Periodic Travelling Waves in Oscillatory Reaction-Diffusion Systems, and Applications to Ecology

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The work on ecological applications is in collaboration with:

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Matthew Smith

Outline

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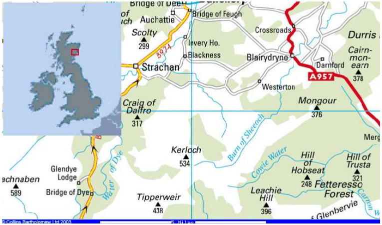
Habitat Boundaries in Ecology

- Often ecological habitats are surrounded by unfavourable environments
- Examples: a wood surrounded by open terrain
  moorland surrounded by farmland
  marsh surrounded by dry ground

Example: Red Grouse on Kerloch Moor



- Red grouse is a cyclic population (period about 4-6 years)
- The study site is moorland, with farmland at its Northern edge
- Farmland is very hostile for red grouse

Mathematical Representation

$$\begin{array}{rlrcl} \text{Habitat} & x>0: & \partial w/\partial t & = & D\partial^2 w/\partial x^2 + f(w) \\ \text{Surroundings} & x<0: & \partial w/\partial t & = & D\partial^2 w/\partial x^2 - \gamma w \end{array}$$

where $w(x,t)$ denotes population density.

- For $x<0$, finiteness as $x \to -\infty \Rightarrow w \propto \exp(x\sqrt{\gamma/D})$ at equilibrium
- Equating w and w_x at $x=0$ implies the Robin boundary condition $\sqrt{D}w_x + \sqrt{\gamma}w = 0$
- Note that γ is large, so that the boundary condition will be close to the Dirichlet limit.

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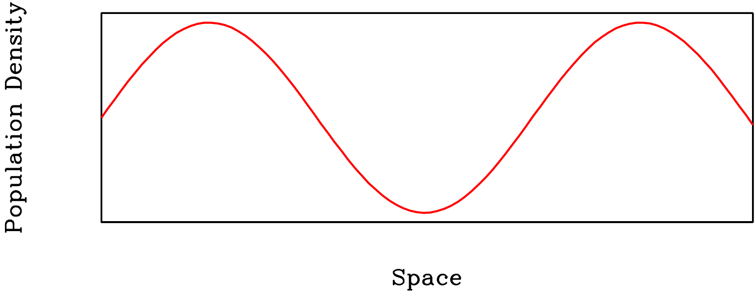
Spatiotemporal data from Kerloch Moor shows that the red grouse cycles are spatially organised into a periodic travelling wave



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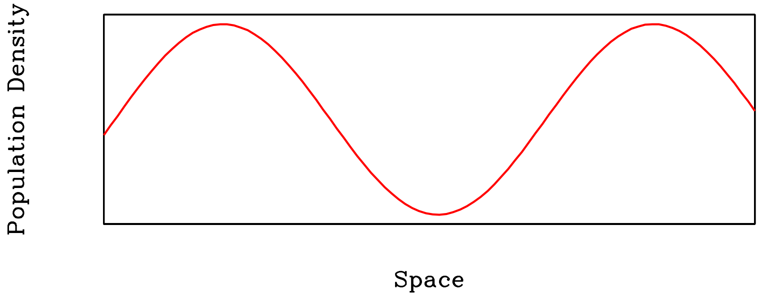

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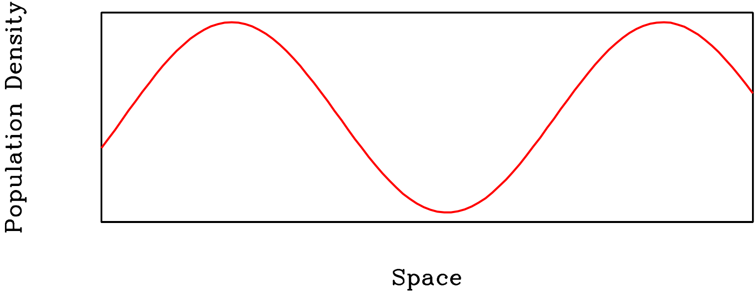

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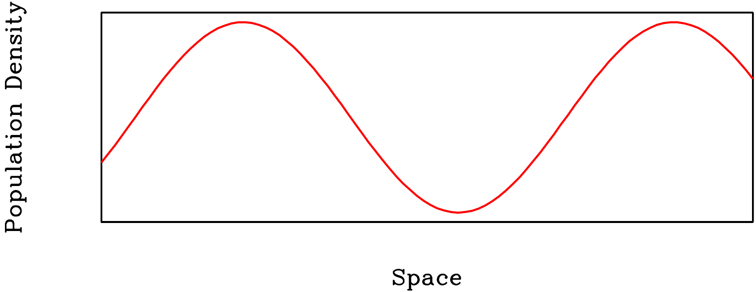

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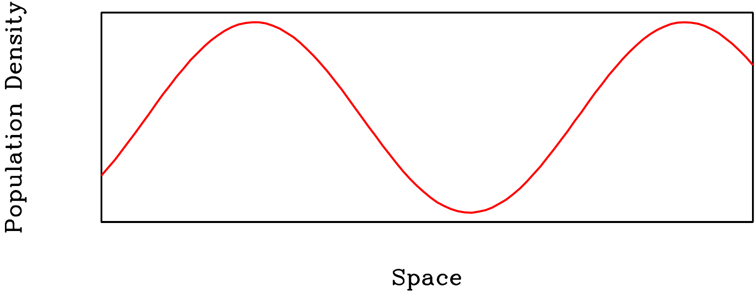

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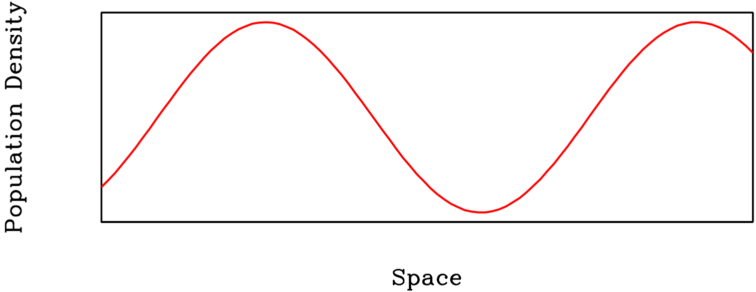

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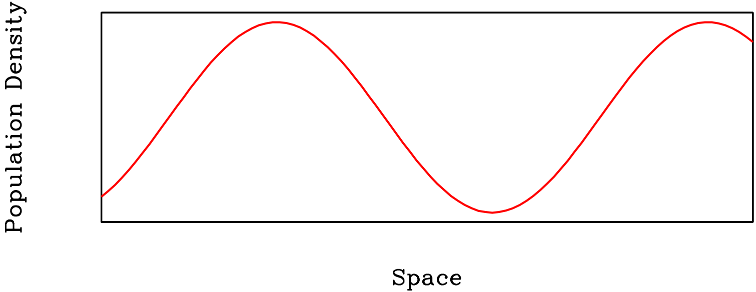

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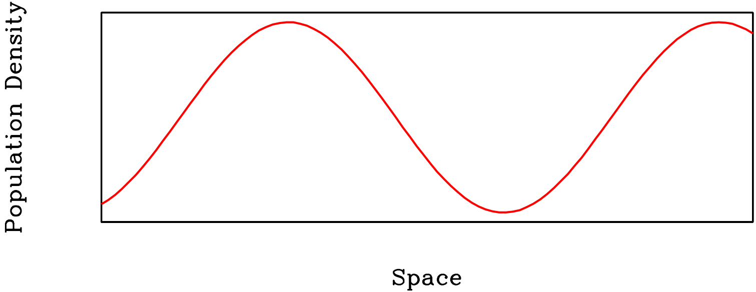

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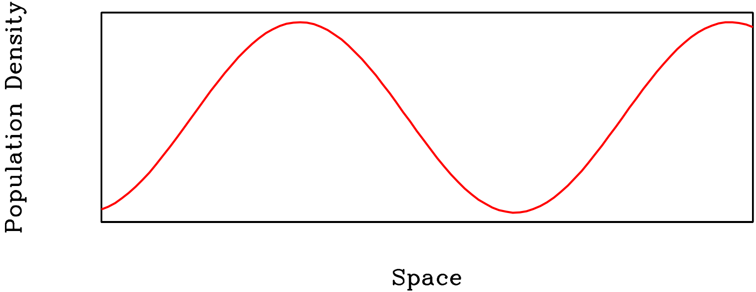

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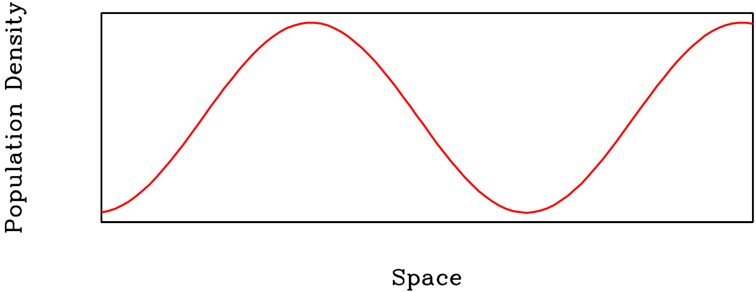

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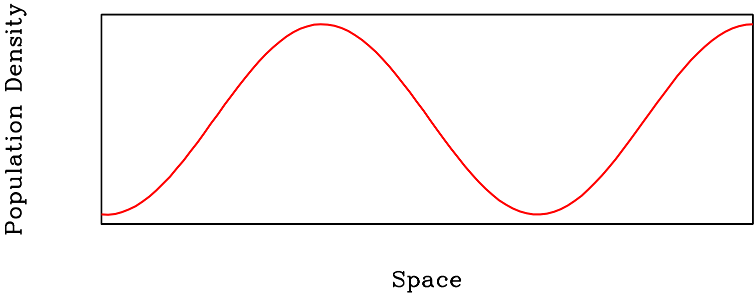

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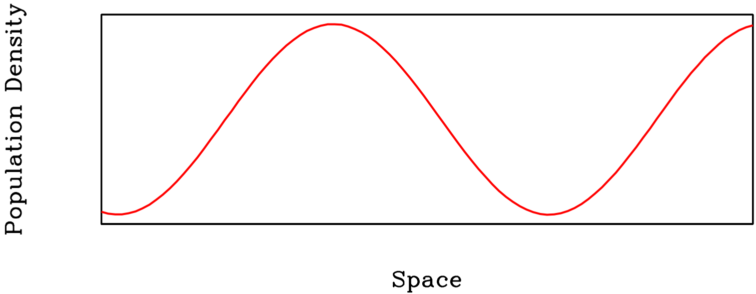

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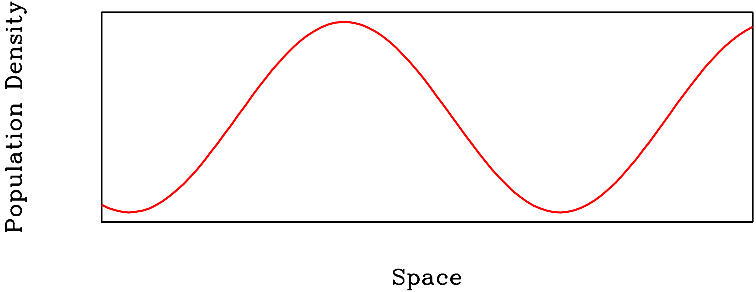

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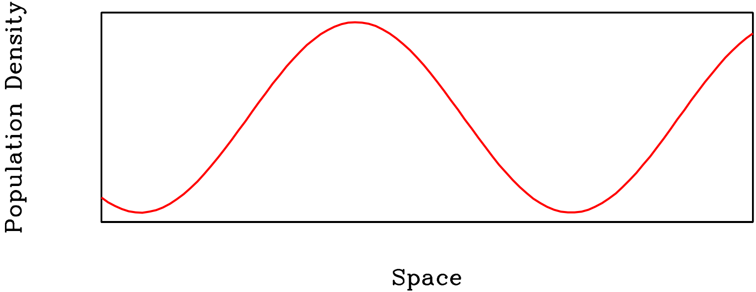

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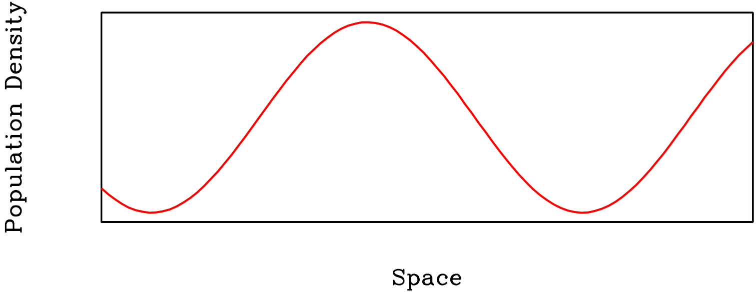

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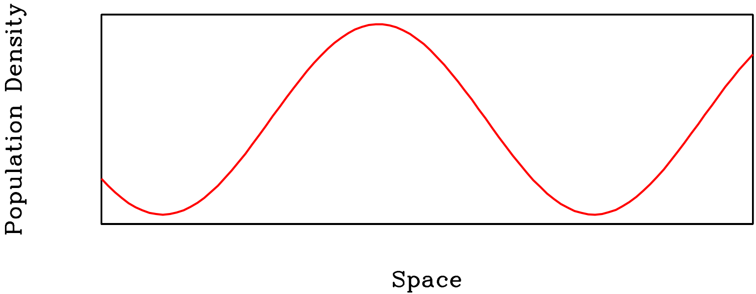

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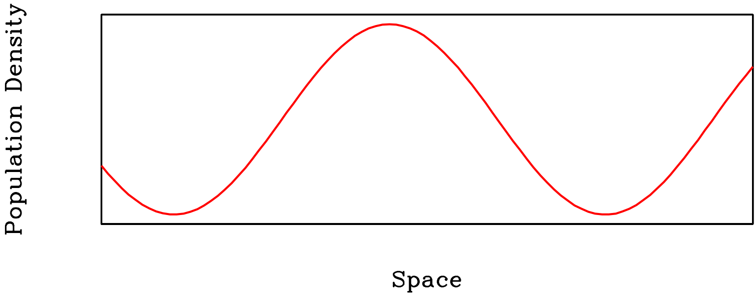

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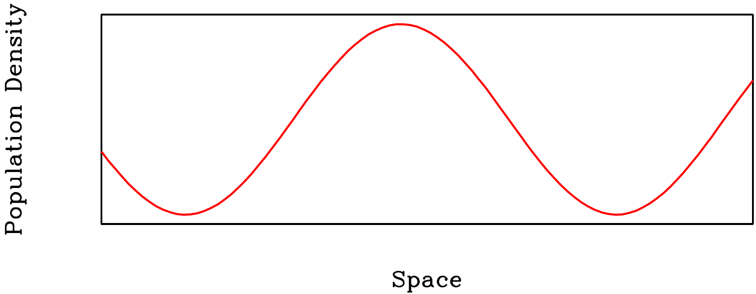

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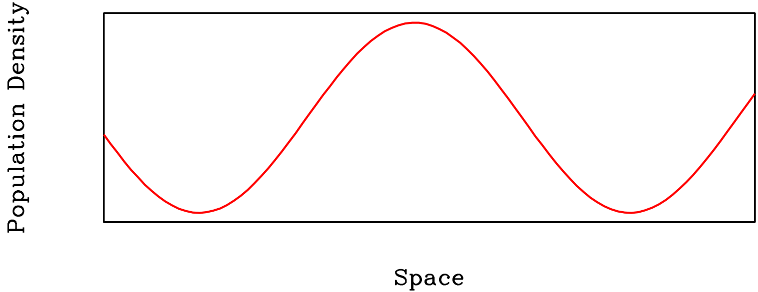

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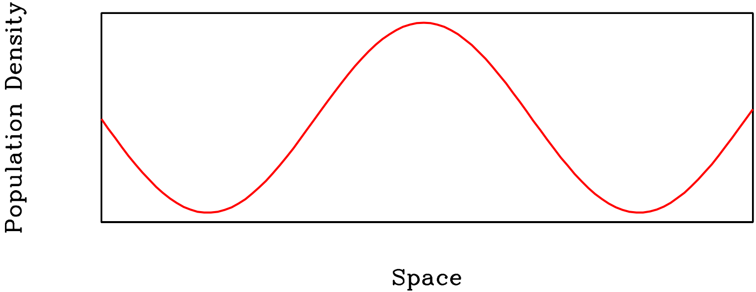

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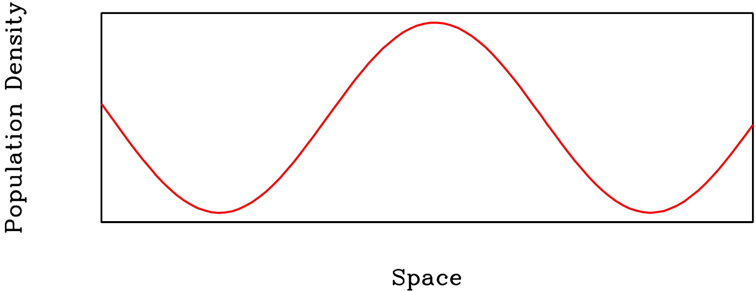

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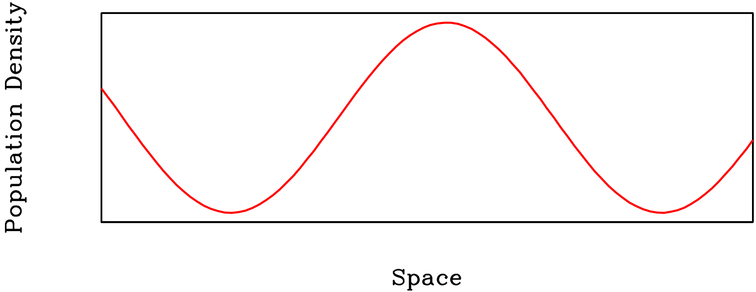

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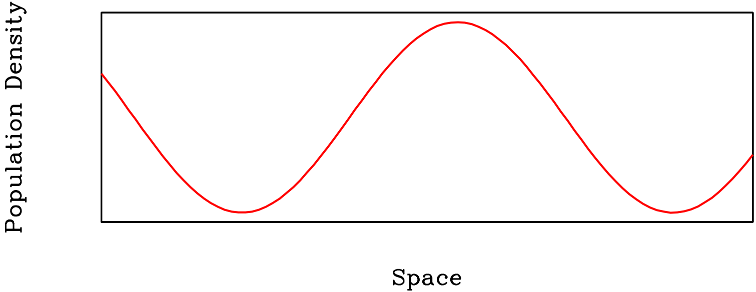

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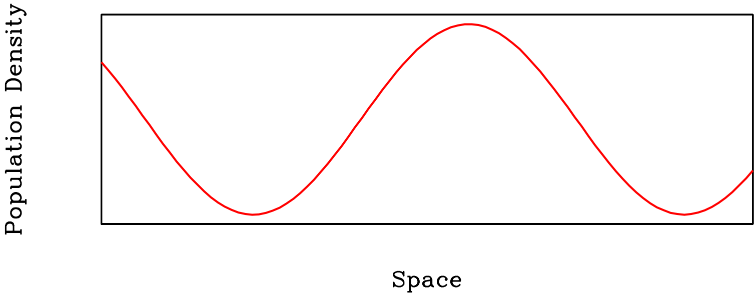

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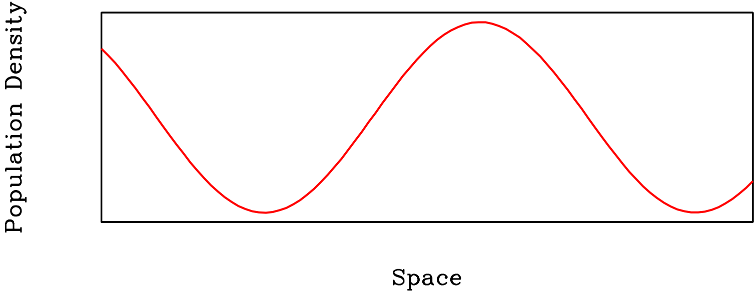

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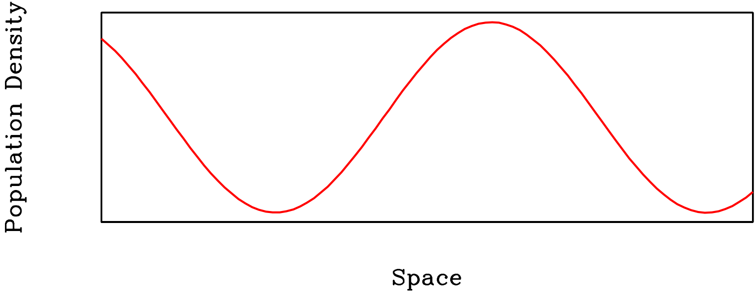

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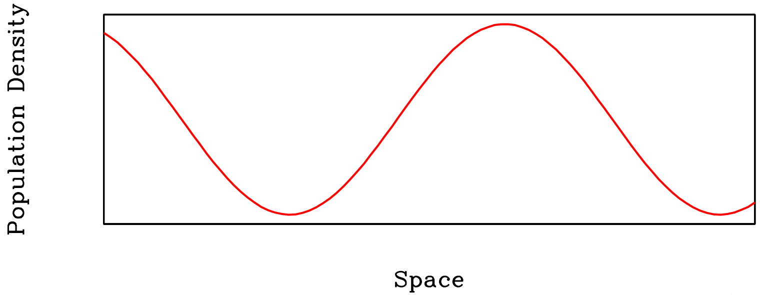

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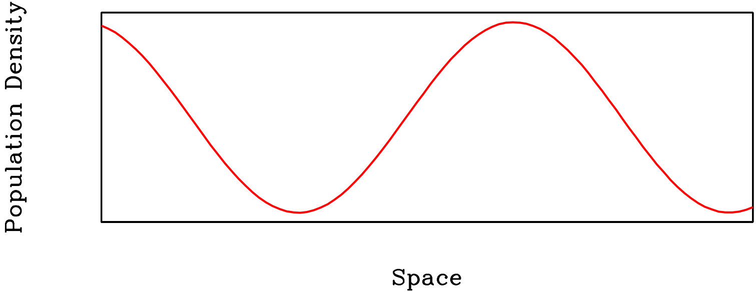

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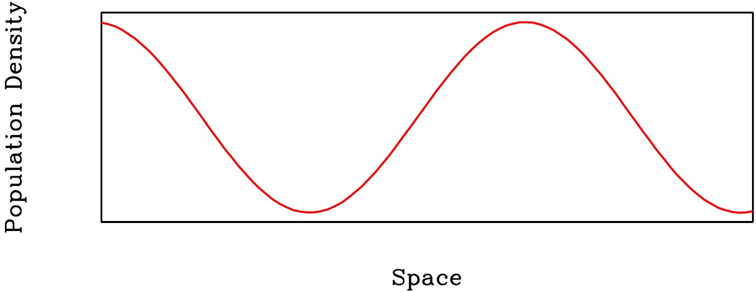

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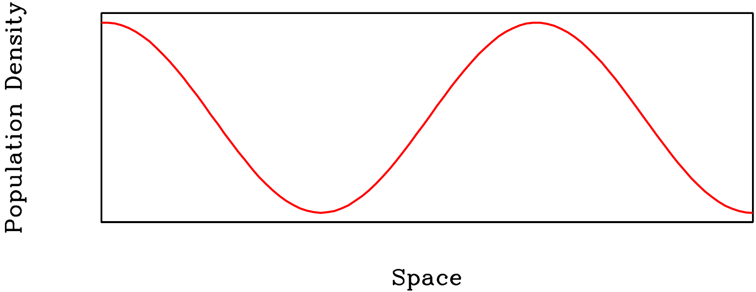

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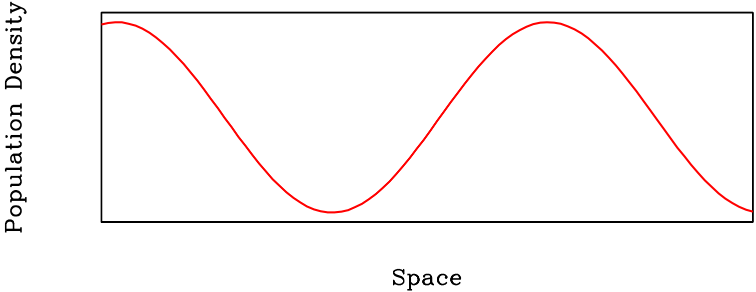

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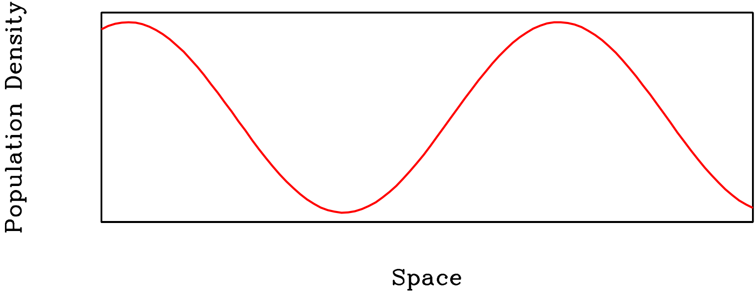

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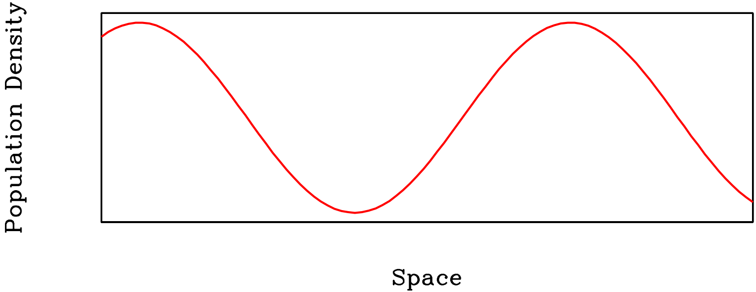

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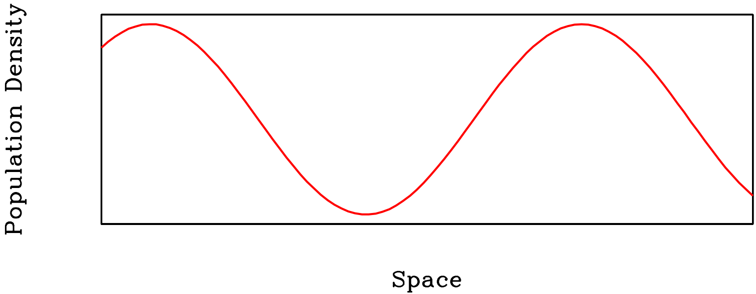

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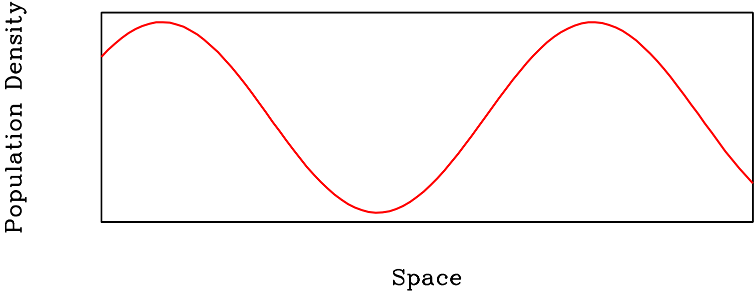

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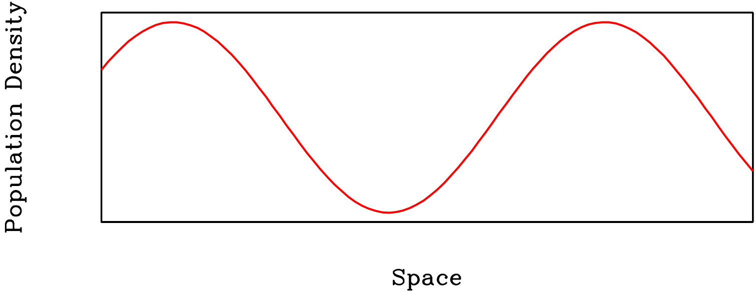

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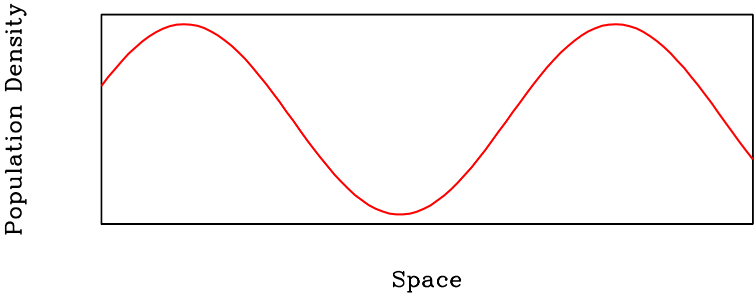

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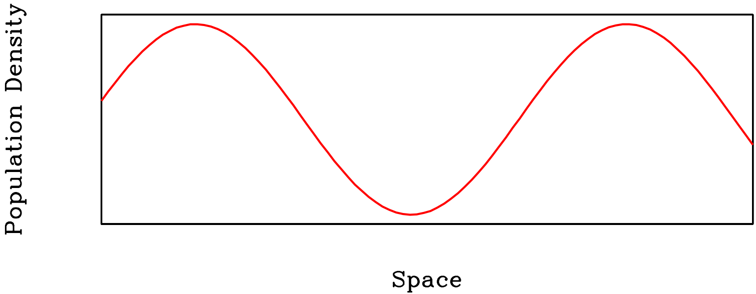

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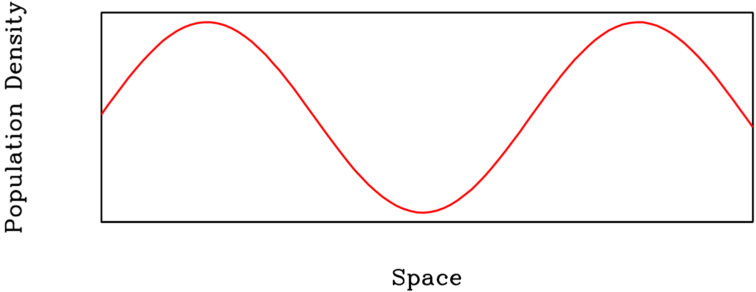

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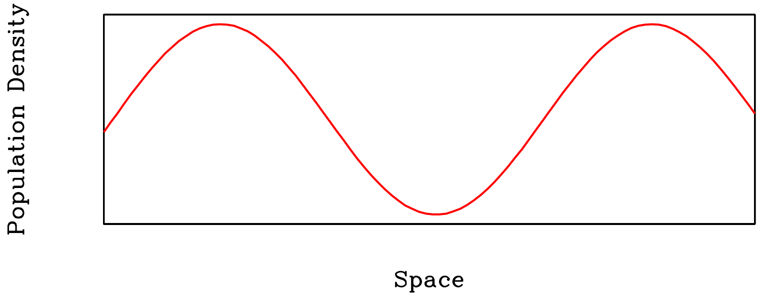

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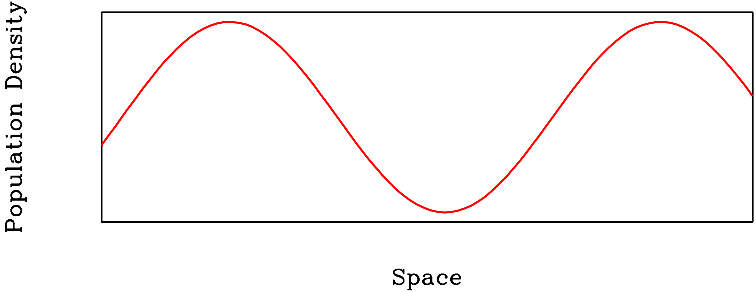

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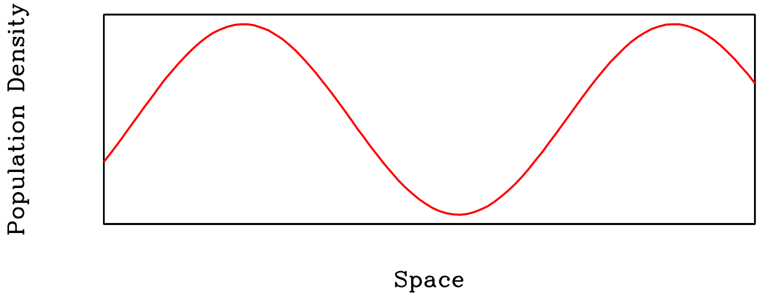

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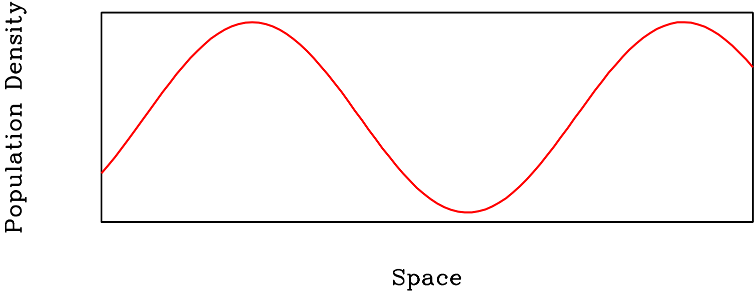

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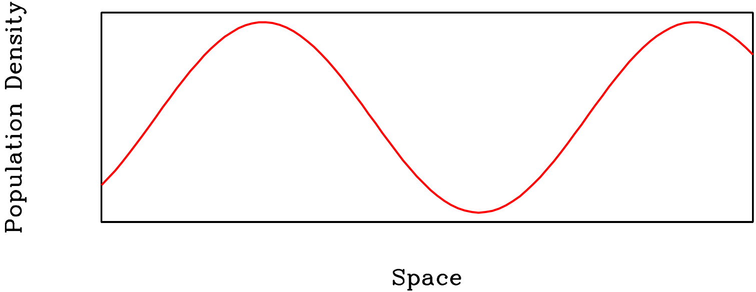

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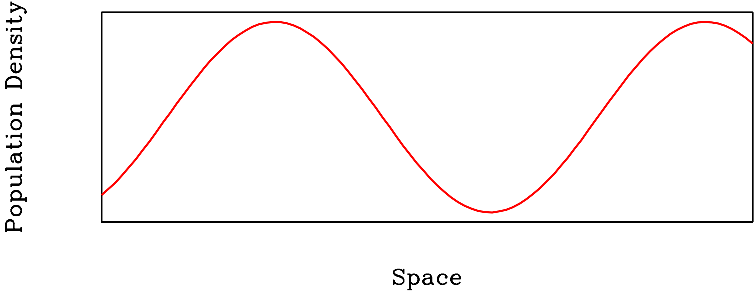

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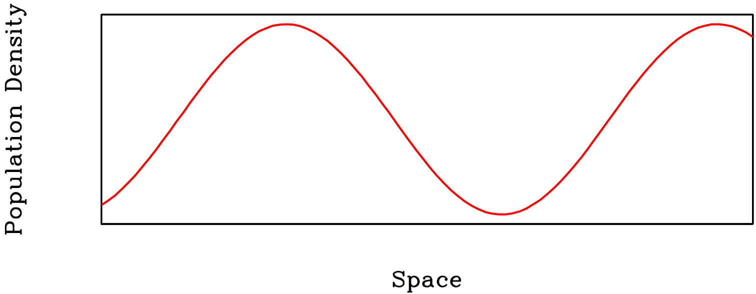

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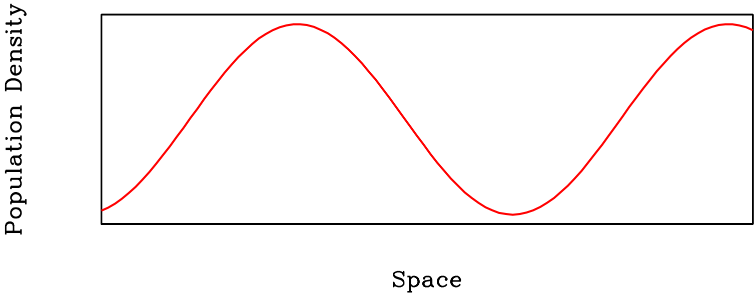

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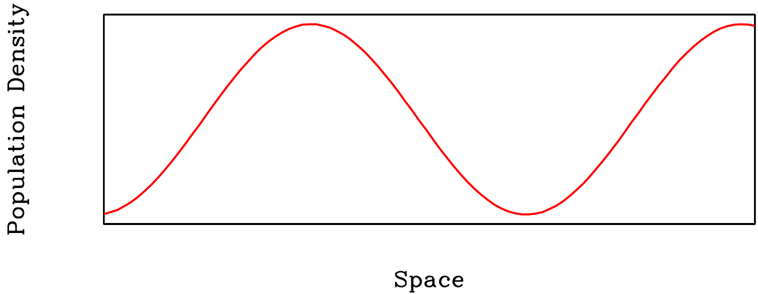

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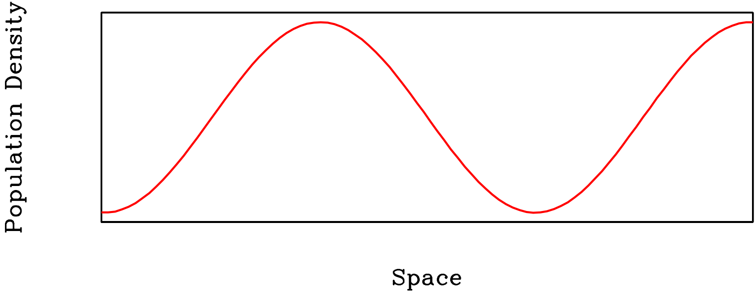

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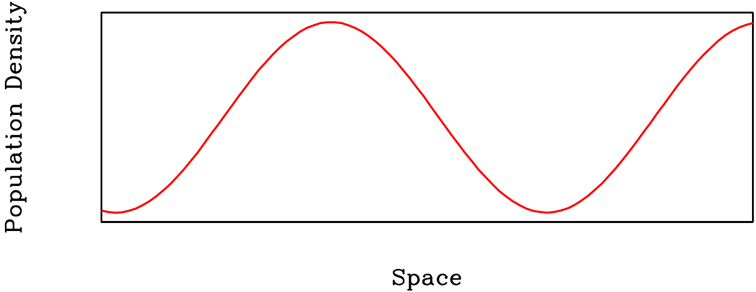

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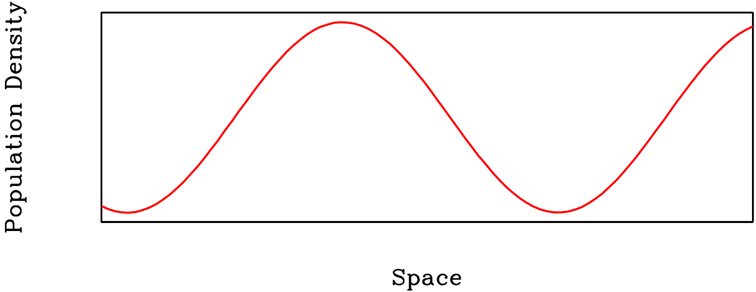

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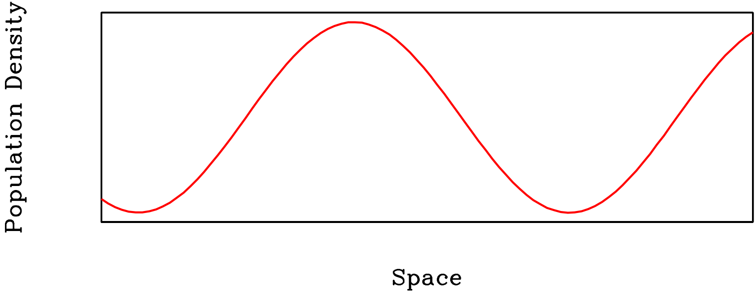

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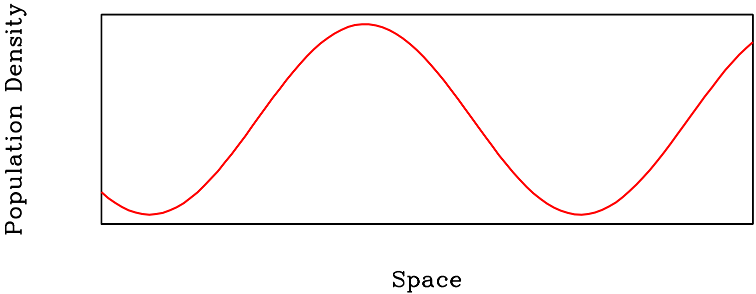

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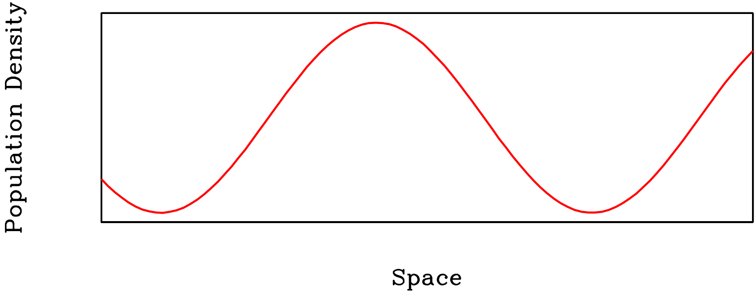

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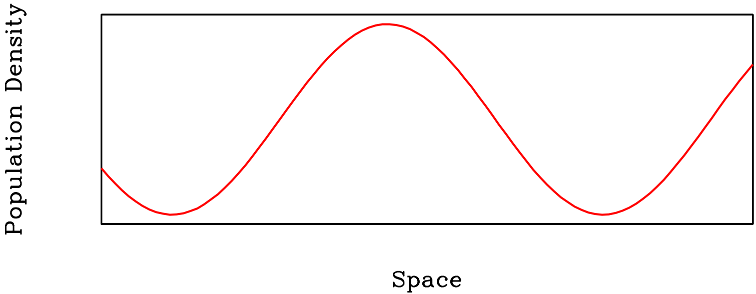

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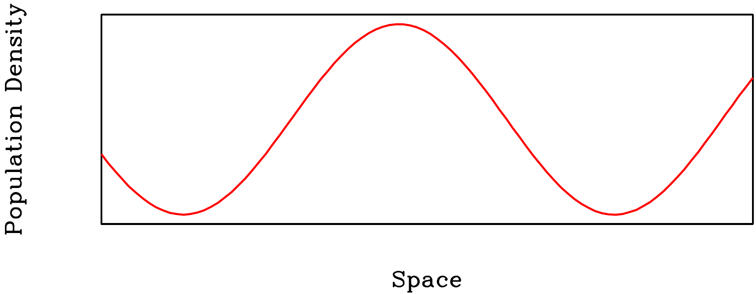

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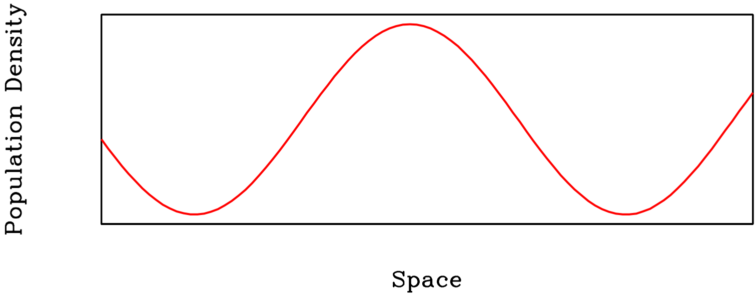

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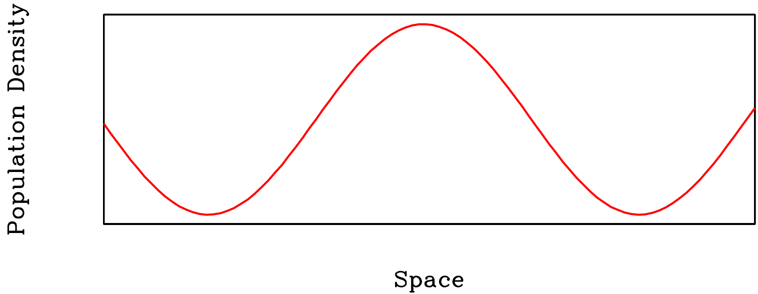

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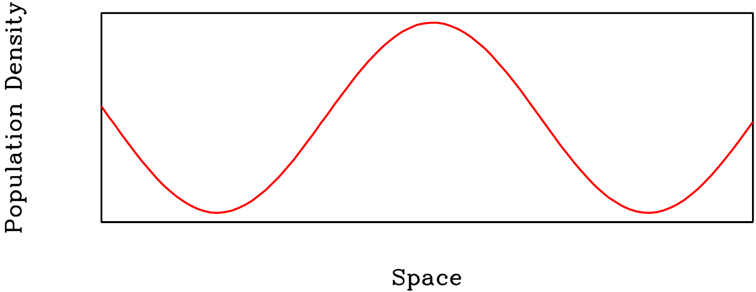

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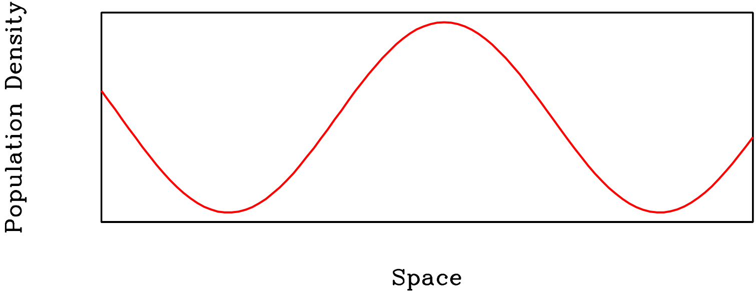

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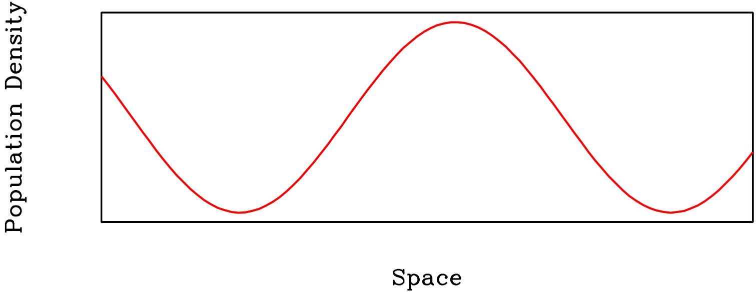

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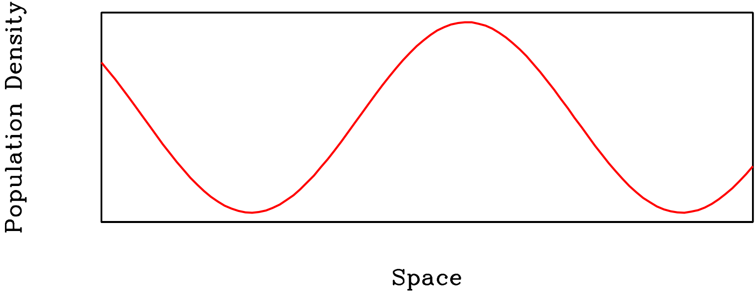

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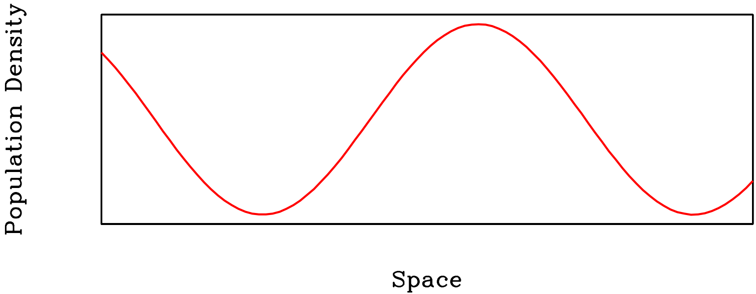

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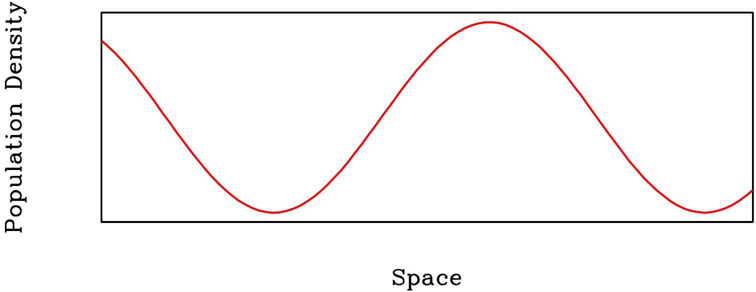

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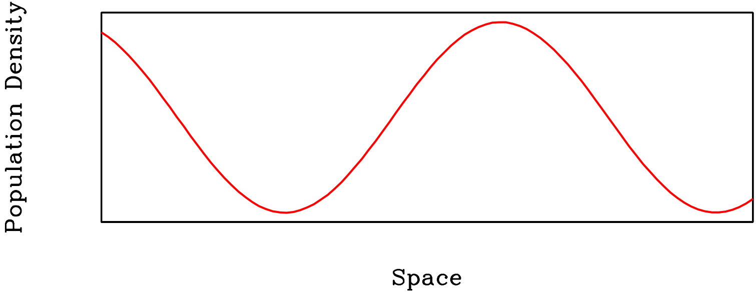

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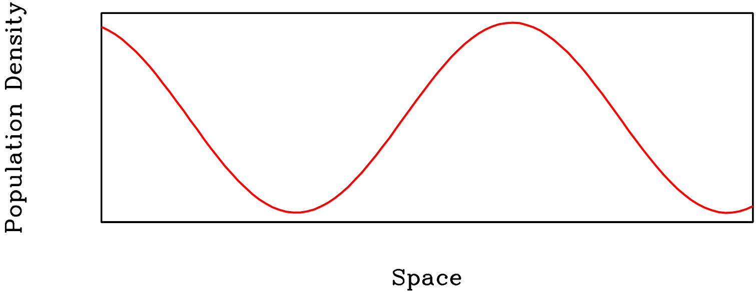

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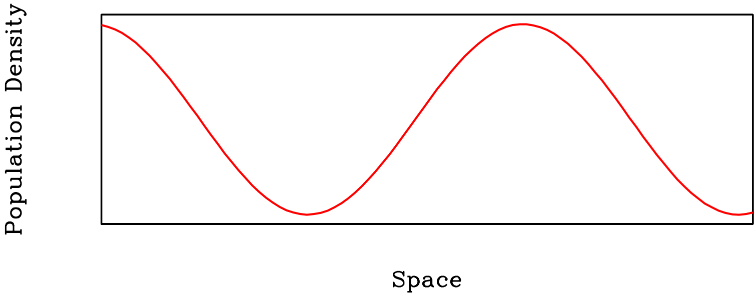

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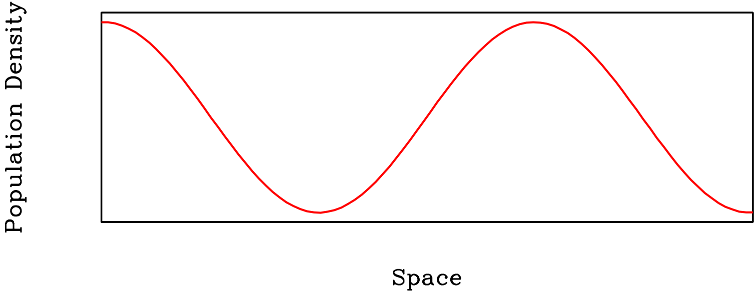

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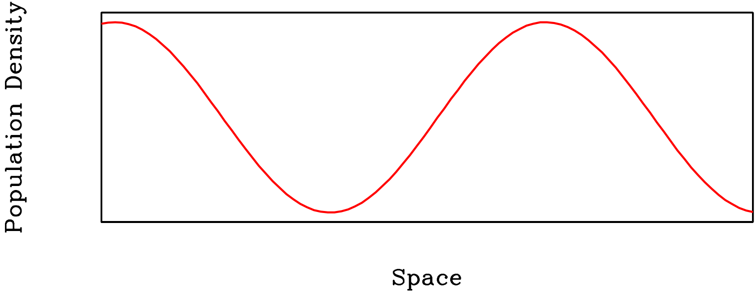

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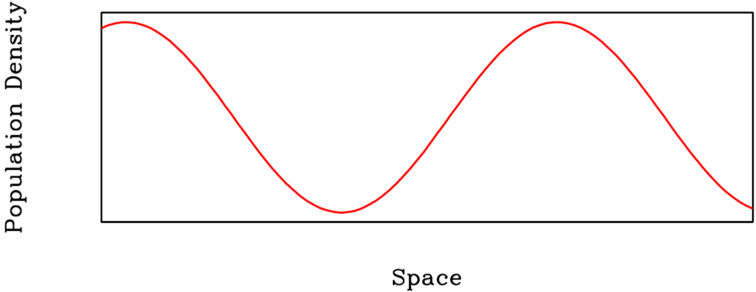

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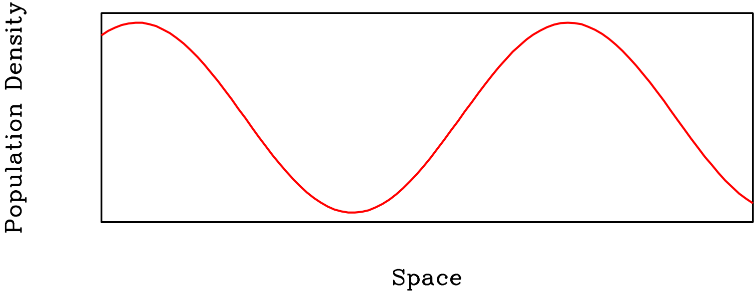

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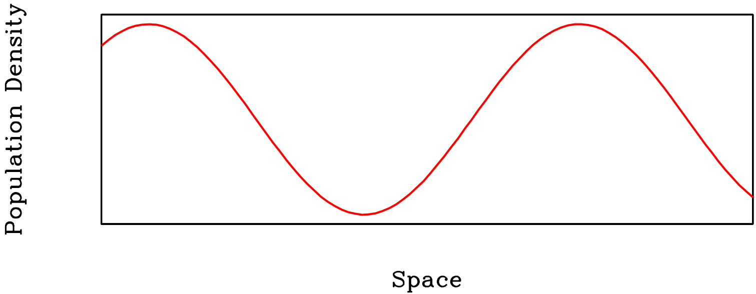

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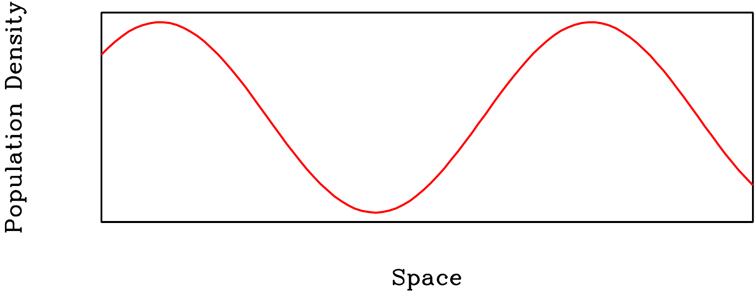

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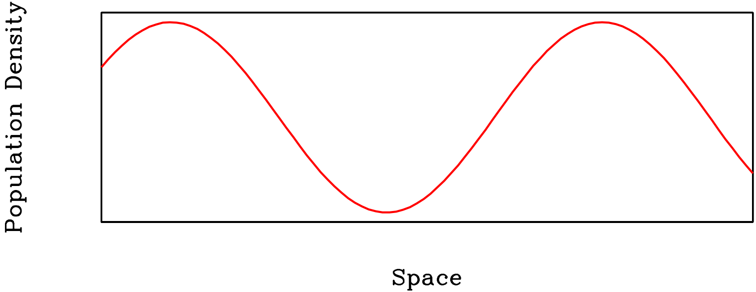

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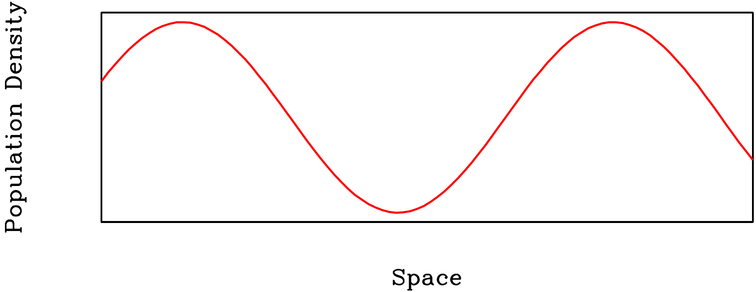

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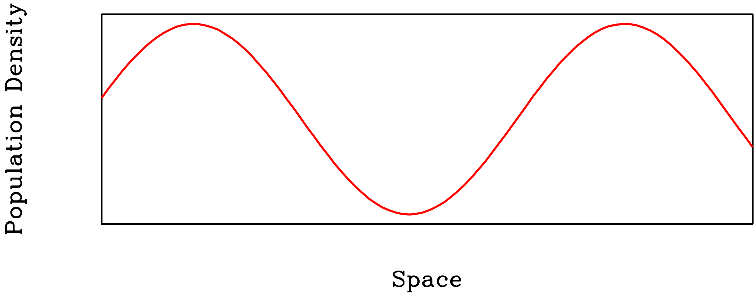

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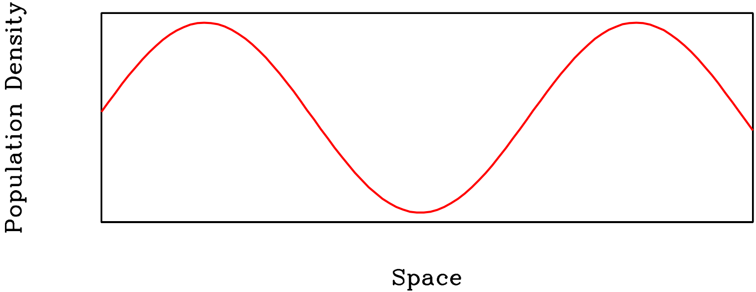

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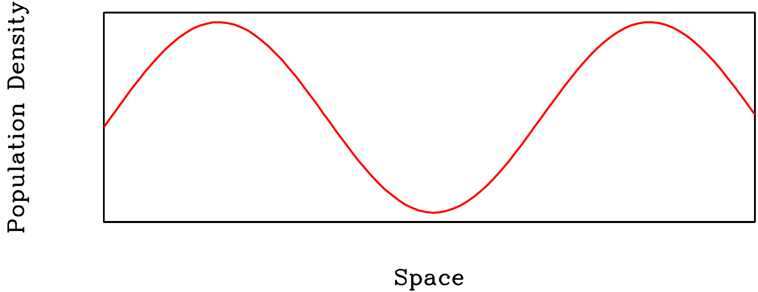

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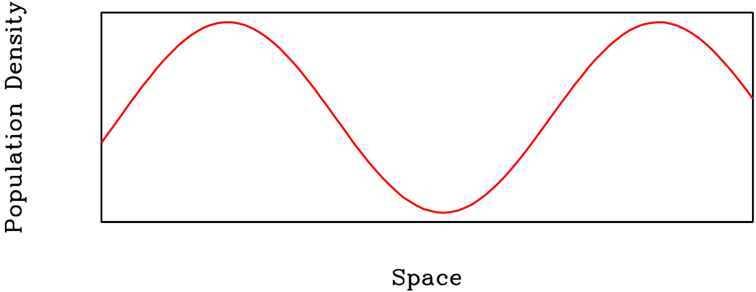

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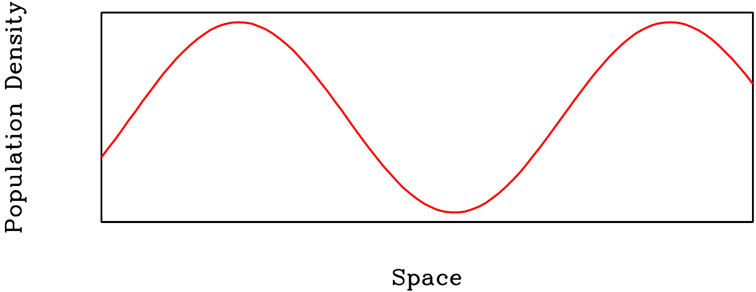
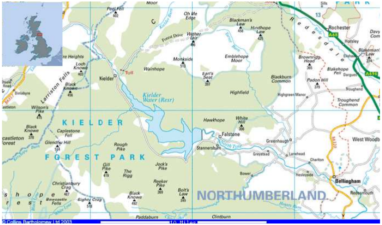


Red Grouse Wave Generation Question

Question

Could the moor/farmland boundary at the Northern edge of the study site play a role in generating the periodic travelling waves?

Second Example: Field Voles in Kielder Forest



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

Again, spatiotemporal field data shows that the cycles are spatially organised into a periodic travelling wave

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

- Voles are an important prey species for owls and kestrels
- 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

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

Field Vole Wave Generation Question

Question

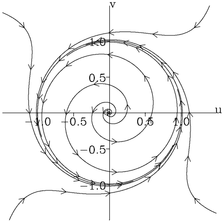
Could the boundary condition at the reservoir edge play a role in generating the periodic travelling waves?

Outline

Mathematical Model

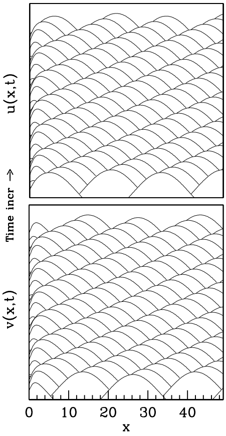
I consider a generic oscillator model ("λ–ω equations")

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



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

Typical Model Solutions

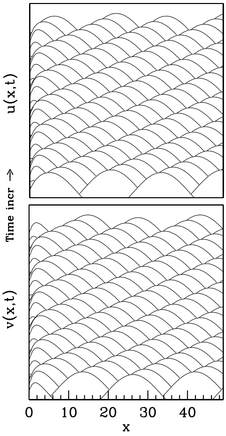


$$\text{Eqns:}\quad \begin{aligned} \frac{\partial u}{\partial t} &= \frac{\partial^2 u}{\partial x^2} + \lambda(r)u - \omega(r)v \\ \frac{\partial v}{\partial t} &= \frac{\partial^2 v}{\partial x^2} + \omega(r)u + \lambda(r)v \\ r &= \sqrt{u^2+v^2} \\ \lambda(r) &= 1 - r^2 \\ \omega(r) &= \omega_0 +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

$$\text{Bcs:}\quad \epsilon u_x = u \quad \epsilon v_x = v \quad \text{at} \quad x = 0$$

$$u_x = v_x = 0 \quad \text{at} \quad x = 50$$

Typical Model Solutions



Interim Conclusion

Robin boundary conditions do generate periodic travelling waves

Amplitude and Phase Equations

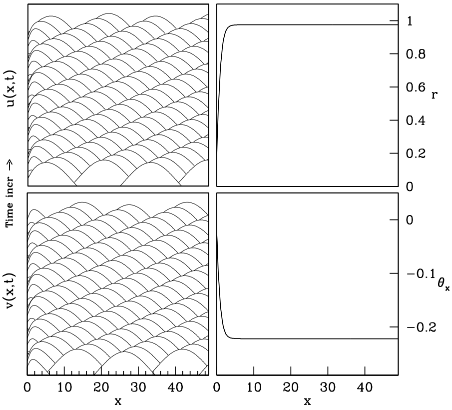
To study the λ–ω equations, it is helpful to replace u and v by $r = \sqrt{u^2 + v^2}$ and $\theta = \tan^{-1}(v/u)$, giving

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

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

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

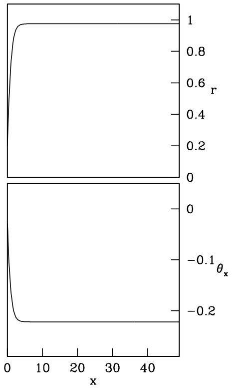
Typical Solutions Replotted



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

Equilibrium Equations

Solns $r = R(x)$, $\theta_x = \Psi(x)$ on $0 < x < \infty$



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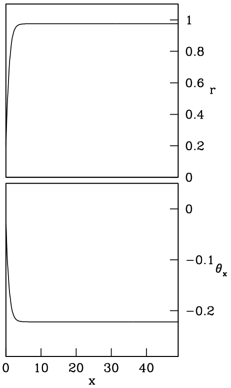


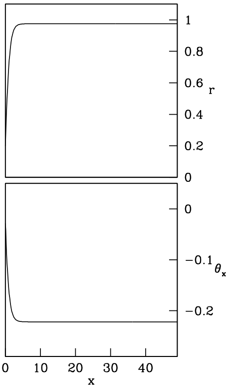
Solns $r = R(x)$, $\theta_x = \Psi(x)$ on $0 < x < \infty$

$$\begin{aligned} \Rightarrow R_{xx} + R(1 - R^2 - \Psi^2) &= 0 \\ \Psi_x + 2\Psi R_x / R + K - \omega_1 R^2 &= 0 \end{aligned}$$

with $\epsilon R_x - R = \Psi = 0$ at $x = 0$.

Here K is a constant of integration.

Equilibrium Equations



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Key question: what is $R(\infty)$, the amplitude of the periodic travelling wave?

Note that $R(\infty) = \sqrt{K/\omega_1}$

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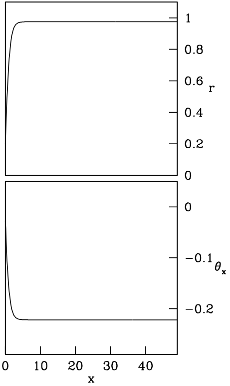

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Note that $R(\infty) = \sqrt{K/\omega_1}$

I consider this question first for $\epsilon = 0$ then for $\epsilon \neq 0$

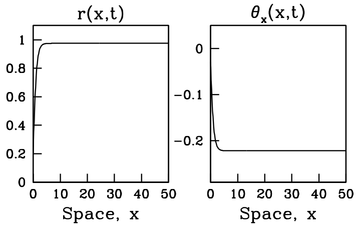
Outline

Steady Solutions for r and θ_x

For the case $\epsilon = 0$ (Dirichlet boundary condition), we look for solutions of

$$\begin{aligned} R_{xx} + R(1 - R^2 - \Psi^2) &= 0 \\ \Psi_x + 2\Psi R_x/R + (\omega_0 - K) - \omega_1 R^2 &= 0 \end{aligned}$$

subject to $R = 0$ at $x = 0$ and $R, \Psi \to$ constants as $x \to \infty$.



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subject to $R = 0$ at $x = 0$ and $R, \Psi \to$ constants as $x \to \infty$.

Hypothesis 1: There is a solution that is monotonic in R for exactly one value of K

Hypothesis 2: Any non-monotonic solutions are unstable as solutions of the original partial differential equations

Steady Solutions for r and θ_x

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subject to $R = 0$ at $x = 0$ and $R, \Psi \to$ constants as $x \to \infty$.

Exact solution: In fact there is an exact (monotonic) solution for $K = \omega_0 + (9 - \sqrt{81 + 72\omega_1^2})/(4\omega_1)$:

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

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

Steady Solutions for r and θ_x

For the case $\epsilon = 0$ (Dirichlet boundary condition), we look for solutions of

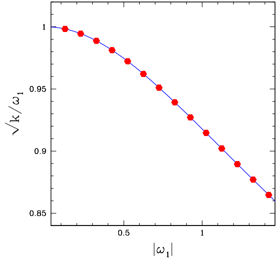
$$\begin{aligned} R_{xx} + R(1 - R^2 - \Psi^2) &= 0 \\ \Psi_x + 2\Psi R_x/R + (\omega_0 - K) - \omega_1 R^2 &= 0 \end{aligned}$$

subject to $R = 0$ at $x = 0$ and $R, \Psi \to$ constants as $x \to \infty$.

Exact solution: the wave amplitude

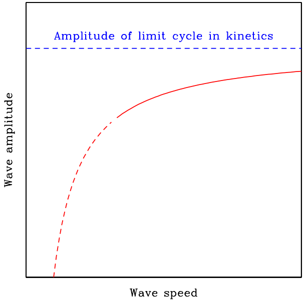
$$r_{ptw} = \left\{ \frac{1}{2}\left[1+\sqrt{1+\frac{8}{9}\omega_1^2}\right]\right\}^{-1/2}$$

is in very good agreement with that found in numerical 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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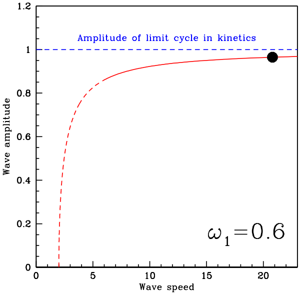

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$$\Leftrightarrow \quad r_{ptw} > \left(\frac{2 + 2\omega_1^2}{3 + 2\omega_1^2} \right)^{1/2}$$

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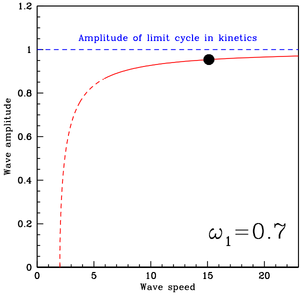

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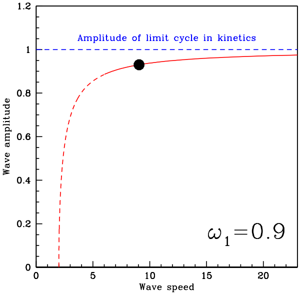

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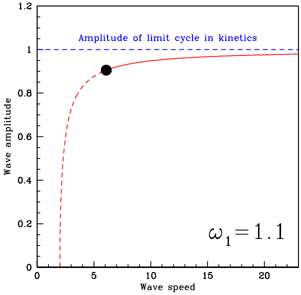

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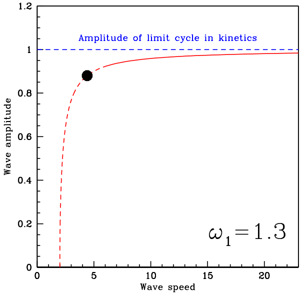

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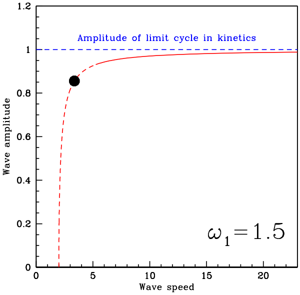

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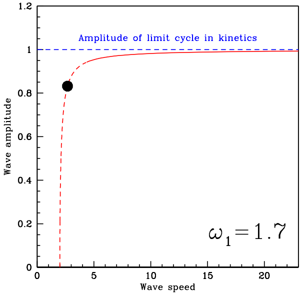

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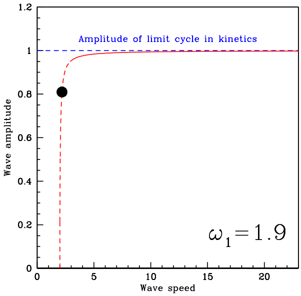
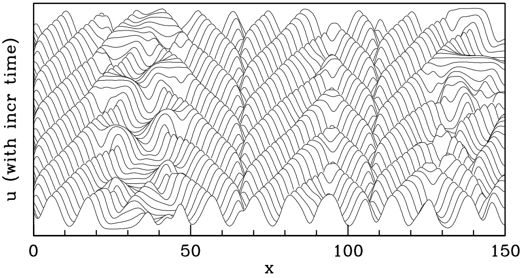


Typical Solution in an Unstable Case



Outline

Review of Boundary Condition

The zero Dirichlet boundary condition considered previously is an approximation to a Robin condition. For the λ–ω equations, it is possible to quantify the quality of this approximation.

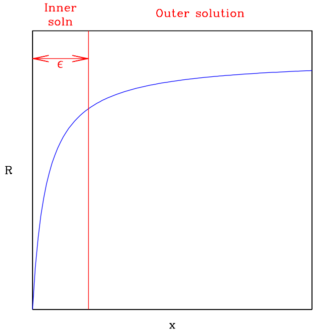
$$
\begin{aligned}
u_t &= u_{xx} + \lambda(r)u - \omega(r)v \\
v_t &= v_{xx} + \omega(r)u + \lambda(r)v \\
r &= \sqrt{u^2 + v^2} \\
\lambda(r) &= 1 - r^2 \\
\omega(r) &= \omega_0 + \omega_1 r^2.
\end{aligned}
$$

Boundary conditions at $x = 0$:

Dirichlet: $u = v = 0$
Robin: $u_x = (1/\epsilon)u$, $v_x = (1/\epsilon)v$

Perturbation theory calculation

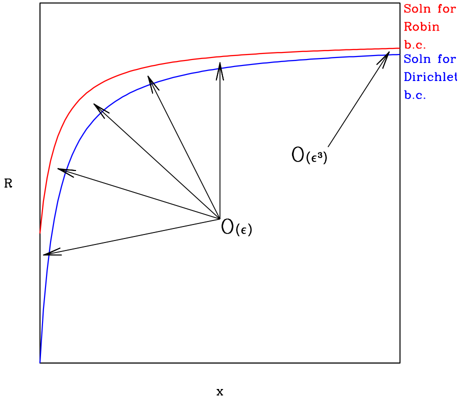
- For $\epsilon = 0$ we have an exact solution.
- For $\epsilon > 0$, this exact solution can be used as the basis for a power series expansion



Inner layer rescalings:
$\tilde{R} = R/\epsilon \quad \tilde{\Psi} = \Psi/\epsilon \quad \tilde{x} = x/\epsilon$

Perturbation theory calculation

- For $\epsilon = 0$ we have an exact solution.
- For $\epsilon > 0$, this exact solution can be used as the basis for a power series expansion
- Conclusion: the solution for $R(x)$ changes at $O(\epsilon)$, but the periodic wave amplitude $R(\infty)$ changes only at $O(\epsilon^3)$.



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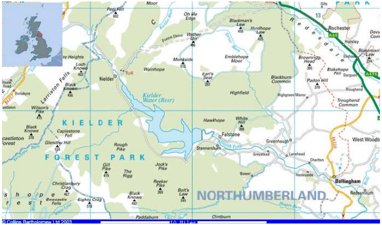
- So: the Dirichlet boundary condition is a very good approximation to the Robin condition.
- This result is for the λ–ω equations. Future work: is this true for other oscillatory reaction-diffusion systems?

Outline

Conclusions

- A Robin boundary condition does generate periodic travelling waves
- The periodic wave given by the Robin boundary condition is very well approximated by that given by the Dirichlet boundary condition
- This is important because a Dirichlet boundary condition is much simpler both analytically and numerically
- Most ecological models use Dirichlet rather than Robin conditions, without any justification. My results provide justification in the context of periodic travelling wave generation

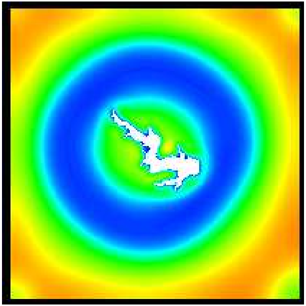
Back to the Example of Field Voles in Kielder Forest



Back to the Example of Field Voles in Kielder Forest

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

Numerical Simulation of Field Vole Waves



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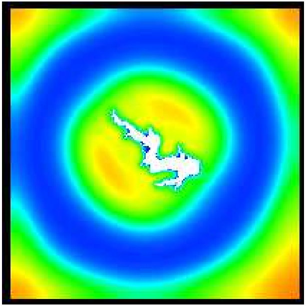

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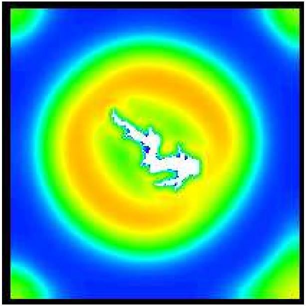

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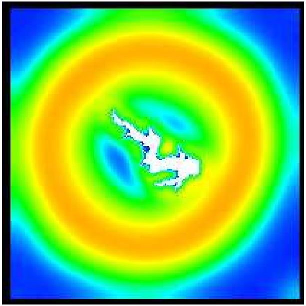

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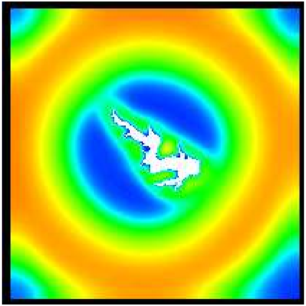

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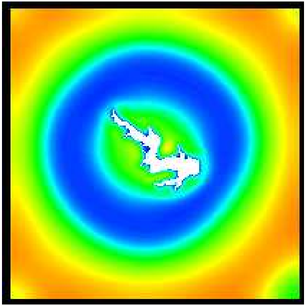


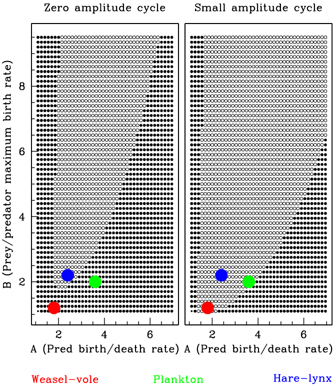
Movie of Field Vole Wave Simulation

Click here to
play the movie

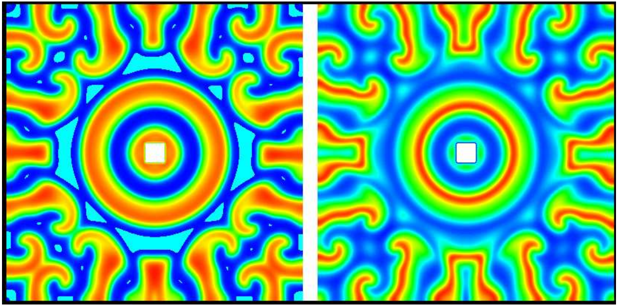
List of Frames

An Application of the Dirichlet Bdy Cond$^{\mathrm{n}}$ 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 a predator-prey model (close to Hopf bifurcation)



Typical Predator-Prey Solution in the Unstable Parameter Regime



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