# Lecture 17: Biological Waves

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# Outline

1. Wave Fronts I: Modelling Epidermal Wound Healing
2. Wave Fronts II: The Speed of Epidermal Repair
3. Wave Fronts III: Bistable Kinetics (Spruce Budworm)
4. Periodic Travelling Waves

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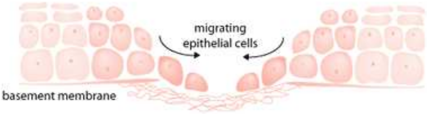
# Epidermal Wound Healing

Epidermal wounds are very shallow (no bleeding), e.g. blisters



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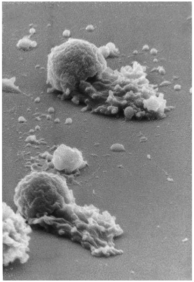

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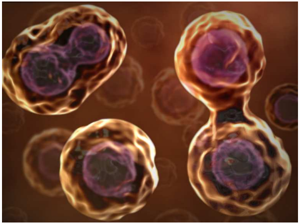

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*Cell division is upregulated by chemicals produced by the cells*

# A Mathematical Model

Cell division is upregulated by chemicals produced by the cells
Model variables: $n(\underline{x}, t)$ and $c(\underline{x}, t)$.

Model equations:

$$\begin{aligned}
\partial n/\partial t &= \overbrace{D\nabla^2 n}^{\text{cell movement}} + \overbrace{s(c)(N-n)n}^{\text{cell division}} - \overbrace{\delta n}^{\text{cell death}} \\
\partial c/\partial t &= \underbrace{D_c\nabla^2 c}_{\text{chemical diffusion}} + \underbrace{An/(1+\alpha n^2)}_{\text{production by cells}} - \underbrace{\lambda c}_{\text{decay}}
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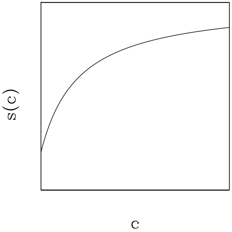

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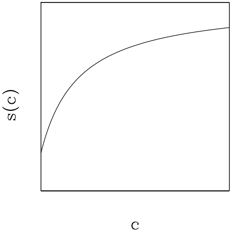

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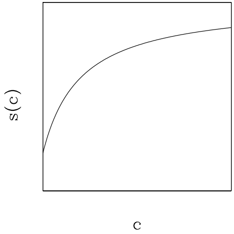

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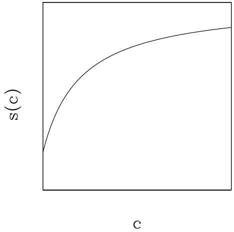

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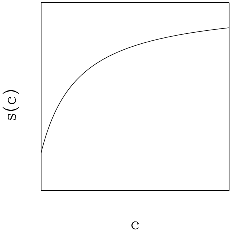

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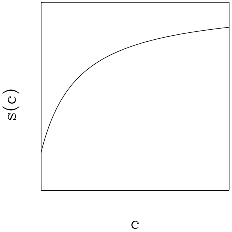

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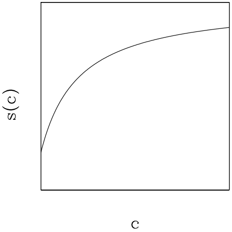

# Reduction to One Equation

$$\begin{aligned} \partial n/\partial t &= D\nabla^2 n + s(c)(N-n)n - \delta n \\ \partial c/\partial t &= D_c\nabla^2 c + An/(1+\alpha n^2) - \lambda c \end{aligned}$$

The chemical kinetics are very fast $\Rightarrow A$, $\lambda$ large.
So to a good approximation $c = (A/\lambda)\cdot n/(1+\alpha n^2)$.

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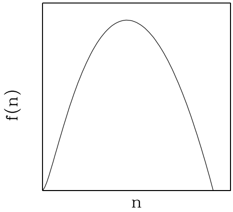
So to a good approximation $c = (A/\lambda)\cdot n/(1+\alpha n^2)$.

$$\Rightarrow \partial n/\partial t = D\nabla^2 n + f(n)$$

where

$$f(n) = s\left(\frac{An}{\lambda(1+\alpha n^2)}\right)(N-n)n - \delta n$$



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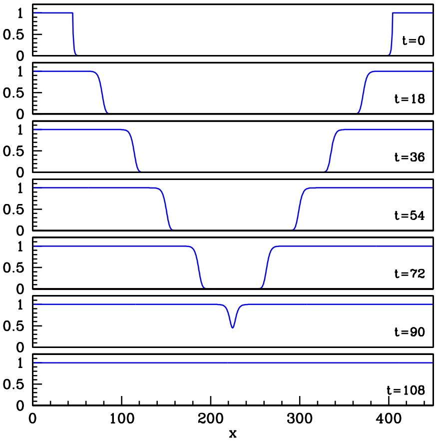
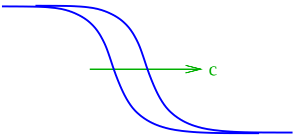
# Typical Model Solution



# Travelling Wave Solutions

During most of the healing, the solution moves with constant speed and shape.

This is a “travelling wave solution”




$$n(x,t) = N(x - at)$$

where $a$ is the wave speed. We will write $z = x - at$. Then $\partial n/\partial x = dN/dz$ and $\partial n/\partial t = -a\,dN/dz$

$$\Rightarrow D\frac{d^2N}{dz^2} + a\frac{dN}{dz} + f(N) = 0$$

# The Speed of Travelling Waves

We know that $N \to 0$ as $z \to \infty$. Recall that

$$D\frac{d^2N}{dz^2} + a\frac{dN}{dz} + f(N) = 0$$

Therefore when $N$ is small

$$D\frac{d^2N}{dz^2} + a\frac{dN}{dz} + f'(0)N = 0$$

to leading order. This has solutions $N(z) = N_0 e^{\lambda z}$ with

$$\lambda^2 + a\lambda + 1 = 0 \Rightarrow \lambda = \tfrac{1}{2}\left(-a \pm \sqrt{a^2 - 4Df'(0)}\right).$$

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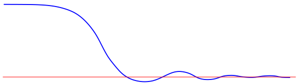
If $a < 2\sqrt{Df'(0)}$ then $\lambda$ is complex $\Rightarrow$ the solutions oscillate about $N = 0$, which does not make sense biologically



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So we require $a \geq 2\sqrt{Df'(0)}$.

# The Speed of Travelling Waves (contd)

- We require $a \geq 2\sqrt{Df'(0)}$
- Mathematical theory implies that in applications, waves will move at the minimum possible speed, $2\sqrt{Df'(0)}$.

# Applications to Wound Healing

For the wound healing model

$$f'(0) = Ns(0) - \delta$$

$$\Rightarrow \text{wave speed } a = 2\sqrt{D(Ns(0) - \delta)}$$

# General Results on Wave Speed

Consider the equation $\partial u/\partial t = D\,\partial^2 u/\partial x^2 + f(u)$ with $f(0) = f(1) = 0$, $f(u) > 0$ on $0 < u < 1$, $f'(0) > 0$ and $f'(u) < f'(0)$ on $0 < u \leq 1$.

For this equation, two important theorems were proved by Kolmogorov, Petrovskii and Piskunov; a similar but slightly less general study was done at the same time by Fisher.

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**Theorem 1.** There is a positive travelling wave solution for all wave speeds $\geq 2\sqrt{Df'(0)}$, and no positive travelling waves for speeds less than this critical value.

*A proof of theorem 1 is in the supplementary material.*

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**Theorem 2.** Suppose that $u(x, t = 0) = 1$ for $x$ sufficiently large and negative, and $u(x, t = 0) = 0$ for $x$ sufficiently large and positive. Then the solution $u(x, t)$ approaches the travelling wave solution with the critical speed $2\sqrt{Df'(0)}$ as $t \to \infty$.

The form of the approach to the travelling wave is discussed in depth by Bramson (1983). *The proof of theorem 2 is extremely difficult.*

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**References:**

Bramson, M.D. 1983 Convergence of solutions of the Kolmogorov equation to travelling waves. *Mem. AMS* 44 no. 285.

Fisher, R.A. 1937 The wave of advance of advantageous genes. *Ann. Eug.* 7, 355-369.

Kolmogorov, A., Petrovskii, I., Piskunov, N. 1937 Etude de l'équation de la diffusion avec croissance de la quantité de matière et son application à un problème biologique. *Moscow Univ. Bull. Math.* 1, 1-25.

# Therapeutic Addition of Chemical

Now return to the wound healing model and consider adding extra chemical to the wound as a therapy.
The equation for the chemical changes to

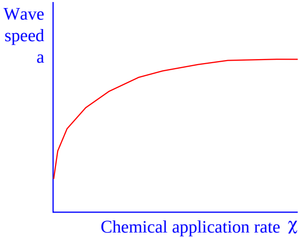
$$\partial c/\partial t = An/(1+\alpha n^2) - \lambda c + \gamma$$

$\Rightarrow$ $f(n)$ changes to

$$s\left(\frac{\gamma}{\lambda} + \frac{An}{\lambda(1+\alpha n^2)}\right)(N-n)n - \delta n$$

$\Rightarrow$ $f'(0)$ changes to $Ns(\gamma/\lambda) - \delta$

$\Rightarrow$ observed (min poss) wave speed $a = 2\sqrt{D(Ns(\gamma/\lambda) - \delta)}$



# Deducing the Chemical Profile

Since we know $c$ as a function of $n$, there is also a travelling wave of chemical, whose form we can deduce. The chemical profile has a peak in the wave front.

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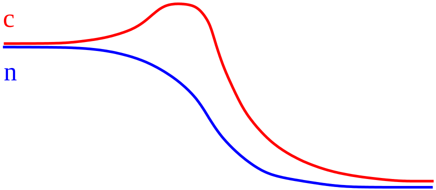

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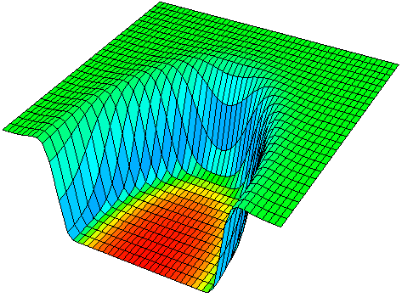

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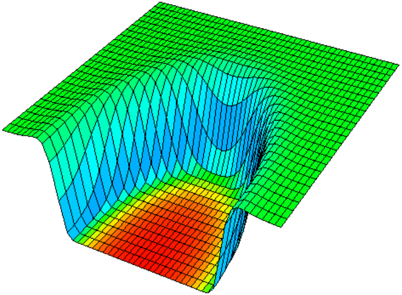

However, there are no theorems on the speed of wave fronts in systems of reaction-diffusion equations, except in a few special cases (which do not include this model).

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# Spruce Budworm Dynamics

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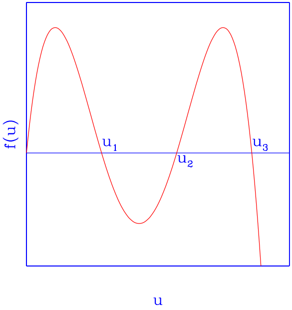
A simple model is

$$\partial u/\partial t = D\,\partial^2 u/\partial x^2 + f(u)$$

where

$$f(u) = \underbrace{k_1 u(1 - u/k_2)}_{\text{logistic growth}} + \underbrace{u^2/(1+u^2)}_{\text{predation by birds}}$$



# Travelling Waves in the Spruce Budworm Model

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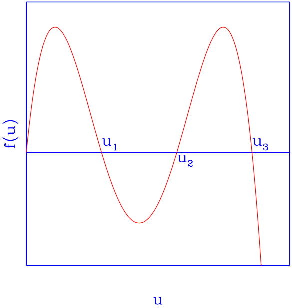


In applications, waves travelling between $u = u_1$ (“refuge state”) and $u = u_3$ (“outbreak state”) are important. Both of these steady states are locally stable. Therefore the direction of wave propagation is not obvious.

# Direction of Wave Propagation

Travelling wave solutions $U(z)$ ($z = x - ct$) satisfy

$$\begin{aligned} DU'' + cU' + f(U) &= 0 \\ \Rightarrow \left[\tfrac{1}{2}DU'^2\right]_{-\infty}^{+\infty} + c\int_{-\infty}^{+\infty} U'^2 dz + \int_{-\infty}^{+\infty} f(U)U' dz &= 0 \end{aligned}$$

We know that $U'(\pm\infty) = 0$. Therefore for a wave front with $U(-\infty) = u_1$ and $U(+\infty) = u_3$, $c$ has the same sign as $-\int_{u_1}^{u_3} f(U)dU$.

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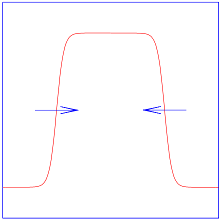
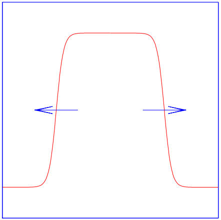
For the spruce budworm model, this can be used to predict whether a local outbreak will die out or spread.



Outbreak dies out



Outbreak spreads

# Existence of Travelling Waves

**Theorem** [Fife & McLeod, 1977]. Consider the equation $\partial u/\partial t = D\,\partial^2 u/\partial x^2 + f(u)$ with $f(u_1) = f(u_2) = f(u_3) = 0$, $f'(u_1) < 0$, $f'(u_2) > 0$, $f'(u_3) < 0$. This equation has a travelling wave solution $u(x,t) = U(x - ct)$ with $U(-\infty) = u_1$ and $U(+\infty) = u_3$ for exactly one value of the wave speed $c$.

*A proof of this theorem is in the supplementary material.*

Reference:
Fife, P.C. & McLeod, J.B. 1977 The approach of solutions of nonlinear diffusion equations to travelling front solutions. *Arch. Rat. Mech. Anal.* 65, 335-361.

# The Value of the Wave Speed

There is no general result on the value of the unique wave speed for a reaction-diffusion equation with bistable kinetics.

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# A Model for Predator-Prey Interactions

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

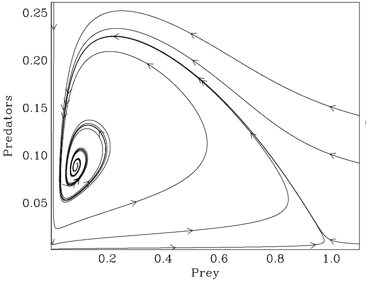
For some parameters, the kinetic ODEs have a stable coexistence steady state.

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

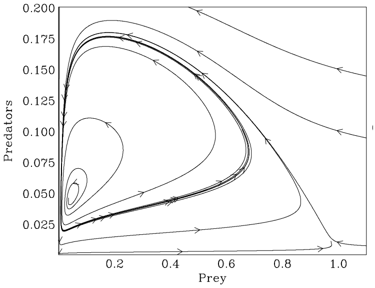
For other parameters, the coexistence steady state is unstable, and there is a stable limit cycle.

predators

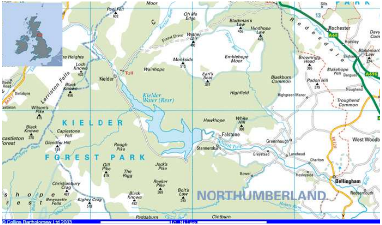
$$\partial p/\partial t = akph/(1+kh) - bp$$

prey

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



# Example of a Cyclic Population

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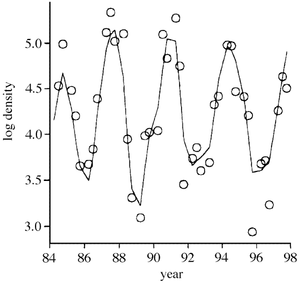
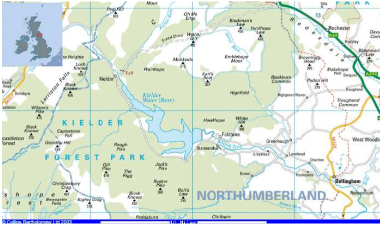



Field voles in Kielder Forest are cyclic (period 4 years)

# Example of a Cyclic Population


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

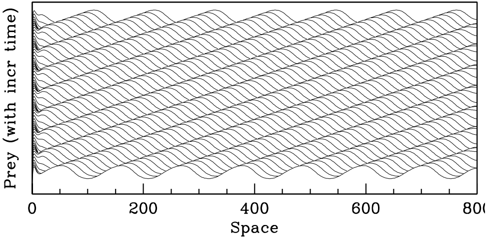
Spatiotemporal field data shows that the cycles are spatially organised into a periodic travelling wave

# What is a Periodic Travelling Wave?

A periodic travelling wave is an oscillatory solution moving with constant shape and speed.

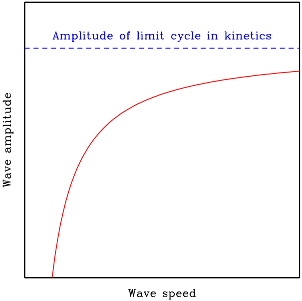
It is periodic as a function of time (at a fixed space point).
It is periodic as a function of space (at a fixed time point).

Speed = space period/ time period



# The Periodic Travelling Wave Family

**Theorem** [Kopell & Howard, 1973]. Any oscillatory reaction-diffusion system has a one-parameter family of periodic travelling waves.




Reference: Kopell, N. & Howard, L.N. 1973 Plane wave solutions to reaction-diffusion equations. *Stud. Appl. Math.* 52, 291-328.

# $\lambda$–$\omega$ Equations

Mathematical analysis is not possible for the predator-prey equations. Instead we consider a simpler example known as the $\lambda$–$\omega$ equations:

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

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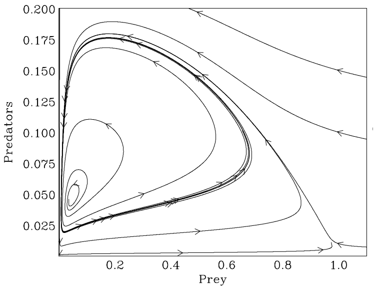


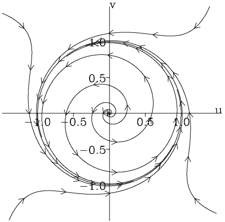

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The periodic travelling wave family is

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

# $\lambda$–$\omega$ Equations in Polar Coordinates

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

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

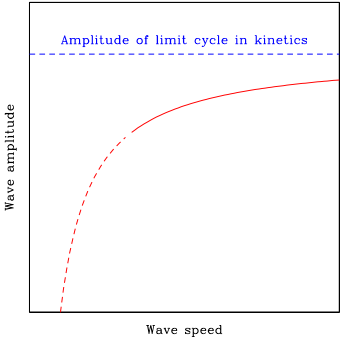
The periodic travelling waves are

$$r = R \qquad \theta = \pm\sqrt{\lambda(R)}x + \omega(R)t$$

$$\text{wavelength} = \frac{2\pi}{\sqrt{\lambda(R)}} \quad \text{time period} = \frac{2\pi}{|\omega(R)|} \quad \text{speed} = \frac{|\omega(R)|}{\sqrt{\lambda(R)}}$$

# 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.



# Stability in the Periodic Travelling Wave Family

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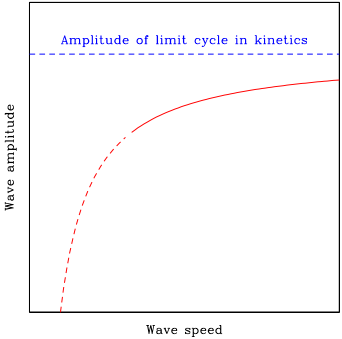
For the $\lambda$–$\omega$ system, the stability condition is

$$4\lambda(R)\left[1+\omega'(R)^2/\lambda'(R)^2\right]+R\lambda'(R)\leq 0\,.$$




This condition is hard to derive in general (see Kopell & Howard, 1973). For the special case of $\omega(.)$ constant, the derivation is given in the supplementary material.

# Generation of Periodic Travelling Waves

One way in which periodic travelling waves develop in the $\lambda$–$\omega$ equations is via the local perturbation of the unstable equilibrium $u = v = 0$. This process selects a particular wave amplitude, that can be calculated explicitly. Details of this are given in the supplementary material.

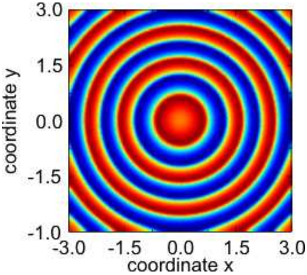
For the predator-prey model, a corresponding process is the generation of periodic travelling waves by the invasion of a prey population by predators. For details of this, see

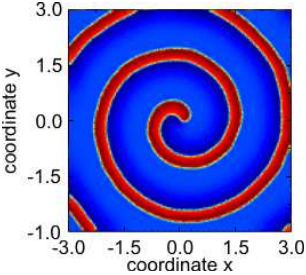
Sherratt, J.A., Lewis, M.A. & Fowler, A.C. 1995 Ecological chaos in the wake of invasion. *Proc. Natl. Acad. Sci. USA* 92, 2524-2528.

(This paper can be downloaded from `www.ma.hw.ac.uk/~jas/publications.html`)

# Extension to Two Space Dimensions: Spiral Waves

Periodic travelling waves are important in their own right, and also as the one-dimensional equivalents of target patterns and spiral waves.




A brief introduction to spiral waves in the $\lambda$–$\omega$ equations is given in the supplementary material.

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