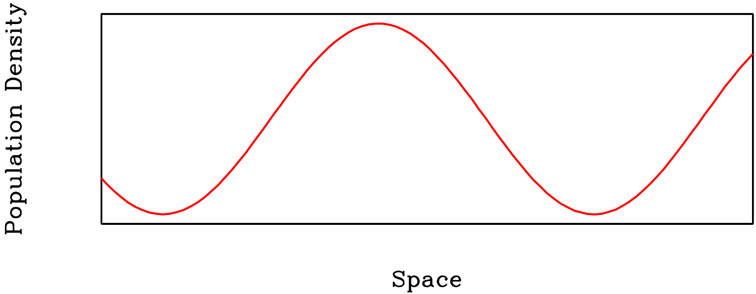

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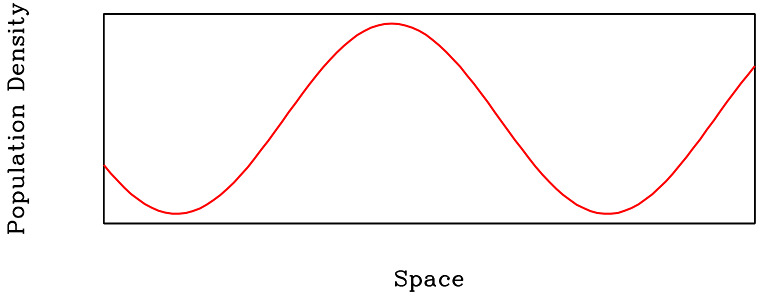

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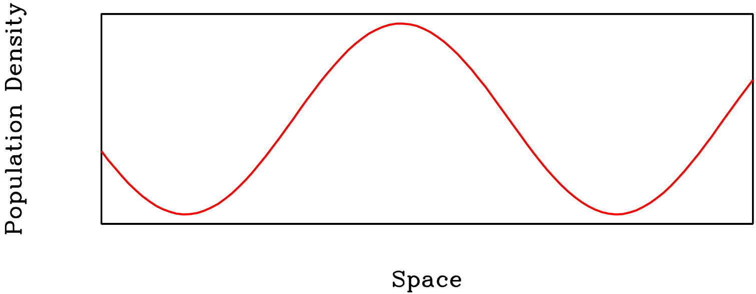

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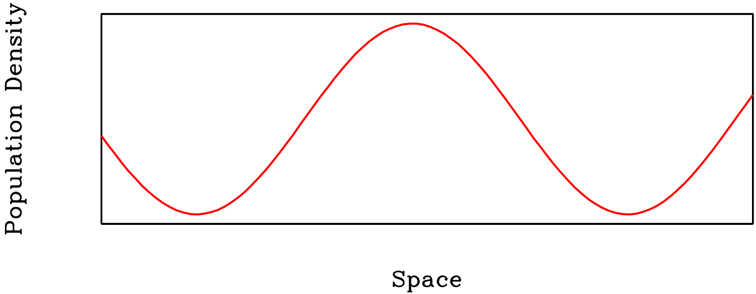

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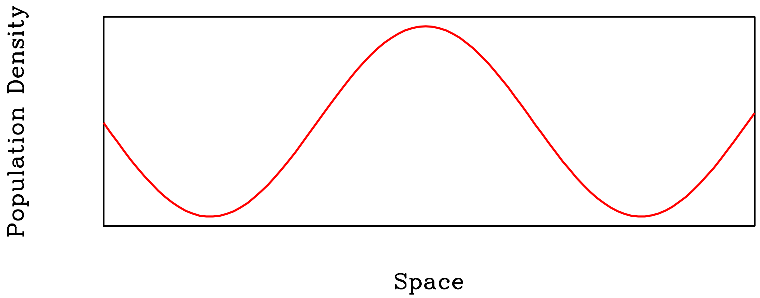

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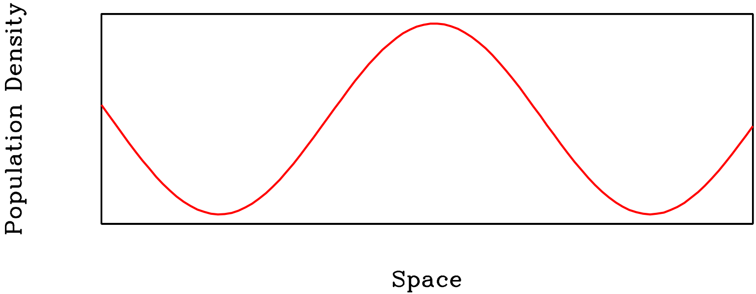

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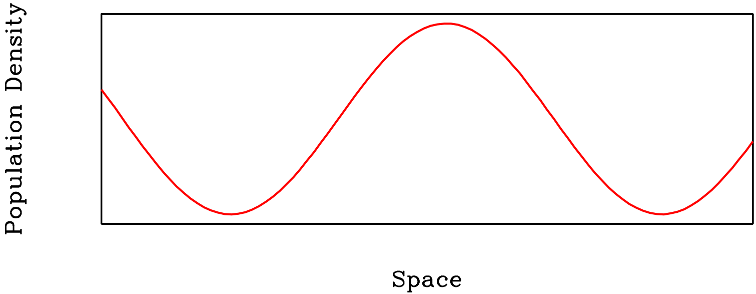

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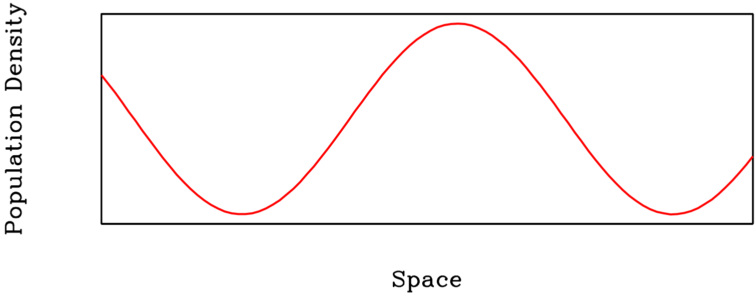

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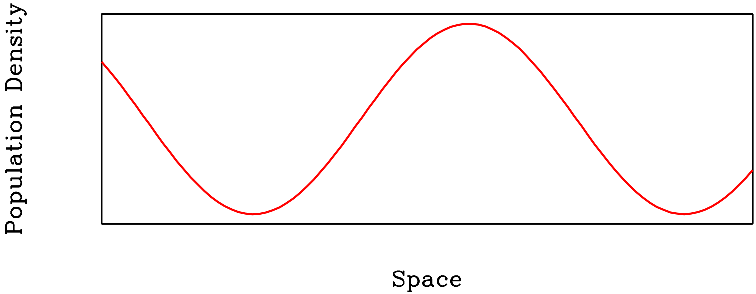

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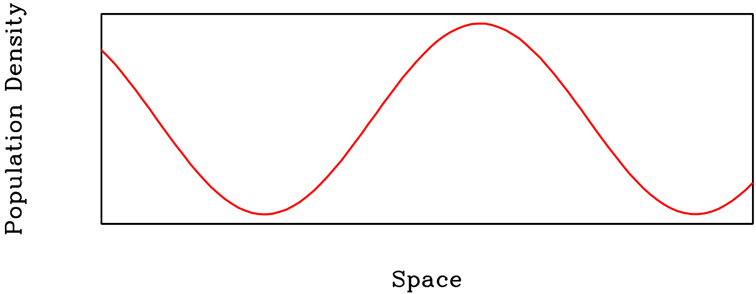

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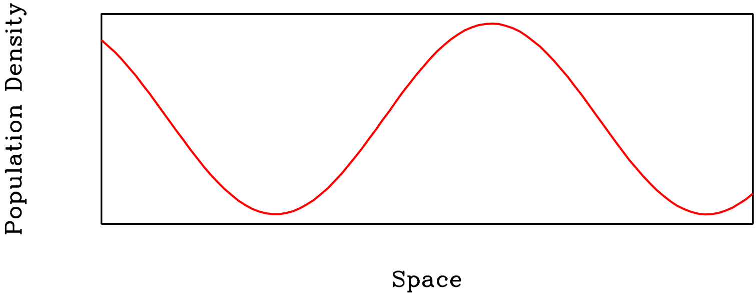

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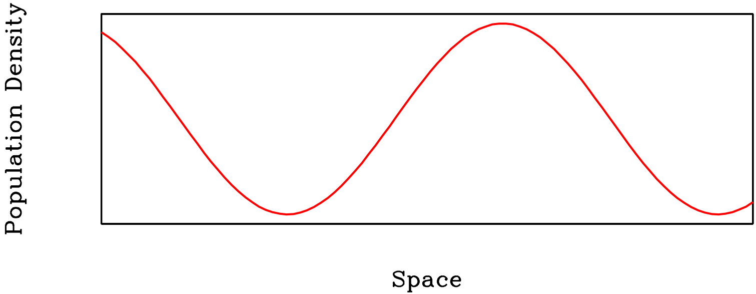

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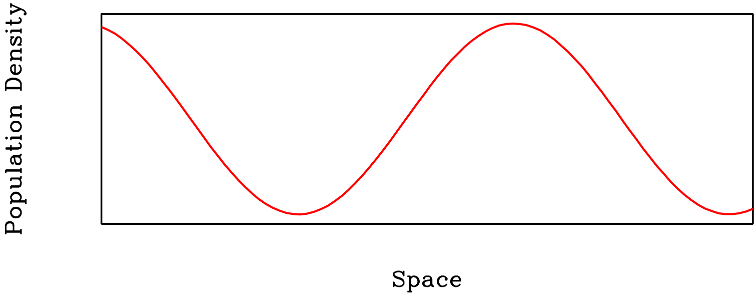

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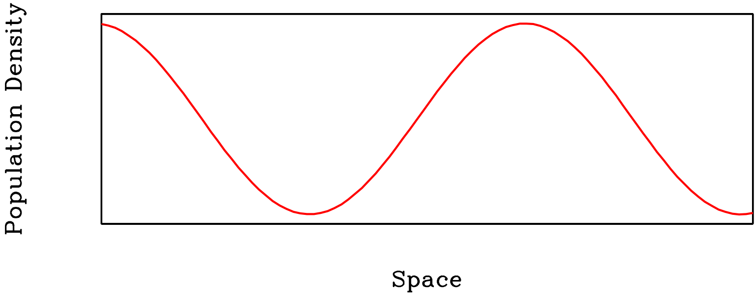

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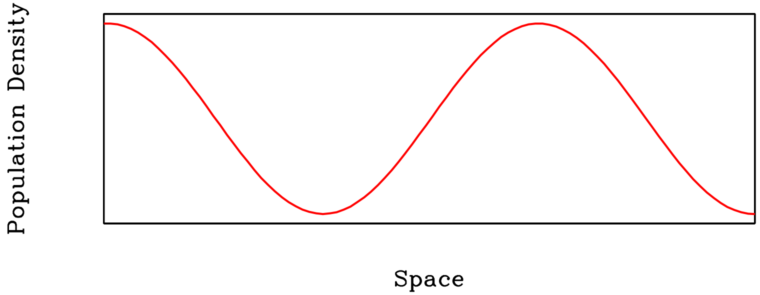

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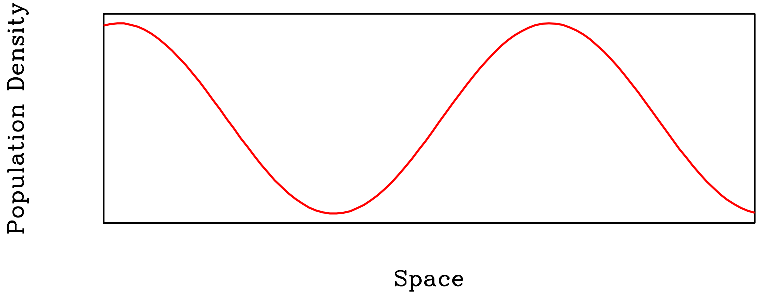

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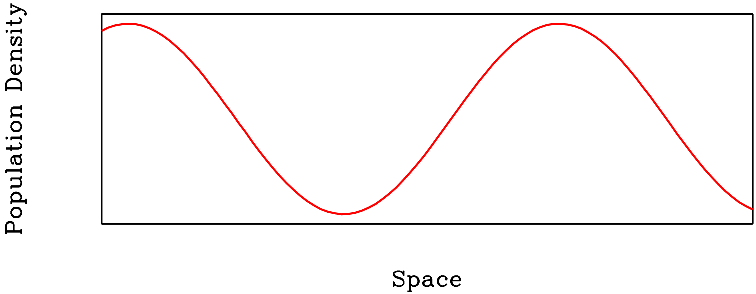

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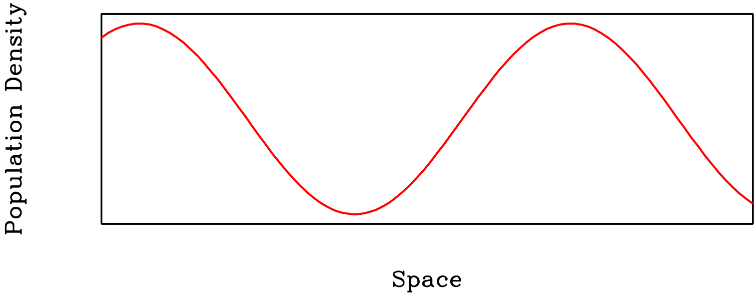

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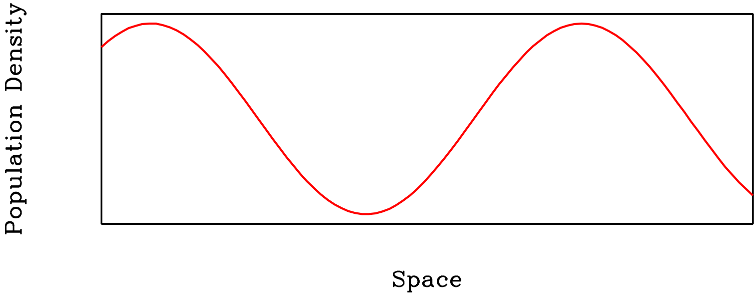

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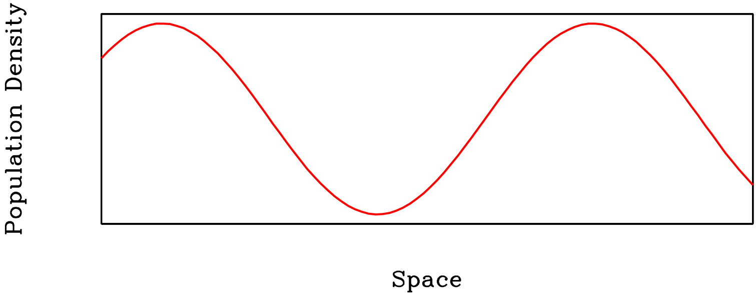

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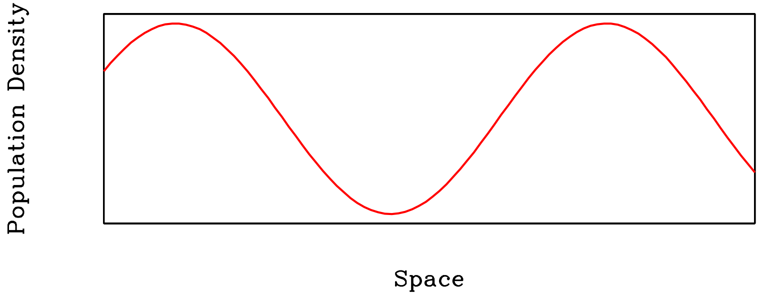

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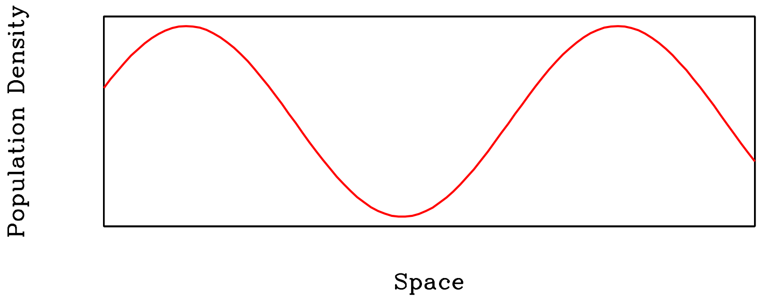

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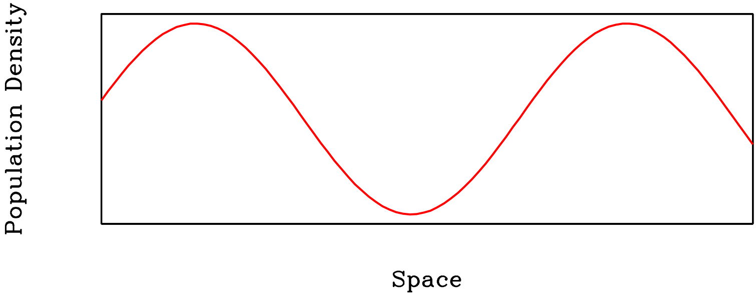

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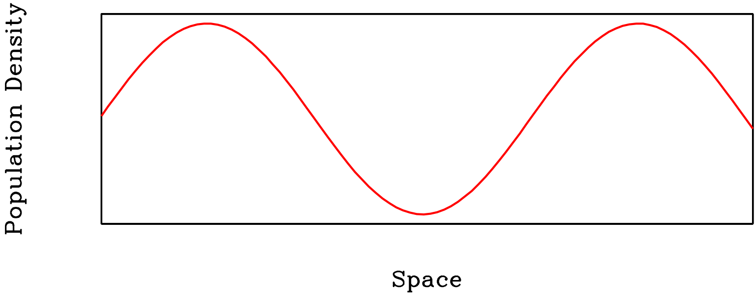

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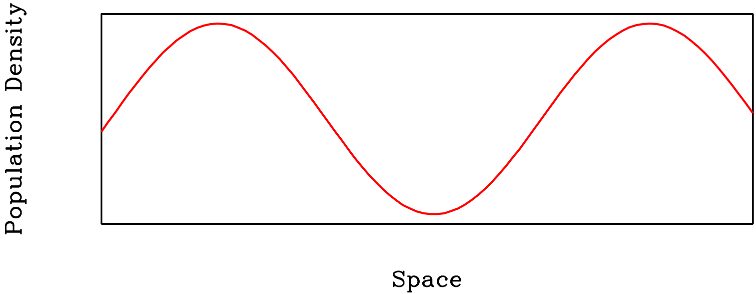

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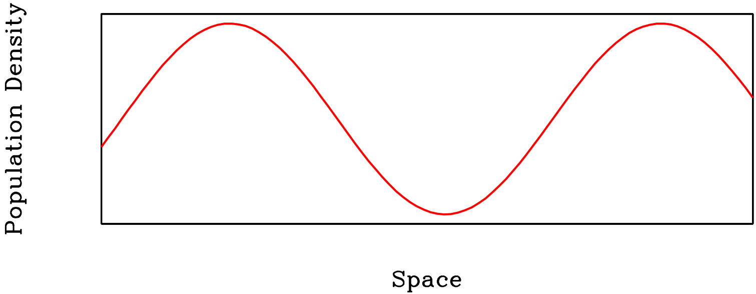

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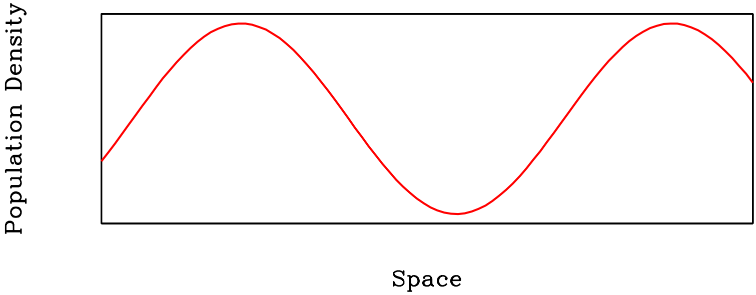

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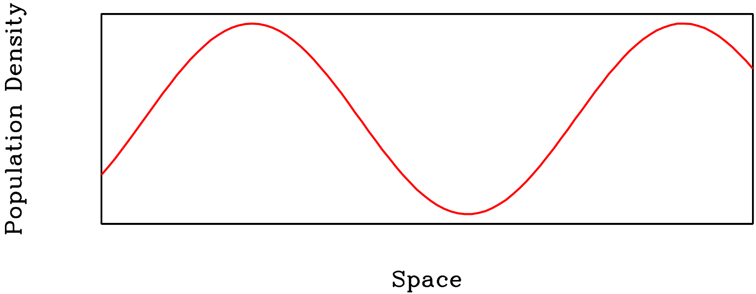

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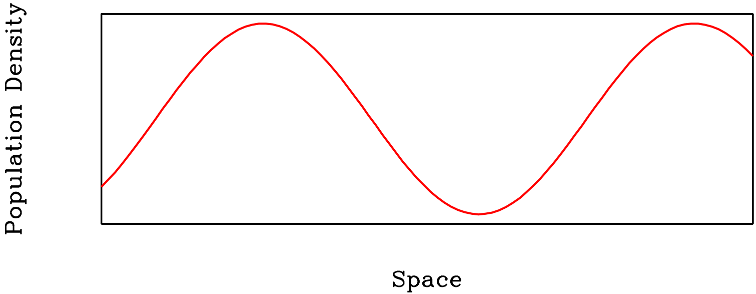

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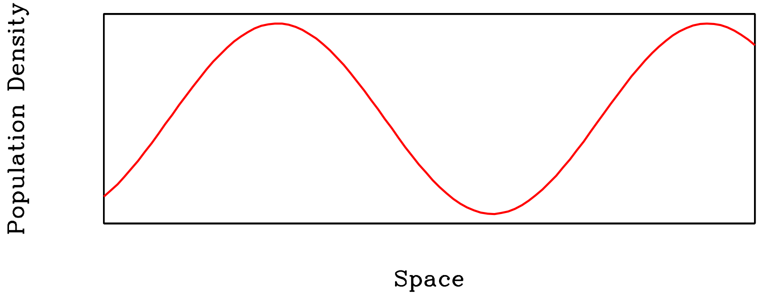

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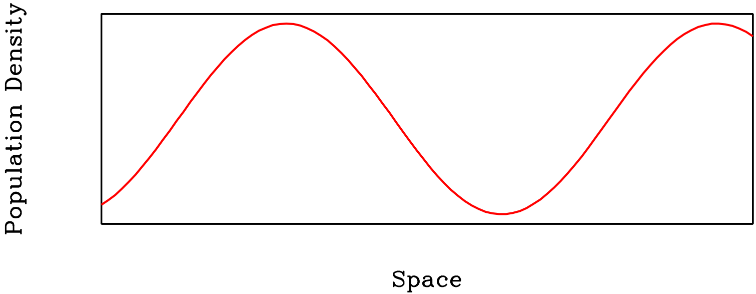

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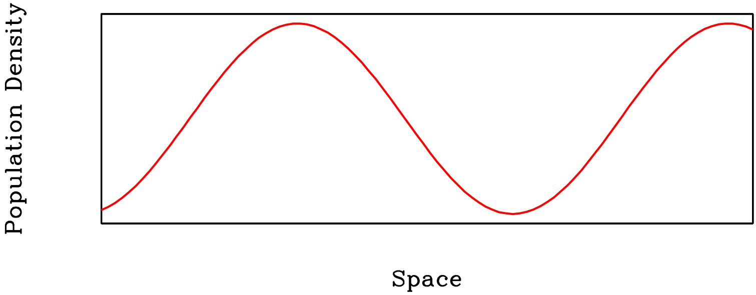

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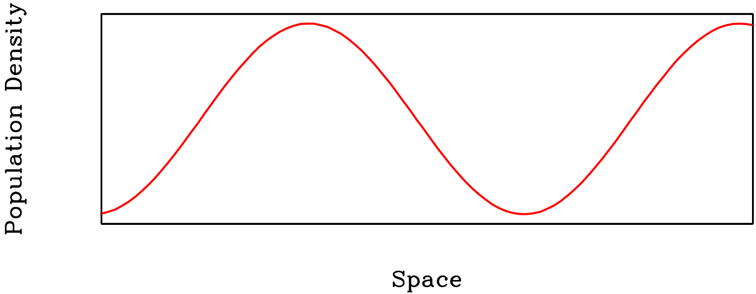

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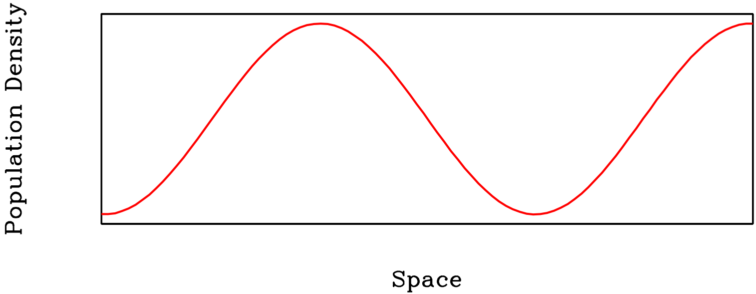

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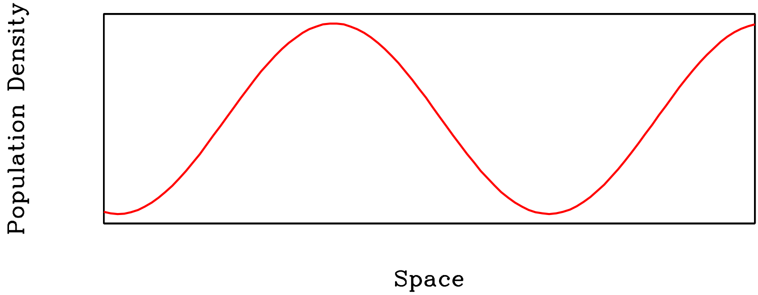

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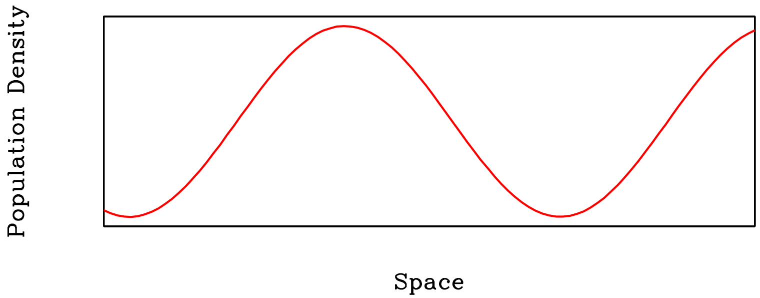

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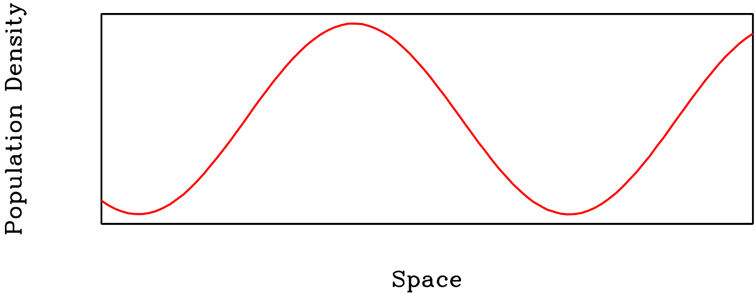

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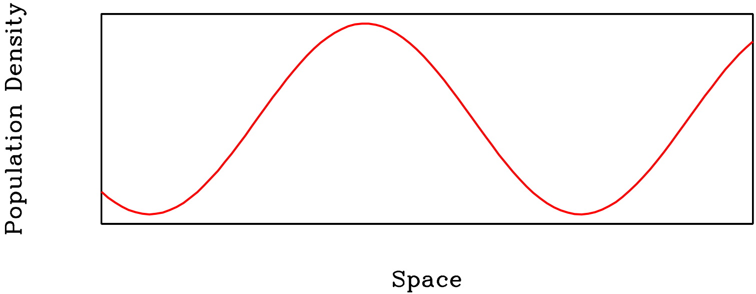

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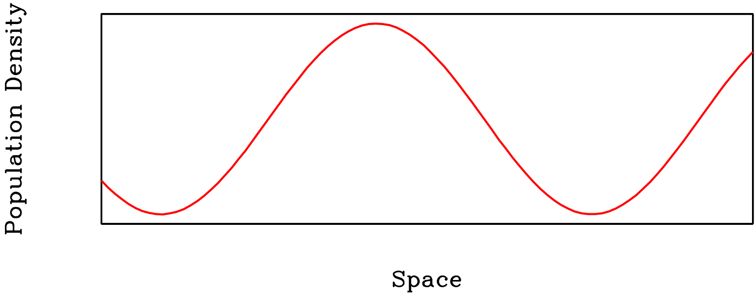

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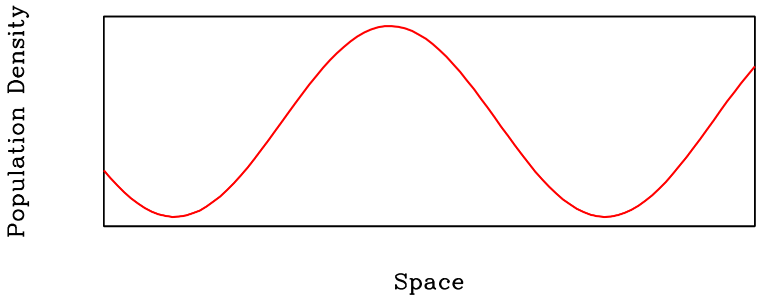

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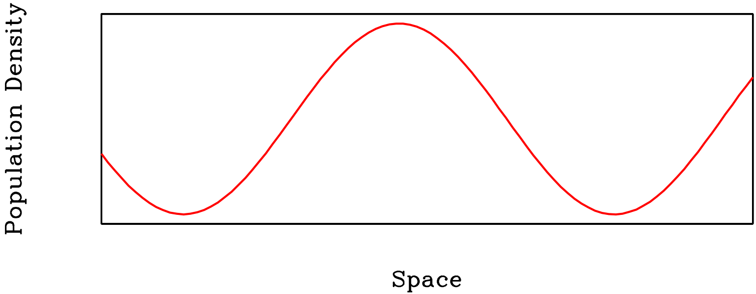

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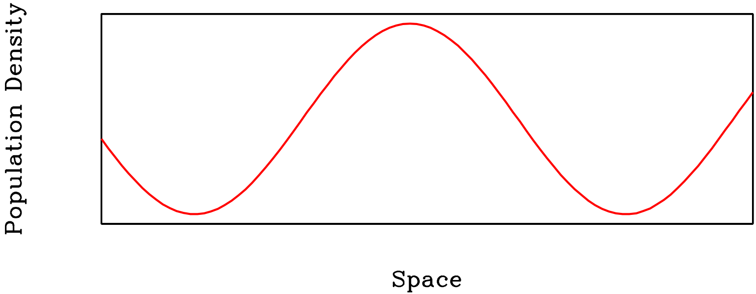

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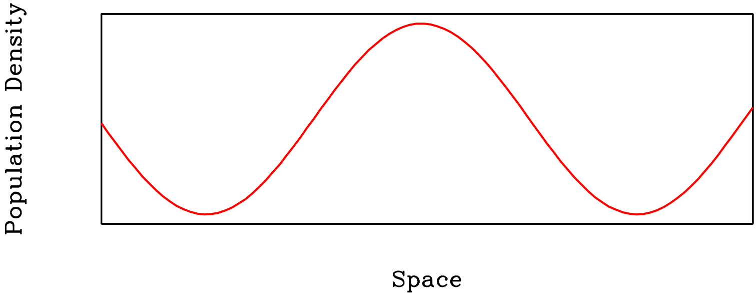

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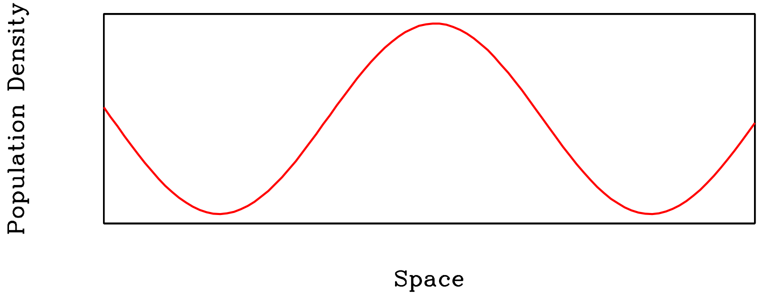

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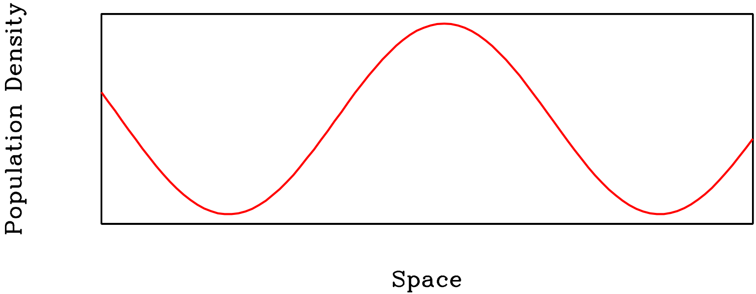

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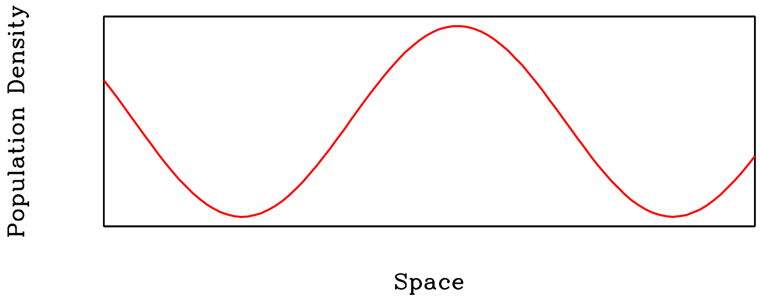

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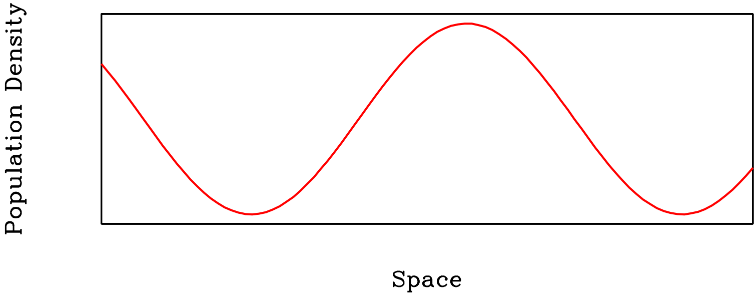

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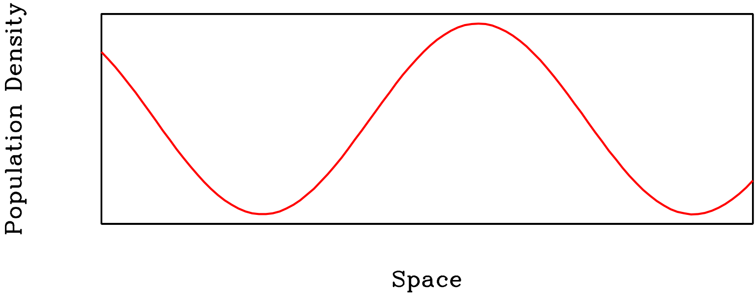

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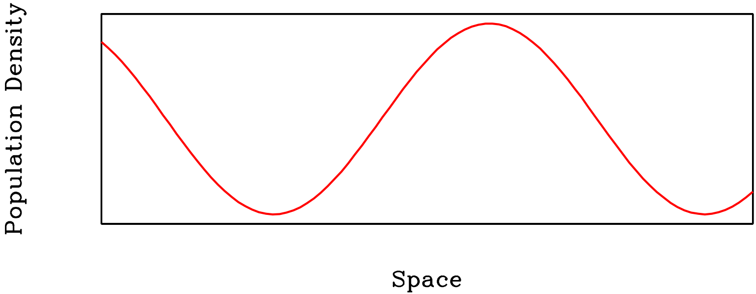

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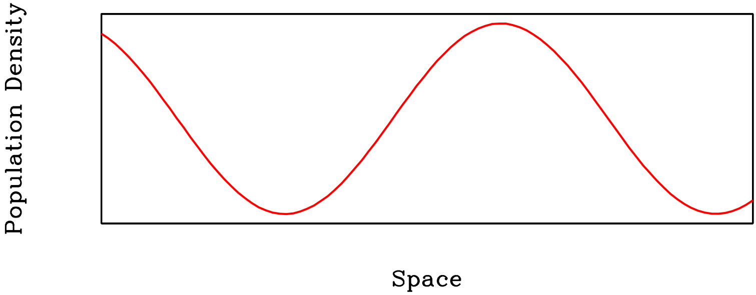

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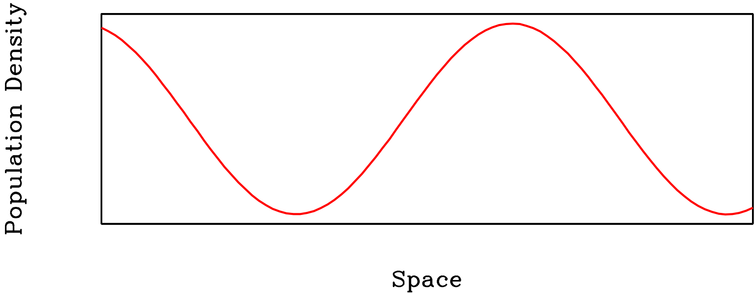

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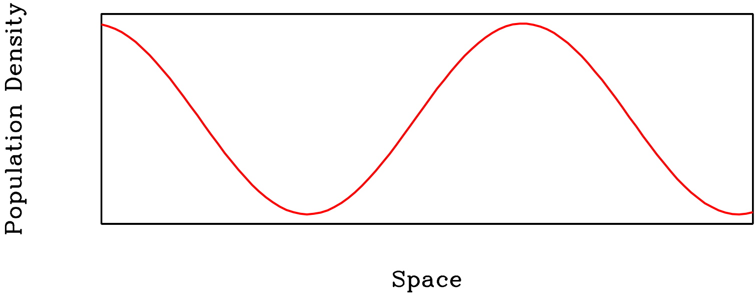

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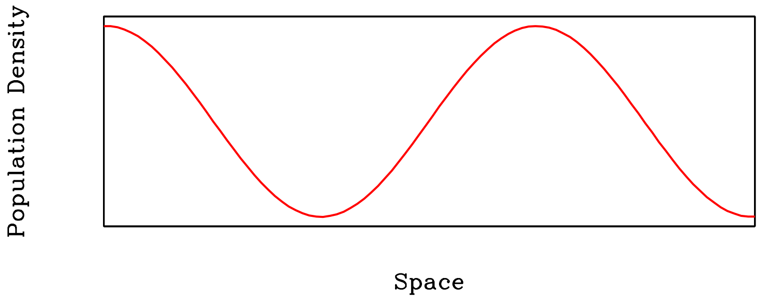

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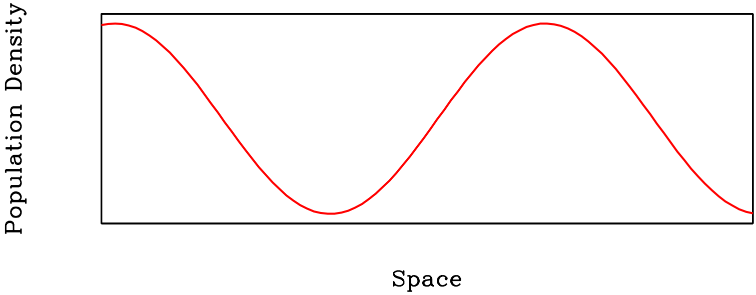

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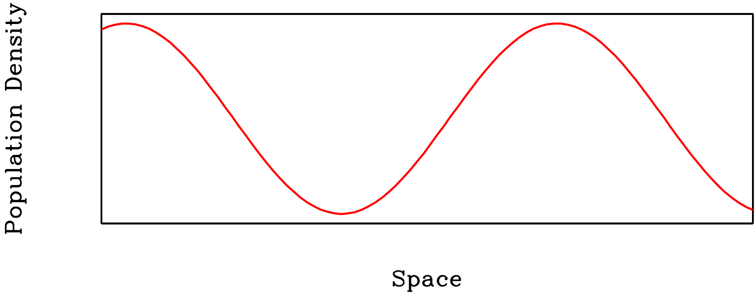

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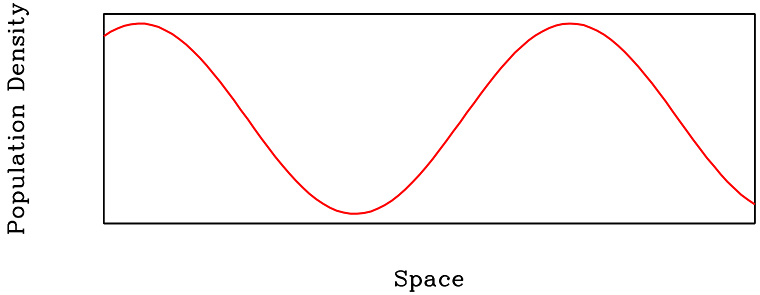

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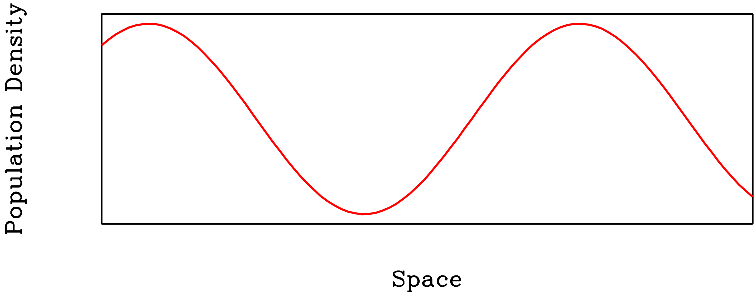

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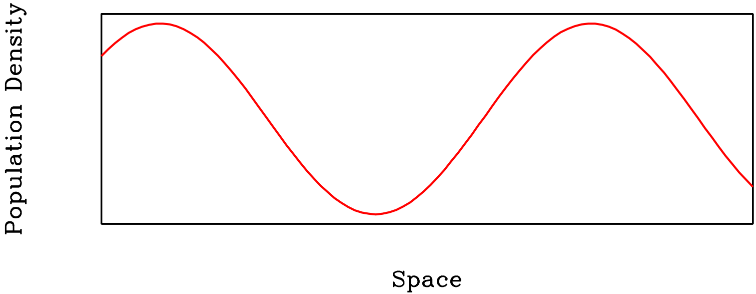

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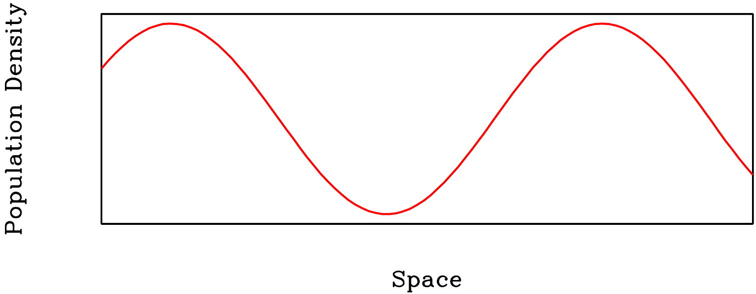

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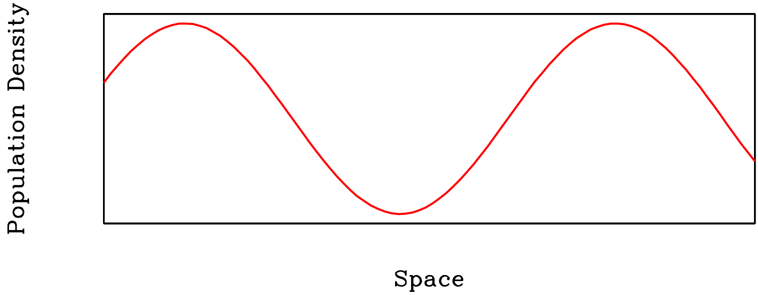

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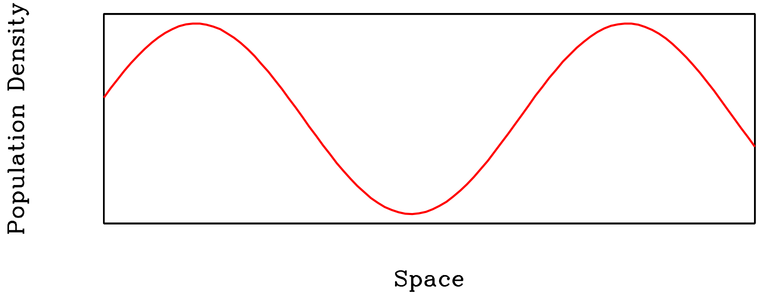

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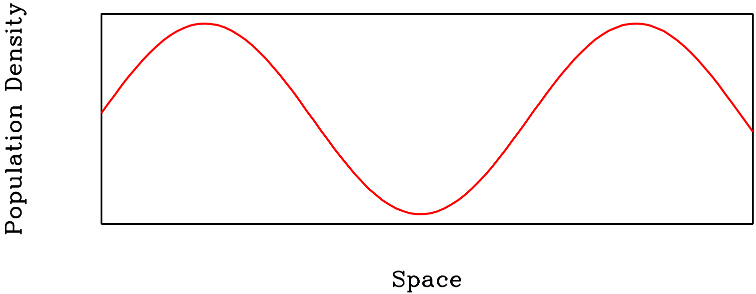

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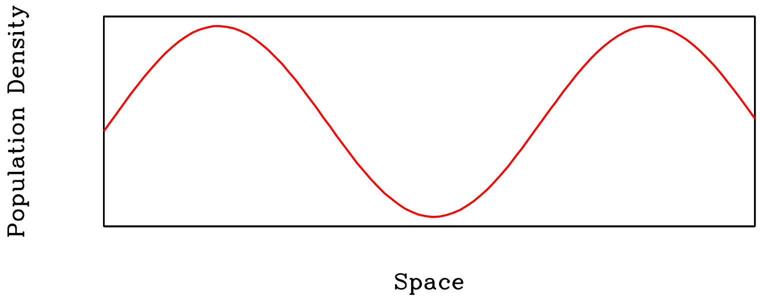

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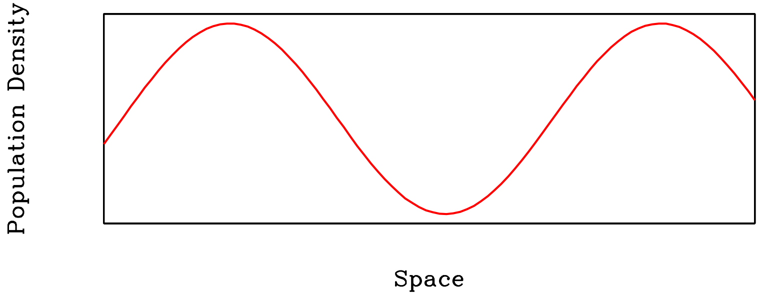

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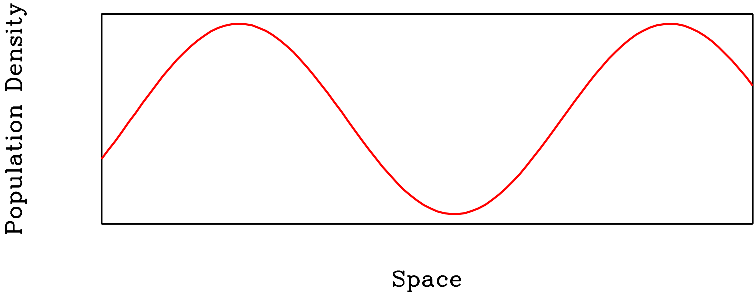

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I consider periodic travelling waves in oscillatory reaction-diffusion equations

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

What is a Periodic Travelling Wave?

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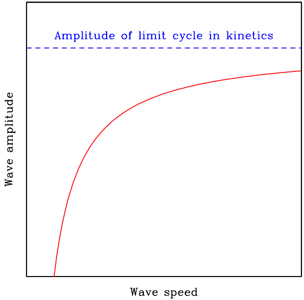
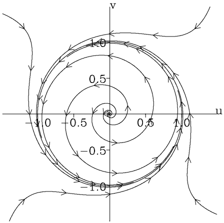
Theorem (Kopell & Howard, 1973):
An oscillatory reaction-diffusion system has a one-parameter family of periodic travelling wave solutions if the diffusion coefficients are sufficiently close to one another.



A Generic Oscillatory Reaction-Diffusion System

I consider first a generic oscillator model ("λ–ω equations")

$$
\begin{aligned}
\frac{\partial u}{\partial t} &= \frac{\partial^2 u}{\partial x^2} + \lambda(r)u - \omega(r)v \\
\frac{\partial v}{\partial t} &= \frac{\partial^2 v}{\partial x^2} + \omega(r)u + \lambda(r)v \\
r &= \sqrt{u^2 + v^2} \\
\lambda(r) &= 1 - r^2 \\
\omega(r) &= \omega_0 + \omega_1 r^2
\end{aligned}
$$



This is the normal form of an oscillatory reaction-diffusion system with scalar diffusion close to a supercritical Hopf bifurcation

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Family of periodic travelling wave solutions

$$u = R \cos\left[\omega(R)t \pm \sqrt{\lambda(R)}x\right]$$
$$v = R \sin\left[\omega(R)t \pm \sqrt{\lambda(R)}x\right]$$

$$(0 < R < 1)$$

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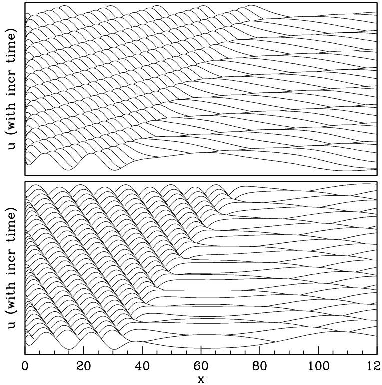
Typical Model Solutions

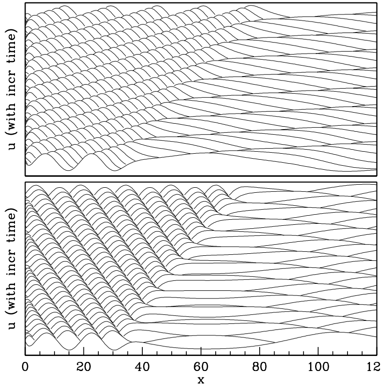


Eqns:
$$\begin{aligned}\frac{\partial u}{\partial t} &= \frac{\partial^2 u}{\partial x^2} + \lambda(r)u - \omega(r)v\\ \frac{\partial v}{\partial t} &= \frac{\partial^2 v}{\partial x^2} + \omega(r)u + \lambda(r)v\\ r &= \sqrt{u^2+v^2}\\ \lambda(r) &= 1 - r^2\\ \omega(r) &= \omega_0 + \omega_1 r^2\end{aligned}$$

Bcs: $u = v = 0$ at $x = 0$

$u_x = v_x = 0$ at $x = 50$

Typical Model Solutions



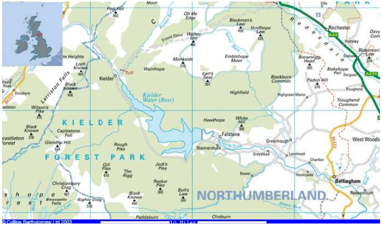
Conclusion

Dirichlet boundary conditions generate periodic travelling waves

Outline

1. Periodic Travelling Wave Generation
2. Application to Field Voles in Kielder Forest
3. Analytical Calculation of Wave Amplitude and Stability
4. Numerical Calculation of Wave Amplitude and Stability
5. Conclusions

Field Voles in Kielder Forest



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

Boundary Condition at the Reservoir Edge

- 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

Boundary Condition at the Reservoir Edge

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- The open expanse of Kielder Water will greatly facilitate hunting at its edge
- Therefore we expect very high vole loss at the reservoir edge, implying a Robin boundary condition

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

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Our Conclusion: this boundary condition could be responsible for the observed periodic travelling waves

Question: how does wave speed/amplitude/stability depend on parameters?

Outline

Amplitude and Phase Equations

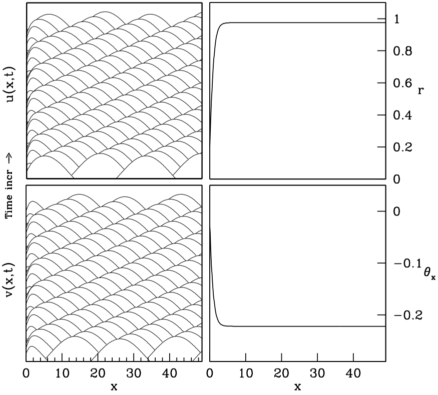
To study the λ–ω equations, it is helpful to replace u and v by $r = \sqrt{u^2 + v^2}$ and $\theta = \tan^{-1}(v/u)$, giving

$$\begin{aligned} r_t &= r_{xx} - r\theta_x^2 + r(1 - r^2) \\ \theta_t &= \theta_{xx} + \frac{2r_x\theta_x}{r} + \omega_0 - \omega_1 r^2 \end{aligned}$$

Family of periodic travelling wave solutions ($0 < R < 1$):

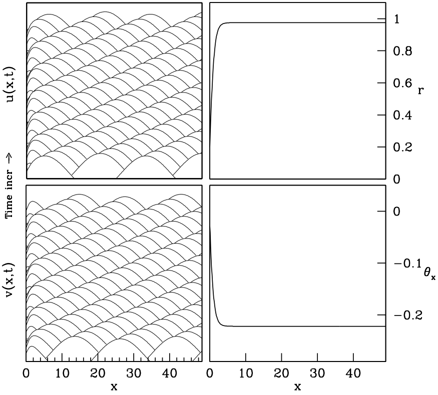
$$\left\{ \begin{array}{l} r = R \\ \theta = \left[\omega(R)t \pm \sqrt{\lambda(R)}x\right] \end{array} \right\} \leftrightarrow \left\{ \begin{array}{l} u = R\ \cos\left[\omega(R)t \pm \sqrt{\lambda(R)}x\right] \\ v = R\ \sin\left[\omega(R)t \pm \sqrt{\lambda(R)}x\right] \end{array} \right\}$$

Typical Solutions Replotted



Replotting the solutions in terms of r and θ_x shows that the long-term solutions for r and θ_x are independent of time

Typical Solutions Replotted



Exact solution:

$$R(x) = r_{ptw} \tanh\left(x/\sqrt{2}\right)$$

$$\Psi(x) = \psi_{ptw} \tanh\left(x/\sqrt{2}\right)$$

where

$$r_{ptw} = \left\{\tfrac{1}{2}\left[1+\sqrt{1+\tfrac{8}{9}\omega_1^2}\right]\right\}^{-1/2}$$

$$\psi_{ptw} = -\mathrm{sign}(\omega_1)\left\{\frac{\sqrt{1+\frac{8}{9}\omega_1^2}-1}{\sqrt{1+\frac{8}{9}\omega_1^2}+1}\right\}^{1/2}$$

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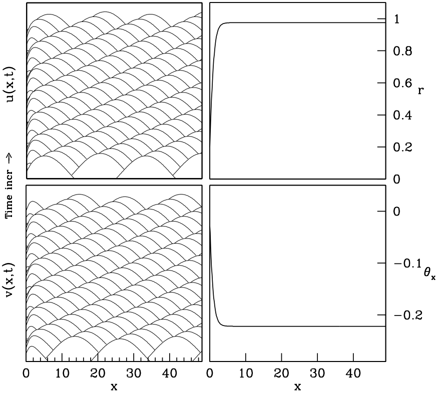
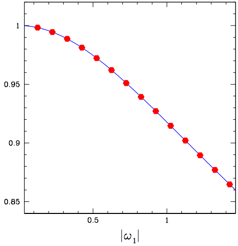


Exact solution:
the wave amplitude

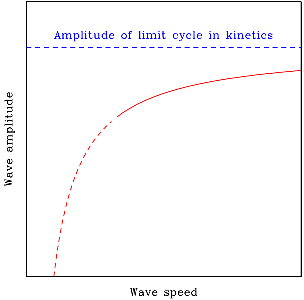
$$r_{ptw} = \left\{ \tfrac{1}{2}\left[1+\sqrt{1+\tfrac{8}{9}\omega_1^2}\right]\right\}^{-1/2}$$

is in very good agreement with that found in simulations



Stability in the Periodic Travelling Wave Family

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



For our λ–ω system, the stability condition is

$$r^* > \left(\frac{2 + 2\omega_1^2}{3 + 2\omega_1^2} \right)^{1/2}$$

Stability of the Selected Wave

The stability of the selected wave depends on ω_1.

$$r_{ptw} = \left\{ \tfrac{1}{2} \left[1 + \sqrt{1 + \tfrac{8}{9}\omega_1^2} \right] \right\}^{-1/2}$$

This is stable

$$\Leftrightarrow \quad r_{ptw} > \left(\frac{2 + 2\omega_1^2}{3 + 2\omega_1^2} \right)^{1/2}$$
$$\Leftrightarrow \quad |\omega_1| < 1.110468\ldots$$

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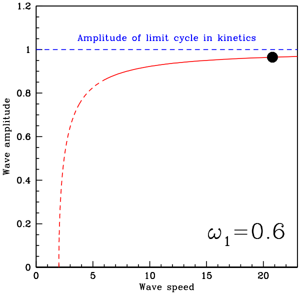

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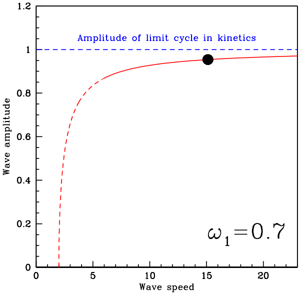

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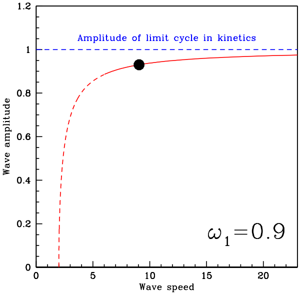

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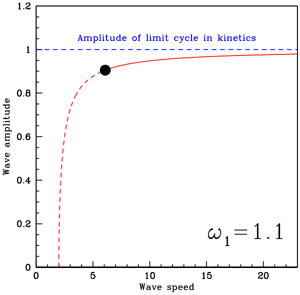

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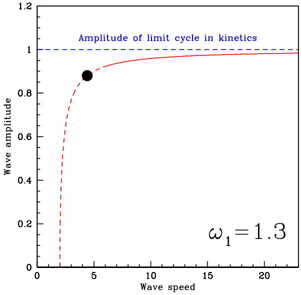
$$r_{ptw} = \left\{ \frac{1}{2} \left[1 + \sqrt{1 + \frac{8}{9}\omega_1^2} \right] \right\}^{-1/2}$$

This is stable

$$\Leftrightarrow \quad r_{ptw} > \left(\frac{2 + 2\omega_1^2}{3 + 2\omega_1^2} \right)^{1/2}$$

$$\Leftrightarrow \quad |\omega_1| < 1.110468\ldots$$



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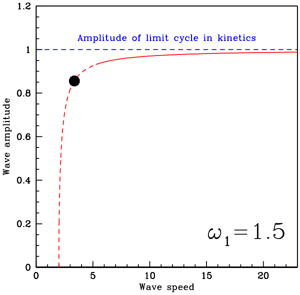
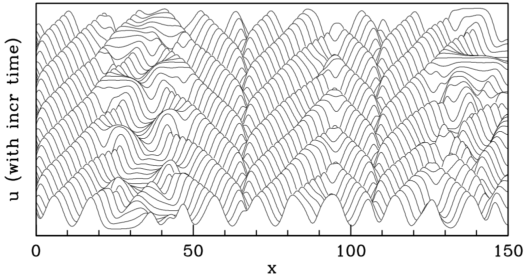


Typical Solution in an Unstable Case



Outline

A Standard Predator-Prey Model

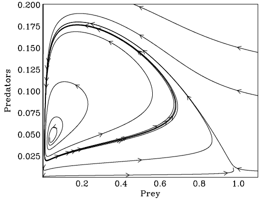
predators

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

prey

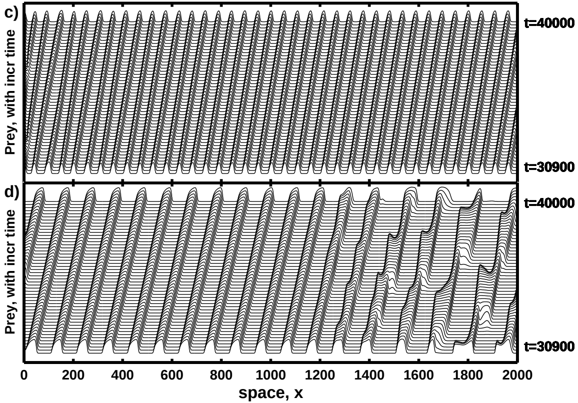
$$\partial h/\partial t = \underbrace{D_h \nabla^2 h}_{\text{dispersal}} + \underbrace{rh(1-h/h_0)}_{\text{intrinsic birth \& death}} - \underbrace{ckph/(1+kh)}_{\text{predation}}$$

Phase plane of kinetics:



Periodic Wave Generation in Predator-Prey Eqns

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



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

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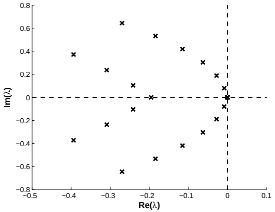

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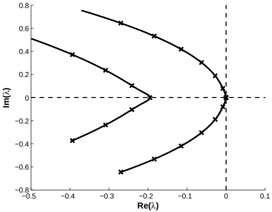

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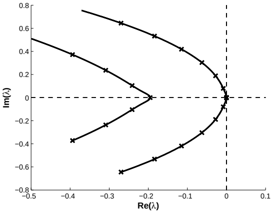

This gives the eigenvalue spectrum, and hence (in)stability

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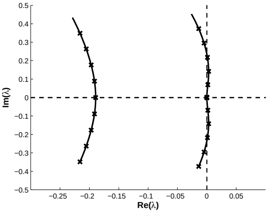
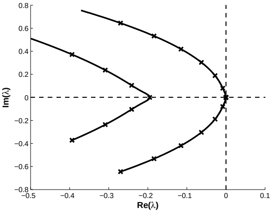


UNSTABLE

Eckhaus instability

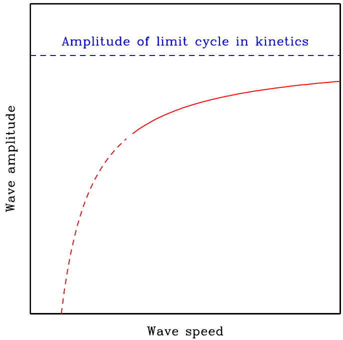


STABLE

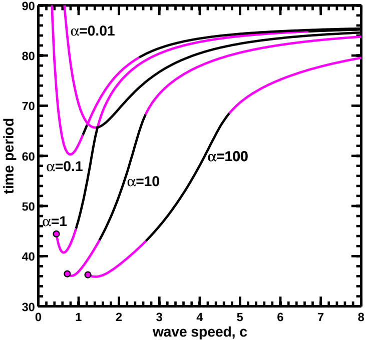
This gives the eigenvalue spectrum, and hence (in)stability

Periodic Wave Families with Stability

λ–ω kinetics



Predator-prey kinetics



$$\alpha = D_{\text{prey}}/D_{\text{predator}}$$

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.

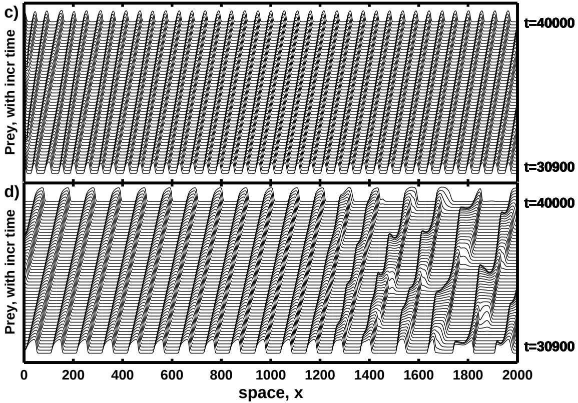
In fact, stable/unstable boundaries can be computed accurately by numerical continuation of the point at which

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

(Eckhaus instability point)

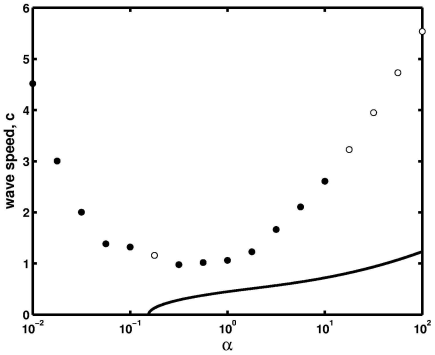
Back to Wave Generation in Predator-Prey Eqns

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



Back to Wave Generation in Predator-Prey Eqns

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



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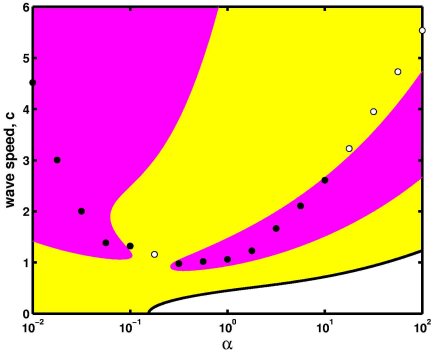
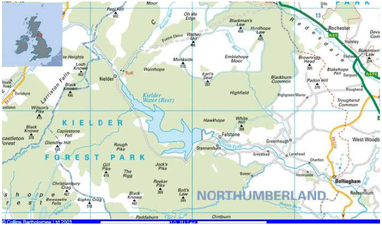


Our stability calculations explain the suprising results from simulations of periodic wave generation

Outline

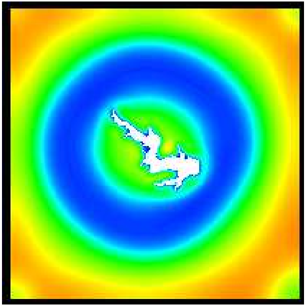
Back to the Example of Field Voles in Kielder Forest



Back to the Example of Field Voles in Kielder Forest

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

Numerical Simulation of Field Vole Waves



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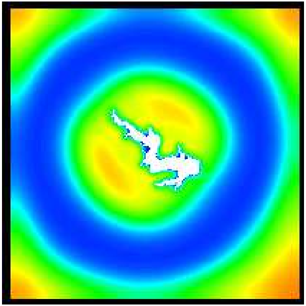

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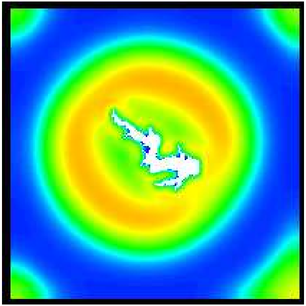

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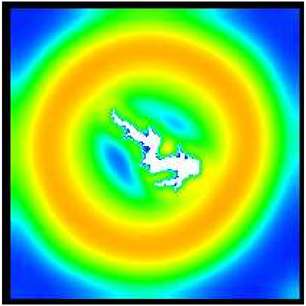

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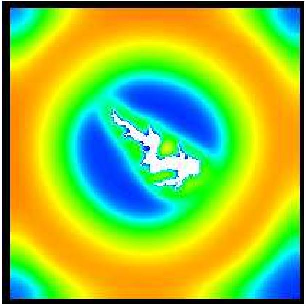

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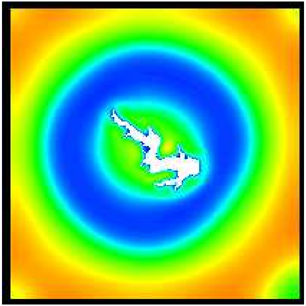
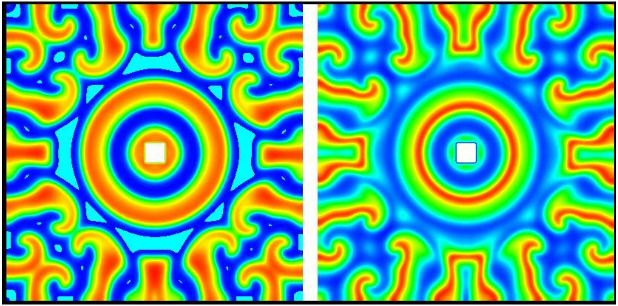


Movie of Field Vole Wave Simulation

Click here to
play the movie

Typical Predator-Prey Solution in the Unstable Parameter Regime



Movie of Predator-Prey Solution in the Unstable Parameter Regime

Click here to
play the movie

List of Frames

An Application of the Dirichlet Bdy Cond$^{\text{n}}$ Formula

Using the formula for the periodic wave amplitude generated by the Dirichlet boundary condition, we can predict the stability of the waves as a function of ecological parameters in the predator-prey model (close to Hopf bifurcation)