APPLIED MATHEMATICS IIIP AND IIIH

Biomathematics

(20% Assignments; 80% Exam)

18 lectures Dr. D.E. Rees

1. Single Species Models

   Density-dependent growth, equilibrium, linearized stability, harvesting and grazing, case study of spruce budworm.

2. Resource Management

   Bioeconomics, bionomic equilibrium, optimal control of fisheries.

3. Multispecies Models

   Phase plane and linearized stability analysis, classical models of predator-prey, competition and symbiosis.

4. Epidemic Models

   Classical General Epidemic model, recurrent epidemics, VD models, case study of European rabies epidemic.

5. Effects of Spatial Diffusion

   Reaction diffusion equations, population waves, critical patch theory, spread of epidemics, pattern formation, morphogenesis.

References:

* N.T.J. Bailey, The Mathematical Theory of Infectious Diseases, Hafner Press, New York, 1975.

* M. Braun, Differential Equations and their Applications, Applied Mathematical Sciences Series, Vol. 15, Springer-Verlag, New York, 1975.

1,2 * C.W. Clark, Mathematical Bioeconomics, Wiley Interscience, 1976.

* P.M. Tuchinsky, Man in Competition with the Spruce Budworm, UMAP Expository Monograph, Birkhäuser, 1981

Plus a selection of recent journal articles.

* Available on closed reserve in Mathematics Library.

Single Species Population Dynamics

Let $x(t)$ = pop^n of species, a continuous function of time.

Intrinsic growth (or instantaneous <u>proportional</u> growth) rate $\quad r \equiv \frac{1}{x}\frac{dx}{dt}$

If only changes in x are due to births & deaths

$$r = b - d$$

<u>Malthusian Growth</u>

$r = $ const. $\quad x(t) = x_0 e^{rt} \quad x(0) = x_0$

<u>Density Dependent Growth</u>

$$r = f(x)$$

Growth in a restricted environment must be eventually limited by shortage of resources.

Competition within pop^n slows growth rate and in our model pop^n will reach a <u>saturation level</u>, or <u>carrying capacity</u> of environment.

$\frac{1}{x}\frac{dx}{dt} = f(x)$ and $f(x)$ decreases as x increases

"Simplest" model $f(x)$ linear in x

$$f(x) = r\left(1 - \frac{x}{K}\right) = r - \frac{rx}{K} \qquad r, K \text{ const.}$$

Logistic "Law"

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right) \qquad K = \text{carrying capacity}$$

Equilibrium

Define an eq$\underset{\sim}{^m}$ soln x^* of

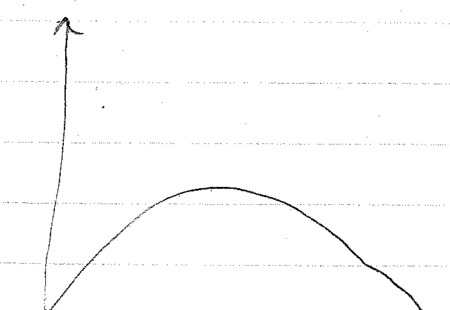
$$\frac{dx}{dt} = xf(x) = F(x) \quad \text{as one where}$$

$\frac{dx}{dt} = 0 \qquad$ Logistic case $\quad F(x) = rx\left(1 - \frac{x}{K}\right) = 0$

$$x^* = 0 \text{ or } K$$

For $0 < x < K \quad \frac{dx}{dt} > 0$

$\qquad x > K \quad \frac{dx}{dt} < 0$



This is a phase-plane sketch giving qualitative idea of time dependence of $x(t)$

$x^* = 0$ is unstable,

$x^* = K$ is stable.

Linearized Stability Analysis

$$\frac{dx}{dt} = F(x) \qquad -① $$

? behaviour of $x(t)$ near eq$^{\underline{m}}$ solution x^* where $F(x^*) = 0$

Let $x(t) = x^* + p(t)$ — ② where $p(t)$ is a perturbation away from eq^m state x^*. We assume $|p(t)|$ is small so that, with ② in ①

$\frac{dx^*}{dt} = 0$

$$\frac{dp}{dt} = F(x^* + p)$$
$$= F(x^*) + F'(x^*)\,p(t) \quad + O(p^2)$$
$$\frac{dp}{dt} \doteqdot F'(x^*)\,p$$

Approx $p(t) \propto e^{\lambda t}$ where $F'(x^*) = \lambda$

If $\lambda < 0$ then p decays in time and remains small

If $\lambda > 0$ p increases with t ie. $|p|$ is not necessarily small

Conclusion: If $F'(x^*) < 0$ eq^m x^* is stable, if $F'(x^*) > 0$ eq^m x^* is unstable.

Logistic case $F(x) = rx\left(1 - \frac{x}{K}\right)$

$F'(x) = r\left(1 - 2x/K\right)$

at $x^* = 0$ $\quad F'(0) = r > 0$ unstable

$x^* = K$ $\quad F'(K) = -r < 0$ stable

Harvesting (Clark p12)

Consider continuous harvesting model. Let $h(t)$ = harvest rate

Unharvested model $\frac{dx}{dt} = F(x)$

With harvesting: $\frac{dx}{dt} = F(x) - h(t)$

Model 1. h = const. Model 2. - Constant Effort

Assume $h = q.E.x$ ie catch/unit effort $\frac{h}{E} \propto x$

(how do we know x?)

Effort E is a rate ~ E (no of vessel days / yr, nets, lines, traps)

q = const of proportionality called catchability coefficient (... ?)

In most cases we set $q = 1$.

Logistic Model

Model 1. $\frac{dx}{dt} = F(x) - h$

$$= rx\left(1 - \frac{x}{K}\right) - h$$

This has 2 equilibrium points

$$x_{1,2} = \frac{1}{2}K\left[1 \mp \sqrt{1 - \frac{4h}{rK}}\right]$$

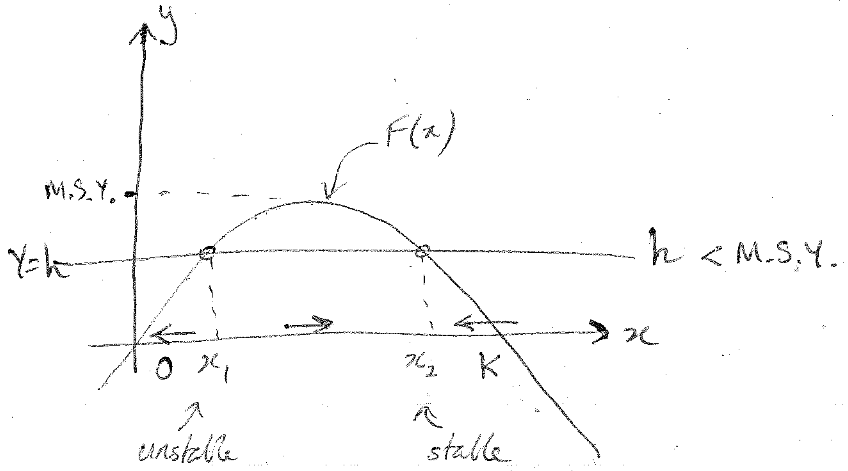
These are real if $h < \frac{rK}{4}$

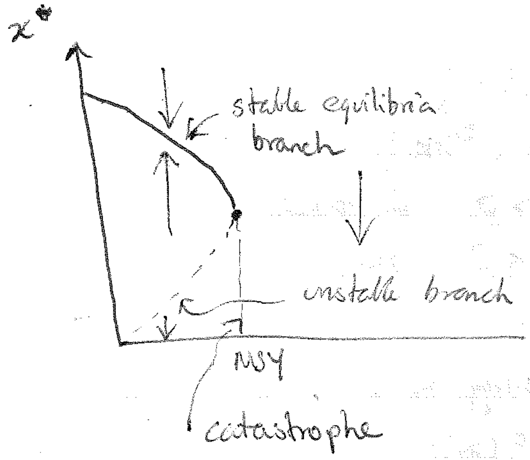
<u>Sustainable yield</u>, Y, is the harvest rate at which the popⁿ is maintained at stable eqᵐ.

Here $Y = h$ as $h = \text{const}$.

<u>Maximum sust yield</u> M.S.Y.

Here $\text{M.S.Y.} = \frac{rK}{4} = \max F(x)$





Equilibrium state x^* as fn of h

Smooth increase in control parameter h leads to a catastrophe

Catastrophe Theory

Write $\frac{dx}{dt} = G(x) = -\frac{\partial V}{\partial x}$

ie. $V = -\int G(x)\,dx$

At equilibrium $\frac{dx}{dt} = 0$ ie $\frac{\partial V}{\partial x} = 0$

$\frac{\partial^2 V}{\partial x^2} = -G'(x)$ For stability / instability? at x^* $G'(x^*) \lessgtr 0$

ie. $\frac{\partial^2 V}{\partial x^2} \gtrless 0$

$V(x)$ is min / max at stable / unstable eqᵐ pt x^*

As $x(t)$ changes in time the function $V(x(t))$ changes

Can think of system as moving on "surface" $V(x)$.

$\frac{dV(x(t))}{dt}$ = rate of change of V as x changes accord to sol^n of D.E.

$$= \frac{\partial V}{\partial x} \cdot \frac{dx}{dt}$$

$$= \frac{\partial V}{\partial x}\left(-\frac{\partial V}{\partial x}\right) = -\left(\frac{\partial V}{\partial x}\right)^2 < 0$$

– flow downhill on $V(x)$

Logistic Model $h = \text{const.}$

$$V = -\int F(x) - h \; dx = -\int rx(1 - x/K) - h$$

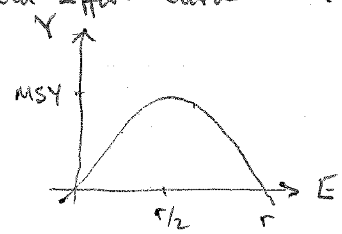
a cubic in x.

Max + Min merged to become a point of inflection at bifurcation point

Logistic Model $h = Ex$

$$\frac{dx}{dt} = rx(1 - x/K) - Ex \qquad x^* = K(1 - E/r) \text{ stable.}$$
$$= 0 \text{ unstable.}$$

Yield-Effort Curve $Y = KE(1 - E/r)$



• sustained yield = harvest rate at x^*

$$Y(E) = Ex^*$$

$$E_{MSY} = r/2 \qquad MSY = \tfrac{1}{4} rK$$

Nonlinear Systems of ODE's

Consider a system

$$\frac{dx}{dt} = f(x,y) \qquad \frac{dy}{dt} = g(x,y) \qquad (1)$$

NB time t does not appear explicitly on RHS. In general f, g are Nonlinear functions of x, y

(1) is a system of autonomous nonlinear ODE's

<u>Phase Plane Analysis</u>

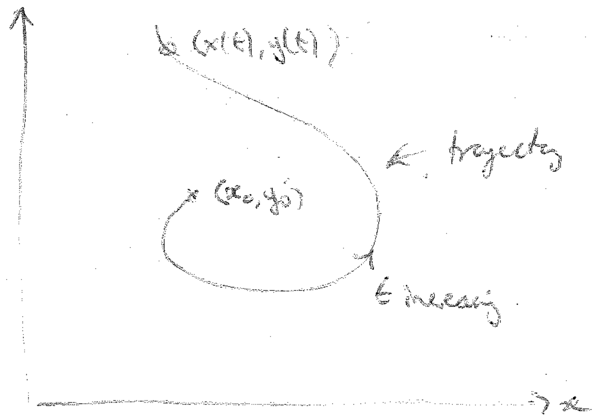
Aim is to solve (1) subject to initial conditions

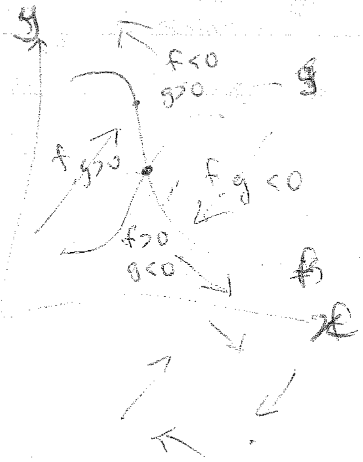
$$x(0) = x_0 \qquad y(0) = y_0$$

to get $x = x(t)$, $y = y(t)$. However explicit form of $x(t)$ + $y(t)$ is not usualy considered in following.

$(x(t), y(t))$ can be plotted on the xy plane – <u>the phase plane</u>

The <u>locus</u> traced by (x,y) as t varies is the phase path or trajectory of the system. Any pt (x,y) on locus is a state of system





From ① $\quad \dfrac{dy}{dx} = \dfrac{\dot y}{\dot x} = \dfrac{g(x,y)}{f(x,y)}$ ②

This is DE for the trajectory

Equilibrium States:

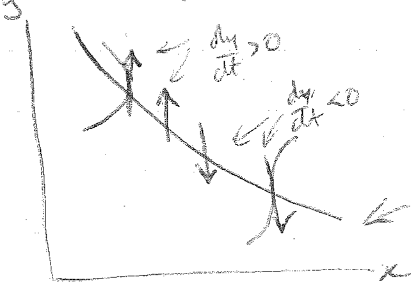
An equilibrium state (x_e, y_e) is one where

$$\frac{dx}{dt} = 0 \quad \text{and} \quad \frac{dy}{dt} = 0$$

i.e. $f(x_e, y_e) = g(x_e, y_e) = 0$ ③

Phase Path Construction

Isoclines: The curve $f(x,y) = 0$ (i.e. $y = g(x)$ defined implicitly) is the locus of pts on the xy plane where $\frac{dx}{dt} = 0$



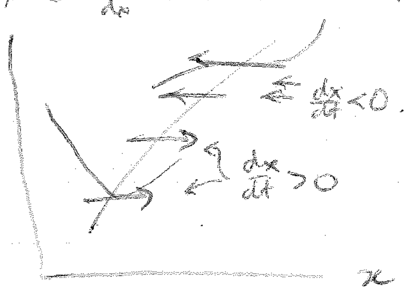
On $f(x,y) = 0$

$\frac{dy}{dx}$ is infinite

i.e. trajectory is vertical as it crosses $f(x,y) = 0$.

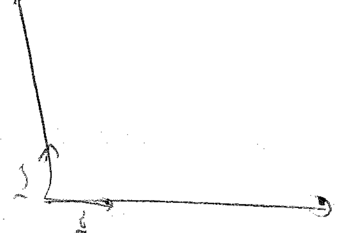
The curve $g(x,y) = 0$ is locus of pts on xy plane where $\frac{dy}{dt} = 0$

On $g(x,y) = 0$ $\frac{dy}{dx}$ is zero i.e. trajectory is horizontal as it crosses $g(x,y) = 0$



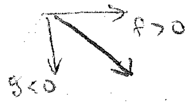
Vector (f, g) $\{ \equiv f\underline{i} + g\underline{j} \}$

indicates direction of trajectory at x, y



eg. (i) $\dot{x} = f > 0 \quad \dot{y} = g > 0$

(ii) $\dot{x} = f > 0 \quad \dot{y} = g < 0$



It is possible to obtain a qualitative solution in phase plane from the direction field composed of such arrows

eg. $\frac{dx}{dt} = y \qquad \frac{dy}{dt} = -x$

Isoclines $\dot{x} = 0 \Rightarrow y = 0$ is a vertical crossing isocline. Direction of flow is governed by $\frac{dy}{dt}$ $\quad \frac{dy}{dt} > 0 \Rightarrow \uparrow$ if $x < 0$

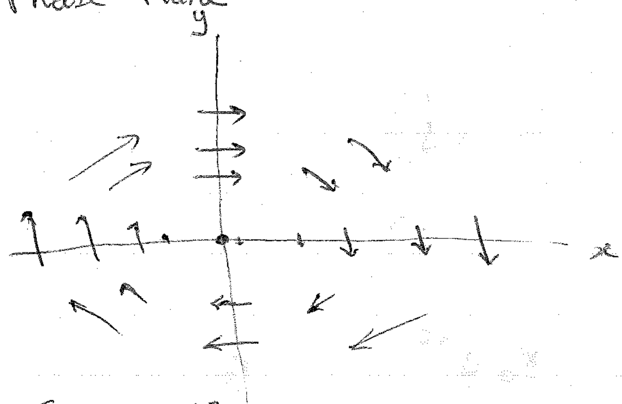
$< 0 \Rightarrow \downarrow$ if $x > 0$

$\dot{y} = 0 \Rightarrow x = 0$ is horiz cross. isocline

Flow: $\frac{dx}{dt} > 0 \Rightarrow \longrightarrow$ if $y > 0$

$< 0 \Rightarrow \longleftarrow$ if $y < 0$

Phase Plane



At other pts

$x > 0, y > 0 \quad \frac{dx}{dt} > 0$

$\frac{dy}{dt} < 0$

Exact sol$^{\underline{n}}$

$\frac{dy}{dx} = -\frac{x}{y} \qquad x\,dx + y\,dy = 0$

$x^2 + y^2 = \text{const.}$

Linearized Stability Analysis

Suppose that the model of 2-species ecosystem

$\frac{dx}{dt} = f(x,y) \qquad \frac{dy}{dt} = g(x,y)$

has an eq^{n} state (x_e, y_e) $\qquad f(x_e, y_e) = g(x_e, y_e) = 0$

intersectn of ~~two~~-isoclines

Consider a small perturbation so

$$x = x_e + p(t) \qquad — \ (2)$$
$$y = y_e + q(t)$$

Put (1) in (2) & expand to 1st order in p, q

$$\frac{dx}{dt} = \frac{dp}{dt} = f(x_e+p, y_e+q)$$

$$= f(x_e, y_e) + f_x(x_e, y_e)\,p + f_y(x_e, y_e)\,q$$

$$\frac{dy}{dt} = \frac{dq}{dt} = g(x_e, y_e) + g_x(x_e, y_e)\,p + g_y(x_e, y_e)\,q$$

Then to first order in p, q we have the linear system

$$\frac{dp}{dt} = f_x p + f_y q$$

$$\frac{dq}{dt} = g_x p + g_y q$$

{ f_x, f_y, g_x, g_y are evaluated at (x_e, y_e) }

Stability of (x_e, y_e) depends on solution of this system

Properties of Linear System of ODE's

For notational convenience we study

$$\frac{dx}{dt} = ax + by$$

$$\frac{dy}{dt} = cx + dy \quad \leftarrow \text{const.}$$

In matrix notation

Let $\underline{\underline{A}} = \begin{pmatrix} a & b \\ c & d \end{pmatrix}$, $\underset{\sim}{x} = \begin{pmatrix} x \\ y \end{pmatrix}$

Then (1) becomes

$$\frac{d\underset{\sim}{x}}{dt} = \underline{\underline{A}}\,\underset{\sim}{x} \quad \ldots (2)$$

Try sol^n of form $\underset{\sim}{x} = \underset{\sim}{x}_0 e^{\lambda t}$ $\qquad \underset{\sim}{x}_0$ is const. vector

In (2) we get $\underset{\sim}{x}_0 \lambda e^{\lambda t} = \underline{\underline{A}}\,\underset{\sim}{x}_0 e^{\lambda t}$

$\therefore$ λ, $\underset{\sim}{x}_0$ must satisfy

$$\underline{\underline{A}}\,\underset{\sim}{x}_0 = \lambda \underset{\sim}{x}_0 \quad \ldots (3)$$

Non-trivial sol^{ns} (ie $\underset{\sim}{x}_0 \neq \underline{0}$) exist only for certain λ

$$(\underline{\underline{A}} - \lambda \underline{\underline{1}})\,\underset{\sim}{x}_0 = 0$$

eg. relevant λ's are eigenvalues of $\underline{\underline{A}}$ satisfying

$$|\underline{\underline{A}} - \lambda \underline{\underline{1}}| = 0 \qquad (4)$$

$$\begin{vmatrix} a-\lambda & b \\ c & d-\lambda \end{vmatrix} = 0 \qquad \lambda^2 - (a+d)\lambda + (ad-bc) = 0$$

Let $p = a+d \qquad q = ad - bc$

$\Delta = p^2 - 4q$ (discriminant)

Soln of 5 $\qquad \lambda_{1,2} = \frac{1}{2}(p \pm \sqrt{\Delta})$

Consider the case $\lambda_1 \neq \lambda_2$ ie $\Delta \neq 0$

For each eigenvalue λ_i $(i = 1,2)$ there is a correspondly solution $\underset{\sim}{x}_i$ of eqn $\underline{A}\,\underset{\sim}{x}_0 = \lambda \underset{\sim}{x}_0$ write $\underline{A}\,\underset{\sim}{x}_i = \lambda_i \underset{\sim}{x}_i$

$\underset{\sim}{x}_i$ is eigenvector ie. $\underset{\sim}{x}_i e^{\lambda_i t}$ $i = 1,2$ are solutions of system ①

& General soln is a linear combn

$$\boxed{\underset{\sim}{x} = \sum_{i=1}^{2} c_i \underset{\sim}{x}_i e^{\lambda_i t}}$$

If $\underset{\sim}{x}_i = \begin{pmatrix} r_i \\ s_i \end{pmatrix}$ then $x = c_1 r_1 e^{\lambda_1 t} + c_2 r_2 e^{\lambda_2 t}$

$y = c_1 s_1 e^{\lambda_1 t} + c_2 s_2 e^{\lambda_2 t}$

eg. $\dfrac{dx}{dt} = -4x + 3y$

$\dfrac{dy}{dt} = -2x + y$ $\qquad \underline{A} = \begin{pmatrix} -4 & 3 \\ -2 & 1 \end{pmatrix}$

$(-4-\lambda)(1-\lambda) - (3)(-2) = 0$

$\lambda^2 + 3\lambda + 2 = 0 \quad = (\lambda+2)(\lambda+1) = 0$

$\lambda_1 = -1, \quad \lambda_2 = -2$

Eigenvector for λ_1

$\underline{A}\,\underset{\sim}{x}_1 = \lambda_1 \underset{\sim}{x}_1 \qquad$ Let $\underset{\sim}{x}_1 = \begin{pmatrix} r_1 \\ s_1 \end{pmatrix}$

$$\begin{pmatrix} -4 & 3 \\ -2 & 1 \end{pmatrix}\begin{pmatrix} r_1 \\ s_1 \end{pmatrix} = -\begin{pmatrix} r_1 \\ s_1 \end{pmatrix}$$

Show $-3r_1 + 3s_1 = 0, \quad -2r_1 + 2s_1 = 0$

$\Rightarrow r_1 = s_1 \qquad \underset{\sim}{x}_1 = r_1 \begin{pmatrix} 1 \\ 1 \end{pmatrix}$ where

r_1 is arbitrary

W.l.o.g. let $r_1 = 1 \qquad \underset{\sim}{x}_1 = \begin{pmatrix} 1 \\ 1 \end{pmatrix}$

Similarly $\underset{\sim}{x}_2 = \frac{r_2}{3}\begin{pmatrix} 3 \\ 2 \end{pmatrix} \qquad$ w.l.o.g. $\underset{\sim}{x}_2 = \begin{pmatrix} 3 \\ 2 \end{pmatrix}$

G.S. is, $\underset{\sim}{x} = \begin{pmatrix} x \\ y \end{pmatrix} = c_1 \begin{pmatrix} 1 \\ 1 \end{pmatrix} e^{-t} + c_2 \begin{pmatrix} 3 \\ 2 \end{pmatrix} e^{-2t}$

$x = c_1 e^{-t} + 3c_2 e^{-2t}$

$y = c_1 e^{-t} + 2c_2 e^{-2t}$

Classification of Solutions in Phase Plane

$$\underset{\sim}{x} = \sum_{i=1}^{2} c_i \underset{\sim}{x}_i e^{\lambda_i t}$$

$$\frac{d\underset{\sim}{x}}{dt} = \sum_{i=1}^{2} c_i \lambda_i \underset{\sim}{x}_i e^{\lambda_i t}$$

$$\frac{dy}{dx} = \frac{dy/dt}{dx/dt}$$

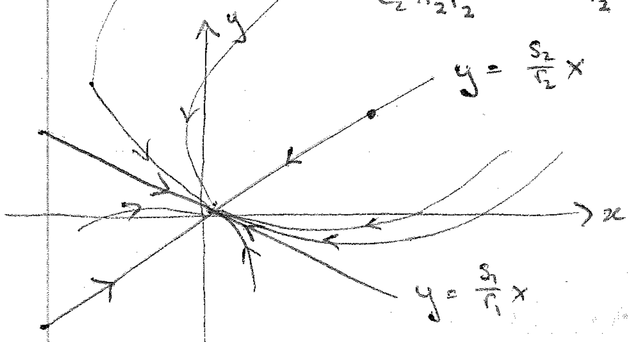
$$= \frac{c_1\lambda_1 s_1 e^{\lambda_1 t} + c_2\lambda_2 s_2 e^{\lambda_2 t}}{c_1\lambda_1 r_1 e^{\lambda_1 t} + c_2\lambda_2 r_2 e^{\lambda_2 t}}$$

i) λ_1, λ_2 real, same sign, $\lambda_1 \neq \lambda_2$ NODE

Suppose $\lambda_2 < \lambda_1 < 0$

Now $$\frac{dy}{dx} = \frac{c_1\lambda_1 s_1 + c_2\lambda_2 s_2 e^{-(\lambda_1-\lambda_2)t}}{c_1\lambda_1 r_1 + c_2\lambda_2 r_2 e^{-(\lambda_1-\lambda_2)t}}$$

Solutions for which $c_1 = 0$ approach origin at $t \to \infty$ along line which has d.e. $\frac{dy}{dx} = \frac{c_2\lambda_2 s_2}{c_2\lambda_2 r_2} = \frac{s_2}{r_2}$ ie. along line $y = \frac{s_2}{r_2}x$



Solution for which $c_2 = 0$ approach origin along line $y = \frac{s_1}{r_1}x$

If $c_1 \neq 0, c_2 \neq 0$

$$\lim_{t\to\infty} \frac{dy}{dx} = \frac{s_1}{r_1}$$

$$\lim_{t\to-\infty} \frac{dy}{dx} = \frac{s_2}{r_2}$$

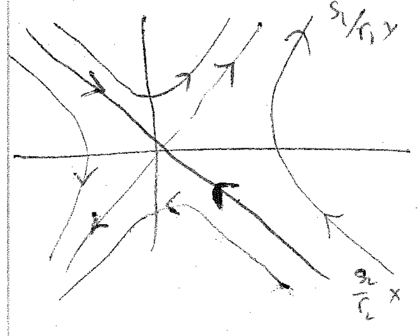
Thus when $\lambda_1 < 0$ & $\lambda_2 < 0$ (real), the flow is always back to $(0,0)$ ie. $(0,0)$ is a STABLE NODE.

If $\lambda > 0$ flows in opposite direction. ie. $(0,0)$ is an UNSTABLE NODE.

ii) λ_1, λ_2 real, opposite sign SADDLE PT

eg. $\lambda_1 > 0$ $\lambda_2 < 0$

Exercise: Show for $c_1 = 0$ solutions move towards origin along $y = \frac{s_2}{r_2}x$. Solutions with $c_2 = 0$ leave origin along $y = \frac{s_1}{r_1}x$



$$\lim_{t\to\infty} \frac{dy}{dx} = \frac{s_1}{r_1}x$$

$$\lim_{t\to-\infty} \frac{dy}{dx} = \frac{s_2}{r_2}x$$

ASYMPTOTES are SEPARATRICES

(iii) λ_1, λ_2 complex conjugates

$$\lambda_1 = \alpha + i\beta \qquad \lambda_2 = \alpha - i\beta$$

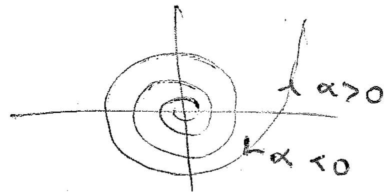
We can show

$$x = C e^{\alpha t} \cos(\beta t + \gamma)$$

$$y = C K e^{\alpha t} \cos(\beta t + \gamma + \delta)$$

Eq^n $(0,0)$ is a $\left.\begin{matrix}\text{STABLE} \\ \text{UNSTABLE}\end{matrix}\right\}$ FOCUS

if $Re(\lambda_i) = \alpha < 0$
$\qquad\qquad\qquad > 0$



or the other way.

Multispecies Models

$x(t)$, $y(t)$ interacting species populations

$$\frac{dx}{dt} = f(x,y)$$

$$\frac{dy}{dt} = g(x,y)$$

Classification of Interaction

(i) Predator - prey $(+,-)$, $(-,+)$

Here existence of one species (prey) enhances other (predator), pred. obviously has -ve effect on prey

(2) Competition $(-,-)$

Each species is detrimental to the other

(3) Symbiosis (mutualism) $(+,+)$

Each species enhances the other

Predator - Prey Model

x = prey $\quad \dfrac{dx}{dt} = ax - bxy$

y = predator $\quad \dfrac{dy}{dt} = -cy + dxy$

$$\dot{p} = (a - by)p - bxq$$

$$\dot{q} = (-c + dx)q + dyp$$

$x = c/d \quad y = a/b$

$$\dot{p} = -\frac{bc}{d} q$$

$$\dot{q} = +\frac{ab}{d} p$$

$$\begin{vmatrix} -\lambda & -\frac{bc}{d} \\ \frac{ad}{b} & -\lambda \end{vmatrix}$$

$$\lambda^2 + \frac{ab^2c}{d^2} = 0$$

$$\lambda = \pm i \sqrt{ac}$$

Centre

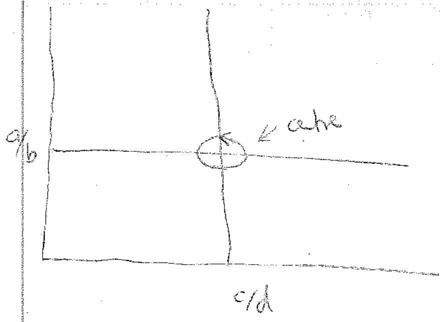
$x = 0 \quad y = 0$

$$\dot{p} = ap$$

$$\dot{q} = -cq.$$

$$\begin{vmatrix} a - \lambda & 0 \\ 0 & -c-\lambda \end{vmatrix}$$

$\lambda = a \quad \lambda = -c$



Linearized analysis indicates that eq^n $(\frac{c}{d}, \frac{a}{b})$ is neutrally stable.

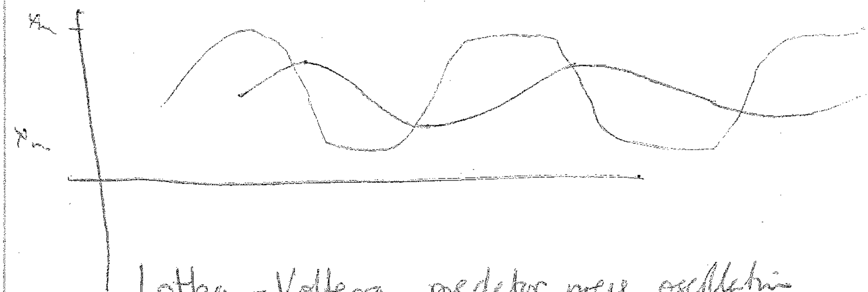
To decide once & for all about nature of $(\frac{c}{d}, \frac{a}{b})$ we need to study the full non-linear system

One can show that the non-linear system has closed trajectories

Pop^n of Predator & Prey are periodic around eq^n $(\frac{c}{d}, \frac{a}{b})$

N.B. trajectories never get there.

$\Rightarrow$ y_{min} at x_e, y_e at x_{max}, y_{max} at x_e, y_e at x_{min}



Lotka-Volterra predator prey oscillation

Increase in predator (sharks) lags behind increase in prey (fish)

Average population

For prey $\frac{1}{x}\frac{dx}{dt} = a - by$

We want $\bar{x} = \frac{1}{T}\int_{t_1}^{T+t_1} x \, dt$ $\quad \bar{y} = \frac{1}{T}\int_{t_1}^{t_1+T} y \, dt$

$$\frac{1}{x}dx = a\,dt - by\,dt$$

$$\cancel{\frac{1}{T}\int_{x(t_1)}^{x(T+t_1)} \frac{1}{x}\,dx} = \frac{1}{T}\int_{t_1}^{t_1+T} a\,dt - b\int_{t_1}^{t_1+T} y\,dt$$

$$0 = a - b\bar{y}$$

$\bar{y} = a/b$ Similarly $\bar{x} = c/d$

Regardless of trajectory

$$(\bar{x}, \bar{y}) = (x_e, y_e) = (c/d, a/b)$$

<u>Volterra's Principle</u>

Suppose we harvest at constant effort E with catchability coeff'nts q_1 & q_2 for x & y resp.

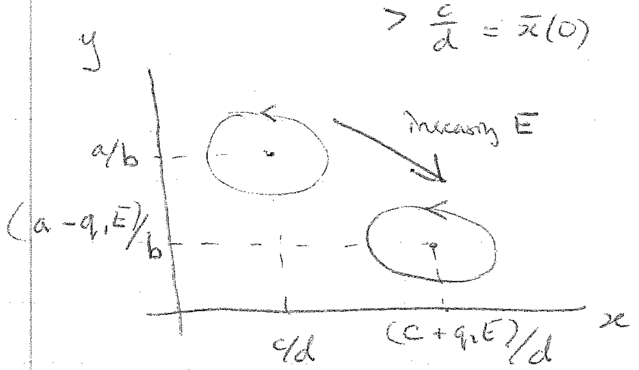
Prey : $\frac{dx}{dt} = x(a-by) - q_1 E x \quad = x\left((a - q_1 E) - by \right)$

Predator : $\frac{dy}{dt} = y(-c+dx) - q_2 E y \quad = y\left(-(c + q_2 E) + dx \right)$

Provided $q_1 E < a$, the new system has same structure as old & equilibrium or average population

$$\bar{x}(E) = \frac{c + q_2 E}{d} \qquad \bar{y}(E) = \frac{a - q_1 E}{b}$$

$$> \frac{c}{d} = \bar{x}(0) \qquad\qquad < \frac{a}{b} = \bar{y}(0)$$



~~$\frac{d\bar{x}}{dt} = 0$~~ Turn Plus

Competition Models (Gause 1935)

Two species ecosystem in which both species ~~compete~~ exploit the same resource. Let x, y be pop^ns & suppose in isolation each grows logistically

If $y = 0$ $\qquad \frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right)$

If $x = 0$ $\qquad \frac{dy}{dt} = sy\left(1 - \frac{y}{L}\right)$

When $x \neq 0$ & $y \neq 0$ the species interact so as to reduce each other's growth rate

We assume
$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right) - \alpha x y$$
$$\frac{dy}{dt} = sy\left(1 - \frac{y}{L}\right) - \beta x y$$

α, β are taken as positive constants which govern the degree of niche overlap. The species may occupy the same geographical region but not compete for same food - then $\alpha = 0, \beta = 0$.

If y exploits common resource more efficiently than x then $\alpha \gg \beta$.

Qualitative Analysis in Phase Plane

Isoclines: (i) $\dot{x} = 0$ (vertical crossing)

$$x = 0 \quad \text{or} \quad y = \frac{r}{\alpha}\left(1 - \frac{x}{K}\right)$$

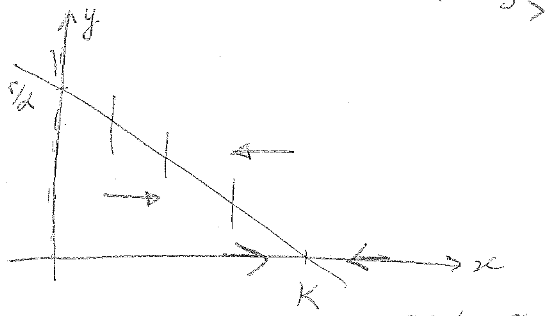
(ii) $\dot{y} = 0$ (horizontal crossing)

$$y = 0 \quad \text{or} \quad x = \frac{s}{\beta}\left(1 - \frac{y}{L}\right)$$

Plots. (i) on $x=0$ $\quad \dot{y} \gtrless 0$ if $y \lessgtr L$

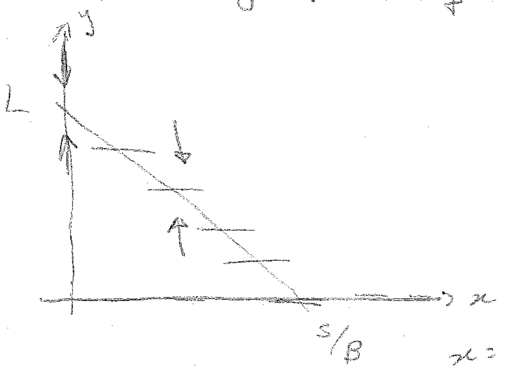
(ii) on $y=0$ $\quad \dot{x} \gtrless 0$ if $x \lessgtr K$

(iii) $\dot{x} \gtrless 0$ if $y \lessgtr r/\alpha\,(1 - x/K)$



$y = r/\alpha\,(1 - x/K)$

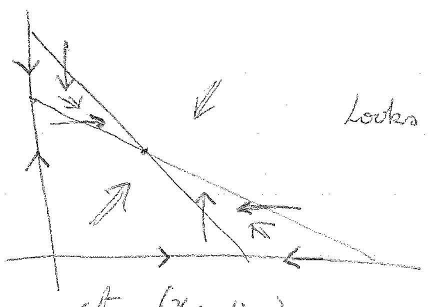
(iv) $\dot{y} \gtrless 0$ if $x \lessgtr \frac{s}{\beta}(1 - y/L)$



$x = s/\beta\,(1 - y/L)$

Competitive Co-existence

If $r/\alpha > L$ & $s/\beta > K$ then isoclines intersect at eq^m pt (x_e, y_e)



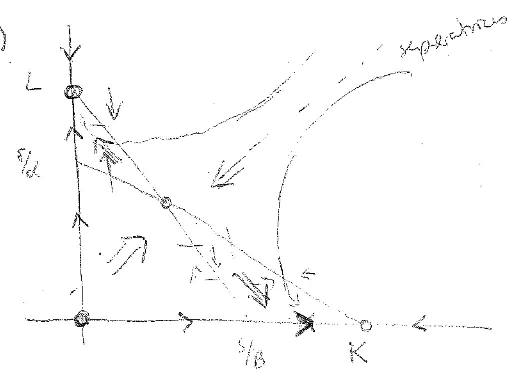
Looks like a stable node

i.e. regardless of initial state the system will end up asymptotically at (x_e, y_e)

2 species co-exist stably

Principle of Competitive Exclusion

If $r/\alpha < L$ & $s/\beta < K$ the isoclines intersect at non-zero (x_e, y_e)



Qualitatively (x_e, y_e) appears to be a saddle point while $(0, L)$ and $(K, 0)$ appear to be stable nodes. $(0,0)$ is unstable node.

Only one species survives, which one depends on critical conditions

Epidemic Models

Bailey "Math. Theory of Infectious Diseases"

Simple Epidemic Model With No Removals

i) Disease is assumed to be transmitted by contact between an infected individual (infective) + a susceptible individual

ii) There is no incubation period i.e. disease is instantaneously transmitted upon contact, the newly infected individual is immediately infectious.

iii) All susceptibles are equally susceptible; all infected are equally infectious

iv) Total pop^n is fixed

Let n = total size of community

x = no. of susceptibles at t

y = no. of infectives at t.

No removal from circulation by death, recovery or isolation

Assume that pop^n is subject to homogeneous mixing such that in Δt the no. of new infectives Δy is

$$\Delta y = \beta x y \Delta t \qquad \beta \text{ is contact rate}$$

$$\boxed{\frac{dy}{dt} = \beta x y}$$, We assume β = constant

$$\boxed{x} \xrightarrow{\beta} \boxed{y}$$

Since $x + y = n$ const.

$$\boxed{\frac{dx}{dt} = -\beta x y}$$

Ex. Show that $x = \dfrac{n(n-1)}{(n-1) + e^{n\beta t}}$ given $x = n-1$ at $t=0$

i.e. initially $y = 1$

Hence show $y = \dfrac{n}{1 + (n-1)e^{-n\beta t}}$

$\lim_{t \to \infty} y = n$ all sick

Classical General Epidemic Model

Let n = community size = const.

x = susceptibles

y = infectives

z = removals

Removals are individuals who have recovered & are immune & are no longer carriers or they may be quarantined or dead

All that is needed is that z's be unavailable to spread infection

Let γ = removal rate

Assume γ = constant

$$\boxed{x} \xrightarrow{\beta} \boxed{y} \xrightarrow{\gamma} \boxed{z}$$

$$\frac{dx}{dt} = -\beta xy$$

$$\frac{dy}{dt} = \beta xy - \gamma y \qquad x+y+z = n \text{ const.}$$

$$\frac{dz}{dt} = \gamma y$$

Define relative removal rate $\rho = \gamma/\beta$

Then $\frac{dx}{dt} = -\beta xy$

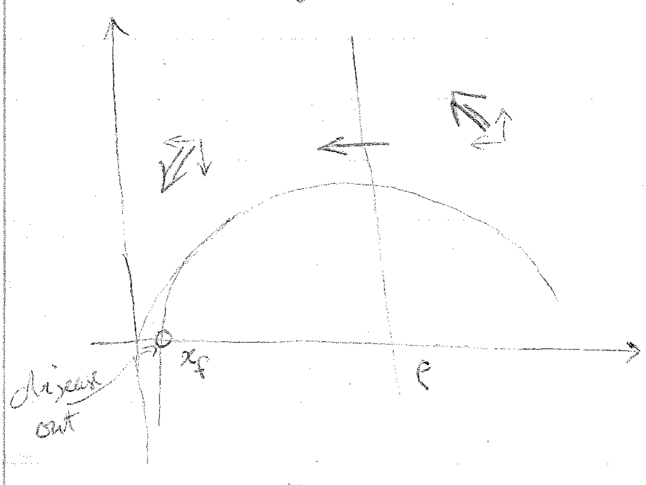
$$\frac{dy}{dt} = \beta y(x-\rho)$$

Phase Plane Analysis

$\forall\ x, y > 0 \qquad \frac{dx}{dt} < 0$ so $\leftarrow$

$\frac{dy}{dt} \gtrless 0 \quad \uparrow\downarrow$ if $x \gtrless \rho$

Isoclines $\dot{y} = 0$ (horiz. cross) on $x = \rho$



Ex: Show that $y = y_0 + x_0 - x + \rho \ln\left(\frac{x}{x_0}\right)$

$\lim_{x \to 0} y = -\infty$

so $y = 0$ at x_f with $0 < x_f < \rho < x_0$

x_f = final population when disease has died out

Threshold behaviour

An epidemic (in the sense of an increase in no. of infectious) occurs only if the no. of susceptibles exceeds the threshold ρ.

V.D. Models

Criss - Cross Epidemic Process

For V.D. infections postulate 2 interacting populations.

n males ♂

n females ♀

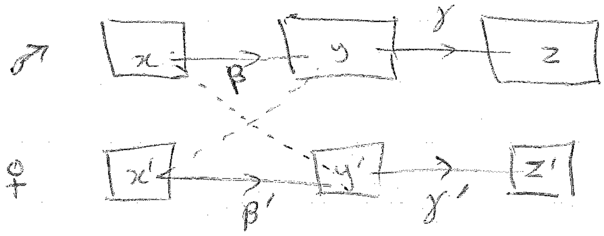
Let no. of susceptible, infectives & removals in each group be

(x, y, z) ♂

(x', y', z') ♀

$$\left.\begin{aligned} x+y+z &= n \\ x'+y'+z' &= n' \end{aligned}\right\} \text{const.}$$

Homogeneous mixing with uniform, promiscuous heterosexual behaviour.
No incubation period



Male x is infected by female y' : female x' is infected by male y . β, β' contact rate . γ, γ' are removal rates

♂		♀	
$\frac{dx}{dt} = -\beta x y'$	(1)	$\frac{dx'}{dt} = -\beta' x' y$	(1')
$\frac{dy}{dt} = \beta x y' - \gamma y$	(2)	$\frac{dy'}{dt} = \beta' x' y - \gamma' y'$	(2')
$\frac{dz}{dt} = \gamma y$	(3)	$\frac{dz'}{dt} = \gamma' y'$	(3')

Suppose at $t=0$ $(x_0, y_0, 0)$ ♂
$(x_0', y_0', 0)$ ♀

(1) ÷ (3')

$$\frac{dx}{dt} \Big/ \frac{dz'}{dt} = \frac{-\beta x y'}{\gamma' y'} = -\frac{\beta}{\gamma'} x$$

Integrate by separation

$$-\ln\left(\frac{x}{x_0}\right) = \frac{\beta z'}{\gamma'} \qquad (4)$$

Similarly $$-\ln\left(\frac{x'}{x_0'}\right) = \frac{\beta' z}{\gamma} \qquad (5)$$

Def^n: The intensity of an epidemic that is triggered by the initial nos. of infectives y_0, y_0' is defined as proportion i, i' who finally contract the disease.

ie. $\lim_{t\to\infty} (x,y,z) = (n(1-i), 0, ni)$

$$(x', y', z') = (n'(1-i'), 0, n'i')$$

Let $t \to \infty$ in ④

$$-\ln\left(\frac{n(1-i)}{x_0}\right) = \frac{\beta n' i'}{\gamma'}$$

$$-\ln(1-i) = \frac{\beta}{\gamma'} n' i' + \ln\left(\frac{n}{x_0}\right)$$

Assume initially $y_0 \ll n$ ie. $x_0 \approx n$ $\therefore \ln\left(\frac{n}{x_0}\right) \sim 0$

Then $-\ln(1-i) \approx \frac{\beta}{\gamma'} n' i'$ — ⑥

Similarly $y_0' \ll n'$

$$-\ln(1-i') \approx \frac{\beta'}{\gamma} n i \quad — ⑦$$

⑥ × ⑦ $\frac{\beta\beta' n n' i i'}{\gamma\gamma'} \approx \{\ln(1-i)\}\{\ln(1-i')\}$

$$\approx \left(i + \frac{i^2}{2} + \dots\right)\left(i' + \frac{i'^2}{2} + \dots\right)$$

$$\approx i i' + \frac{1}{2} i i'(i + i') + \dots$$

$$\frac{\beta\beta' n n'}{\gamma\gamma'} \approx 1 + \frac{1}{2}(i + i') \quad ⑧$$

Let $\rho = \gamma/\beta$ $\quad \rho' = \gamma'/\beta'$ $\qquad \frac{n n'}{\rho\rho'} - 1 \approx \frac{1}{2}(i + i')$

As $i, i' > 0$ $\;nn' > \rho\rho'$ for an epidemic joint threshold cstn

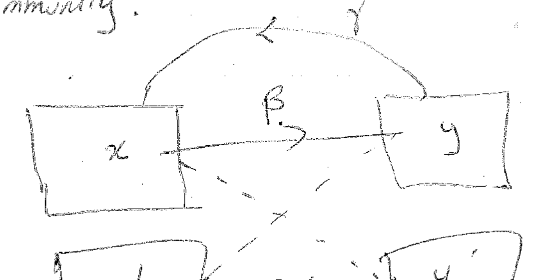
Criss-Cross Infection Without Immunity

x, y susc. & infective ♂

x', y' " ♀

We suppose that once an individual has left the class of infectives then she/he returns to susceptibles class.

$\nexists$ immunity.



β, β' contact rates , γ, γ' recovery rates

$$\frac{dx}{dt} = -\beta x y' + \gamma y \qquad \frac{dx'}{dt} = -\beta' x' y + \gamma' y'$$

$$\frac{dy}{dt} = +\beta x y' - \gamma y \quad (1) \qquad \frac{dy'}{dt} = +\beta' x' y - \gamma' y' \quad (2)$$

$$x + y = n \qquad x' + y' = n'$$

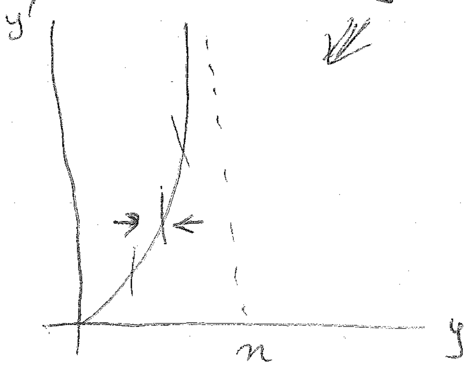
Take $\dfrac{dy}{dt} = \beta(n-y)y' - \gamma y = \beta(n-y)\left[y' - \dfrac{ey}{n-y}\right] \quad e = \gamma/\beta \quad (3)$

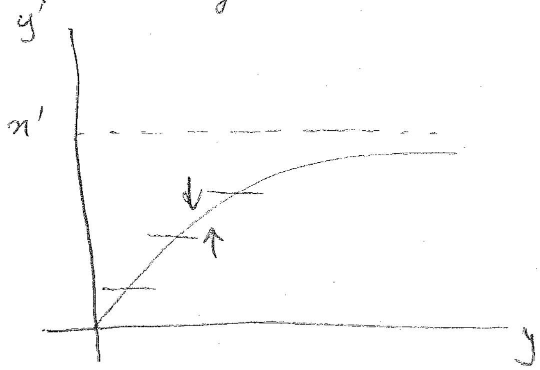
$$\frac{dy'}{dt} = \beta'(n'-y')\left[y - \frac{e'y'}{n'-y'}\right] \quad e' = \gamma'/\beta' \quad (4)$$

$\dfrac{dy}{dt} = f(y, y') \quad \dfrac{dy'}{dt} = g(y, y')$

Since $y \le n$ & $y' \le n'$ the isoclines of interest are

$\dot{y} = 0 \Rightarrow y' = \dfrac{ey}{n-y} \qquad \dot{y}' = 0 \Rightarrow y = \dfrac{e'y'}{n'-y'}$





Flows : $\dot{y} \gtrless 0 \rightleftarrows$ if $y' \gtrless \dfrac{ey}{n-y}$

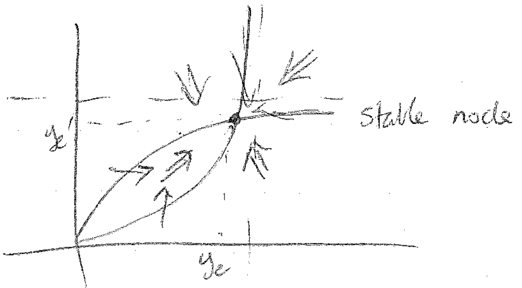
$\dot{y}' \gtrless 0 \uparrow\downarrow$ if $y \gtrless \dfrac{e'y'}{n'-y'}$

$Eq^{\underline{m}}$ occurs at intersection of isoclines

$$y_e' = \frac{e y_e}{n - y_e}, \quad y_e = \frac{e' y_e'}{n' - y_e'}$$

One possibility $(y_e, y_e') = (0, 0)$

Hence we have possibility of non-zero $eq^{\underline{m}}$ if $nn' > ee'$

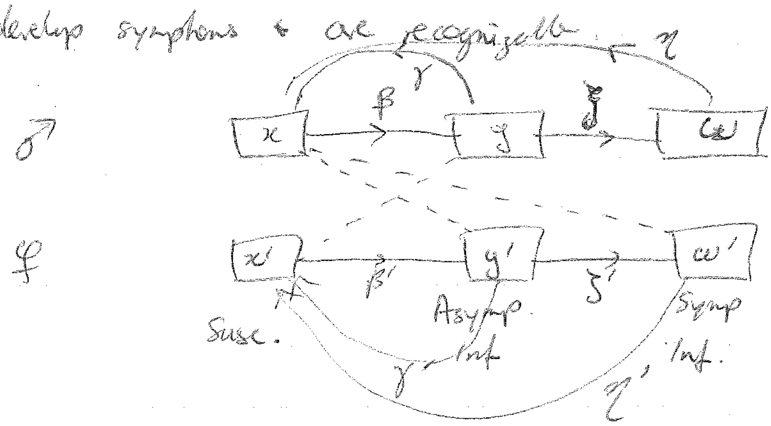


For fixed n, n' endemic state can be shifted towards origin by increasing the relative recovery rates ρ, ρ'.

If $\rho\rho' > nn'$ then $y_e < 0$ $y_e' < 0$ &
$(0,0)$ is stable state

Allowance for Asymptomatic Infectives.

Suppose recognizable infectives continue to circulate, though they may undergo some degree of treatment & return to susceptible class at a different rate (probably faster) than untreated asymptomatic infectives (who show no symptoms). Assume asymptomatics are never recognized, but return directly to susc. class; the rest develop symptoms & are recognizable.

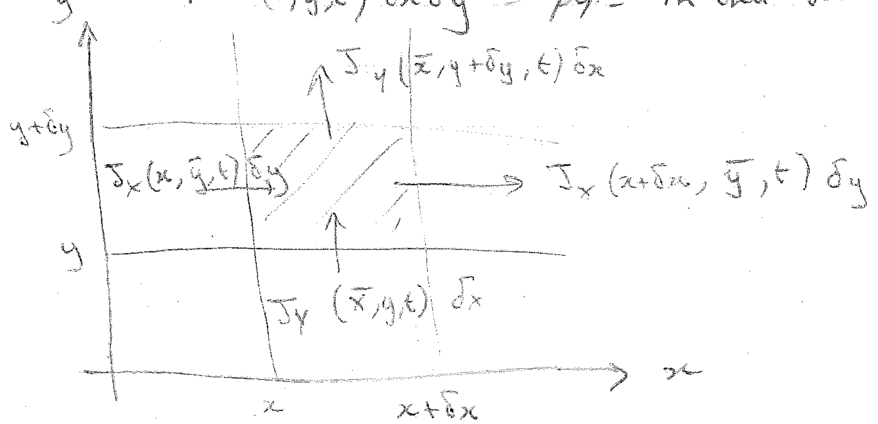


Single Species Growth in Spatial Dispersal

Pop^n growth in space & time

Consider a species dispersing on the xy plane. At time t let $S(x,y,t)$ be the pop^n density at (x,y).

ie. $S(x,y,t)\,\delta x\,\delta y$ = pop^n in area $\delta x \times \delta y$



Let $J_x(x,y,t)$ = pop^n flux in the x direction at (x,y) at time t

Let $F(S)$ = rate of growth of pop^n – in general density dependent (eg. Logistic)

In absence of diffusion

$$\frac{\partial S}{\partial t} = F(S) \quad \text{as before.}$$

Consider now the growth in the rectangle, accounting for fluxes in and out

$$\frac{\partial S}{\partial t}\,\delta x\,\delta y = \text{rate of growth of pop}^n \text{ in } \delta x\,\delta y$$

$$= F(S)\,\delta x\,\delta y + \left[J_x(x,\bar{y},t) - J_x(x+\delta x,\bar{y},t)\right]\delta y + \left[J_y(\bar{x},y,t) - J_y(\bar{x},y+\delta y,t)\right]\delta x.$$

Divide by $\delta x\,\delta y$ take limit in 1st order x, y

$$\frac{\partial S}{\partial t} = F(S) - \frac{\partial}{\partial x}J_x - \frac{\partial}{\partial y}J_y \qquad (1)$$

$$\nabla \cdot \underset{\sim}{J} + \frac{\partial S}{\partial t} = F(S)$$

Fick's Law of Diffusion

One of simplest models of diffusion is based on Fick's phenomenological law of molecular diffusion in solutions.

Pop^n Flux $\propto$ − Gradient of pop^n density

$$J_x = -K\frac{\partial S}{\partial x} \qquad J_y = -K\frac{\partial S}{\partial y} \qquad K \text{ is } \text{scalar} \text{ for isotropic diffusion.}$$

$$\boxed{\underset{\sim}{J} = -K\nabla S} \qquad K = \text{coeff. of diffusivity} \qquad (2)$$

−ve sign indicates pop^n tends to disperse from high density towards low density regions.

$$\boxed{\frac{\partial S}{\partial t} = F(S) + K\nabla^2 S} \qquad (3)$$

Critical Patch Theory

Consider a species growing in a favourable habitat surrounded by a hostile environment

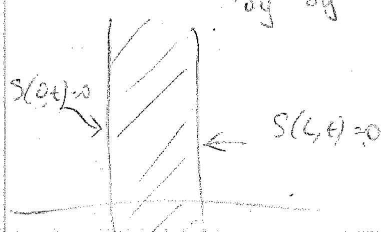
KISS - model (Kierstead, Slobodkin & Skellam)

One-dimensional dispersal & Malthusian growth.

Growth occurs in a strip $0 \le x \le L$, $-\infty < y < \infty$ with net flows only in the x-direction

i.e. $\frac{\partial}{\partial y}J_y = 0 = \frac{\partial^2 S}{\partial y^2}$ & $F(S) = rS$

$r = \text{const.}$



$$\frac{\partial S}{\partial t} = rS + K\frac{\partial^2 S}{\partial x^2} \qquad B.C.'s \quad S(0,t) = S(L,t) = 0$$

Initial conditions

Suppose $S(x,0) = f(x)$

Using separation of variables verify that

$$S(x,t) = \sum_{n=1}^{\infty} A_n \sin\left(\frac{n\pi x}{L}\right) e^{\lambda_n t} \qquad \lambda_n = r - \frac{K n^2 \pi^2}{L^2}$$

$$= r\left(1 - n^2\left(\frac{L_c}{L}\right)^2\right)$$

$$L_c = \pi\left(\frac{K}{r}\right)^{1/2}$$

If $L < L_c$ $\lambda_n < 0$ for all n

Then $\lim_{t\to\infty} S(x,t) = 0$

Thus $L_c = \pi\left(\frac{K}{r}\right)^{1/2}$ is the critical patch size for pop^n survival since

if $L > L_c$ at least one λ_n is > 0

$\lim_{t\to\infty} S(x,t) = \infty$

Consider the logistic model with one-dimensional dispersal

$$\frac{\partial S}{\partial t} = K\frac{\partial^2 S}{\partial x^2} + rS\left(1 - \frac{S}{K}\right)$$

B.C.'s $S(-\frac{L}{2},t) = S(+\frac{L}{2},t) = 0$ — totally hostile

Non-dimensionalize problem. Let $u = S/K$, $\tau = rt$

$X = x\left(\frac{r}{K}\right)^{1/2}$, $\ell = L\left(\frac{r}{K}\right)^{1/2}$

Then problem becomes

$$\frac{\partial u}{\partial \tau} = \frac{\partial^2 u}{\partial X^2} + u(1-u)$$

B.C. $u(-\frac{\ell}{2},\tau) = u(+\frac{\ell}{2},\tau) = 0$

Avoid time dependent problem, seek a steady state sol^n

$u(X,\tau) = v(X)$

i.e. $\frac{d^2 v}{dX^2} + v(1-v) = 0$ — ① $\quad v(-\frac{\ell}{2}) = v(\frac{\ell}{2}) = 0$ — ②

We want a solution where $v(X) > 0$ in $-\frac{\ell}{2} < X < \frac{\ell}{2}$.

Then since $v = 0$ at $-\ell/2$ and $\ell/2$ v must attain a maximum in $-\ell/2 < X < \ell/2$. Let this be at $X = a$

Then $0 < v(X) \le v(a) = \mu$ $\quad (v_{max} = \mu)$

Also $v'(a) = 0$

$v''(a) < 0$

In ① $v''(a) = -v(a)(1-v(a))$

$= -\mu(1-\mu) < 0$ by ③.

$\mu(1-\mu) > 0$ ie. $0 < \mu < 1$

Recall $u(X,t) = \dfrac{S(x,t)}{K}$

$S_{\text{steady state}} < K \quad \forall x.$

Soln of D.E. for v

$$\frac{d^2v}{dX^2} + v(1-v) = 0 \qquad \text{Let } v' = \frac{dv}{dX}$$

$$\frac{d}{dv}\left(\tfrac{1}{2}v'^2\right) + v(1-v) = 0.$$

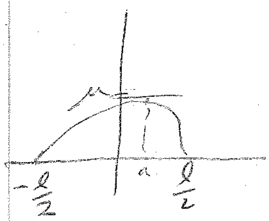
Let $F(v) = \int_0^v v(1-v)\,dv = \frac{1}{2}v^2 - \frac{1}{3}v^3$

Then $\dfrac{d}{dv}\left\{\tfrac{1}{2}v'^2 + F(v)\right\} = 0$

$$\tfrac{1}{2}v'^2 + F(v) = \text{const.}$$

But at $X = a \quad v = \mu,\ v' = 0 \quad \therefore\ 0 + F(\mu) = \text{const.}$

$$\therefore\ v'^2 = 2\left[F(\mu) - F(v)\right]$$



Then $v' = +\sqrt{2}\sqrt{F(\mu) - F(v)} \qquad -\frac{l}{2} \le X < a$

$= -\sqrt{2}\sqrt{F(\mu) - F(v)} \qquad a < X \le l/2$

For $X < a$ separate variables.

$$\frac{dv}{\sqrt{F(\mu) - F(v)}} = \sqrt{2}\,dX$$

Integrate from X to a. $(X < a)$

$$\int_{v(X)}^{\mu} \frac{dv}{\sqrt{F(\mu) - F(v)}} = \sqrt{2}\int_X^a dX = \sqrt{2}(a - X) \qquad ④$$

For $X > a$ show

$$\int_{v(X)}^{\mu} \frac{dv}{\sqrt{F(\mu) - F(v)}} = \sqrt{2}(X - a) \qquad ⑤$$

Apply BCs at $X = -l/2 \quad v(X) = 0$

Put $X = -l/2$ in ④.

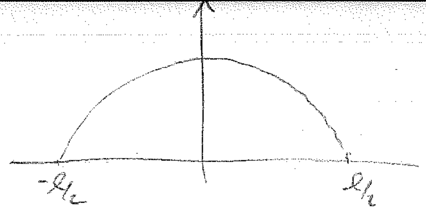
$$\int_0^{\mu} \frac{dv}{\sqrt{F(\mu) - F(v)}} = \sqrt{2}\left(a + \frac{l}{2}\right) \qquad ⑥a$$

At $X = +l/2 \quad v(x) = 0 \quad$ Put $X = +l/2$ in ⑤.

$$\int^{\mu} \frac{dv}{\ldots} = \sqrt{2}\left(\frac{l}{\ldots}\right.\ldots \qquad (6\ldots$$

(6) $\therefore\ a + \frac{l}{2} = \frac{l}{2} - a$

$\therefore\ a = 0$



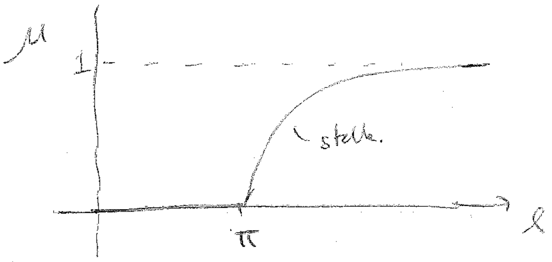
From 6a or 6b

$$l = \sqrt{2}\int_0^{\mu} \frac{dz}{\sqrt{F(\mu) - F(z)}} \qquad F(z) = \tfrac{1}{2}z^2 - \tfrac{1}{3}z^3$$

Let $z = w\mu$ and show

$$l = 2\sqrt{3}\int_0^1 \frac{dw}{\sqrt{3(1-w^2) - 2\mu(1-w^3)}} = h(\mu)$$

We have an implicit relation between the strip width l & max of $v = \mu$



For what values of l do we get $\mu > 0$

Properties of $h(\mu)$

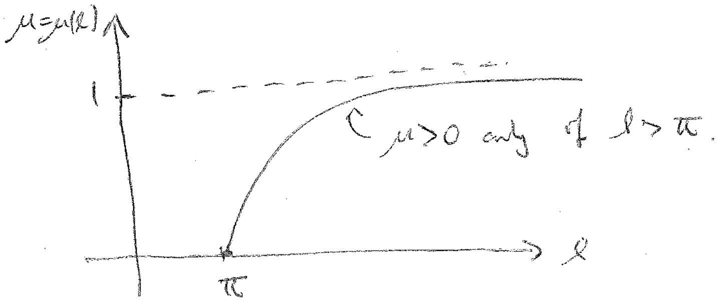
(i) $\frac{dh}{d\mu} > 0$ in $0 < \mu < 1$

h is incr. fn of μ.

(ii) $h(\mu) \to \infty$ as $\mu \to 1$

(iii) $h(\mu) \to \pi$ as $\mu \to 0$

$\left[h(0) = 2\sqrt{3}\int_0^1 \frac{dw}{\sqrt{3(1-w^2)}} = \left[2\sin^{-1} w\right]_0^1 = \pi \right.$



Thus to get a positive steady state solution for $v(X)$ or equivalently a positive value for the max of $v(X)$ (ie. $\mu > 0$) we must have a patch size $l > \pi$

Critical patch size is $l_c = \pi$ or in terms of original x dimensions. $l_c = L_c\left(\frac{r}{K}\right)^{1/2} = \pi$

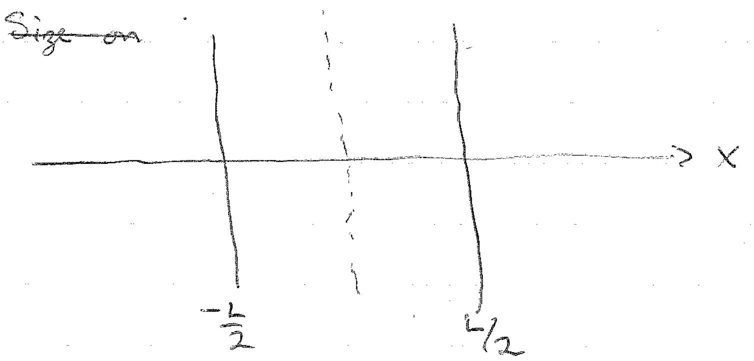
$$L_c = \pi\left(\frac{K}{r}\right)^{1/2}$$

This is same critical patch size as obtained with the linear model $F(S) = rS$.

this is a "linearization" of $F(S) = rS(1 - S/K)$

Dependence of Critical Patch Size on Exterior Conditions.

~~Size on~~



Suppose species can venture into the region $|X| > L/2$ survive, and return to $|X| < \frac{L}{2}$.

In $|X| < \frac{L}{2}$ let $\quad \dfrac{\partial S}{\partial t} = K_i \dfrac{\partial^2 S}{\partial x^2} + r_i S(1 - S/K)$

In $|X| > \frac{L}{2}$ let $\quad \dfrac{\partial S}{\partial t} = K_o \dfrac{\partial^2 S}{\partial x^2} - r_o S$

i (inside patch), o (outside patch)

r_o = net mortality rate outside. In absence of diffusion species dies out in $|X| > L/2$

Assume S is continuous, across the boundaries and also that there are no sources or sinks of animals at the boundaries.

ie. we have continuity of animal flux.

At $\frac{L}{2}$ $\quad \displaystyle\lim_{x \to L/2^-} S(x,t) = \lim_{x \to \frac{L}{2}^+} S(x,t)$

$$S_i\left(\tfrac{L}{2}, t\right) = S_o\left(\tfrac{L}{2}, t\right)$$

$$\lim_{x \to \frac{L}{2}^-} \left(K \frac{\partial S}{\partial x}\right) = \lim_{x \to \frac{L}{2}^+} \left(K \frac{\partial S}{\partial x}\right)$$

$$K_i \frac{\partial S_i}{\partial x}\left(\tfrac{L}{2}, t\right) = K_o \frac{\partial S_o}{\partial x}\left(\tfrac{L}{2}, t\right)$$

What is critical L_c for a positive steady state solution in $|X| < \frac{L}{2}$?

Non-dimensionalizing the eq^{n}s.

$\tau = r_i t \qquad X = \left(\dfrac{r_i}{K_i}\right)^{1/2} x \qquad l = \left(\dfrac{r_i}{K_i}\right)^{1/2} L \qquad u = \dfrac{S}{K}$

Eq^{n}s are

$$\frac{\partial u}{\partial \tau} = \frac{\partial^2 u}{\partial X^2} + u(1-u) \qquad |X| < l/2$$

$$\frac{\partial u}{\partial \tau} = D \frac{\partial^2 u}{\partial X^2} - \rho u \qquad |X| > l/2 \qquad D = \frac{K_o}{K_i} \qquad \rho = \frac{r_o}{r_i}$$

$$u_i(\pm \tfrac{l}{2}, \tau) = u_o(\pm \tfrac{l}{2}, \tau)$$

$$\frac{\partial u_i}{\partial X}(\pm \tfrac{l}{2}, \tau) = D \frac{\partial u_o}{\partial X}(\pm \tfrac{l}{2}, \tau)$$

For the patch to be a refuge for the species we want a positive steady state solution

$$u(X, \tau) = v(X)$$

ie. we want positive $v(X)$ to be soln of

$$\frac{d^2 v}{dX^2} + v(1-v) = 0 \qquad |X| < l/2 \qquad ①$$

$$D \frac{d^2 v}{dX^2} - \rho v = 0 \qquad |X| > l/2 \qquad ②$$

$$v_i(\pm \tfrac{l}{2}) = v_o(\pm \tfrac{l}{2}) \quad ③ \qquad \frac{dv_i}{dX}(\pm \tfrac{l}{2}) = D \frac{dv_o}{dX}(\pm \tfrac{l}{2}) \quad ④$$

Consider 2, a 2^{nd} order ODE with const coeffs.

Try $v \propto e^{\lambda X}$

$$D\lambda^2 - \rho = 0 \qquad \lambda = \pm\sqrt{\frac{\rho}{D}}$$

General Soln $v(X) = Ce^{+\sqrt{\frac{\rho}{D}}X} + C^* e^{-\sqrt{\frac{\rho}{D}}X}$

For region $X < -l/2$ require $C^* = 0$ for bounded solution

" $X > +l/2$ " $C = 0$ "

Now $v_i'(-\tfrac{l}{2}) = D v_o'(-l/2) = D\sqrt{\frac{\rho}{D}}\, v_o(-\tfrac{l}{2})$ $\quad$ fr ④

and $v_i(-\tfrac{l}{2}) = v_o(-l/2)$ $\quad$ fr ③

$$\therefore \boxed{v_i'(-\tfrac{l}{2}) = \sqrt{\rho D}\, v_i(-l/2)}$$

Similarly $\boxed{v_i'(+\tfrac{l}{2}) = -\sqrt{\rho D}\, v_i(+\tfrac{l}{2})}$

Problem now is $v'' + v(1-v) = 0$ subject to $v'(+\tfrac{l}{2}) = -\sqrt{\rho D}\, v(\tfrac{l}{2})$

$v'(-\tfrac{l}{2}) = +\sqrt{\rho D}\, v(-\tfrac{l}{2})$

Let $\gamma = \sqrt{\rho D} = \left(\frac{K_o r_o}{K_i r_i}\right)^{1/2}$ $\quad$ Fix K_o, K_i, r_i

Then $\gamma \propto r_o^{1/2}$

r_o = net death rate outside $\quad$ γ is measure of external hostility

If we write BC's as

$$v(\pm \tfrac{l}{2}) = \mp \frac{1}{\gamma} v'(\pm \tfrac{l}{2})$$

ie. $\lim_{r_o \to \infty} RHS = 0$

ie. when outside is infinitely hostile we recover the original zero boundary conditions

To get critical l we consider the linearized problem

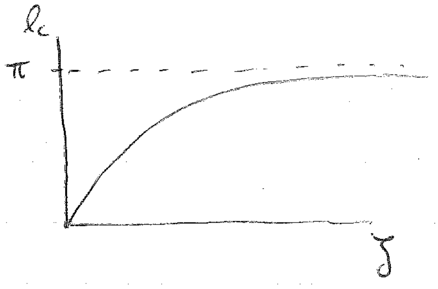
$$v'' + v = 0 \qquad v'(\pm \tfrac{l}{2}) = \mp \gamma v(\pm \tfrac{l}{2})$$

G.S. $\quad v = a\cos X + b\sin X$

$\quad v' = -a\sin X + b\cos X$

Apply B.C.'s and show for a non trivial a, b

$$\gamma = \tan \frac{l_c}{2}$$



In general $l_c < \pi$ ie. the critical patch size is reduced as species can survive outside (with difficulty)

Examinable Stuff

Up to but excluding logistic diffusion problem