7. Systems of reaction-diffusion equations

- Recall coupled ODE models considered earlier, e.g. for reacting chemical species or interacting populations.
- If chemicals or populations are diffusing, so that there is spatial as well as temporal variation in concentrations, then we obtain reaction-diffusion systems of the type

$$\left.\begin{aligned} \frac{\partial U}{\partial t} &= F(U,V) + D_U \nabla^2 U \\ \frac{\partial V}{\partial t} &= G(U,V) + D_V \nabla^2 V \end{aligned}\right\} \tag{30}$$

- These must be solved on domain of interest (call it Ω) subject to initial conditions ($U(\boldsymbol{x},0)$, $V(\boldsymbol{x},0)$ specified) and boundary conditions (typically a linear combination of each of U, V and their normal derivatives specified on bdy of Ω).
- Can write system (30) in matrix form if we define

$$\boldsymbol{U} = \begin{pmatrix} U \\ V \end{pmatrix} \quad \boldsymbol{F}(\boldsymbol{U}) = \begin{pmatrix} F(U,V) \\ G(U,V) \end{pmatrix} \quad D = \begin{pmatrix} D_U & 0 \\ 0 & D_V \end{pmatrix}$$

$$\Rightarrow \quad \boldsymbol{U}_t = \boldsymbol{F}(\boldsymbol{U}) + D\nabla^2 \boldsymbol{U}.$$

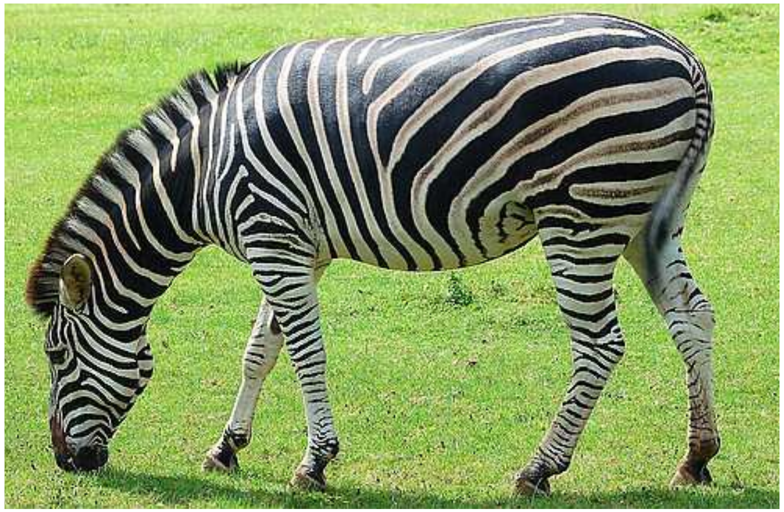
7.1 Diffusion driven instability

$$\boldsymbol{U}_t = \boldsymbol{F}(\boldsymbol{U}) + D\nabla^2\boldsymbol{U} \tag{31}$$

- Turing showed that the simple combination of two reacting and diffusing chemicals (he called them “Morphogens”), could generate spatial patterns (but diffusion is *supposed* to spread things out):
- Diffusion driven instability (DDI) occurs when a constant solution of the model that is stable in the absence of diffusion becomes unstable when diffusion is present.
- Equivalently, this constant solution is stable to spatially homogeneous perturbations but unstable to spatially varying perturbations.
- Also known as the Turing instability, after its discoverer.
- Occurs in many chemical and biological systems, and can lead to patterning (e.g. it is hypothesised to be responsible for the different patterns that occur on animal skins and on some plant leaves, among other things).
- From the point of view of our reaction-diffusion models, “patterns” are stable, steady (in time), spatially nonuniform solutions.
- Investigate possibility of DDI by considering the linear stability of constant solutions $\boldsymbol{U}^*$ to diffusionless problem (31):

$$\boldsymbol{F}(\boldsymbol{U}^*) = \boldsymbol{0}.$$

Leopard's spots and tiger bush...



7.1.1 Linear stability of constant solutions

- Investigate possibility of DDI by considering the linear stability of constant solutions $\boldsymbol{U}^*$ to diffusionless problem (31):

$$\boldsymbol{U}_t = \boldsymbol{F}(\boldsymbol{U}) + D\nabla^2\boldsymbol{U}, \qquad \boldsymbol{F}(\boldsymbol{U}^*) = \mathbf{0} \tag{32}$$

- In usual way set $\boldsymbol{U} = \boldsymbol{U}^* + \epsilon\boldsymbol{W}(\boldsymbol{x}, t) + O(\epsilon^2)$.
- Substituting in (32) and Taylor expanding $\boldsymbol{F}(\boldsymbol{U})$ about $\boldsymbol{U}^*$ gives linear equation

$$\boldsymbol{W}_t = M\boldsymbol{W} + D\nabla^2\boldsymbol{W}, \quad M = \begin{pmatrix} F_U & F_V \\ G_U & G_V \end{pmatrix}_{(U^*, V^*)}$$

  (M is the Jacobian matrix of $\boldsymbol{F}$).

- Require an initial condition, and boundary conditions at edge of spatial domain Ω. E.g., might have no-flux condition,

$$\frac{\partial \boldsymbol{W}}{\partial n} = (\boldsymbol{n}\cdot\nabla U, \boldsymbol{n}\cdot\nabla V)^T = \mathbf{0} \quad \text{on } \partial\Omega.$$

  Suppose this, for definiteness.

Linearised problem for perturbation $\boldsymbol{W}$

$$\boldsymbol{W}_t = M\boldsymbol{W} + D\nabla^2\boldsymbol{W}, \quad M = \begin{pmatrix} F_U & F_V \\ G_U & G_V \end{pmatrix}_{(U^*,V^*)} \qquad \frac{\partial \boldsymbol{W}}{\partial n} = \boldsymbol{0} \quad \text{on } \partial\Omega. \tag{33}$$

- Seek separable solutions $\boldsymbol{W} = \exp(\lambda t)\boldsymbol{w}(\boldsymbol{x})$, where

$$\begin{aligned} \lambda\boldsymbol{w} &= M\boldsymbol{w} + D\nabla^2\boldsymbol{w} \quad \text{in } \Omega, \\ \frac{\partial \boldsymbol{w}}{\partial n} &= 0 \quad \text{on } \partial\Omega. \end{aligned} \tag{34}$$

  We seek solutions $\boldsymbol{w}$ with sinusoidal spatial dependence, $\boldsymbol{w} = \Re(\exp(i\boldsymbol{k}\cdot\boldsymbol{x})\boldsymbol{w}_0)$, where $\boldsymbol{w}_0$ is a constant vector.
  - e.g. consider a 1D problem, and take Ω to be the interval $0 < x < L$, then in order to satisfy conditions (33) we take

$$\boldsymbol{w} = \boldsymbol{w}_0 \cos\left(\frac{n\pi x}{L}\right)$$

    and wavevector $\boldsymbol{k} = (1,0)n\pi/L$.
- In general, substituting in (34) then gives. . .

Eigenvalue problem for $\boldsymbol{w}$ *(*$\boldsymbol{W} = \exp(\lambda t)\boldsymbol{w}(\boldsymbol{x})$*)*

Substituting $\boldsymbol{w} = \Re(\exp(i\boldsymbol{k}\cdot\boldsymbol{x})\boldsymbol{w}_0)$ in problem for $\boldsymbol{w}$

$$\lambda\boldsymbol{w} = M\boldsymbol{w} + D\nabla^2\boldsymbol{w} \quad \text{in } \Omega, \qquad \frac{\partial\boldsymbol{w}}{\partial n} = 0 \quad \text{on } \partial\Omega,$$

gives eigenvalue problem for $\boldsymbol{w}_0$

$$(M - k^2D - \lambda I)\boldsymbol{w}_0 = 0, \quad k^2 = |\boldsymbol{k}|^2.$$

- As in 1D example, allowable $\boldsymbol{k}$ restricted by requiring bdy conditions to be satisfied.
- For nontrivial solutions λ must be an eigenvalue of $(M - k^2D)$. Since M and D known, can write down quadratic satisfied by λ:

$$\lambda^2 + \lambda(k^2(D_1 + D_2) - (F_U + G_V)) + h(k^2) = 0, \tag{35}$$

where $\quad h(k^2) = k^4D_1D_2 - k^2(D_1G_V + D_2F_U) + F_UG_V - F_VG_U.$

- If $\Re(\lambda) < 0$ for all allowable k^2 then steady solution is stable and there is no spatial instability.
- If however $\Re(\lambda) > 0$ for some k^2 then the steady state is unstable to spatially inhomogeneous perturbations.

Diffusion driven instability?

- With spatially-dependent perturbations ($k \neq 0$), stability of constant solution $\boldsymbol{U}^*$ determined by eigenvalue problem

$$\lambda^2 + \lambda(k^2(D_1 + D_2) - (F_U + G_V)) + h(k^2) = 0, \tag{36}$$

where $\quad h(k^2) = k^4 D_1 D_2 - k^2(D_1 G_V + D_2 F_U) + F_U G_V - F_V G_U.$

- For DDI, first requirement is that U^* be stable to spatially homogeneous perturbations, $k = 0$ (no diffusion)
- When $k = 0$ (or $D_1 = D_2 = 0$) eigenvalue problem (36) becomes

$$\lambda^2 - (F_U + G_V)\lambda + F_U G_V - F_V G_U = 0$$

$$\Rightarrow \quad 2\lambda = (F_U + G_V) \pm \sqrt{(F_U + G_V)^2 - 4(F_U G_V - F_V G_U)}$$

- For stability require

$$\text{(a) } F_U + G_V < 0 \quad \text{and} \quad \text{(b) } F_U G_V - F_V G_U > 0. \tag{37}$$

- Assume (37) holds. If we now allow $k \neq 0$ can stability conditions be violated?

Diffusion driven instability? (2)

For stability with $k = 0$ require

$$\text{(a) } F_U + G_V < 0 \quad \text{and} \quad \text{(b) } F_U G_V - F_V G_U > 0. \tag{38}$$

- With $k \neq 0$, analogous to stability condition (38a) is

$$F_U + G_V - k^2(D_1 + D_2) < 0,$$

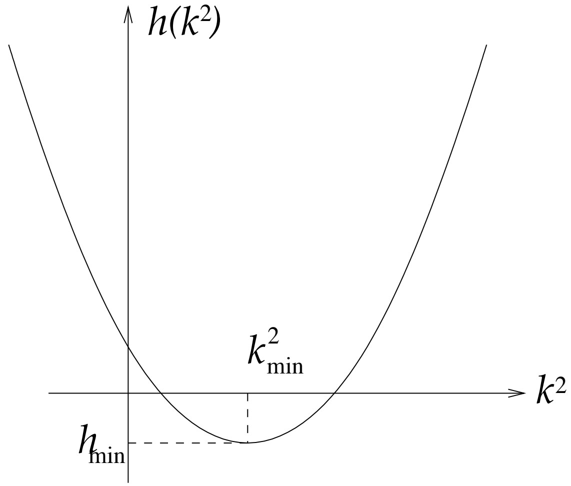
  which by (38a) always holds.

- 2nd requirement for stability (analogous to (38b)) is

$$h(k^2) = k^4 D_1 D_2 - k^2(D_1 G_V + D_2 F_U) + F_U G_V - F_V G_U > 0,$$

  thus we have instability if and only if

$$h(k^2) < 0 \quad \text{for some allowable } k^2.$$



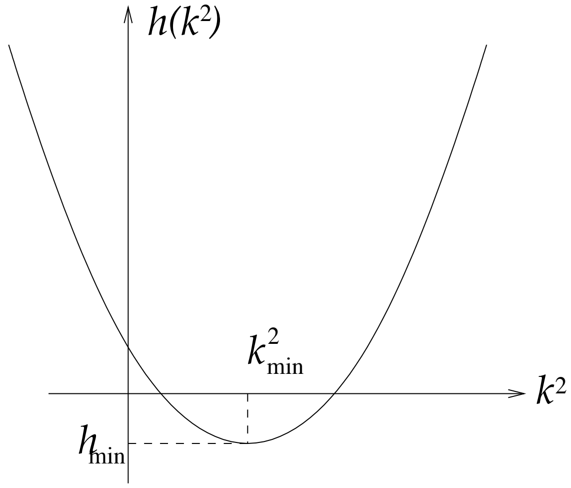
- Instability condition
  $h(k^2) = k^4 D_1 D_2 - k^2(D_1 G_V + D_2 F_U) + F_U G_V - F_V G_U < 0$ illustrated above.
  Note that $h(0) = F_U G_V - F_V G_U > 0$ by (38b)
- Find h_{min} by completing the square – if $h(k^2) = ak^4 - bk^2 + c$ then can write

$$h(k^2) = a\left(k^2 - \frac{b}{2a}\right)^2 + c - \frac{b^2}{4a},$$

  thus $h_{min} = c - b^2/(4a)$ is attained for $k^2_{min} = b/(2a)$.
- For instability require both (a) $k^2_{min} > 0$ and (b) $h_{min} = h(k^2_{min}) < 0$, thus:

$$D_1 G_V + D_2 F_U > 0, \tag{39}$$

$$4D_1 D_2 (F_U G_V - F_V G_U) < (D_1 G_V + D_2 F_U)^2. \tag{40}$$



- Instability condition
  $h(k^2) = k^4 D_1 D_2 - k^2(D_1 G_V + D_2 F_U) + F_U G_V - F_V G_U < 0$.
- When conditions (39) and (40) satisfied $\exists$ range of unstable wavenumbers k^2 lying between the roots of $h(k^2) = 0$ (when roots exist, both must be of same sign since $h(0) > 0$).
- NB: This ignores fact that on finite domains with spatial boundary conditions, only certain values of k are allowed! Need to check finally that, in specific examples, allowable wavenumbers lie in this range.

Diffusion-driven instability: Summary

- For DDI require first that system is stable to spatially-homogeneous perturbations (no diffusion). This requires conditions (38a) and (38b):

$$\text{(DDI1)}\ F_U + G_V < 0 \quad \text{and} \quad \text{(DDI2)}\ F_U G_V - F_V G_U > 0.$$

- Secondly, we require that system is unstable to spatially-varying perturbations – conditions (39), (40):

$$\begin{aligned} &\text{(DDI3)} \quad & D_1 G_V + D_2 F_U > 0 \\ \text{and} \quad &\text{(DDI4)} \quad & 4D_1 D_2 (F_U G_V - F_V G_U) < (D_1 G_V + D_2 F_U)^2. \end{aligned}$$

- If (DDI1)–(DDI4) hold then will have DDI on spatially-unbounded domains.
- Comparing (DDI1) and (DDI3), we see that DDI can never arise when $D_1 = D_2$. The two interacting species must diffuse at different rates.
- Given that we have DDI, which of the allowable wavenumbers k are associated with the fastest growth-rate λ_{max}? These are the unstable spatial modes that will be observed first, and usually provide good predictions of the steady pattern that the system eventually evolves to.
- λ_{max} can be found by considering how λ varies as function of k^2 in (36).

7.1.2 Example: 1D diffusion, no flux boundary conditions

- Activator-inhibitor kinetics and diffusion, in one space dimension, given by

$$\left.\begin{aligned} U_t &= \frac{aU^2}{V} - bU + D_1 U_{xx} \\ V_t &= cU^2 - dV + D_2 V_{xx} \end{aligned}\right\} \quad 0 \le x \le L_1, \quad U_x = 0 = V_x \text{ at } x = 0,\ L_1. \tag{41}$$

- Unique positive steady state (check) at $(U^*, V^*) = (ad/bc, a^2 d/b^2 c)$.
- Begin by nondimensionalising system, writing

$$U = U^* u, \quad V = V^* v, \quad t = T\tau, \quad x = l\xi. \tag{42}$$

- Substituting these scalings into (41) reveals suitable choices for T and l to be $T = 1/b$, $l = \sqrt{D_1/b}$, giving reduced parameter system

$$\left.\begin{aligned} u_\tau &= \frac{u^2}{v} - u + u_{\xi\xi} \\ v_\tau &= \delta(u^2 - v) + \bar{D} v_{\xi\xi} \end{aligned}\right\} \quad 0 \le \xi \le L, \quad u_\xi = 0 = v_\xi \text{ at } \xi = 0,\ L,$$

where $\delta = d/b$, $\bar{D} = D_2/D_1$, $L = L_1\sqrt{b/D_1}$.

Dimensionless model

$$\left.\begin{aligned} u_\tau &= \frac{u^2}{v} - u + u_{\xi\xi} \\ v_\tau &= \delta(u^2 - v) + \bar{D} v_{\xi\xi} \end{aligned}\right\} \quad 0 \le \xi \le L, \quad u_\xi = 0 = v_\xi \text{ at } \xi = 0,\ L. \tag{43}$$

- Steady state of dimless model at $(u^*, v^*) = (1, 1)$. Linearise:

$$\boldsymbol{u} = (u, v) = (1, 1) + \epsilon \boldsymbol{u}_1 + O(\epsilon^2),$$

and substitute in (43), leading to

$$\boldsymbol{u}_{1\tau} = M\boldsymbol{u}_1 + D\boldsymbol{u}_{1\xi\xi}, \quad M = \begin{pmatrix} 1 & -1 \\ 2\delta & -\delta \end{pmatrix} \quad D = \begin{pmatrix} 1 & 0 \\ 0 & \bar{D} \end{pmatrix}.$$

- As usual $\boldsymbol{u}_1 = e^{\lambda\tau}\boldsymbol{w}(\xi)$, so that

$$\lambda\boldsymbol{w} = M\boldsymbol{w} + D\boldsymbol{w}_{\xi\xi}, \quad \frac{\partial \boldsymbol{w}}{\partial \xi} = 0 \text{ at } \xi = 0,\ L.$$

Linearised problem

- $\boldsymbol{u} = (1,1) + \epsilon \boldsymbol{u}_1 + O(\epsilon^2)$, $\boldsymbol{u}_1 = e^{\lambda\tau}\boldsymbol{w}(\xi)$, led to

$$\lambda \boldsymbol{w} = M\boldsymbol{w} + D\boldsymbol{w}_{\xi\xi}, \quad \frac{\partial \boldsymbol{w}}{\partial \xi} = 0 \text{ at } \xi = 0,\ L. \tag{44}$$

- Seek wavelike solutions for $\boldsymbol{w}$. Since domain boundary and conditions specified, can now determine allowable wavenumbers k, and write solution as

$$\boldsymbol{w} = \sum_{n=0}^{\infty} \boldsymbol{w}_n, \quad \boldsymbol{w}_n = \boldsymbol{w}_{0n}\cos(k_n\xi), \quad k_n = n\pi/L.$$

- Equations (44) then yield eigenvalue problem to be solved for λ:

$$\lambda^2 + \lambda\big(k^2(1+\bar{D}) + \delta - 1\big) + [k^4\bar{D} + k^2(\delta - \bar{D}) + \delta] = 0$$

  (this can also be read off from equation (36)).

- For DDI require stable to spatially-homogeneous perturbations, and unstable to spatially-varying perturbations.

Stable to spatially homogeneous perturbations?

- Eigenvalue problem with spatial variation ($k \neq 0$)

$$\lambda^2 + \lambda\big(k^2(1+\bar{D}) + \delta - 1\big) + [k^4\bar{D} + k^2(\delta - \bar{D}) + \delta] = 0 \qquad (45)$$

- To check for stability with no spatial variation, either read off conditions from (DDI1), (DDI2), or check directly by setting $k = 0$ in (45).
  Note: cannot simply set $\bar{D} = 0$ since in dimless problem have scaled so that one diffusion coefficient is unity.
- Leads to “spatially homogeneous” eigenvalue problem

$$\lambda^2 + \lambda(\delta - 1) + \delta = 0 \quad \Rightarrow \quad 2\lambda = 1 - \delta \pm \sqrt{(1-\delta)^2 - 4\delta},$$

  which has stable eigenvalues provided

$$1 - \delta < 0, \quad \text{and} \quad \delta > 0$$

  that is, provided

$$\delta > 1. \qquad (46)$$

Unstable to spatially-varying perturbations?

- With spatial variation, require positive real part to eigenvalues of

$$\lambda^2 + \lambda\big(k^2(1+\bar{D}) + \delta - 1\big) + [k^4\bar{D} + k^2(\delta - \bar{D}) + \delta] = 0.$$

- With restriction $\delta > 1$ in place this can hold only if

$$h(k^2) = k^4\bar{D} - k^2(\bar{D} - \delta) + \delta < 0$$

for some allowable k^2, that is,

$$k^4 - k^2(1-\hat{\delta}) + \hat{\delta} < 0, \qquad \hat{\delta} = \delta/\bar{D}$$

$$\Rightarrow \quad (k^2 - \frac{1}{2}(1-\hat{\delta}))^2 - \frac{1}{4}(1 - 6\hat{\delta} + \hat{\delta}^2) < 0.$$

- Sketching $h(k^2)$ and noting again that $h(0) = \delta > 0$, need $k^2_{min} > 0$, that is,

$$0 < \hat{\delta} < 1, \tag{47}$$

and $h(k^2_{min}) < 0$, that is, $1 - 6\hat{\delta} + \hat{\delta}^2 > 0 \quad \Rightarrow (\hat{\delta} - 3)^2 > 8 \quad \Rightarrow |\hat{\delta} - 3| > 2\sqrt{2}$

$$\Rightarrow \quad \hat{\delta} > 3 + 2\sqrt{2} > 1 \quad \text{or} \quad \hat{\delta} < 3 - 2\sqrt{2} \approx 0.171. \tag{48}$$

Diffusion-driven instability conditions

- Final conditions for DDI to be possible are (46), (47) and (48):

$$\delta > 1, \quad 0 < \hat{\delta} < \hat{\delta}_{max} = 3 - 2\sqrt{2} \approx 0.171. \tag{49}$$

- When (49) satisfied, range of unstable wavenumbers lies between roots of $h(k^2) = 0$:

$$\frac{1}{2}\left((1-\hat{\delta}) - \sqrt{1 - 6\hat{\delta} + \hat{\delta}^2}\right) < k^2 < \frac{1}{2}\left((1-\hat{\delta}) + \sqrt{1 - 6\hat{\delta} + \hat{\delta}^2}\right). \tag{50}$$

- Recalling that allowable k-values are $k_n = n\pi/L$, (50) gives constraints on domain size L for instabilities to be manifested – if L is so small that π^2/L^2 is larger than the upper bound in (50) then no instability is possible.
- There is a critical domain size necessary for a spatial instability.
- Note that for $\hat{\delta} \ll 1$, $\sqrt{1 - 6\hat{\delta} + \hat{\delta}^2} \approx 1 - \frac{6\hat{\delta}}{2}$, and the above range for k^2 approximates to:

$$\hat{\delta} < k^2 < 1 - 2\hat{\delta}. \tag{51}$$

Fastest-growing modes

- DDI conditions: $\delta > 1, \quad 0 < \hat{\delta} < \hat{\delta}_{max} = 3 - 2\sqrt{2}.$
  If $\hat{\delta} < \hat{\delta}_{max}$, can determine fastest-growing modes k_*^2, such that $\lambda(k_*^2)$ is a maximum.
- Suppose $\delta = 2$, and $\hat{\delta} = 0.1 \Rightarrow \bar{D} = 20$ (recall, $\hat{\delta} = \delta/D$).
  λ then satisfies equation (45):

$$\lambda^2 + \lambda(21k^2 + 1) + 20k^4 - 18k^2 + 2 = 0, \tag{52}$$

  and we can track how λ_1 and λ_2 vary with k^2.
- Growth-rates are real over unstable range, and largest root is

$$2\lambda(k^2) = -21k^2 - 1 + \sqrt{361k^4 + 114k^2 - 7}$$

- Can find maximum value of this expression by solving $d\lambda/d(k^2) = 0$, giving

$$21 = \frac{722k^2 + 114}{2\sqrt{361k^4 + 114k^2 - 7}} \quad \Rightarrow \quad k_*^2 = 0.336 \quad \Rightarrow \quad k_* = 0.580$$

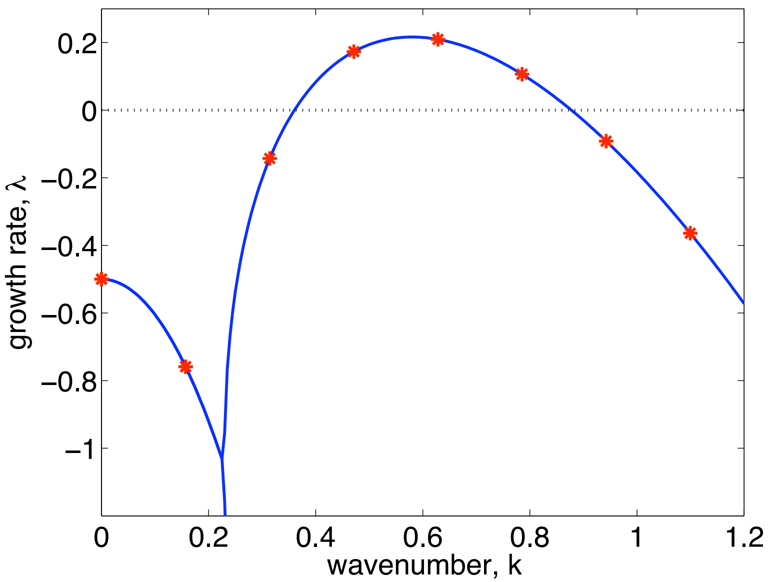
- In present example, the allowed k's are $k_n = n\pi/L$, thus the fastest-growing spatial mode is given by the value of n closest to Lk_*/π.

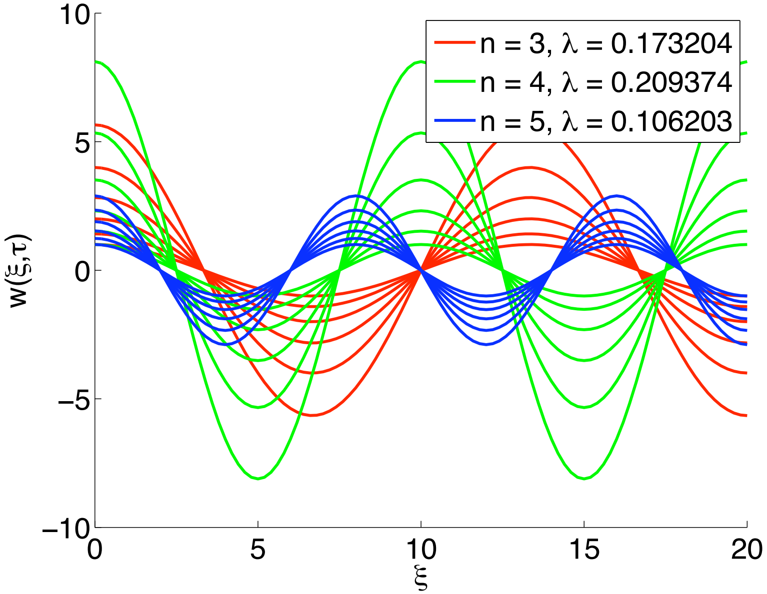
Fastest-growing modes

- Suppose domain length $L = 20$. Then $n^* = Lk_*/\pi = 3.69$, so fastest-growing spatial mode will be $n = 3$ or $n = 4$, corresponding to $k = 3\pi/20$ or $k = \pi/5$.
- These two values give positive growth rates $\lambda = 0.173,\ 0.209$ respectively (from (52)), thus $n = 4$ is the fastest-growing mode.
- The perturbations to the steady state are of the form

$$\boldsymbol{u}_1 \sim \sum \boldsymbol{w}_{0n} e^{\lambda_n \tau} \cos k_n \xi, \qquad k_n = \frac{n\pi}{L},$$

thus the dominant term in the perturbation will be $\boldsymbol{w}_{04} e^{0.209\tau} \cos\left(\frac{\pi\xi}{5}\right)$.

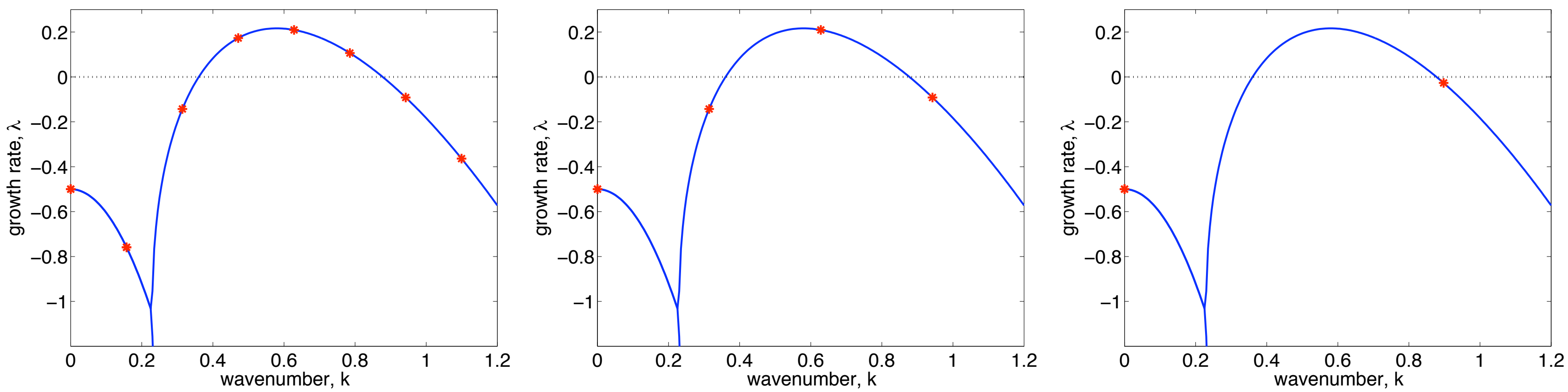




Fastest-growing modes

- $L = 20$. Then $n^* = Lk_*/\pi = 3.69$, so fastest-growing spatial mode will be $n = 2, 3$ or $n = 4$, with positive growth rates $\lambda = 0.173,\ 0.209$ respectively.
- $L = 10$. Then $n^* = Lk_*/\pi = 1.85$, so fastest-growing spatial mode will be $n = 1$ or $n = 2$, with growth rates $\lambda = -0.1428$ and 0.2094 respectively.
- $L = 3.5$. Then $n^* = Lk_*/\pi = 0.6462$, so fastest-growing spatial mode will be $n = 0$ or $n = 1$, with negative growth rates $\lambda = -0.5 + 1.3i,\ -0.0268$ respectively.

  The domain is too short to support a spatial instability.



7.1.3 Extension to two space dimensions

Consider the same problem (43) but in two space dimensions,

$$\left.\begin{aligned} u_\tau &= \frac{u^2}{v} - u + u_{\xi\xi} + u_{\eta\eta} \\ v_\tau &= \delta(u^2 - v) + \bar{D}(v_{\xi\xi} + v_{\eta\eta}) \end{aligned}\right\} \quad (\xi,\eta) \in [0,L]\times[0,P], \quad \begin{aligned} &u_\xi = 0 = v_\xi \text{ at } \xi = 0,\ L, \\ &u_\eta = 0 = v_\eta \text{ at } \eta = 0,\ P, \end{aligned}$$

and consider the stability of the steady state $(1,1)$ to 2D perturbations,
$\boldsymbol{u} = (1,1) + \epsilon e^{\lambda\tau}\boldsymbol{w}(\xi,\eta)$. Same steps as before lead to problem analogous to (44):

$$\lambda\boldsymbol{w} = M\boldsymbol{w} + D(\boldsymbol{w}_{\xi\xi} + \boldsymbol{w}_{\eta\eta}), \quad \frac{\partial\boldsymbol{w}}{\partial\xi} = 0 \text{ at } \xi = 0,\ L, \quad \frac{\partial\boldsymbol{w}}{\partial\eta} = 0 \text{ at } \eta = 0,\ P.$$

Wavelike solutions satisfying boundary conditions:

$$\boldsymbol{w}_{n,m} = \boldsymbol{w}^{(0)}_{n,m}\cos(k_n\xi)\cos(q_m\eta), \quad k_n = \frac{n\pi}{L},\ q_m = \frac{m\pi}{P}.$$

Then, if $\kappa^2 = \pi^2(n^2/L^2 + m^2/P^2)$ we obtain the same equation as before for the eigenvalues λ:

$$\lambda^2 + \lambda\big(\kappa^2(1+\bar{D}) + \delta - 1\big) + [\kappa^4\bar{D} + \kappa^2(\delta - \bar{D}) + \delta] = 0$$

Conditions for Turing instability

$\kappa^2 = k_n^2 + q_m^2$, where k_n and q_m are the wavenumbers in the ξ and η directions respectively

$$\lambda^2 + \lambda\big(\kappa^2(1+\bar{D}) + \delta - 1\big) + [\kappa^4\bar{D} + \kappa^2(\delta - \bar{D}) + \delta] = 0.$$

Requirements for stability to spatially homogeneous perturbations ($\kappa = 0$) and instability to spatially inhomogeneous perturbations ($\kappa \neq 0$) then follow exactly as before, leading to a range of unstable wavenumbers κ, which for $\hat{\delta} \ll 1$ is approximated by

$$\hat{\delta} < \kappa^2 < 1 - 2\hat{\delta}.$$

Again, dimensions of domain $L,\ P$ critically influence observed instability. We require

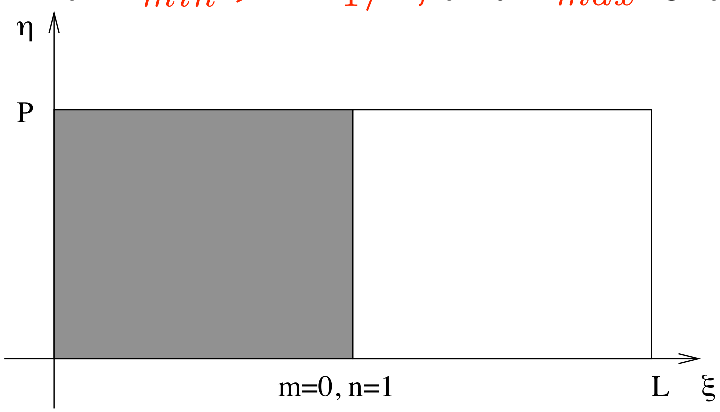
$$\frac{\kappa_1^2}{\pi^2} = \frac{\hat{\delta}}{\pi^2} < \frac{n^2}{L^2} + \frac{m^2}{P^2} < \frac{1-2\hat{\delta}}{\pi^2} = \frac{\kappa_2^2}{\pi^2}$$

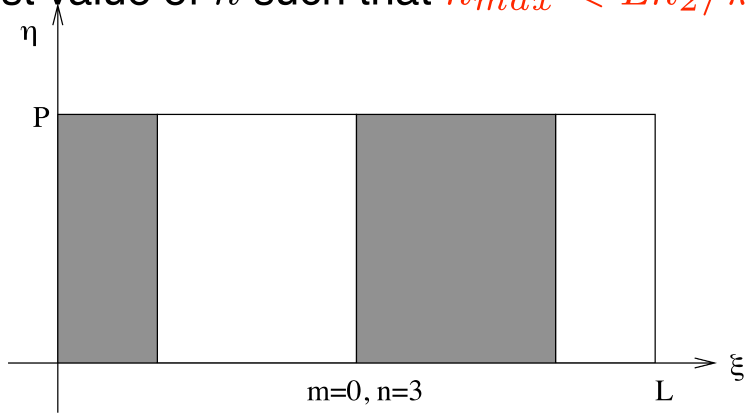
thus, if the domain is sufficiently small in the η-direction, such that $P^2 < \pi^2/(1-2\hat{\delta})$, then we require $m = 0$, so that no instability in this direction can be observed.
(A similar conclusion applies to L too of course.)

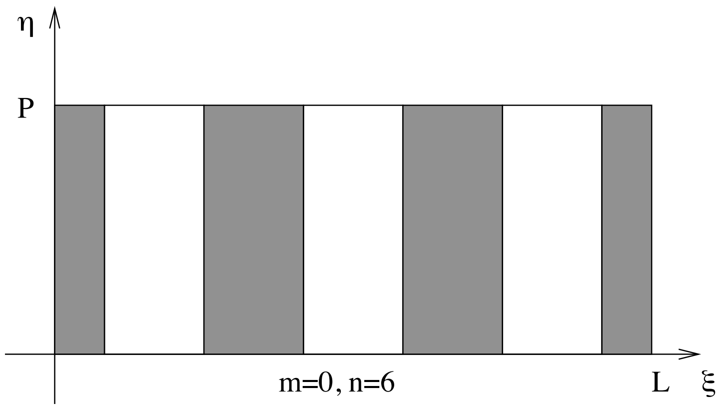
Possible instability modes

$$\frac{\kappa_1^2}{\pi^2} < \frac{n^2}{L^2} + \frac{m^2}{P^2} < \frac{\kappa_2^2}{\pi^2}$$

- Suppose P is fixed such that $\kappa_1^2/\pi^2 < 1^2/P^2 < \kappa_2^2/\pi^2$, but $2^2/P^2 > \kappa_2^2/\pi^2$. Then the only allowable η-instability modes are $m = 0,\ 1$.
- Consider $m = 0$ (1D instability modes). Then possible instability modes in ξ-direction are $n = n_{min}, \ldots, n_{max}$, where n_{min} is the smallest value of n such that $n_{min} > L\kappa_1/\pi$, and n_{max} is largest value of n such that $n_{max} < L\kappa_2/\pi$.





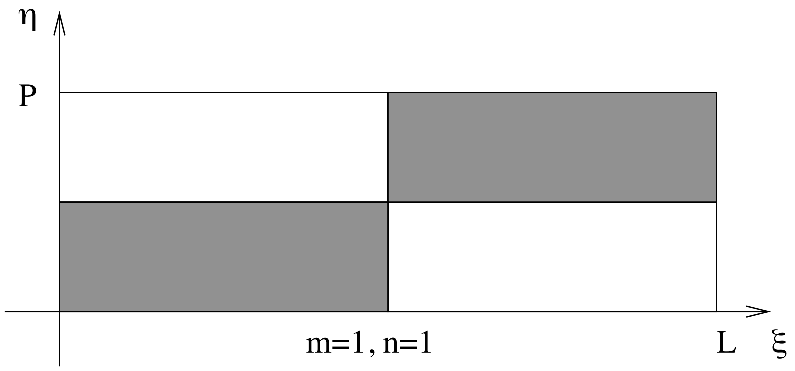


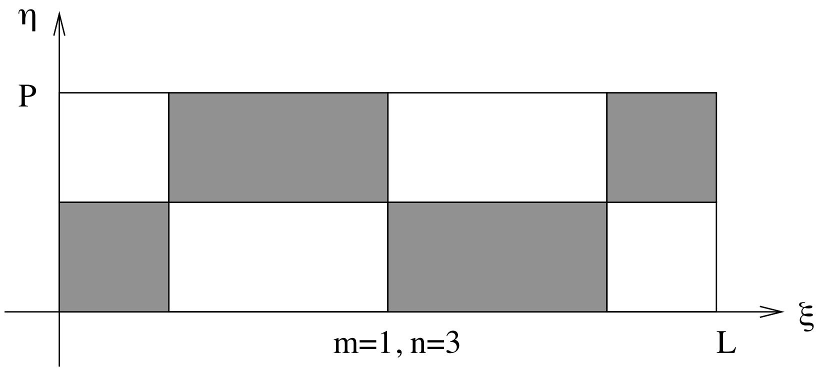
Possible instability modes (2)

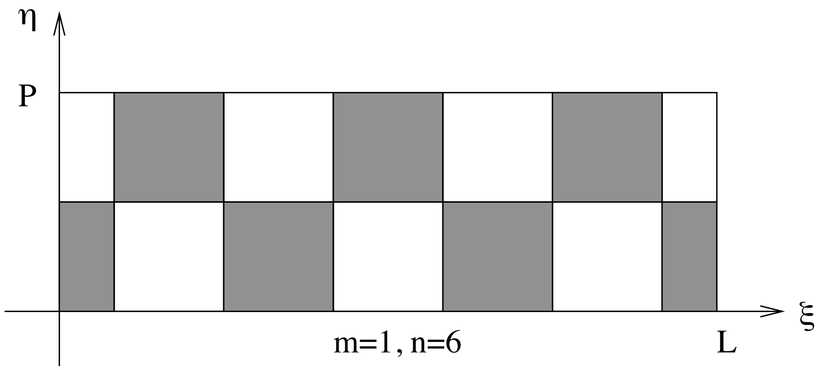
$$\frac{\kappa_1^2}{\pi^2} < \frac{n^2}{L^2} + \frac{m^2}{P^2} < \frac{\kappa_2^2}{\pi^2}$$

- Consider $m = 1$. Now possible instability modes in ξ-direction are $n = 0,\ 1, \ldots n_{max}$, where n_{max} is largest value of n such that

$$n_{max} < L\left(\frac{\kappa_2^2}{\pi^2} - \frac{1}{P^2}\right)^{1/2}.$$







Possible instability modes (3)

$$\frac{\kappa_1^2}{\pi^2} < \frac{n^2}{L^2} + \frac{m^2}{P^2} < \frac{\kappa_2^2}{\pi^2}$$

As P increases, we are able to fit in more instability modes in the η-direction. In general, the maximum numbers of modes possible in ξ and η directions are n_{max} and m_{max} respectively, where n_{max} and m_{max} are the largest integers such that

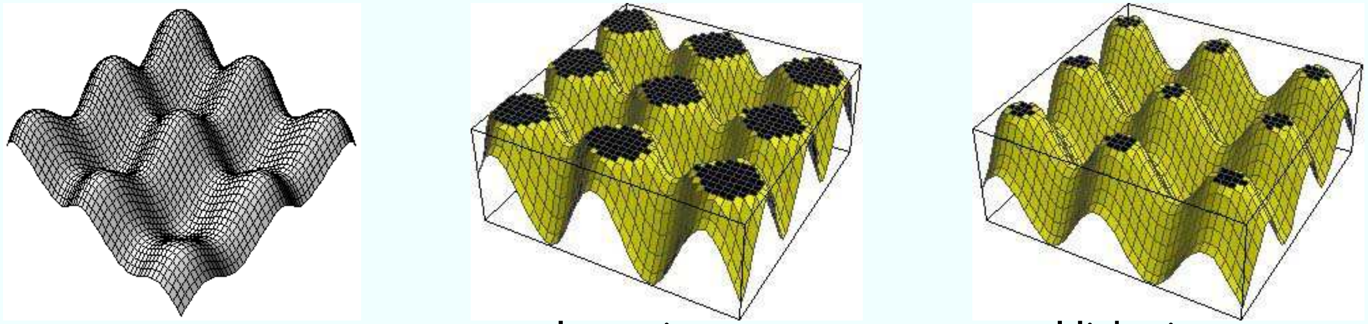
$$n_{max} < \frac{L\kappa_2}{\pi}, \qquad m_{max} < \frac{P\kappa_2}{\pi}.$$

Assuming a domain long in the ξ-direction, so that several instability modes are always possible in this direction, consider what happens as P increases.

- For $P < \pi/\kappa_2$ no instability modes are possible in the η-direction. The only patterns that can form are 1D “stripes” in the ξ-direction.
- As P increases above this threshold truly 2D patterns become possible, the degree of complexity increasing as P increases.

7.1.4 Implications for animal coat patterns

Hypothesis: Morphogens in the developing embryo, satisfy a reaction-diffusion system. The subsequent differentiation of the cells to produce melanin simply reflects spatial pattern of morphogen concentration.



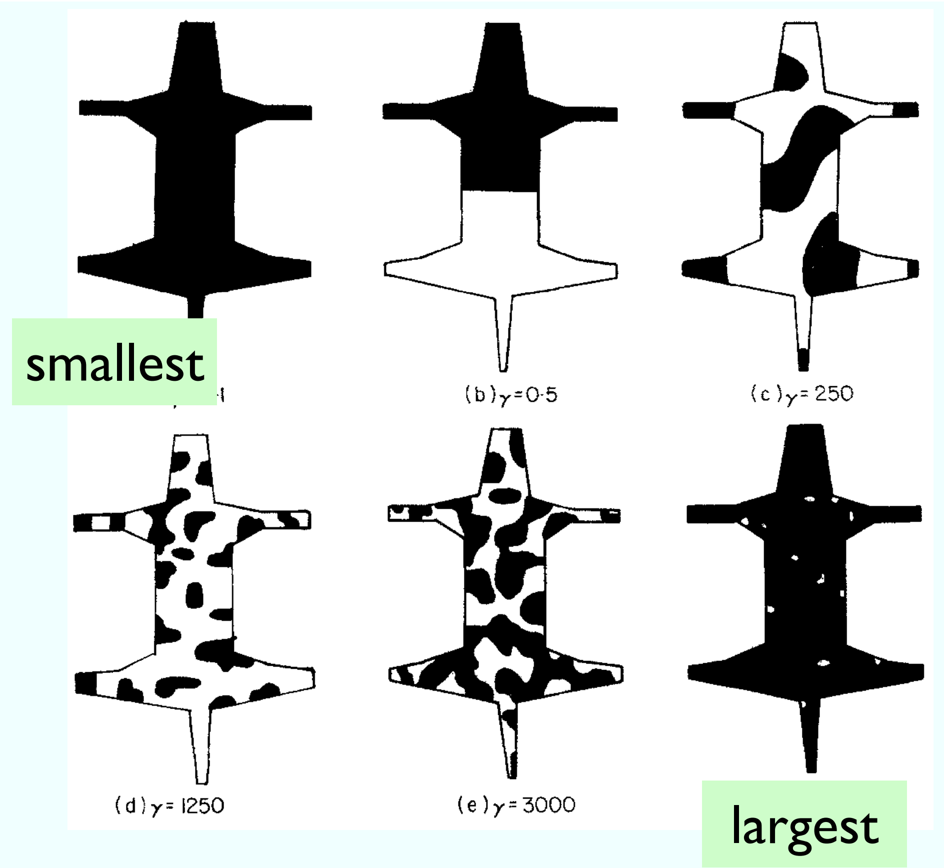
Activator pattern — Low pigment threshold, large spots — High pigment threshold, small spots

Only stripes possible in case $P < \pi/\kappa_2$ (previous slide):

Belted Galloway cattle

More generally

Patterns that can form depend also on dimensions of domain as discussed.

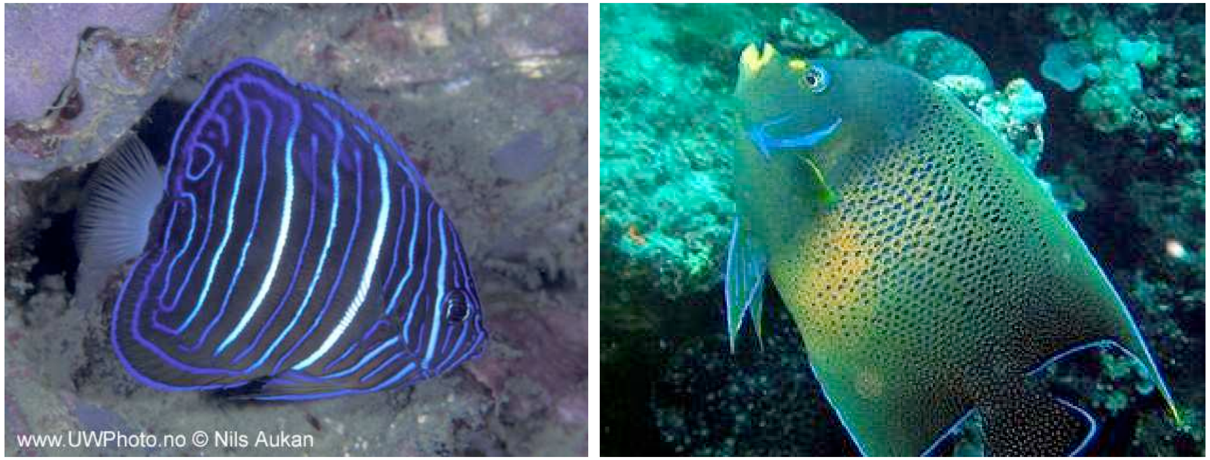


And sometimes juveniles stripy while adults spotty

Juvenile and adult angelfish (Great Barrier Reef)

Some time ago, we idly speculated whether such models could predict patterns on dinosaurs.

And sometimes juveniles stripy while adults spotty



Juvenile and adult angelfish (Great Barrier Reef)

Some time ago, we idly speculated whether such models could predict patterns on dinosaurs.

New evidence suggests that some dinosaurs did have patterned and coloured skin!

7.2 Travelling waves in reaction diffusion systems: spatial effects in disease spread

- So far have only considered time variation in disease epidemics, assuming that infective, susceptible and removed individuals are uniformly distributed.
- However, spatial effects are certainly important in most diseases (you will not get an infectious disease unless you meet someone else who has it).
- Consider how these might be incorporated into our SIR models.
- Classical application is spread of rabies by foxes within Europe. This disease is easy to model, for the following reasons.
    - Rabies, once contracted, is invariably lethal, so the removed class is always dead.
    - Healthy foxes are territorial, while rabid ones will wander large distances randomly (diffuse) and attack other foxes.

  Hence a modified SIR model is proposed, in which infective individuals (but not susceptibles or removed) diffuse:

$$\frac{\partial S}{\partial t} = -\beta IS, \quad \frac{\partial I}{\partial t} = \beta IS - \gamma I + D\nabla^2 I, \quad \frac{\partial R}{\partial t} = \gamma I.$$

7.2.1 Modified SIR model with diffusion of infectives

- Restrict to one space dimension for simplicity, so that $\nabla^2 \mapsto \partial^2/\partial x^2$:

$$\frac{\partial S}{\partial t} = -\beta I S, \quad \frac{\partial I}{\partial t} = \beta I S - \gamma I + D\frac{\partial^2 I}{\partial x^2}, \quad \frac{\partial R}{\partial t} = \gamma I. \tag{53}$$

- As usual we nondimensionalise and scale, setting

$$S = Nu, \quad I = Nv, \quad R = Nw, \quad t = \frac{\tau}{\gamma}, \quad x = \xi\sqrt{D/\gamma}.$$

- Then (53) becomes

$$\frac{\partial u}{\partial \tau} = -r^* uv, \quad \frac{\partial v}{\partial \tau} = r^* uv - v + v_{\xi\xi}, \quad \frac{\partial w}{\partial \tau} = v,$$

  where as before $r^* = \beta N/\gamma$.

- On infinite domain $-\infty < \xi < \infty$ must in general impose far-field and initial conditions to solve PDE system.
- Recall from the spatially uniform case that if $r^* < 1$ disease dies out, whereas if $r^* > 1$ epidemic occurs.

7.2.2 Travelling waves

$$\frac{\partial u}{\partial \tau} = -r^* uv, \quad \frac{\partial v}{\partial \tau} = r^* uv - v + v_{\xi\xi}, \quad \frac{\partial w}{\partial \tau} = v, \tag{54}$$

- Motivated by observation that diseases such as rabies often spread as waves of infection, seek travelling-wave solutions to (54):

$$u(\xi,\tau) = f(z), \quad v(\xi,\tau) = g(z), \quad w(\xi,\tau) = h(z), \quad z = \xi - c\tau.$$

- This leads to a system of ODEs

$$\begin{aligned} cf'(z) - r^* f(z)g(z) &= 0, \\ g''(z) + cg'(z) + r^* f(z)g(z) - g(z) &= 0, \\ ch'(z) + g(z) &= 0, \end{aligned}$$

to be solved subject to

$$\begin{array}{llll} f(z) \to 1 & g(z) \to 0 & h(z) \to 0 & \text{as } z \to +\infty, \\ f(z) \to a & g(z) \to 0 & h(z) \to b & \text{as } z \to -\infty. \end{array}$$

- Unknown constants a and b represent fractions of susceptible and dead foxes in population far behind infection wave. With our scalings, $a + b = 1$.

Solving the travelling wave equations

- Dead foxes h decouple from rest of model so can just consider system for f and g (obtain h afterwards if necessary).

$$cf'(z) - r^* f(z)g(z) = 0, \tag{55}$$

$$g''(z) + cg'(z) + r^* f(z)g(z) - g(z) = 0, \tag{56}$$

$$\text{with} \quad f(z) \to 1, \quad g(z) \to 0 \quad \text{as } z \to +\infty, \tag{57}$$

$$\text{and} \quad f(z) \to a, \quad g(z) \to 0 \quad \text{as } z \to -\infty. \tag{58}$$

- Substituting for g from (55) in (56), obtain integrable ODE:

$$g''(z) + cg'(z) - \frac{cf'(z)}{r^* f(z)} + cf'(z) = 0$$

$$\Rightarrow \quad g'(z) + cg(z) - \frac{c}{r^*} \log f(z) + cf(z) = c,$$

  where conditions (57) were used to fix constant on the right-hand side.

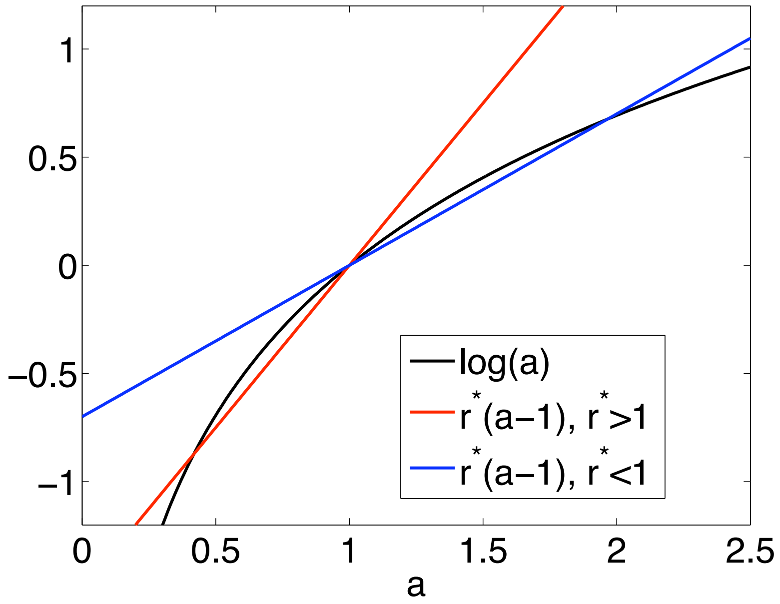
- Conditions (58) must also be satisfied, leading to algebraic relation for surviving susceptible fraction of population after infection has passed:

$$r^*(a-1) = \log a.$$

Can travelling-wave exist?

- Surviving susceptible fraction of population after infection has passed, a, satisfies:

$$r^*(a-1) = \log a, \qquad 0 \le a \le 1. \tag{59}$$



Again case $r^* = 1$ critical.

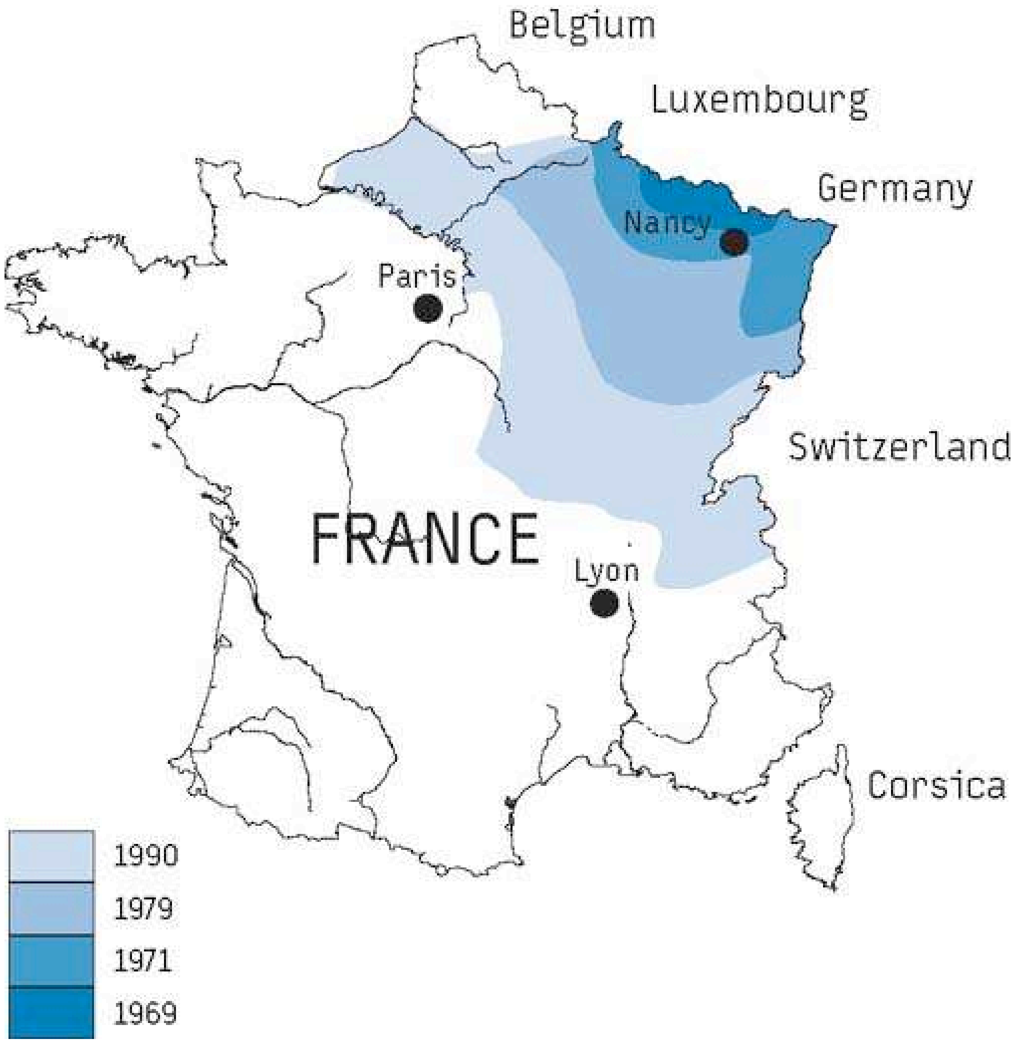
If $r^* = 1$ (59) has only one (repeated) root $a = 1$. In this case eqs (55), (56) plus boundary conditions (57), (58) have the trivial solution $f \equiv 1$, $g \equiv 0$, and so there is no travelling wave.

- For $r^* < 1$ there are two roots, $a = 1$ and $a = a^* > 1$; former root leads to trivial solution above, and latter is not physically relevant (epidemic increases the population with negative deaths $b^* = 1 - a^*$!).
- For $r^* > 1$ there are two roots, $a = 1$ and $a = a^* < 1$. The latter root is physically realistic, and in this case we find a travelling wave of infection, the surviving fraction of the population being given by a^*.
  Bigger $r^* \longrightarrow$ smaller a^*.

7.2.3 Wave of rabies infection in France

FIGURE 2

Situation of the enzootic front of fox rabies in France, 1969-1990



http://www.eurosurveillance.org/em/v10n11/1011-224.asp