Multiannual Cycles in Field Vole Populations: Spatial Data and Spatiotemporal Models

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Collaborators

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Xavier Lambin

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Mike Begon

Outline

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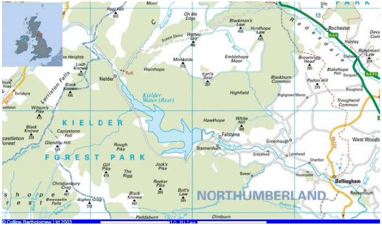
Multiannual Rodent Cycles

- Cyclic rodent populations are one of the most studied systems in ecology
- The multiannual fluctuations in abundance are not driven by the environment
- Despite more than 100 years of study, the underlying mechanisms remain unclear

Field Voles in Kielder Forest

Field vole (*Microtus agrestis*)



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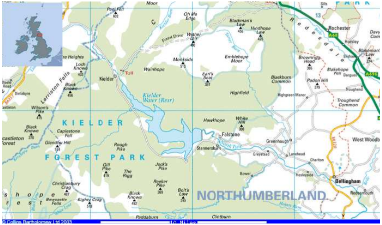

Kielder Forest is a large commercial forest plantation (613km^2). Vole habitat is forest clear cuts (5-100 Ha) that last 12-15 years.

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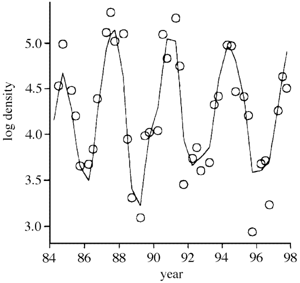

Field voles in Kielder Forest are cyclic (period 4 years)

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Hypothesis I: Predation by Weasels

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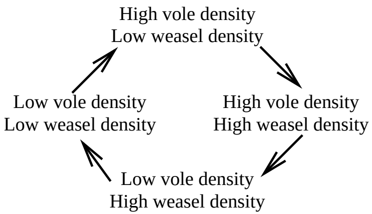

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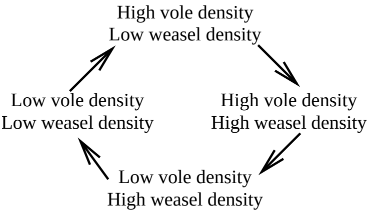
- In Finland, weasels drive multiannual vole cycles. (*Evidence:* live-trapping and removal of weasels changes the vole dynamics to annual cycles).
- However, in Kielder, live-trapping and removal of weasels does not stop multiannual vole cycles.



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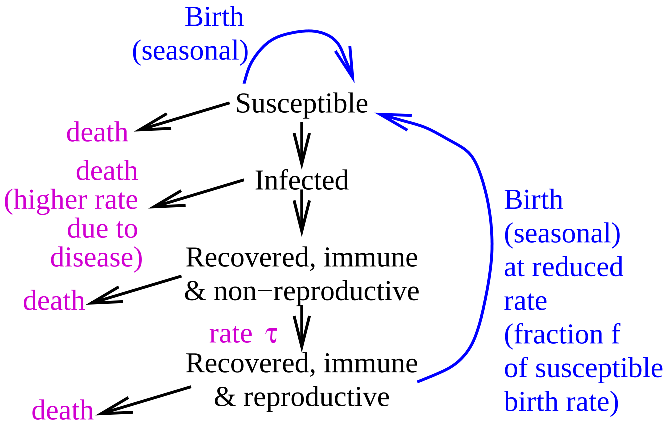
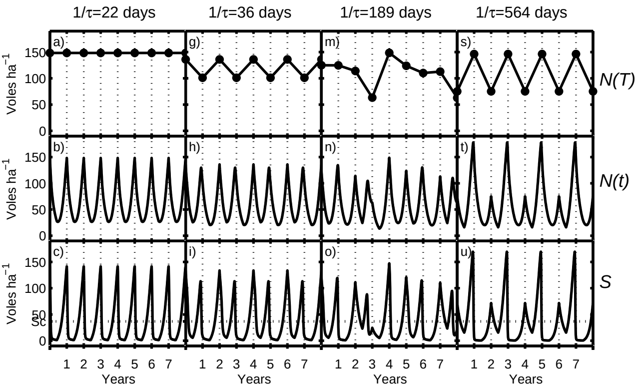
- In Kielder, prevalences of field vole cowpox is significantly correlated with past population densities (also for TB)
- Therefore cowpox and other diseases may alter reproductive timing in a delayed density dependent manner – this could in turn lead to multiannual cycles

Hypothesis II: Schematic Illustration of the Model



Hypothesis II: Examples of Model Solutions



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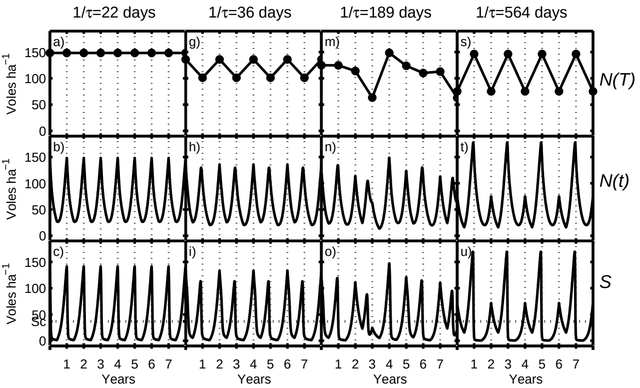

Basic dynamics: population crash in non-breeding season, recovery in breeding season.

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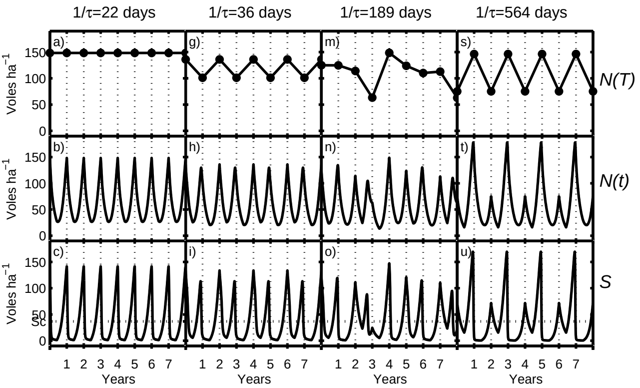

Large τ: recovery is fast enough for annual cycles.

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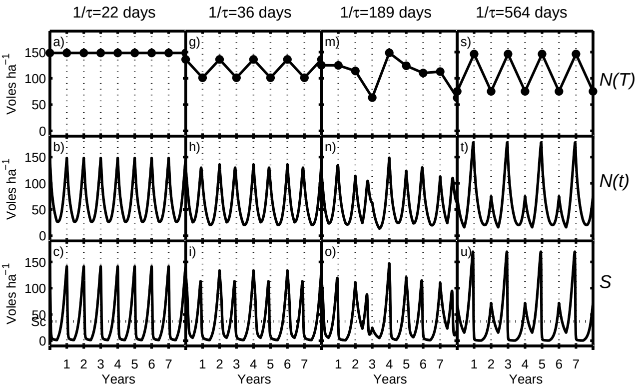
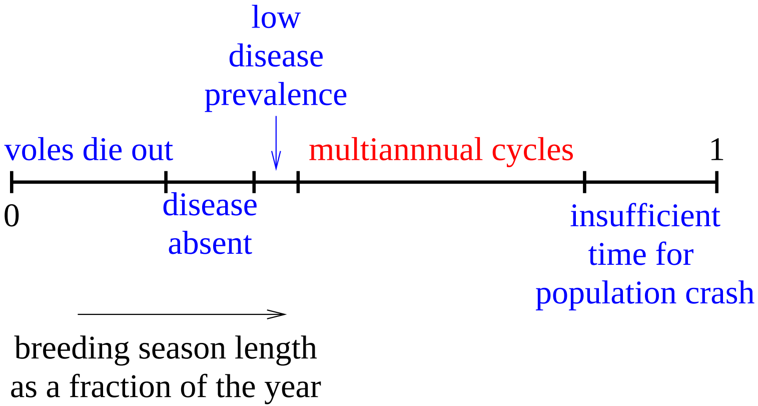


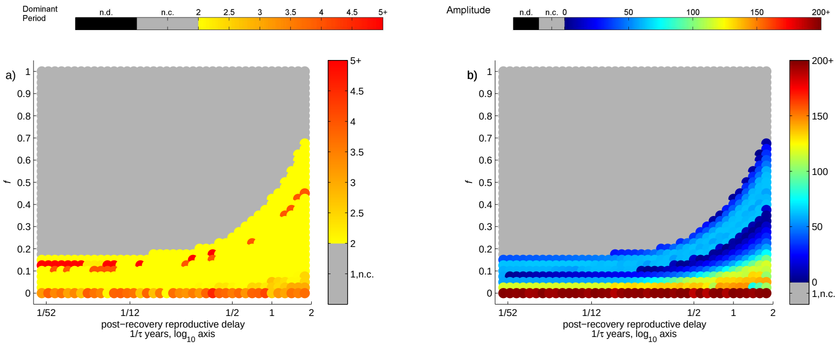
Smaller τ: recovery is too slow for annual cycles.

Hypothesis II: Seasonal Forcing is Important

Multiannual cycles do not occur if the reproductive season is either too short or too long



Hypothesis II: When are Disease-Induced Cycles Expected?



(other param estimates for fi eld voles in Kielder forest and cowpox)

Hypothesis II: Conclusions

- Multiannual cycles can be caused by the combination of
    1. delayed reproduction following infection
    2. reduced fecundity after recovery
    3. annual forcing (seasonal reproduction)
- For cowpox in field voles in Kielder forest, the key requirement is a greatly reduced fecundity after infection (no data currently available)

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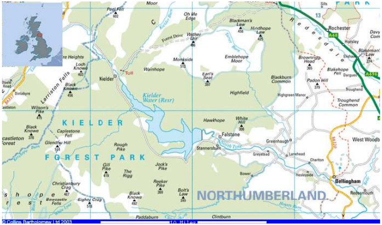
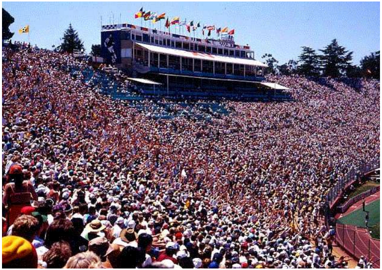


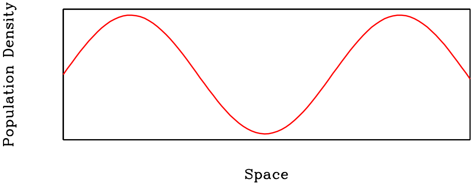
Field voles in Kielder Forest are cyclic (period 4 years)

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

What is a Periodic Travelling Wave?

A useful analogy is the “Mexican Wave”





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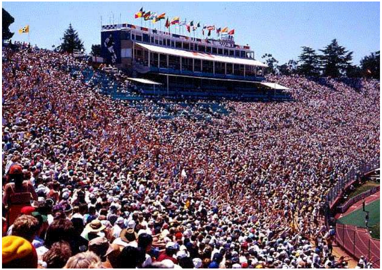

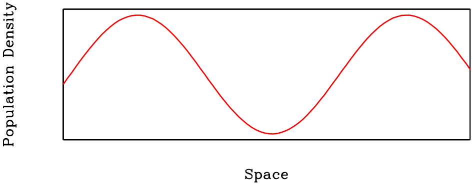

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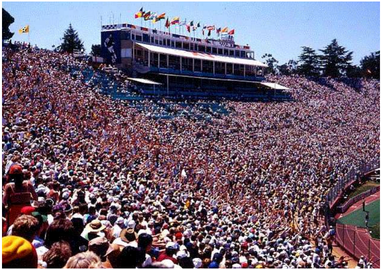

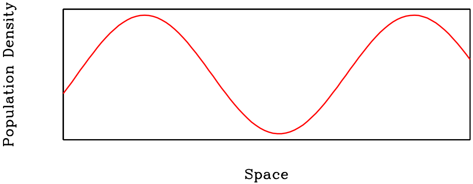

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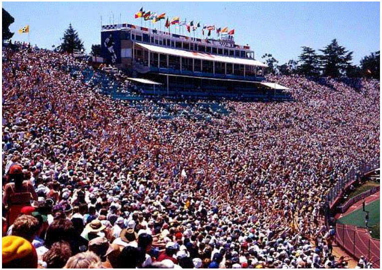

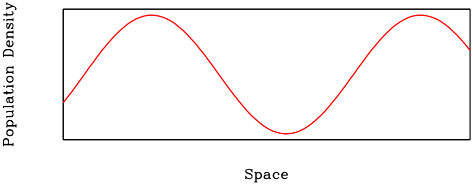

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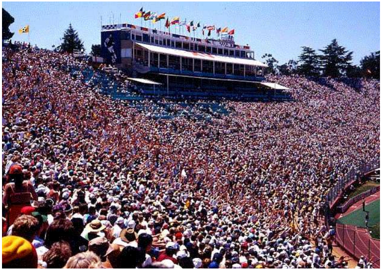

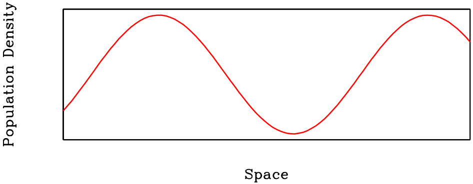

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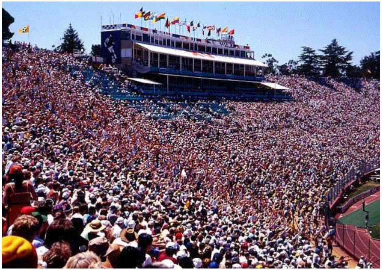

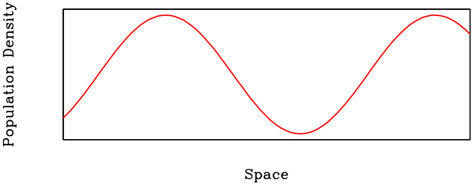

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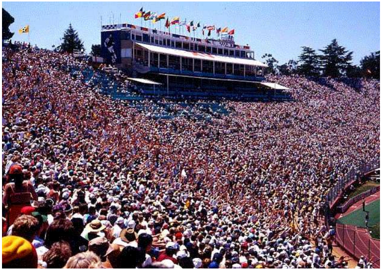

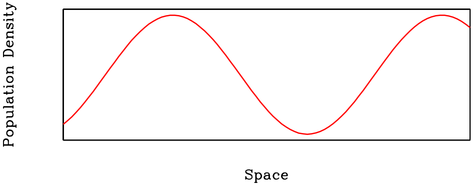

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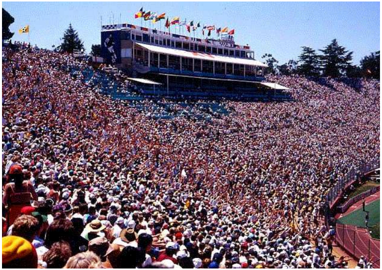

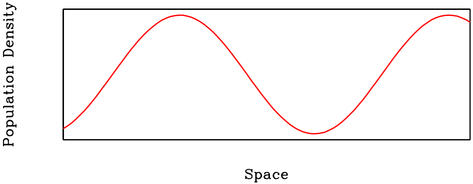

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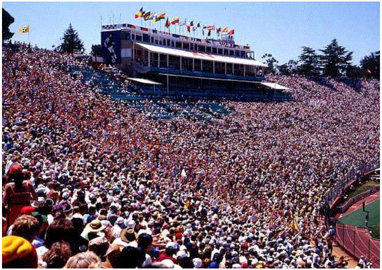

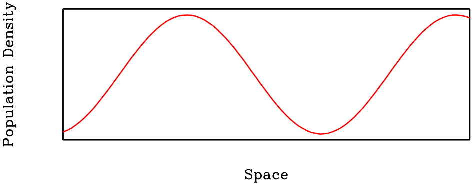

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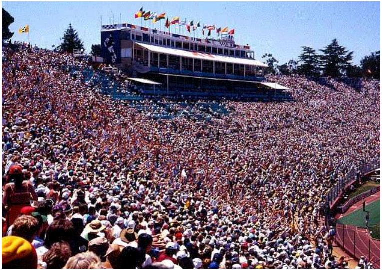

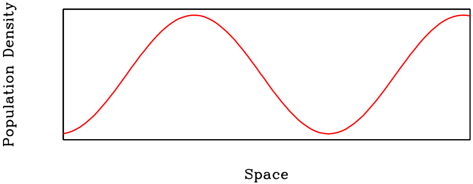

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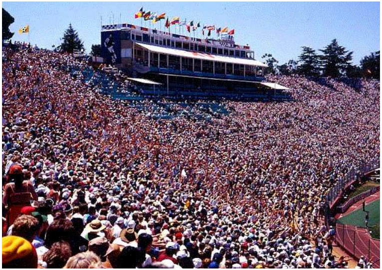

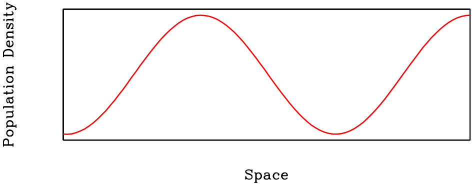

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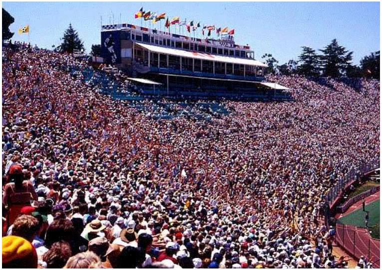

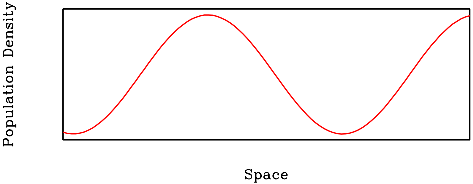

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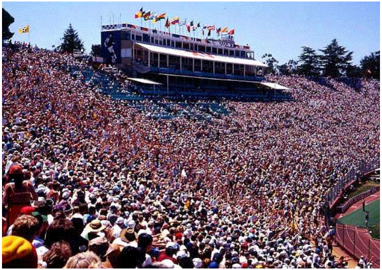

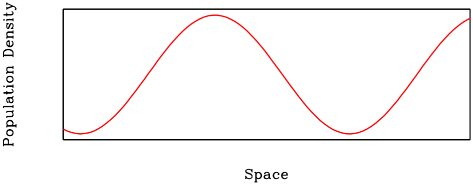

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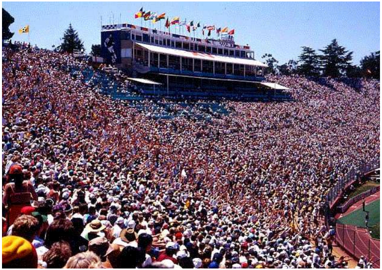

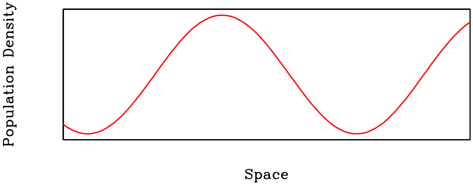

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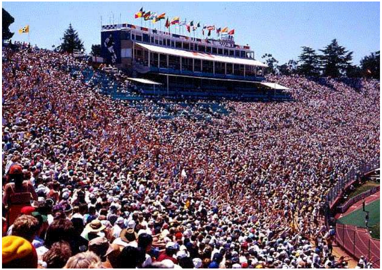

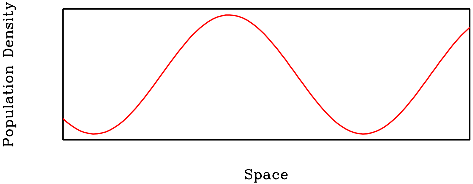

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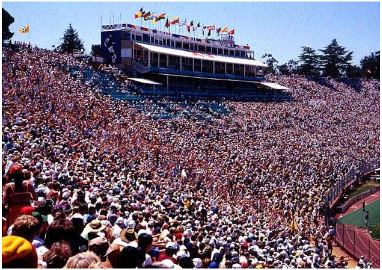

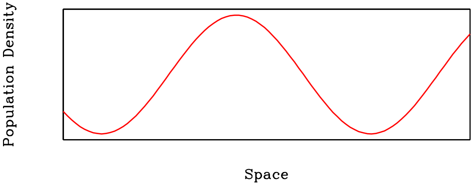

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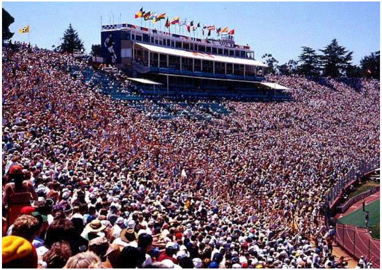

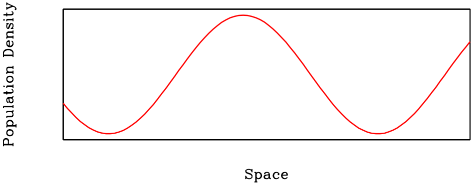

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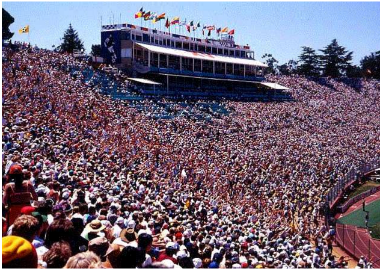

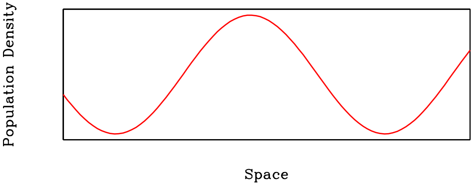

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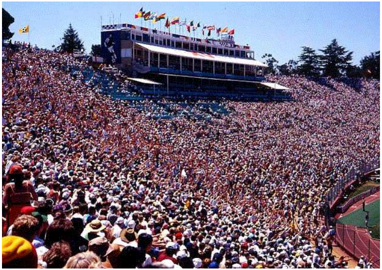

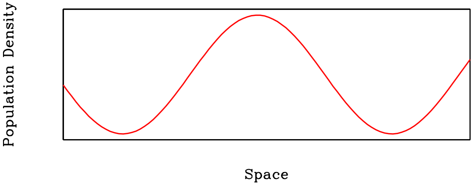

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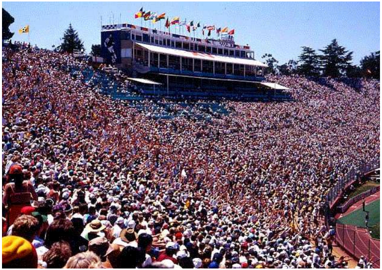

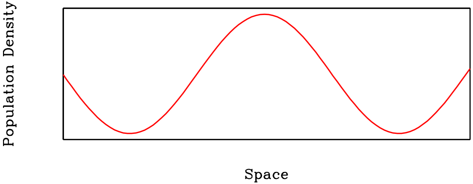

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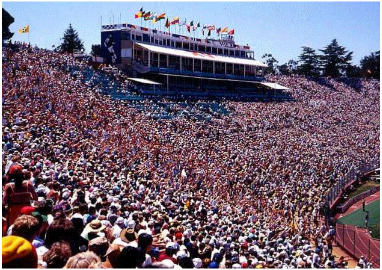

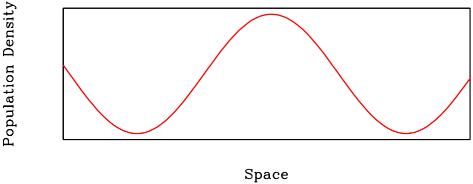

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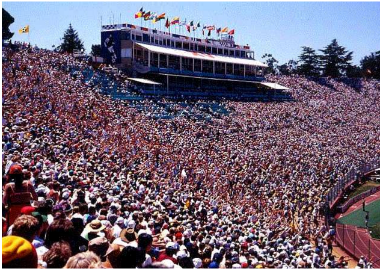

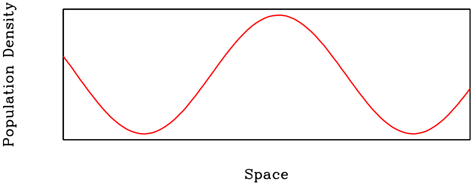

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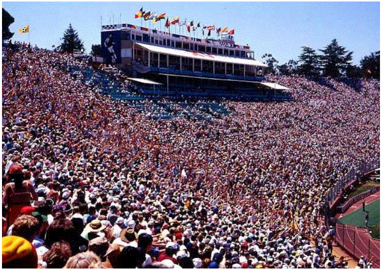

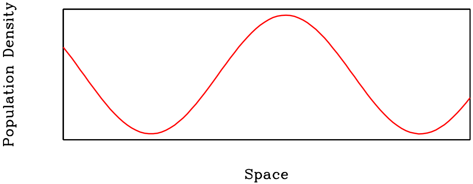

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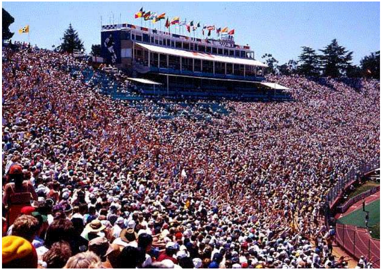

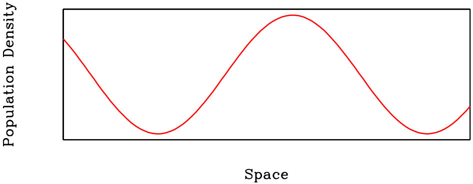

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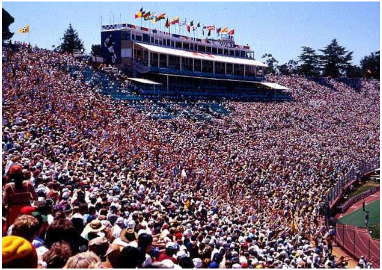

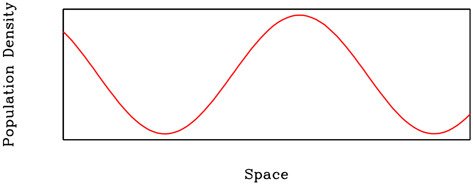

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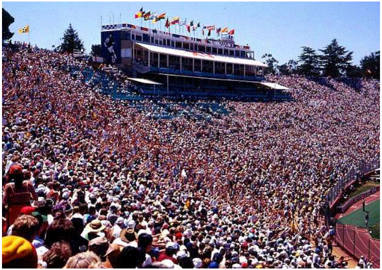

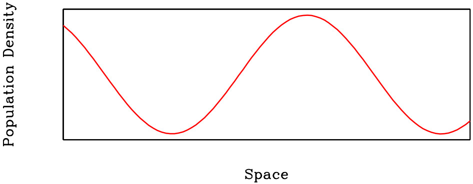

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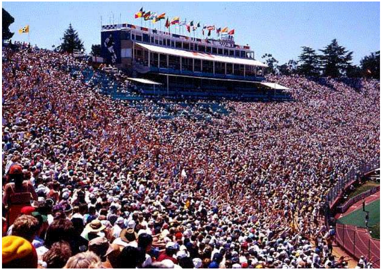

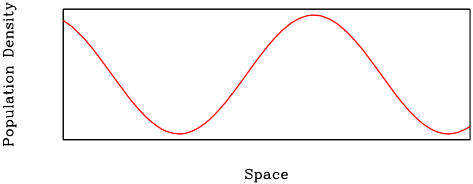

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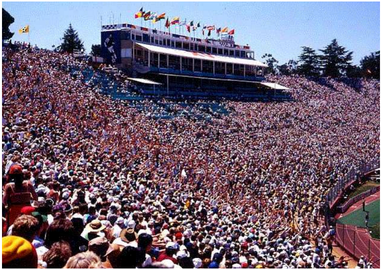

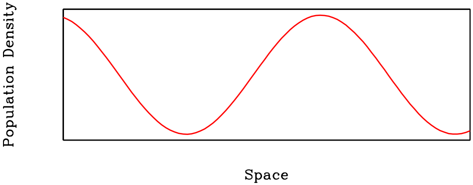

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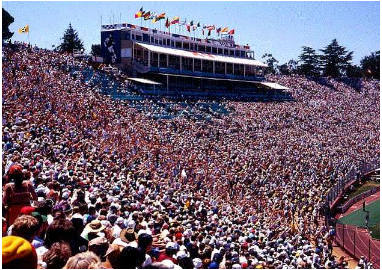

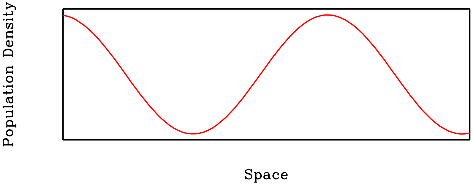

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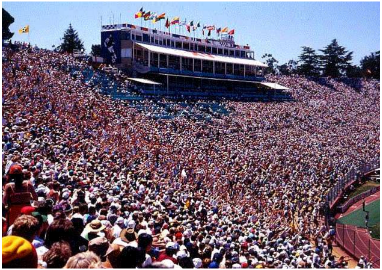

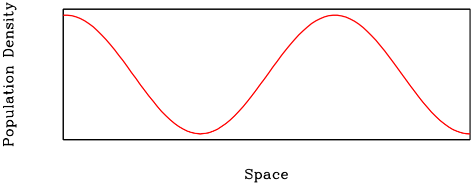

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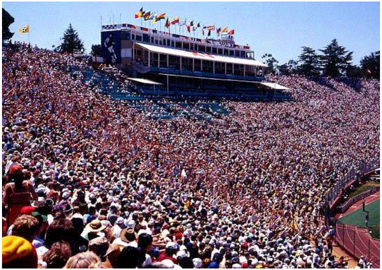

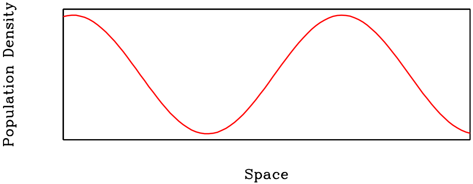

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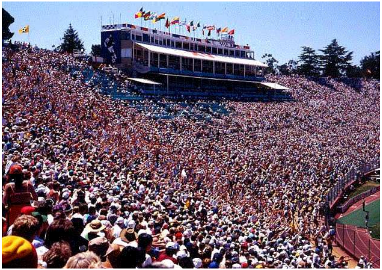

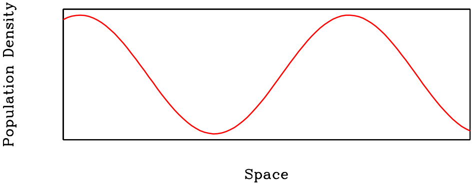

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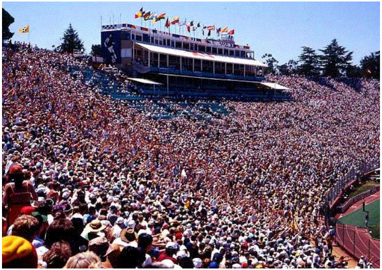

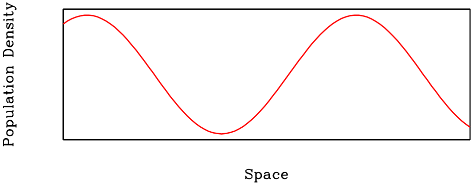

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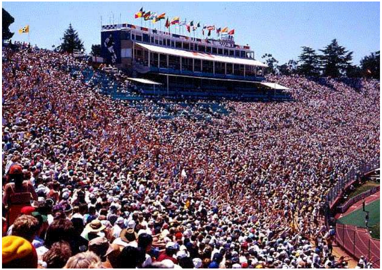

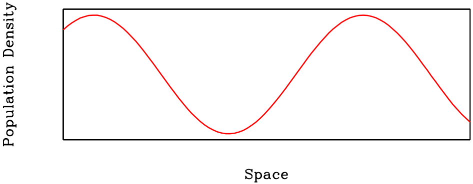

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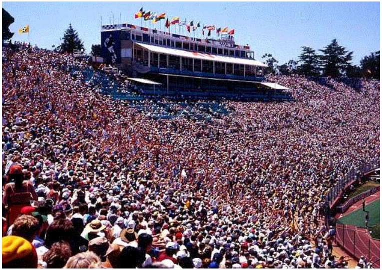

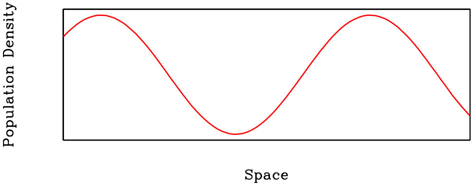

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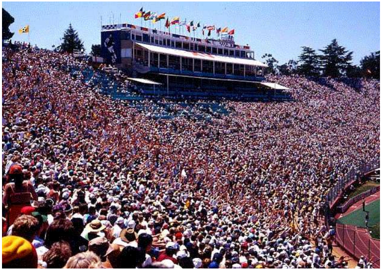

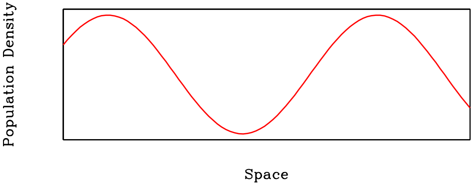

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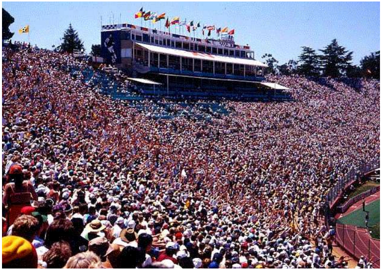

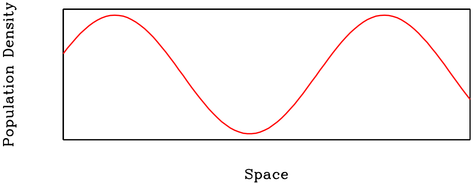

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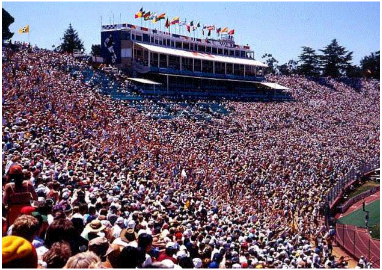

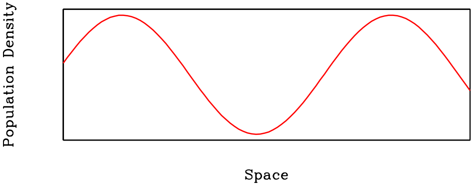

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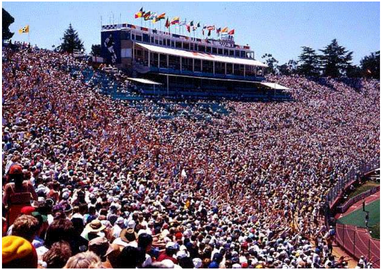

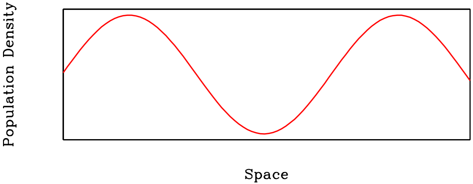

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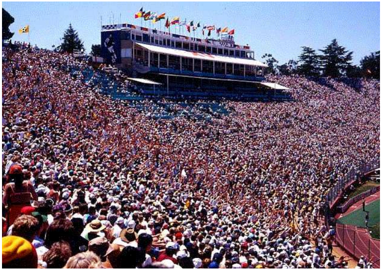

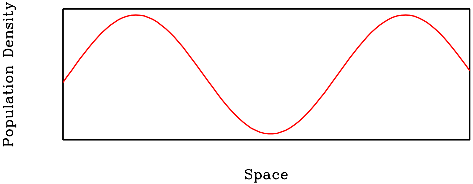

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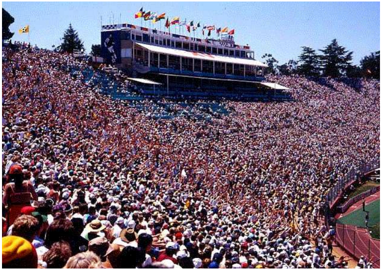

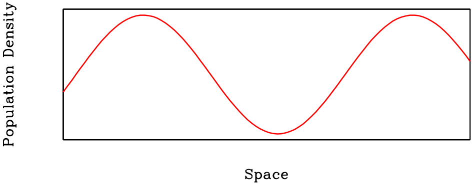

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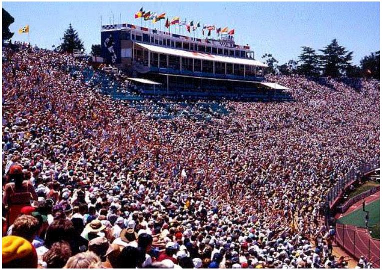

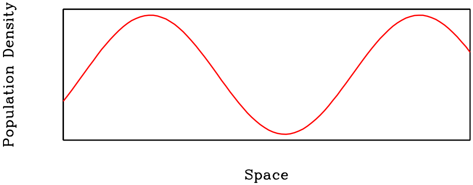

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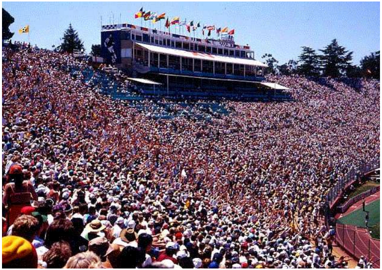

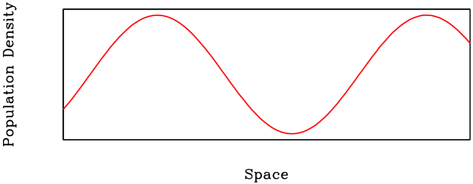

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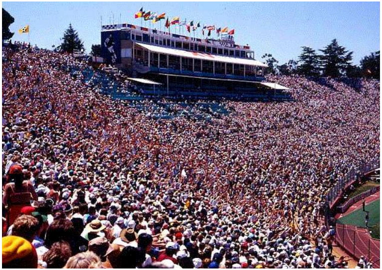

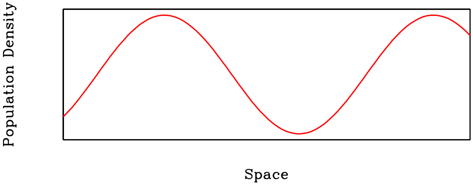

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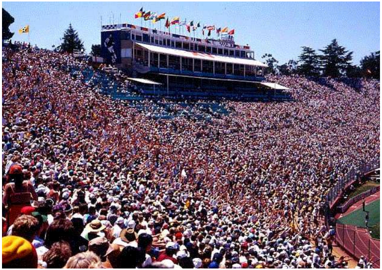

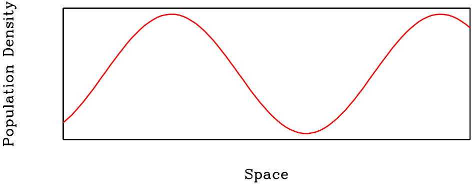

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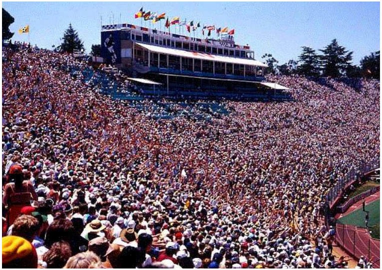

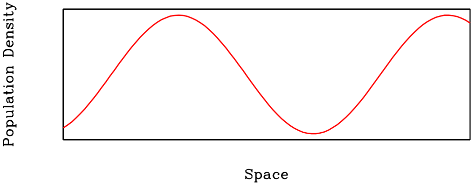

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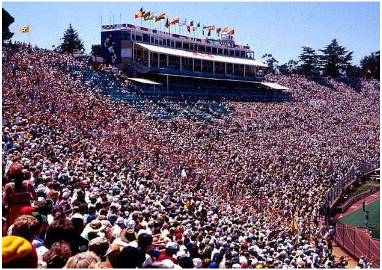

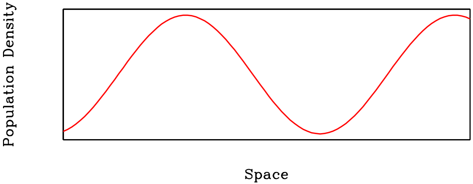

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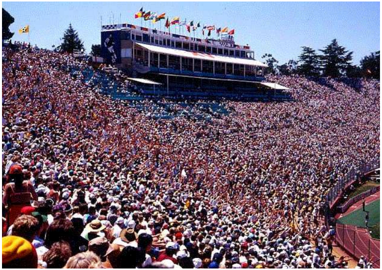

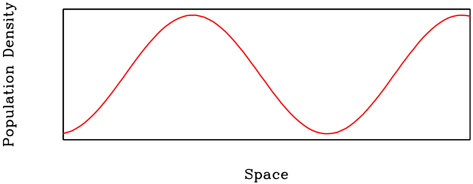

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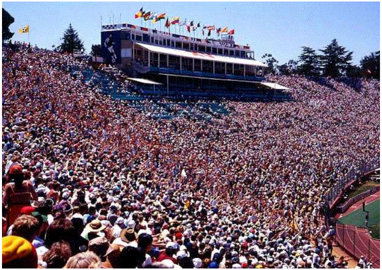

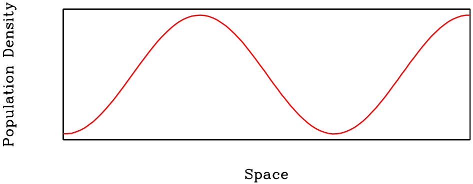

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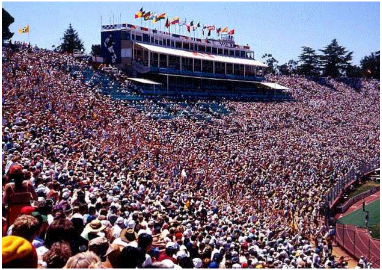

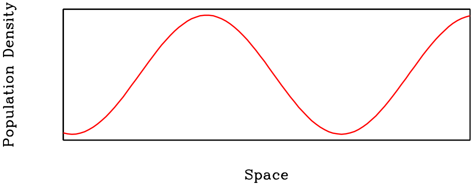

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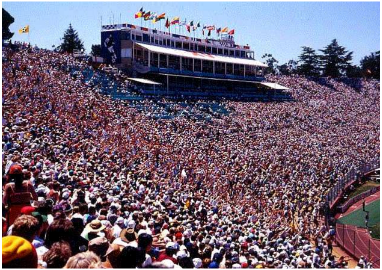

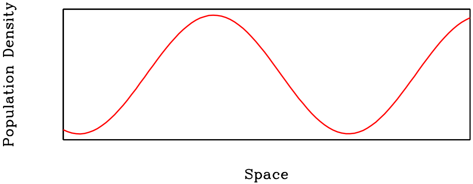

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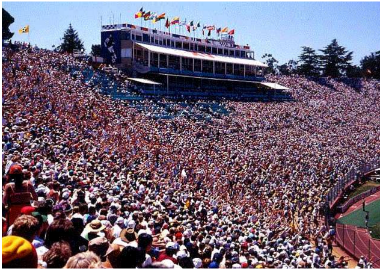

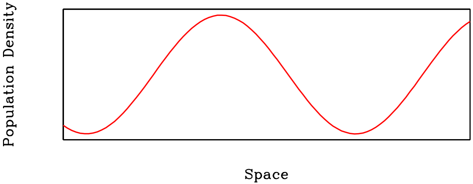

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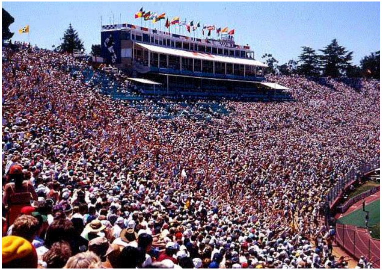

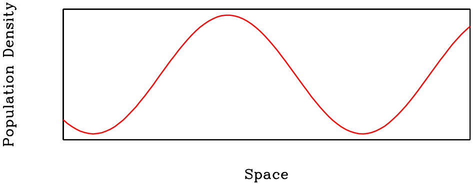

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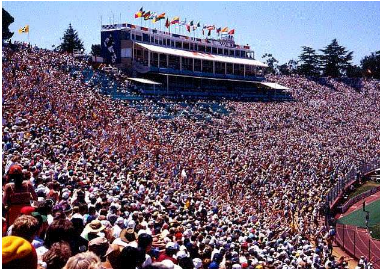

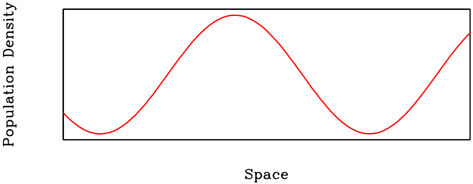

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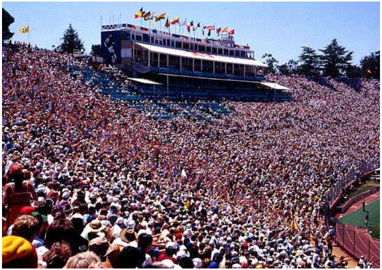

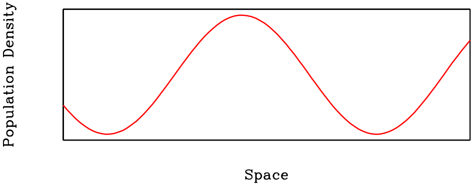

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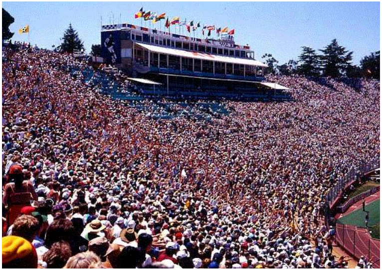

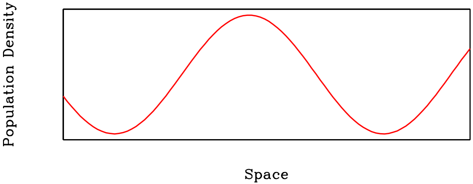

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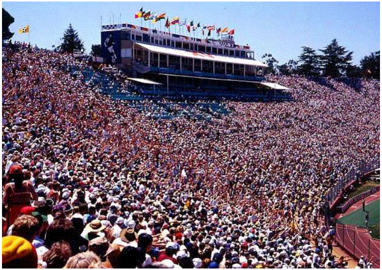

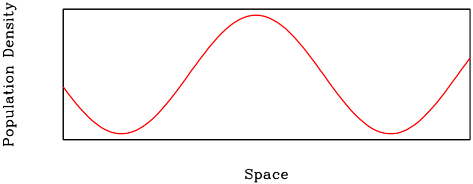

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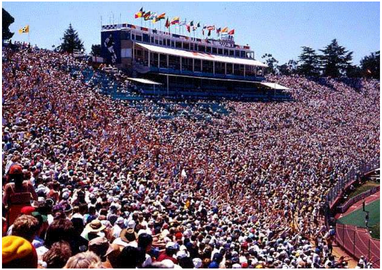

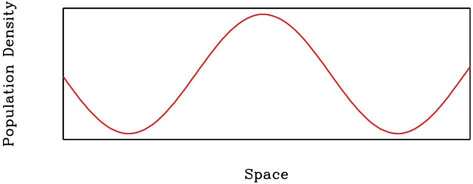

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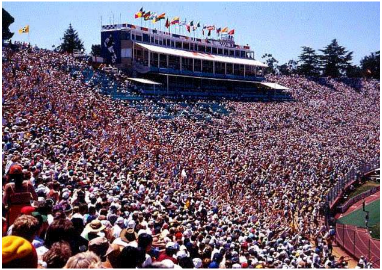

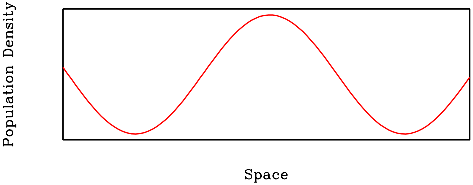

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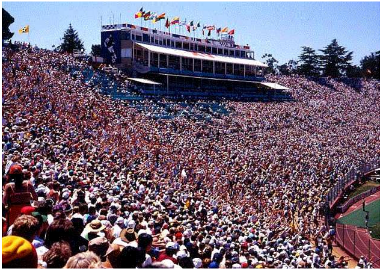

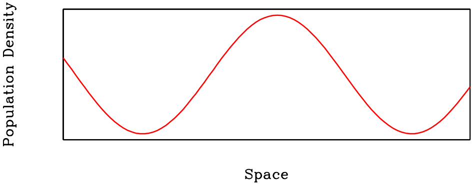

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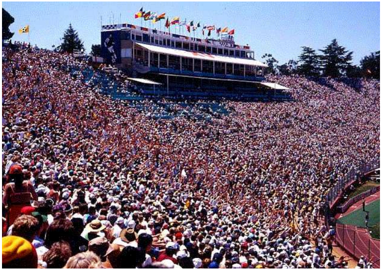

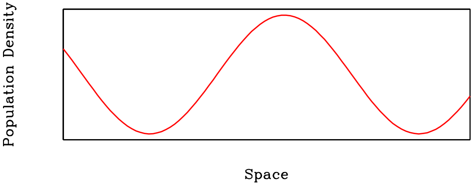

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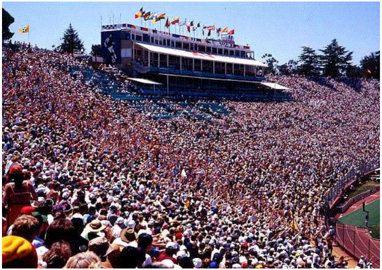

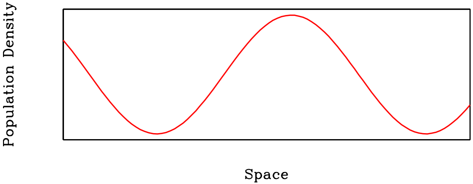

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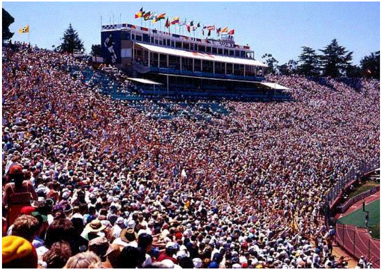

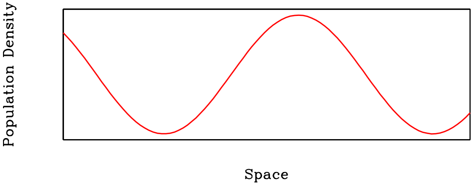

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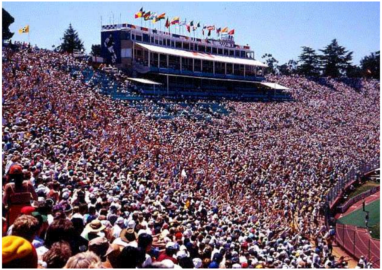

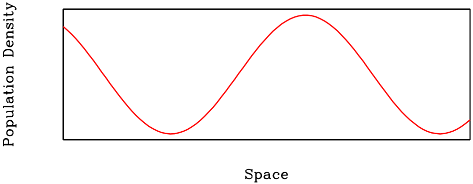

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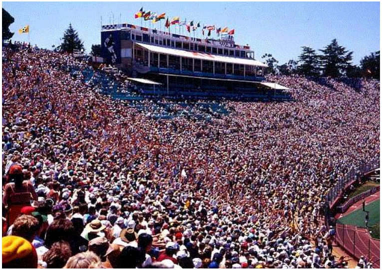

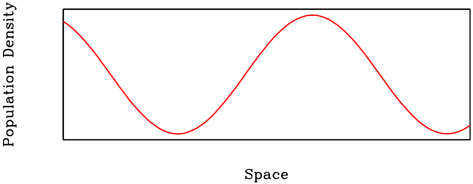

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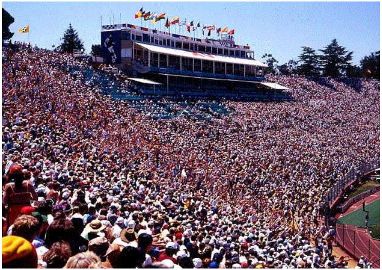

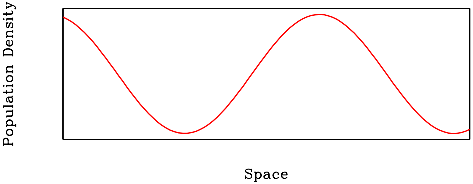

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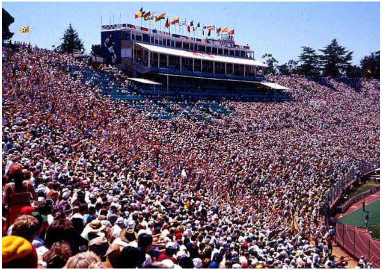

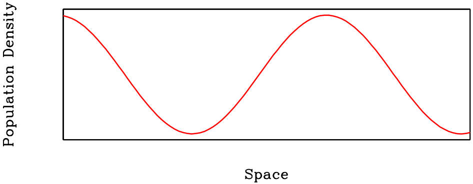

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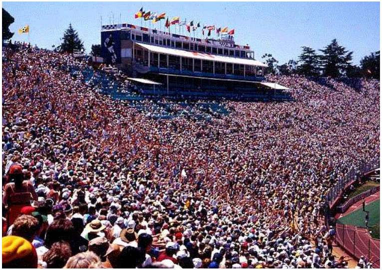

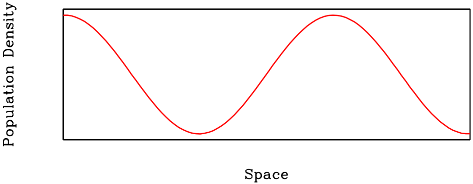

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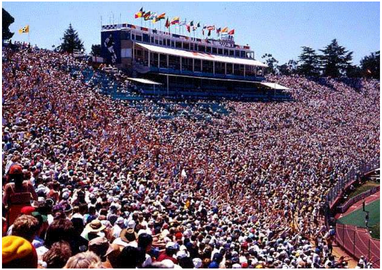

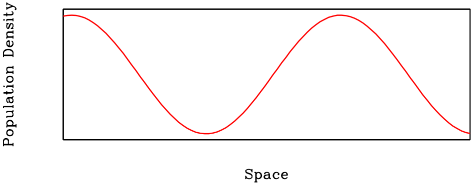

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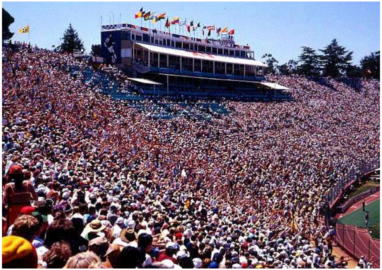

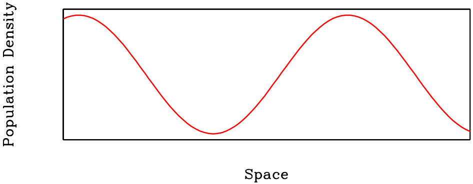

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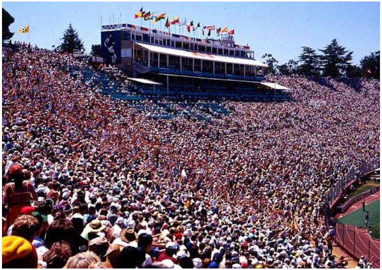

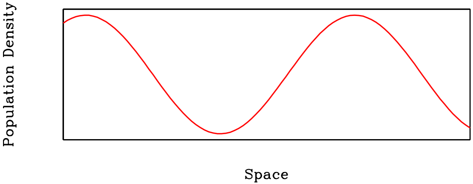

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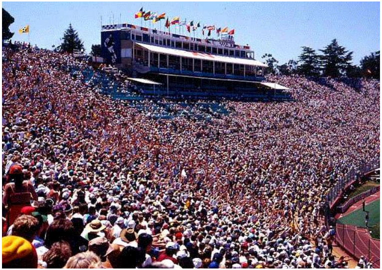

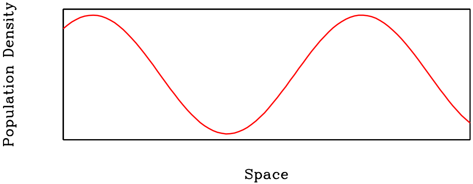

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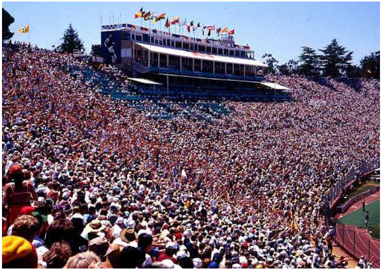

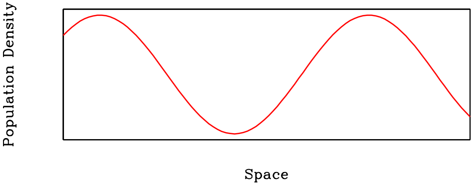

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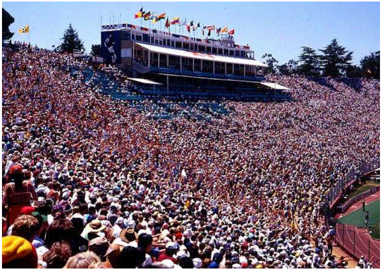

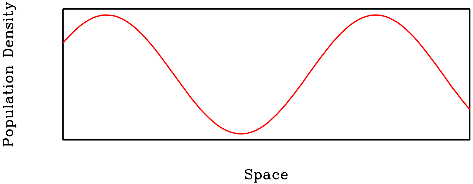

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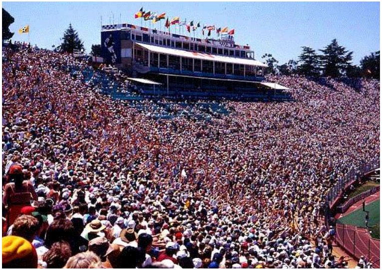

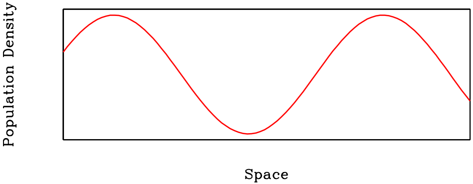

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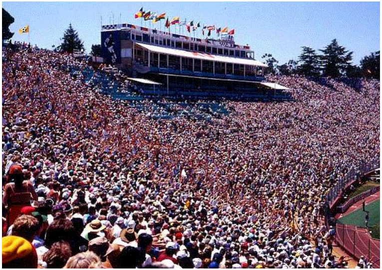

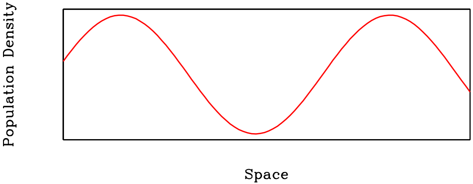

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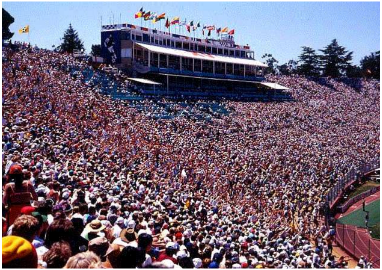

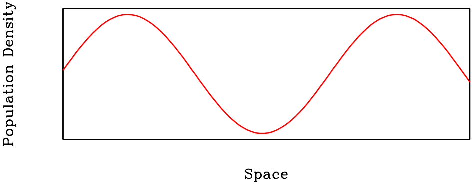

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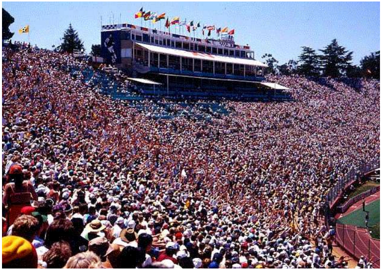

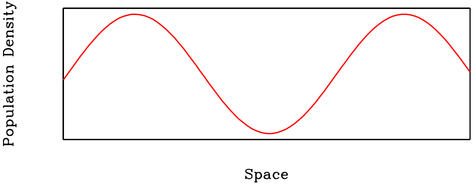

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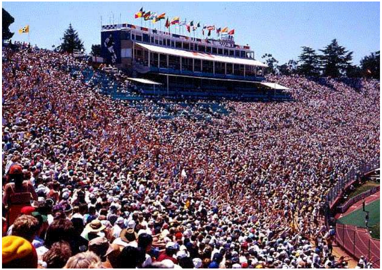

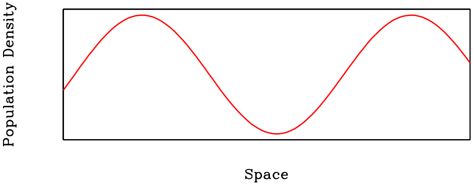

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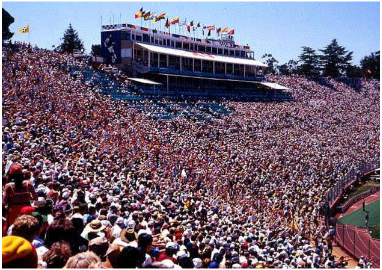

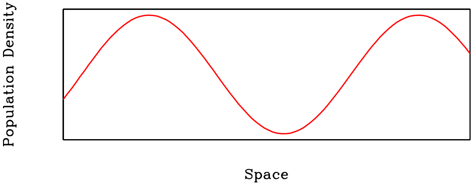

Detection of a Periodic Wave from Field Data

Step 1: At each sampling site i, calculate a time series of growth rates $G_t^i = \log N_t^i - \log N_{t-1}^i$

Step 2: Calculate the cross-correlation coefficient of the growth rates for each pair of sites

$$\rho_{i,j} = \mathrm{cov}\left(G_t^i, G_t^j\right) \;/\; \sqrt{\mathrm{var}(G_t^i), \mathrm{var}(G_t^j)}$$

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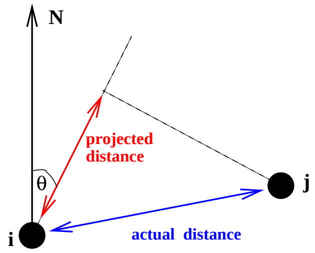

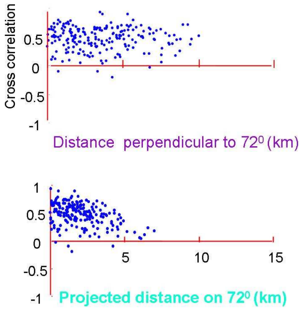

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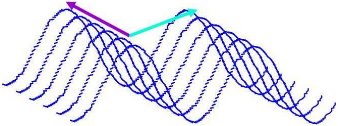

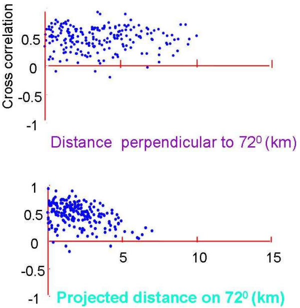

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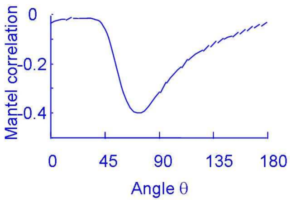
Step 4: For each direction θ, use the Mantel correlogram to calculate the Mantel correlation, and plot this vs θ. A significant reduction in correlation in one direction suggests a travelling wave.



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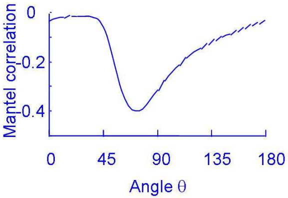
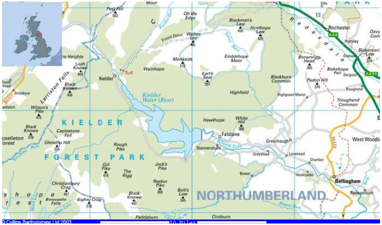
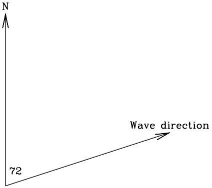


Step 5: Detailed fitting of statistical models, using projected distances, gives robust parameter estimates and significance levels. This implies a wave speed of 19$\mathrm{km}/\mathrm{year}$.

What Causes the Spatial Component of the Oscillations?





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

Outline

Predator-Prey Equations

$$\boxed{\text{predators}}$$

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

$$\boxed{\text{prey}}$$

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

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

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$$\frac{d}{dx}\begin{pmatrix}\text{vole}\\\text{density}\end{pmatrix} = -\begin{pmatrix}\text{large}\\\text{constant}\end{pmatrix}\cdot\begin{pmatrix}\text{vole}\\\text{density}\end{pmatrix}$$

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- To a first approximation, this boundary condition is just

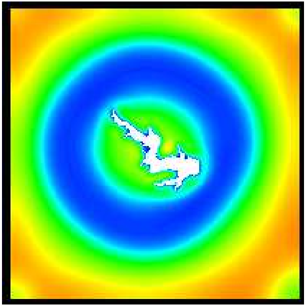
$$\begin{pmatrix}\text{vole}\\\text{density}\end{pmatrix} = 0$$

Field Vole Wave Generation Question

Question

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

Typical Model Solution



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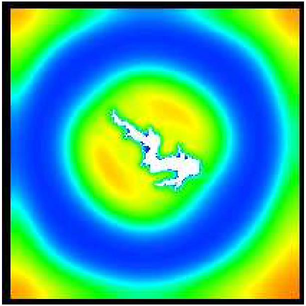

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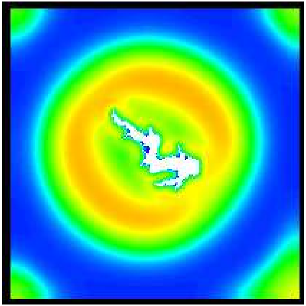

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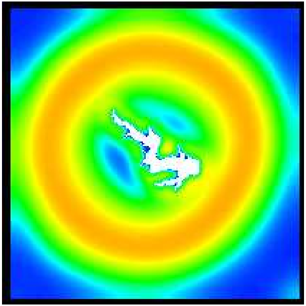

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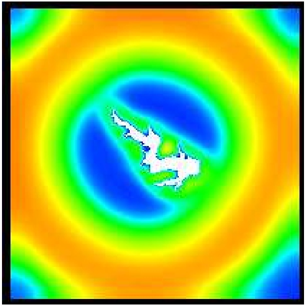

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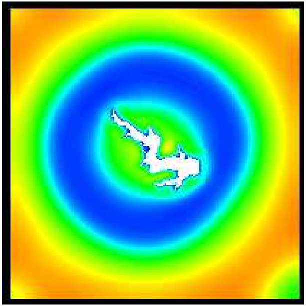
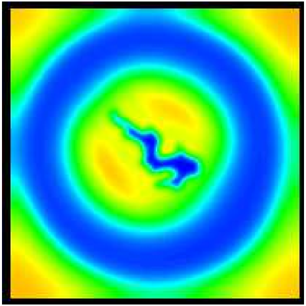


Movie of Typical Model Solution

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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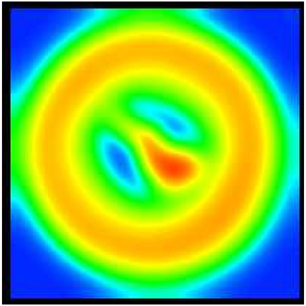

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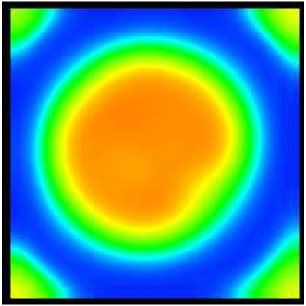

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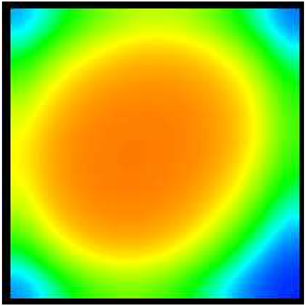

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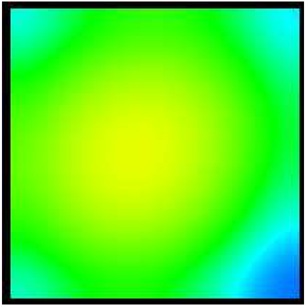
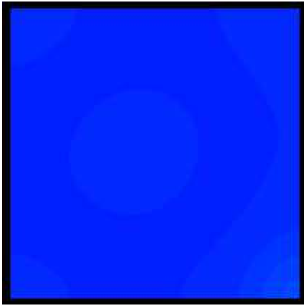


Removing the Reservoir

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



Conclusion of Periodic Travelling Wave Study

The expected behaviour at the edge of Kielder Water provides a possible explanation for the observed periodic travelling waves

Future Work

- Spatiotemporal dynamics of the disease model
- More realistic modelling of the Kielder Forest habitat

List of Frames