Oscillatory Waves in Field Vole Populations

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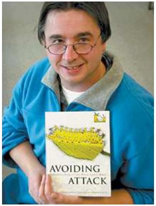
University of Glasgow, 8 December 2006

Collaborators

Xavier Lambin

Matthew Smith

Tom Sherratt



Outline

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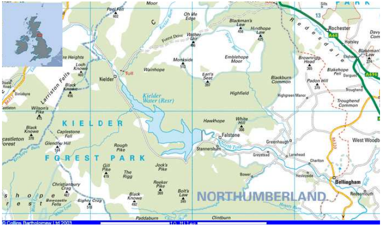
Field Voles in Kielder Forest



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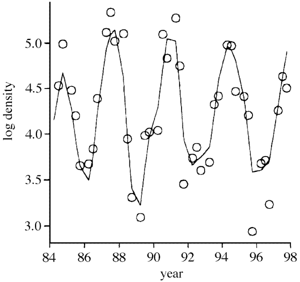

Field voles in Kielder Forest are cyclic (period 4 years)

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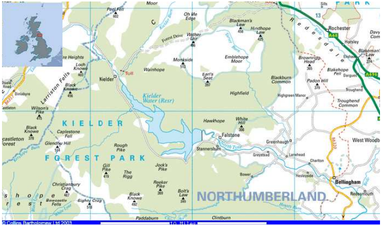

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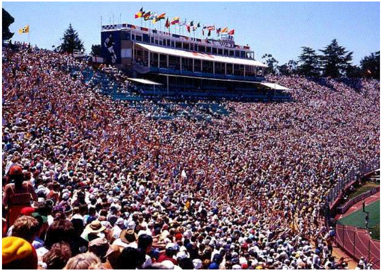
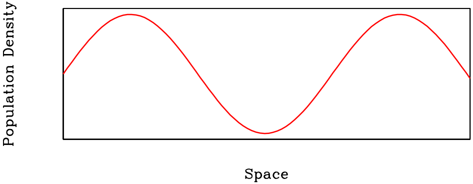
Spatiotemporal field data shows that the cycles are spatially organised into a periodic travelling wave

What is a Periodic Travelling Wave?

A useful analogy is the “Mexican Wave”





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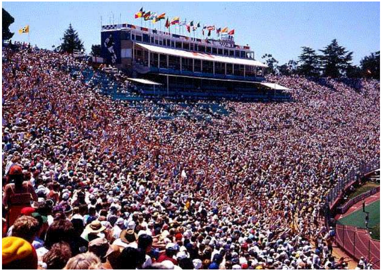

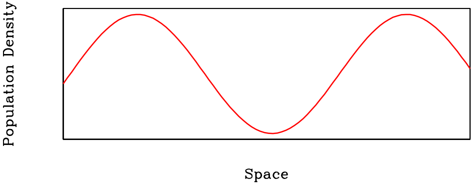

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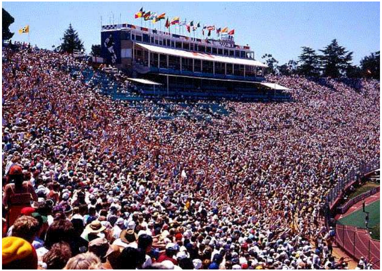

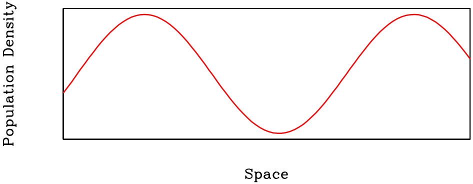

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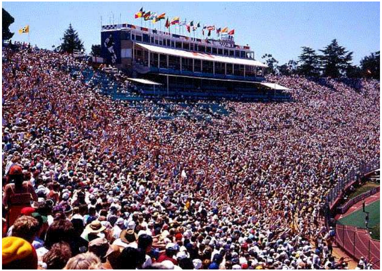

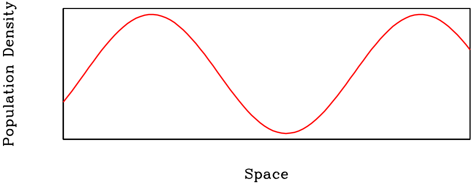

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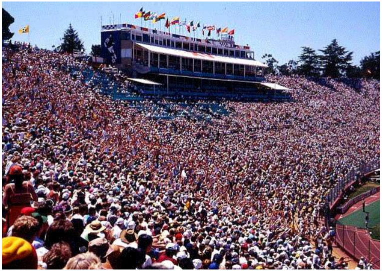

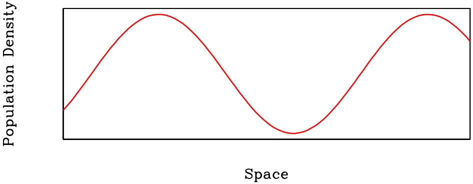

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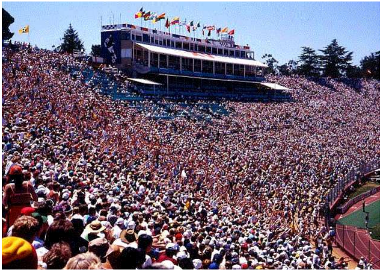

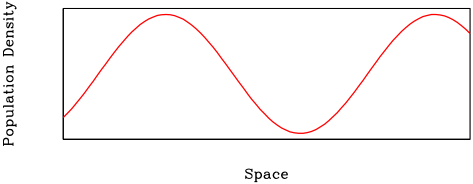

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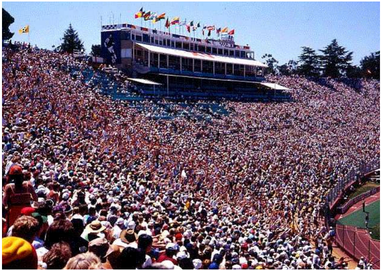

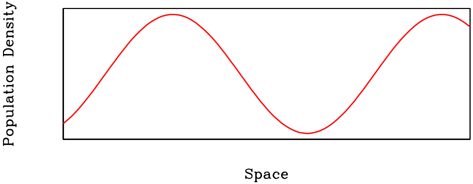

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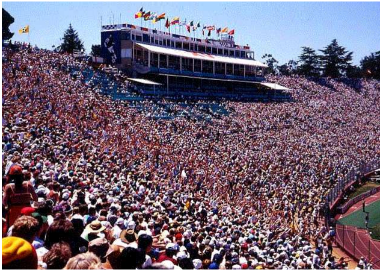

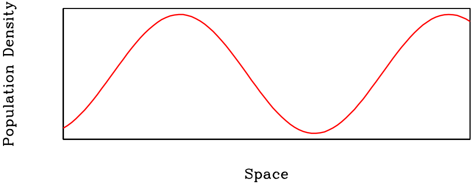

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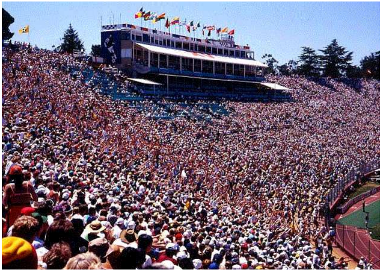

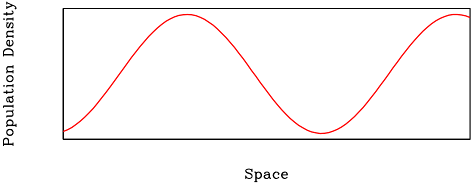

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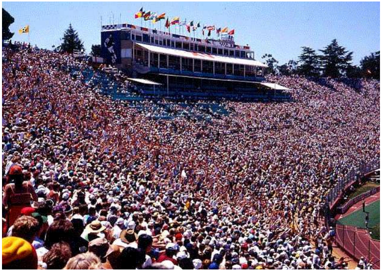

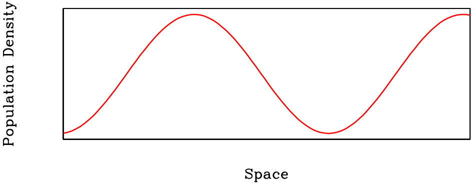

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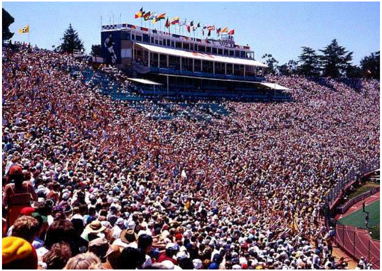

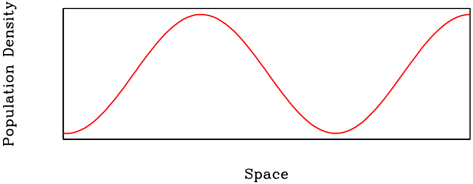

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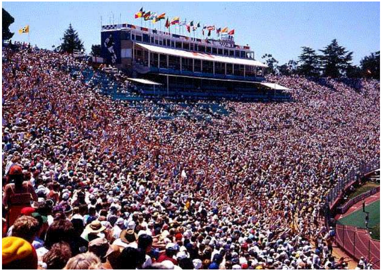

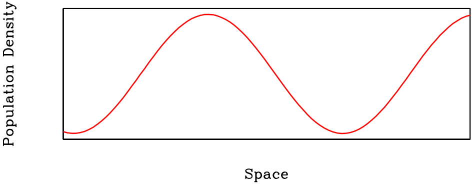

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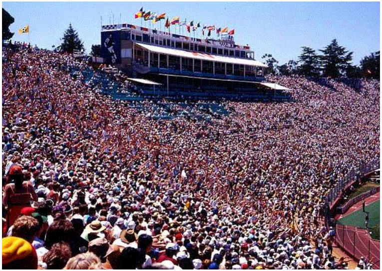

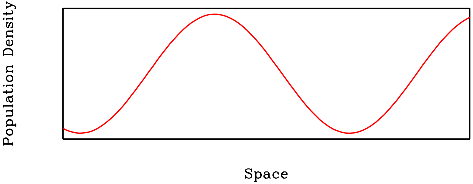

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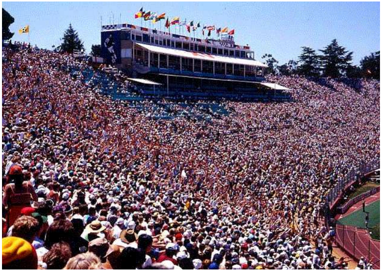

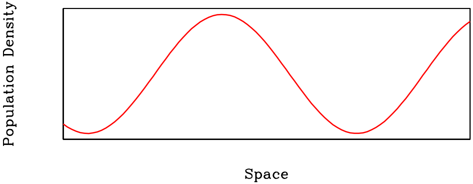

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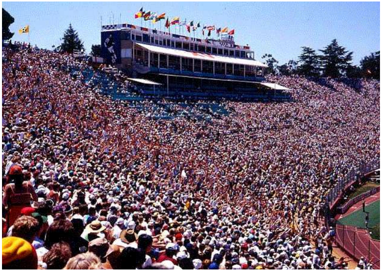

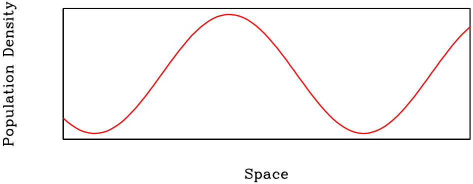

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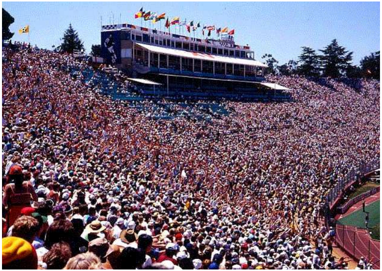

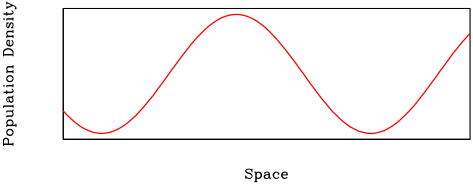

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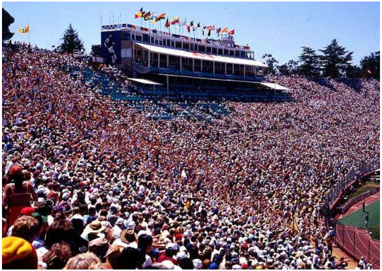

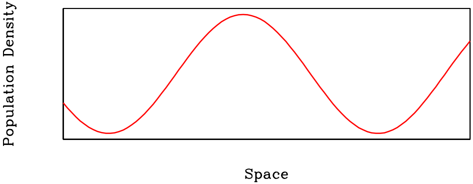

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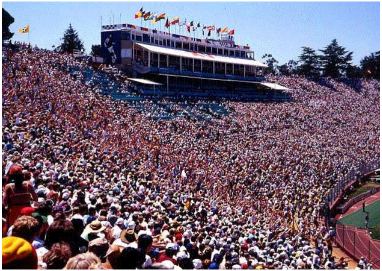

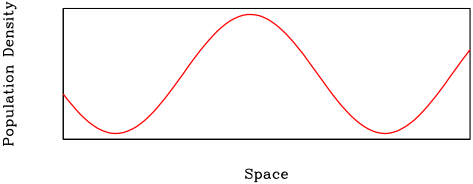

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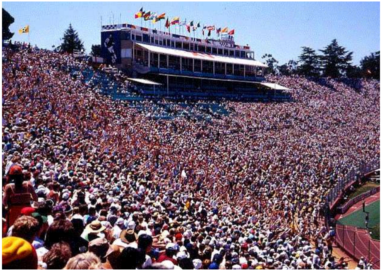

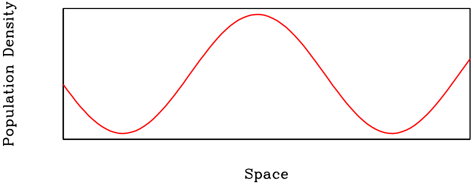

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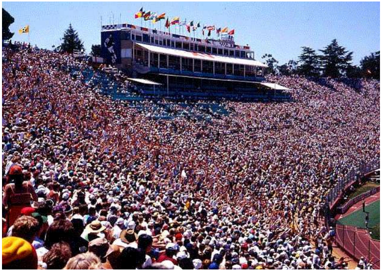

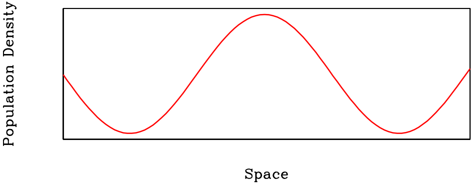

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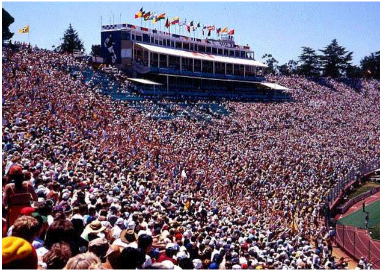

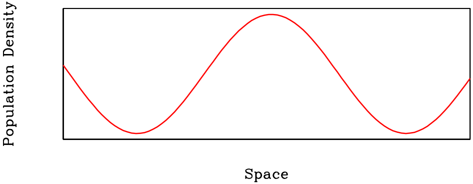

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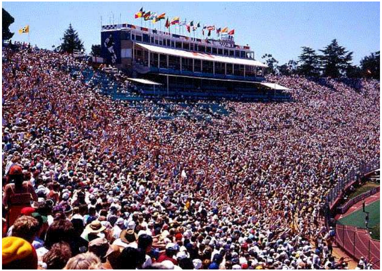

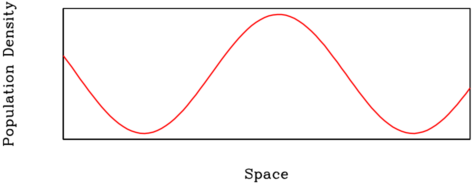

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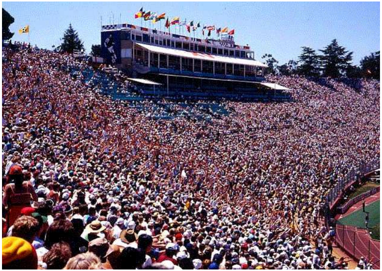

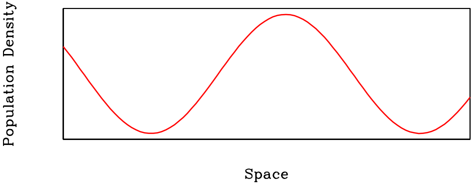

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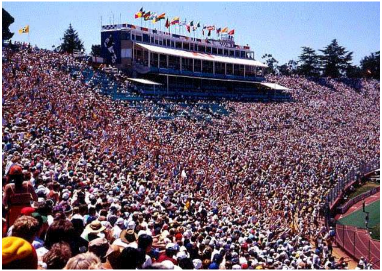

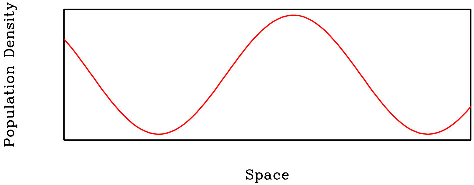

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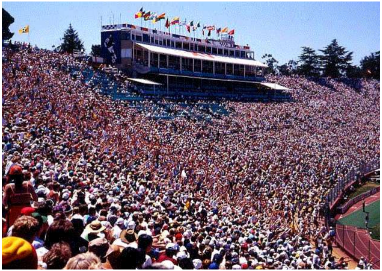

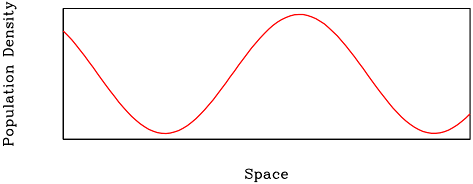

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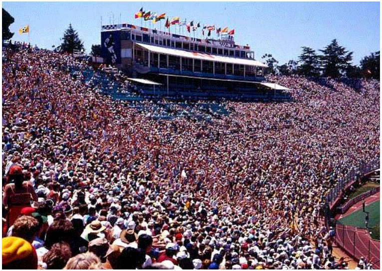

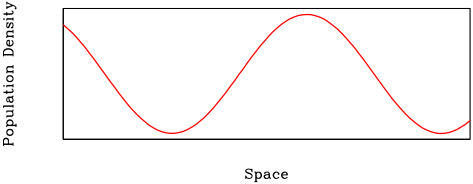

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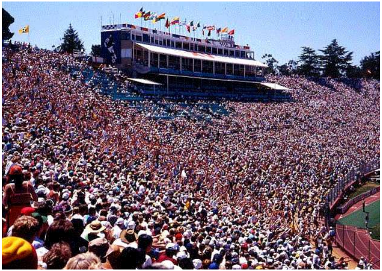

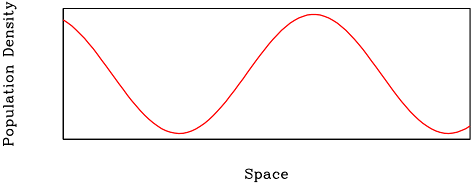

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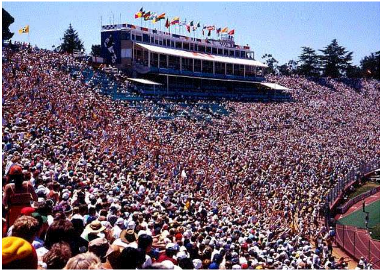

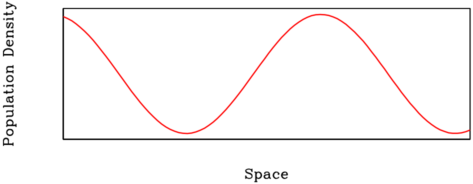

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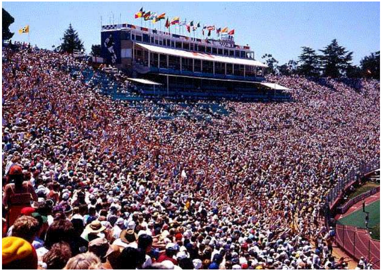

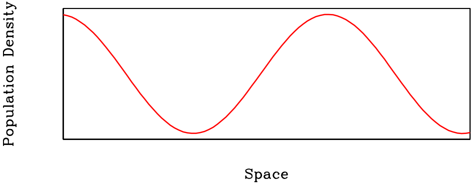

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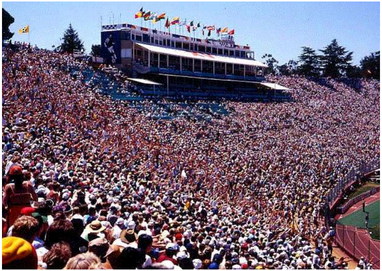

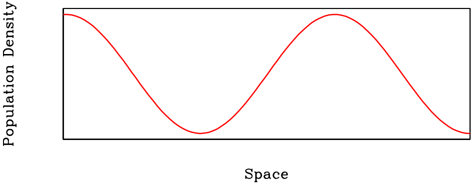

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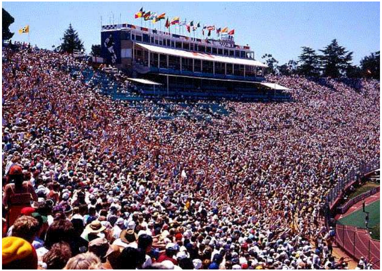

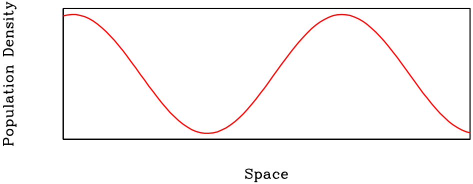

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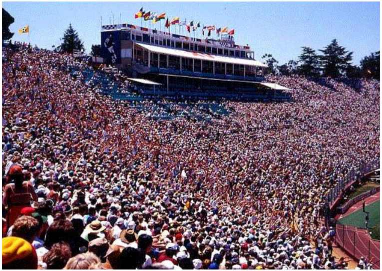

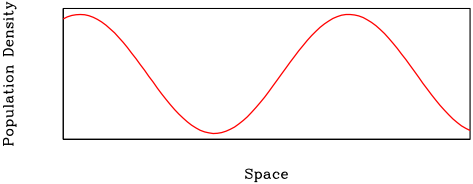

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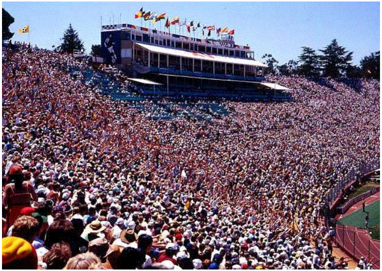

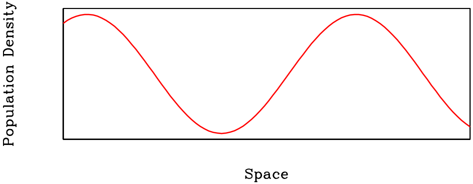

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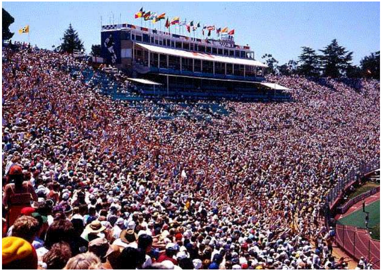

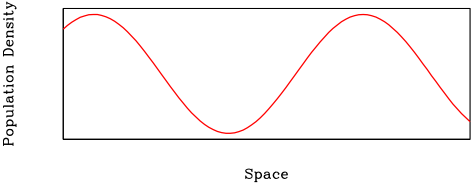

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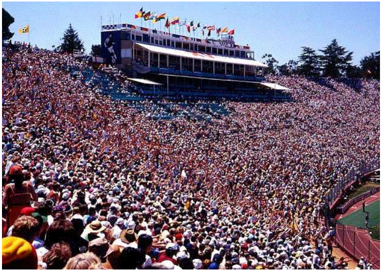

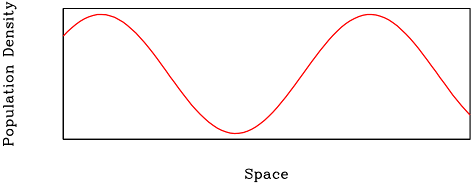

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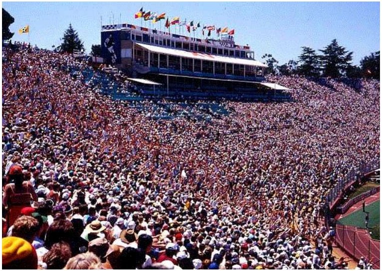

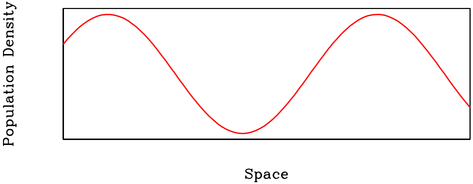

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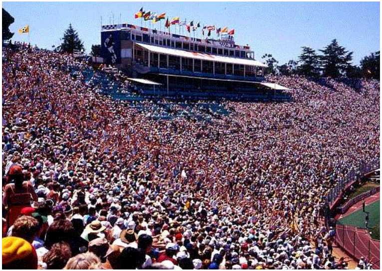

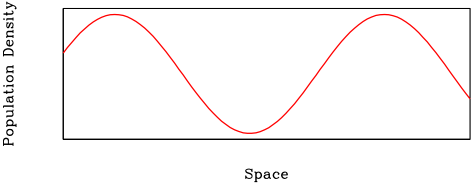

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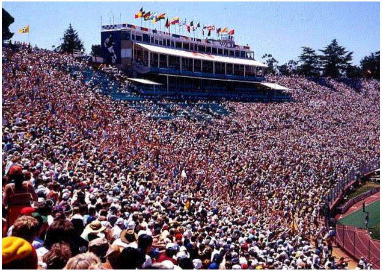

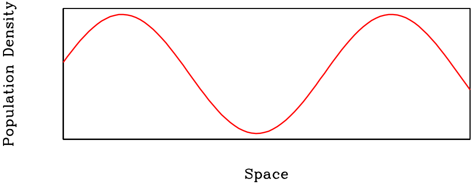

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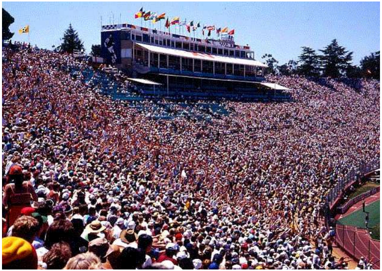

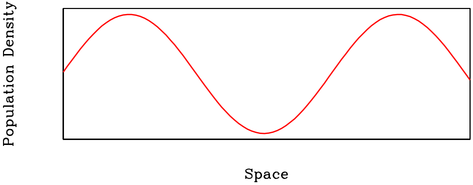

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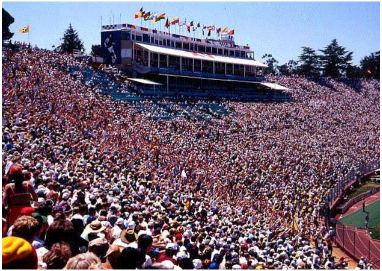

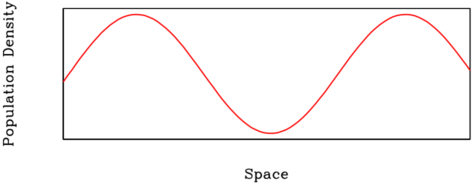

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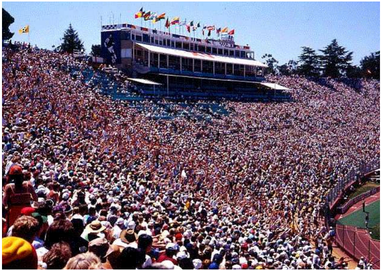

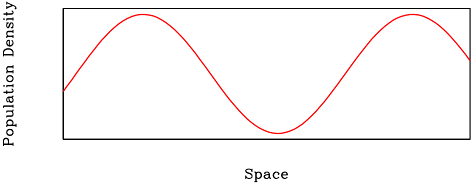

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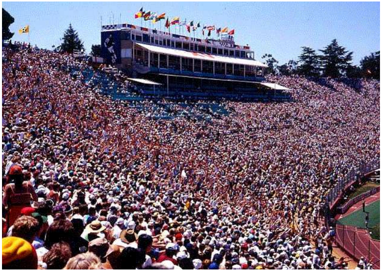

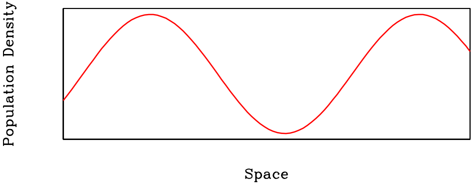

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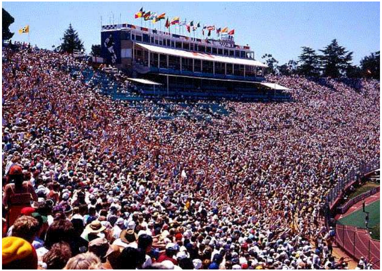

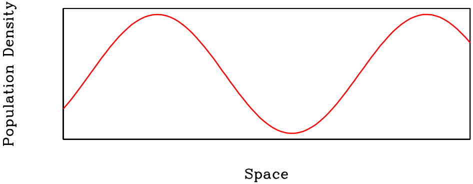

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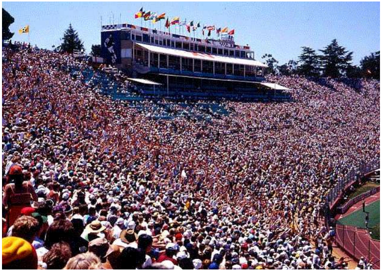

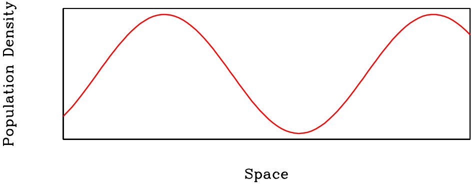

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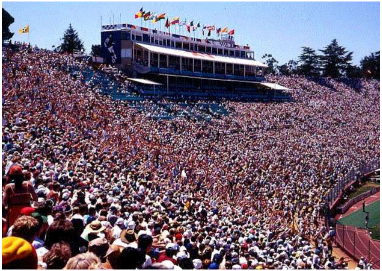

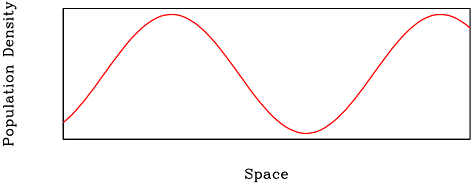

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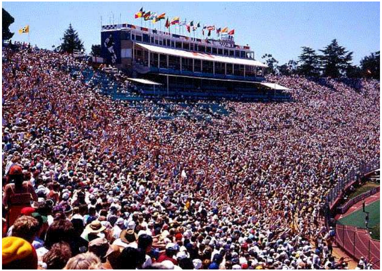

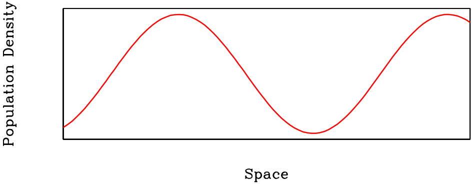

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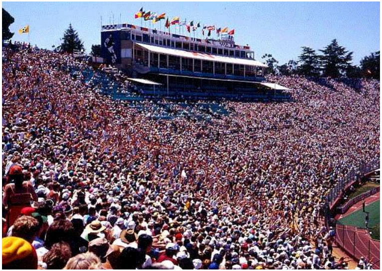

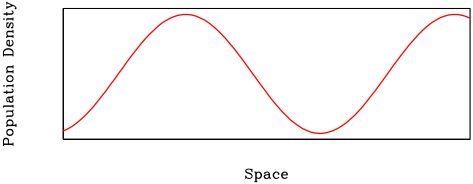

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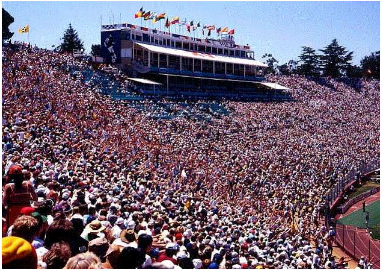

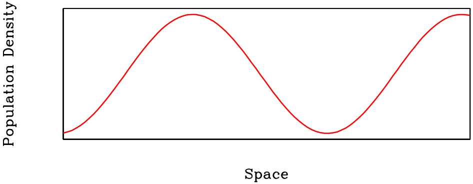

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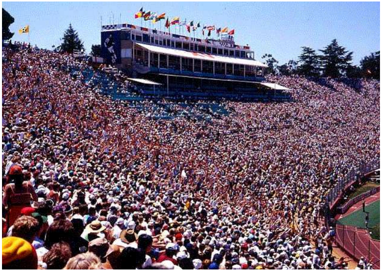

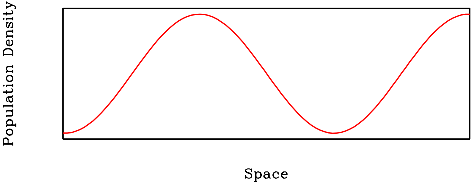

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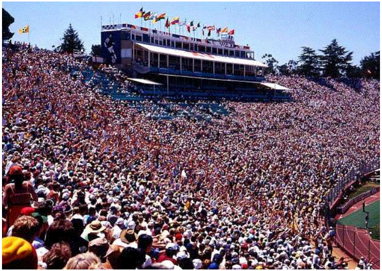

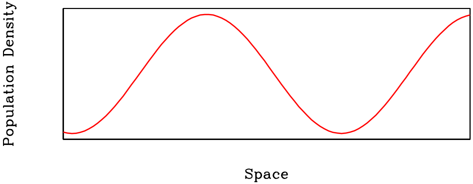

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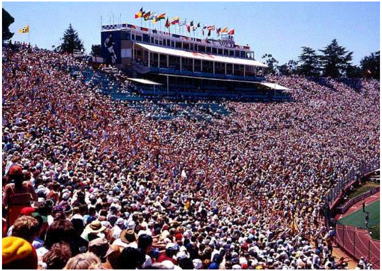

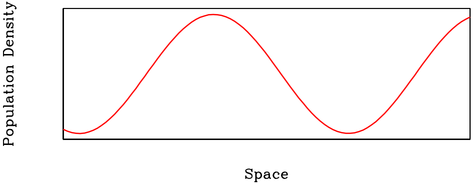

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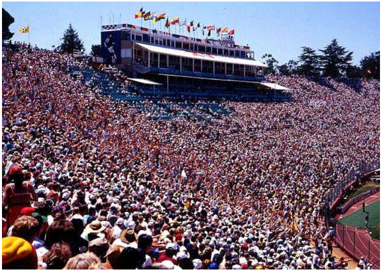

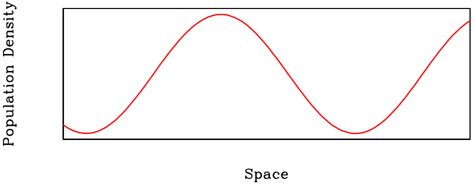

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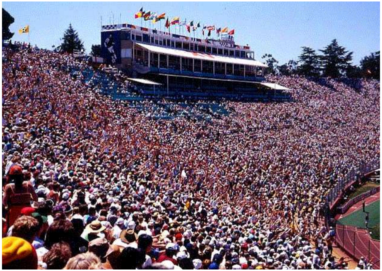

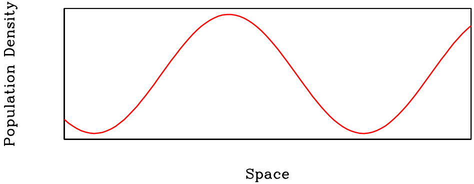

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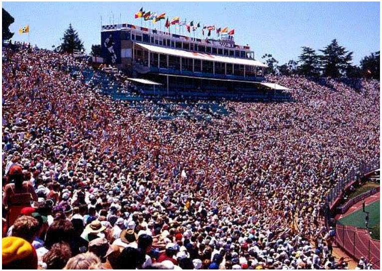

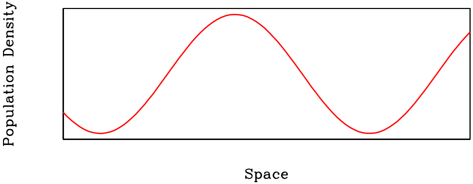

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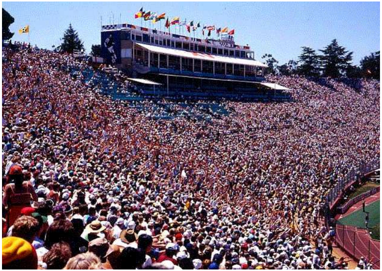

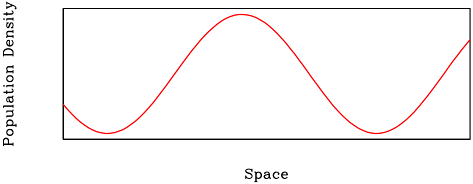

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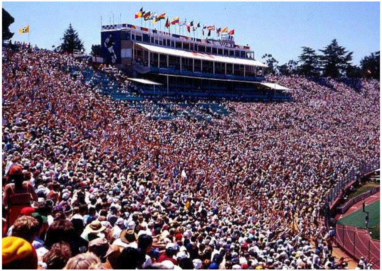

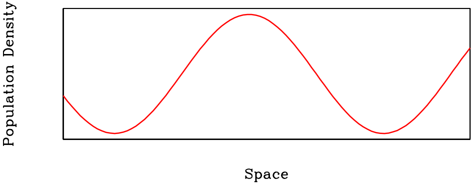

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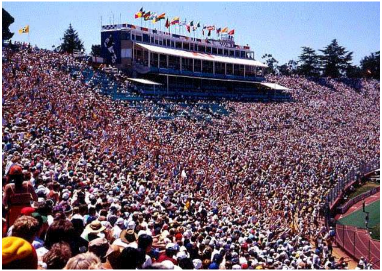

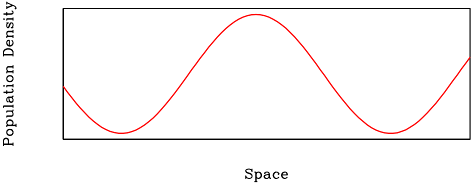

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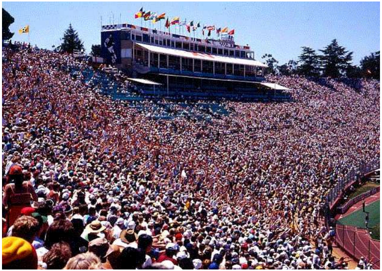

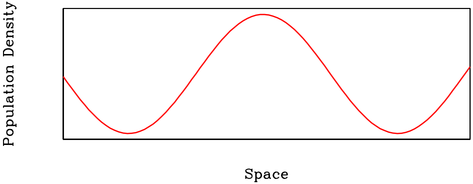

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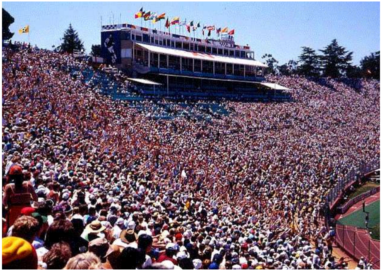

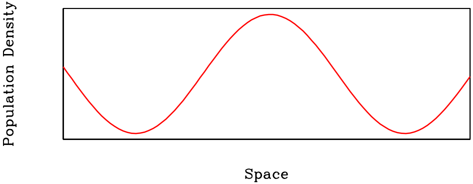

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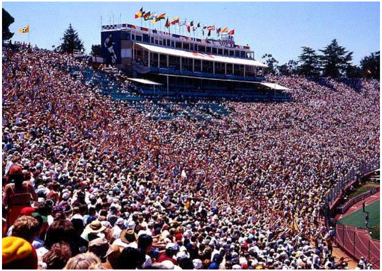

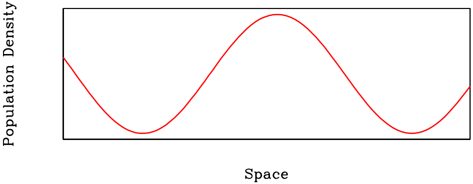

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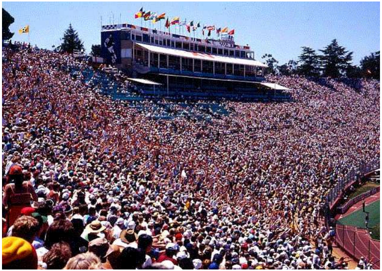

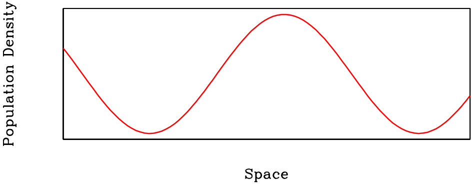

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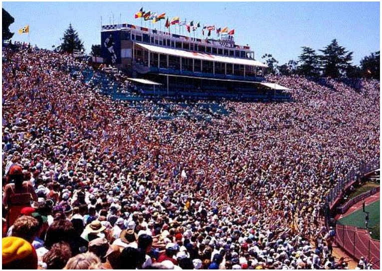

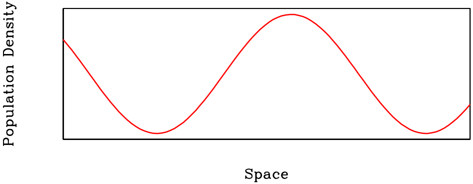

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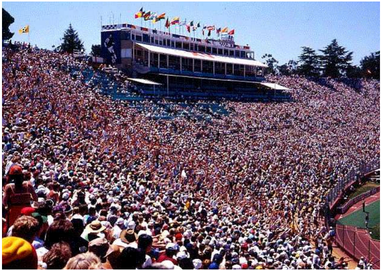

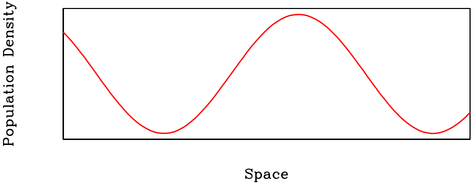

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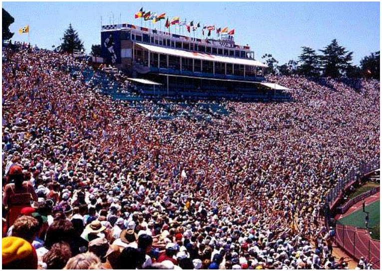

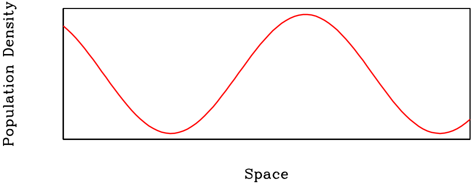

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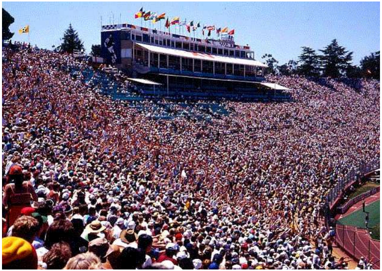

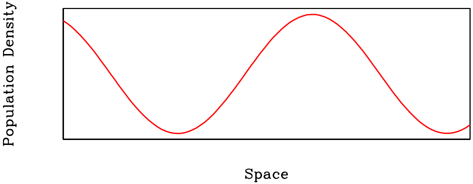

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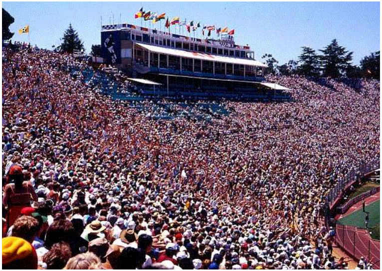

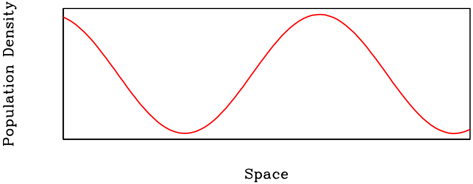

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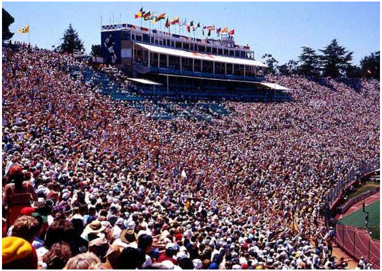

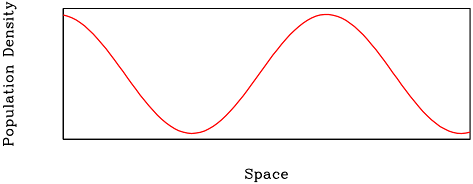

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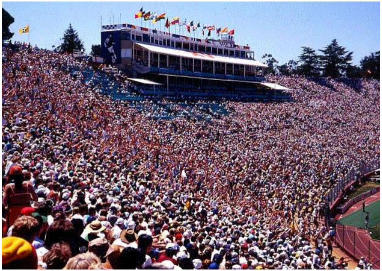

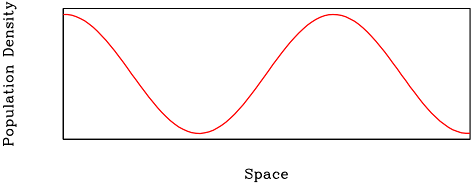

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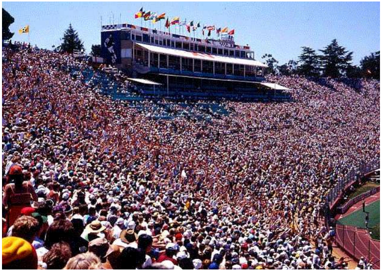

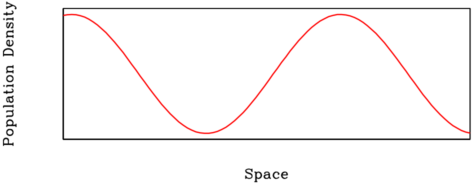

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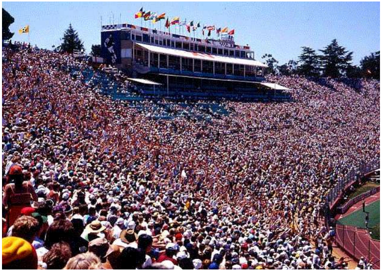

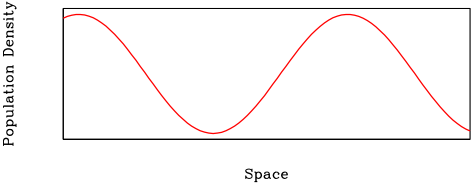

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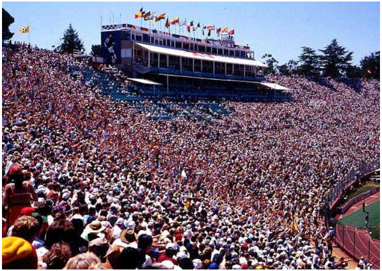

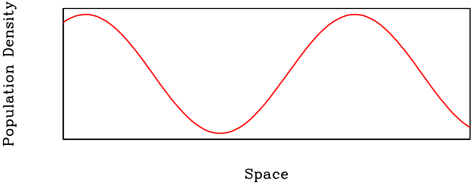

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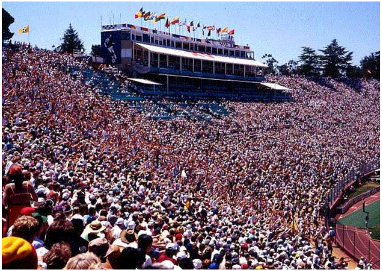

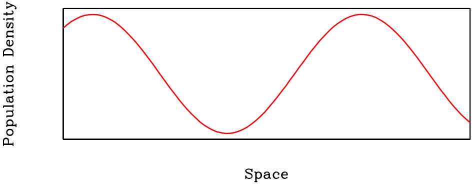

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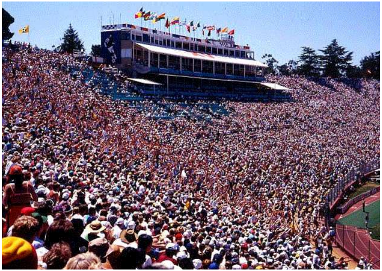

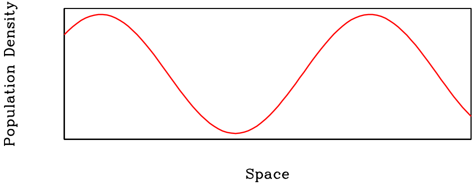

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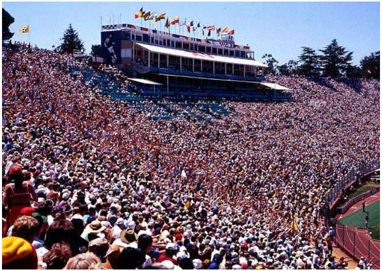

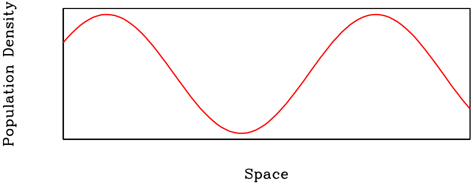

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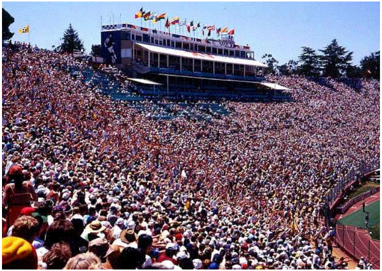

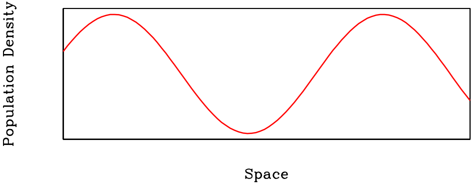

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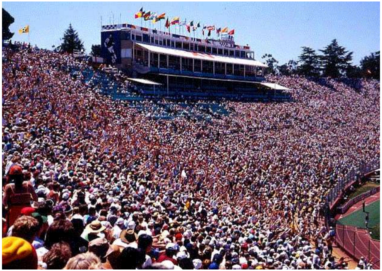

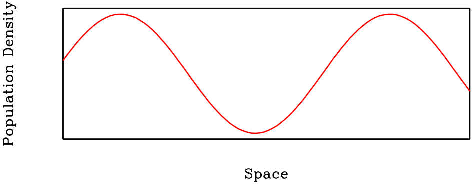

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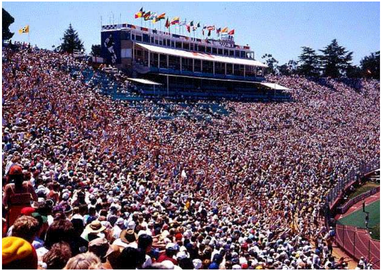

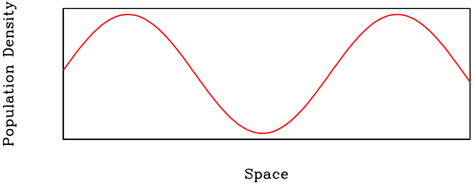

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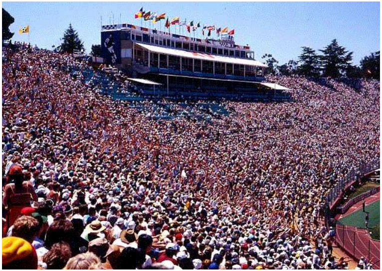

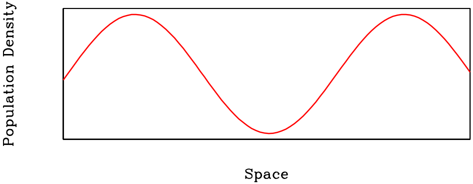

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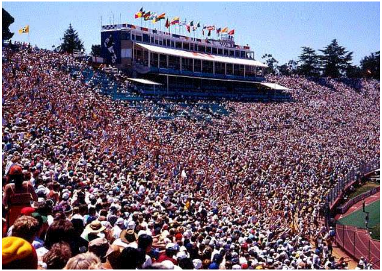

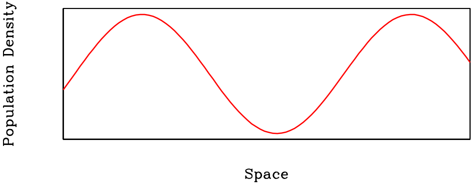

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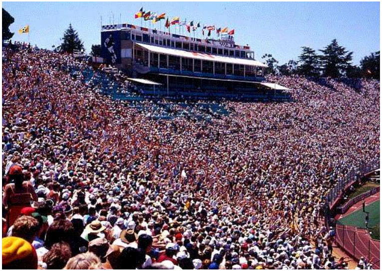

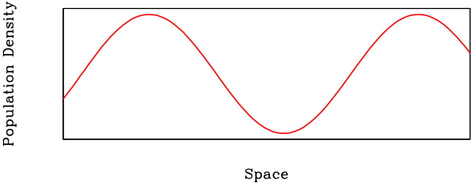

What Causes the Vole Cycles?

This is not known, but there are various hypotheses

- Interactions with predators, esp. weasels
- A disease affecting reproduction
- Complex interaction with grasses

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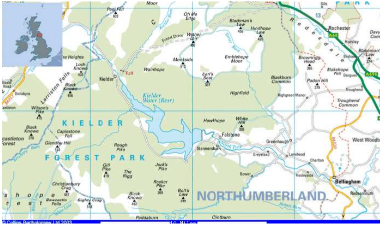
I will focus on vole-weasel dynamics, but many of the conclusions are generic

What Causes the Spatial Component of the Oscillations?



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

Outline

Predator-Prey Equations

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

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

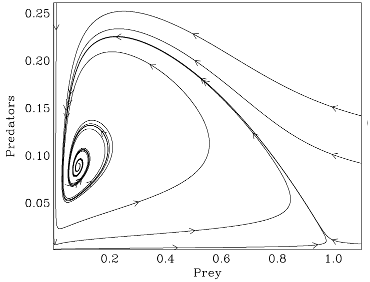
Predator-Prey Kinetics

predators

$$\partial p/\partial t = akph/(1+kh) - bp$$

prey

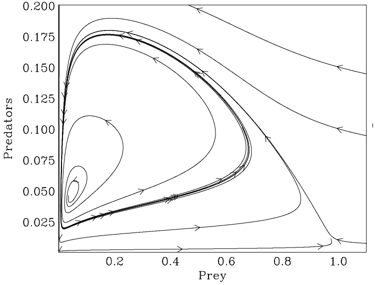
$$\partial h/\partial t = rh(1-h/h_0) - ckph/(1+kh)$$



Predator-Prey Kinetics

$$\frac{\partial p}{\partial t} = \overbrace{akph/(1+kh) - bp}^{\text{predators}}$$

$$\frac{\partial h}{\partial t} = \overbrace{rh(1-h/h_0) - ckph/(1+kh)}^{\text{prey}}$$



Boundary condition at edge of forest

A simple assumption is zero flux

$$\partial h/\partial n = \partial p/\partial n = 0$$

Boundary Condition at the Reservoir Edge

- Voles are an important prey species for owls and kestrels
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$$\frac{d}{dx}\begin{pmatrix}\text{vole}\\ \text{density}\end{pmatrix} = -\begin{pmatrix}\text{large}\\ \text{constant}\end{pmatrix}\cdot\begin{pmatrix}\text{vole}\\ \text{density}\end{pmatrix} \qquad \text{i.e. } \frac{\partial h}{\partial n} = \frac{h}{\epsilon}$$

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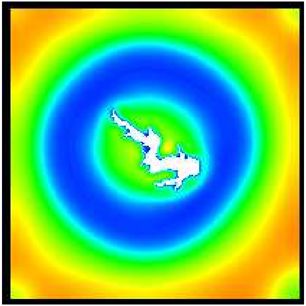
- To a first approximation, this boundary condition is just

$$\left(\begin{array}{c}\text{vole}\\ \text{density}\end{array}\right) = 0 \qquad \text{i.e. } h = 0$$

Typical Model Solution



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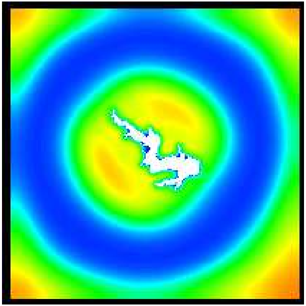

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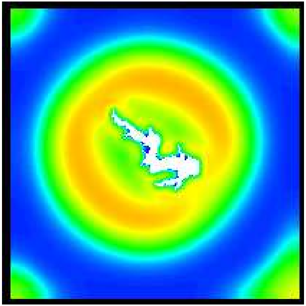

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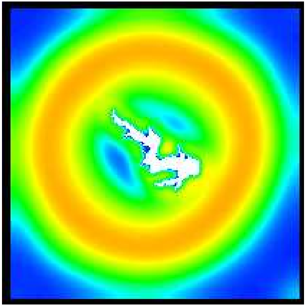

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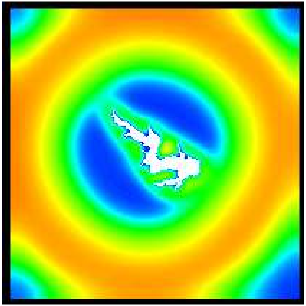

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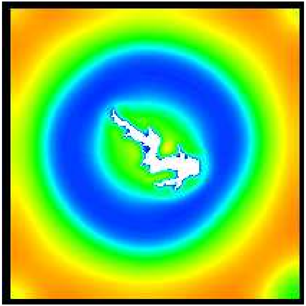
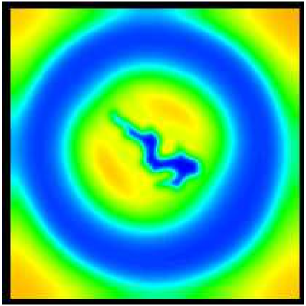


Movie of Typical Model Solution

Click here to
play the movie

Removing the Reservoir

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



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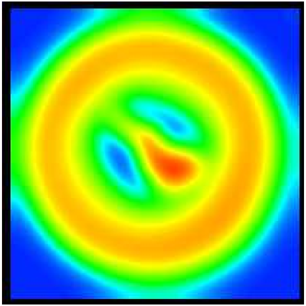

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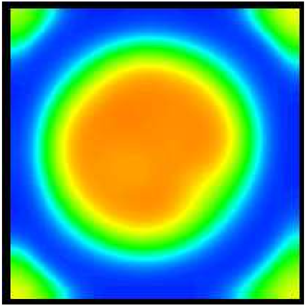

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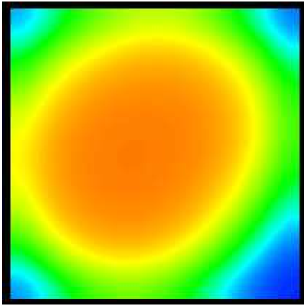

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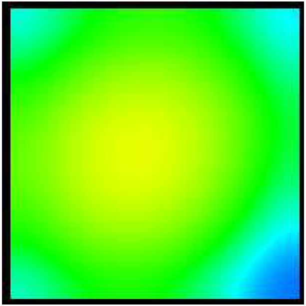

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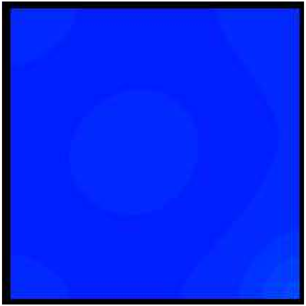
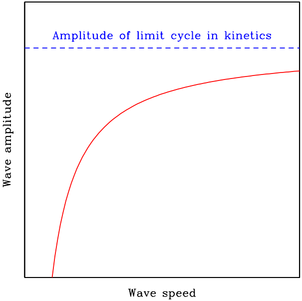


Outline

The Periodic Travelling Wave Family

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



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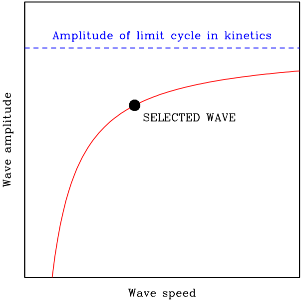
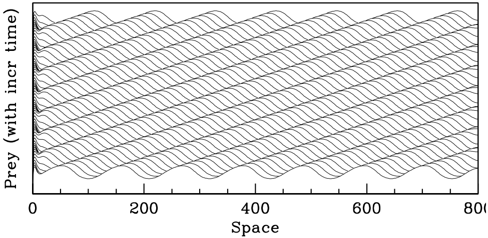


Mathematical question:
which member of the wave family is selected by the reservoir?

One-Dimensional Problem

To simplify, solve on $0 < x < L$ with

$$\begin{array}{llll} h = 0 \quad p_x = 0 & \text{at} & x = 0 & \leftrightarrow \text{edge of reservoir} \\ h_x = p_x = 0 & \text{at} & x = L & \leftrightarrow \text{edge of forest} \end{array}$$



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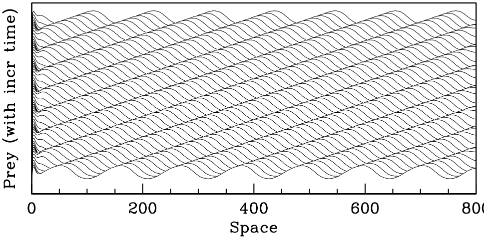

In fact the condition at $x = L$ plays no significant role, and we can consider the equations on $0 < x < \infty$.

λ–ω Equations

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

$$\begin{aligned} u_t &= u_{xx} + \lambda(r)u - \omega(r)v \\ v_t &= v_{xx} + \omega(r)u + \lambda(r)v \end{aligned}$$

where

$$\begin{aligned} \lambda(r) &= 1 - r^2 \\ \omega(r) &= \omega_0 + \omega_1 r^2. \end{aligned}$$

Here

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

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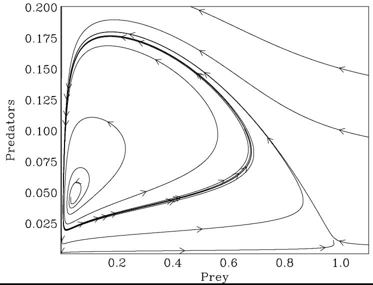

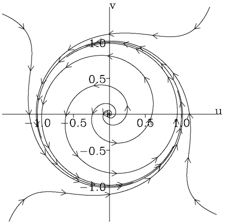

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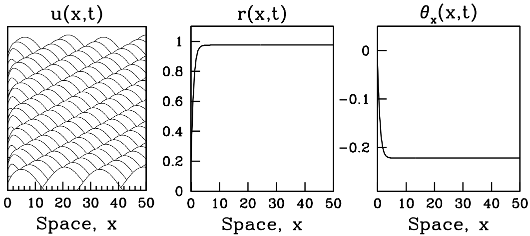
The periodic travelling wave family is

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

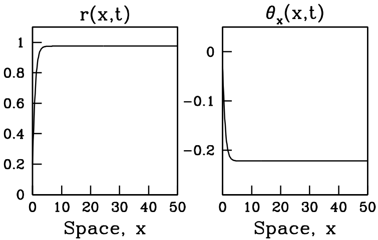
λ–ω Equations in Polar Coordinates

λ–ω equations are simplified by working with $r = \sqrt{u^2 + v^2}$ and $\theta = \tan^{-1}(v/u)$, giving

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



Steady Solutions for r and θ_x



Look for solutions $r(x,t) = R(x)$ and $\theta(x,t) = K + \int \Psi(x)$

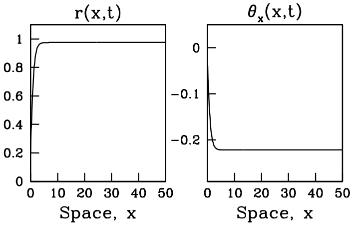
$$\Rightarrow R_{xx} + R(1 - R^2 - \Psi^2) = 0$$
$$\Psi_x + 2\Psi R_x/R + (\omega_0 - K) - \omega_1 R^2 = 0$$

Steady Solutions for r and θ_x (contd)

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 $R, \Psi \rightarrow$ constants as $x \rightarrow \infty$.



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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 (contd)

We look for solutions of

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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 $K = \omega_0 + (9 - \sqrt{81 + 72\omega_1^2})/(4\omega_1)$:

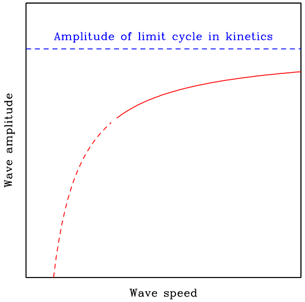
$$R(x) = r_{ptw} \tanh\left(x/\sqrt{2}\right) \qquad \Psi(x) = \psi_{ptw} \tanh\left(x/\sqrt{2}\right)$$

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

Outline

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

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

Stability of the Selected Wave

The stability of the selected wave depends on ω_1.

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

This is stable

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

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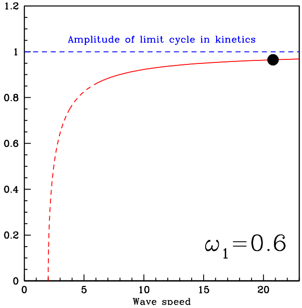

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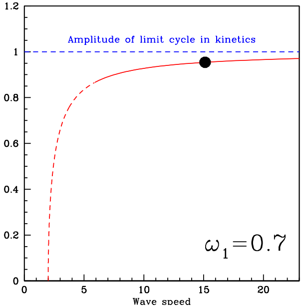

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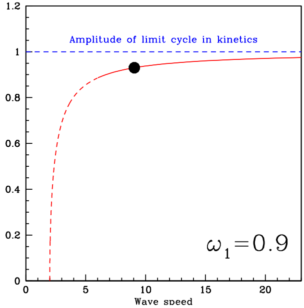

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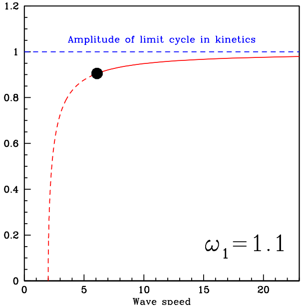

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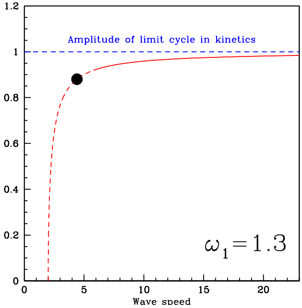

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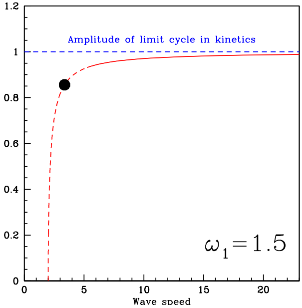

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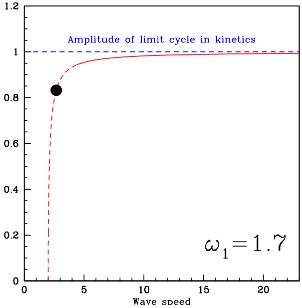

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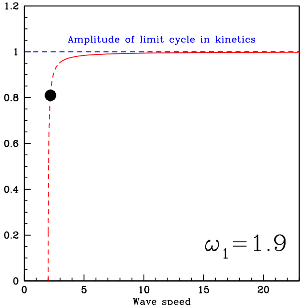
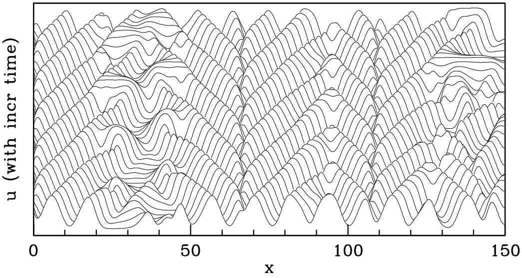
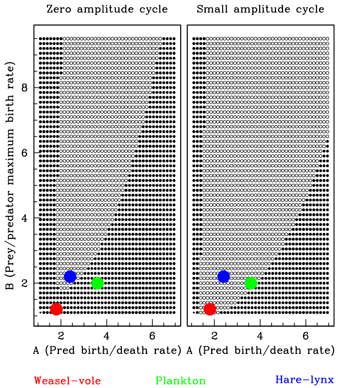


Typical Solution in an Unstable Case

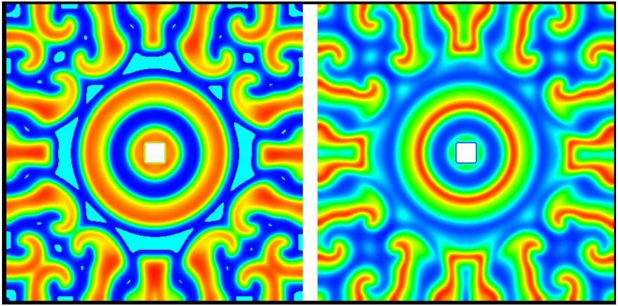


Wave Stability in the Predator-Prey Model

Using the formula for ω_1, we can predict wave stability in the predator-prey model for kinetic parameters close to Hopf bifurcation.



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

Outline

Review of Boundary Condition

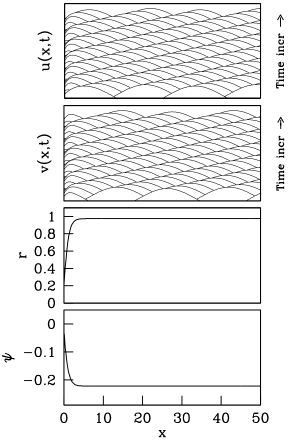
The zero Dirichlet boundary condition at the reservoir edge is an approximation to a Robin condition. For the λ–ω equations, it is possible to quantify the quality of this approximation.

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

Boundary conditions at $x = 0$:

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

Typical Solution with Robin Boundary Condition



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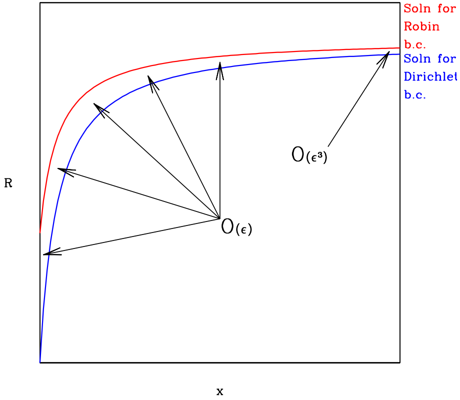

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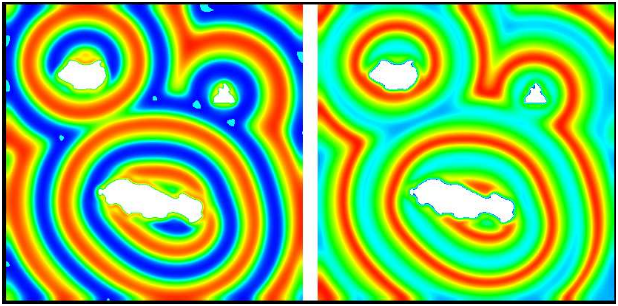
- So: the Dirichlet boundary condition is a very good approximation to the Robin condition.
- Future work: is this true for the predator-prey problem?

Outline

Typical Predator-Prey Solution with Multiple Obstacles

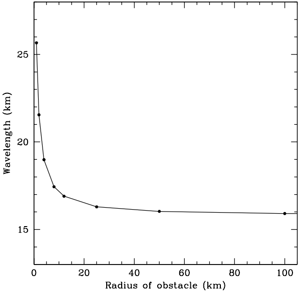


Movie of Solution with Multiple Obstacles

Click here to
play the movie

Wavelength vs Obstacle Radius

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



Competition between Obstacles

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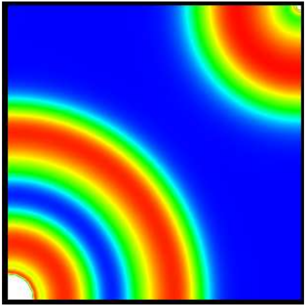

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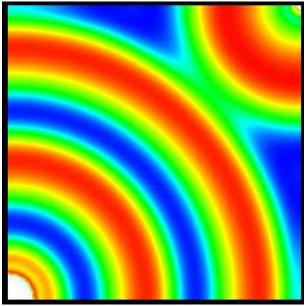

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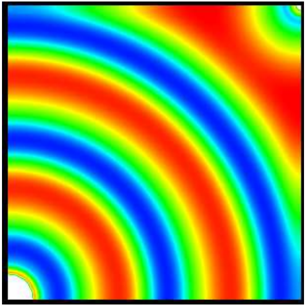

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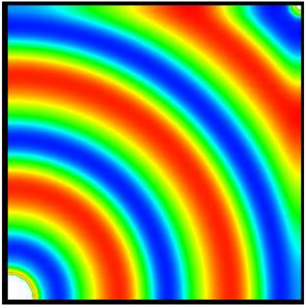

Competition between Obstacles

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

Movie of Competition between Obstacles

Click here to
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Explanation of Competition between Obstacles

Consider an interface between periodic waves in our λ–ω system

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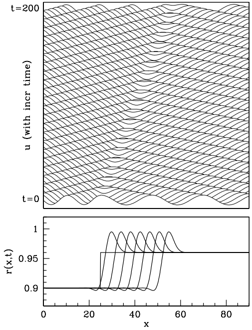

Explanation of Competition between Obstacles

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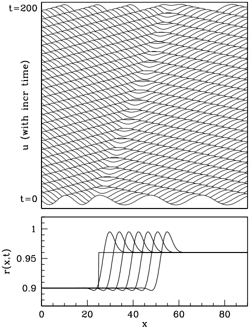

Solutions $r = \hat{r}(x-at)$, $\theta_x = \hat{\psi}(x-at)$

$$\Rightarrow \hat{r}'' + a\hat{r}' + \hat{r}(1-\hat{r}^2-\hat{\psi}^2) = 0$$

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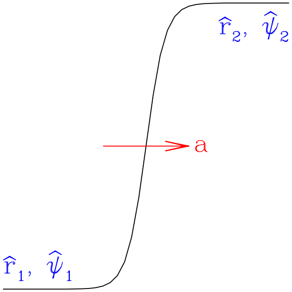

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Substitute in values at $\pm\infty$ and subtract

$$\Rightarrow a = \omega_1(\hat{r}_r^2 - \hat{r}_l^2)/(\hat{\psi}_r - \hat{\psi}_l).$$

Periodic wave directions $\Rightarrow \hat{\psi}_2 > 0,\ \hat{\psi}_1 < 0.$

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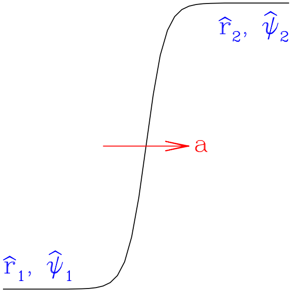

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Therefore a has the same sign as $(\hat{r}_2 - \hat{r}_1)$.

(Recall that larger obstacle radius $\Rightarrow$ smaller wavelength $\Rightarrow$ smaller $\hat{r}$).

Conclusions

- The expected behaviour at the edge of Kielder Water provides a possible explanation for the observed periodic travelling waves
- The generic nature of the λ–ω equations suggests that periodic travelling waves should be common in ecological systems with cyclic populations