DUBLIN INSTITUTE OF TECHNOLOGY KEVIN STREET, DUBLIN 8

Taught Master in Applied Mathematics and Theoretical Physics

Exam 2010

Introduction to Biomathematics

Answer any FOUR Questions

Dept. of Education Tables allowed

Question 1. Consider the following population growth model:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = \frac{rN}{\alpha} \left[1 - \left(\frac{N}{K} \right)^{\alpha} \right],\tag{1}$$

with r > 0, $\alpha > 0$, K > 0 and N(0) > 0.

(i) Analyze the steady states of the model for stability. What is the limit of N(t) when $t \to \infty$?

[7 marks]

(ii) Consider the limit $\alpha \to 0$ in the equation (1). Write the obtained model equation and solve it explicitly for N(t). Compute $\lim_{t\to\infty} N(t)$ for your solution.

[11 marks]

(iii) Prove that (1) does not have any periodic solutions.

[7 marks]

Question 2. (i) Show that an exact travelling wave solution exists for the Fisher-Kolmogorofftype equation

$$\frac{\partial u}{\partial t} = u(1 - u^q) + \frac{\partial^2 u}{\partial x^2},\tag{2}$$

where q > 0. by looking for solutions in the form

$$u(x,t) = U(z) = \frac{1}{(1 + ae^{bz})^s}, \qquad z = x - ct,$$
 (3)

where c > 0 is the wavespeed and b and s are positive constants. Determine the unique values for c, b and s in terms of q. Choose a value for a such that U(0) = 1/2.

[20 marks]

(ii) Take for simplicity q=1 and sketch the solution (3). Explain briefly the relevance of (2) in modelling population dynamics and the meaning of the solution (3) in particular.

[5 marks]

Question 3. The frequency p_n of the allele A of a gene in the n-th generation satisfies the equation of a selection model

$$p_{n+1} = rac{w_{AA}p_n^2 + w_{Aa}p_nq_n}{w_{AA}p_n^2 + 2w_{Aa}p_nq_n + w_{aa}q_n^2}$$

where $q_n = 1 - p_n$ is the frequency of the other allele a of the same gene and w_{AA} , w_{Aa} and w_{aa} are constant positive coefficients called *relative fitness* of the corresponding genotype.

(i) Determine all steady states, their existence and stability in dependence on w_{AA} , w_{Aa} and w_{aa} (assume that these are all different from each other).

[20 marks]

(ii) Explain the biological meaning of the case $w_{AA} = w_{Aa} = w_{aa}$.

[5 marks]

Question 4. Consider the discrete population model

$$N_{t+1} = \frac{rN_t}{1 + bN_t^2} \equiv f(N_t),$$

where t is the discrete time and r and b are positive parameters.

(i) Show that after a long time the population is bounded by

$$N_{\min} = \frac{2r^2}{(4+r^2)\sqrt{b}} \le N_t \le \frac{r}{2\sqrt{b}}$$

[5 marks]

(ii) Determine the steady states and their eigenvalues and hence show that r=1 is a bifurcation value.

[5 marks]

(iii) What do r and b represent in this model? Prove that, for any r, the population will become extinct if b > 4.

[5 marks]

(iv) Consider a delay version of the model, given by

$$N_{t+1} = \frac{rN_t}{1 + bN_{t-1}^2} \equiv f(N_t), \qquad r > 1.$$

Investigate the linear stability about the positive steady state N^* by setting $N_t = N^* + n_t$. Show that the linearized equation is

$$n_{t+1} - n_t + 2\frac{r-1}{r}n_{t-1} = 0. (4)$$

[5 marks]

(v) Show that r=2 is a bifurcation value for (4) and that as $r\to 2$ the steady state bifurcates to a periodic solution of period 6.

[5 marks]

Question 5. A predator-pray interaction is described by the following system of non-dimensional variables

$$\frac{\mathrm{d}u}{\mathrm{d}t} = a\left(u(1-u) - \frac{uv}{1+bu}\right),$$

$$\frac{\mathrm{d}v}{\mathrm{d}t} = v\left(\frac{bu}{1+bu} - c\right)$$

where a, b and c < 1 are positive parameters (Rosenzweig-MacArthur model).

(i) Determine the steady states and the parameter values for which they are biologically relevant.

[5 marks]

(ii) Investigate their stability if $\frac{c}{1-c} < b < \frac{1+c}{1-c}$ and sketch the phase plane trajectories,

[15 marks]

(iii) Explain briefly how the phase plane trajectories will change if $b > \frac{1+c}{1-c}$.

[5 marks]

Question 6. Consider the 'SIR' epidemic model with S(t), I(t) and R(t) as the number of individuals of the three classes: susceptibles, infectives and the removed class correspondingly. The model is described by the system

$$\begin{array}{rcl} \frac{\mathrm{d}S}{\mathrm{d}t} &=& -rSI, \\ \frac{\mathrm{d}I}{\mathrm{d}t} &=& rSI-aI, \\ \frac{\mathrm{d}R}{\mathrm{d}t} &=& aI, \end{array}$$

where r > 0 is the infection rate and a > 0 is the removal rate of infectives. The initial data is $S(0) = S_0 > \rho$, $(\rho = a/r)$, $I(0) = I_0 > 0$, R(0) = 0.

(i) Show that if $S_0 > \rho$ there is an epidemic outbreak.

[3 marks]

(ii) Prove that S(t) + I(t) + R(t) = N = constant. What is the meaning of the constant N?

[2 marks]

(iii) Demonstrate that R(t) satisfies the equation

$$\frac{dR}{dt} = a(N - R - S_0 e^{-R/\rho}), \qquad R(0) = 0.$$
 (5)

[5 marks]

(iv) Show that when R/ρ is small, (5) can be approximated with

$$\frac{dR}{dt} = a \left[N - S_0 + \left(\frac{S_0}{\rho} - 1 \right) R - \frac{S_0 R^2}{2\rho^2} \right], \qquad R(0) = 0.$$
 (6)

[5 marks]

(v) Without solving (6), find $R(\infty) = \lim_{t\to\infty} R(t)$. To this end look at the steady states of this equation. Explain the meaning of $R(\infty)$.

[5 marks]

(vi) Sketch the phase portrait of the system using I (vertical) and S (horizontal) coordinates.

[5 marks]

END OF PAPER

(i) The steady states are N*=0 and N*=K at the zeros of

$$f(N) = \frac{rN}{\alpha} \left[1 - \left(\frac{N}{K} \right)^{\alpha} \right]$$

$$f'(N) = \frac{r}{\alpha} \left[1 - \left(\frac{N}{K} \right)^{\alpha} \right] = \frac{rN}{\alpha} \frac{\alpha N^{\alpha - 1}}{K^{\alpha}}$$

$$f'(0) = \frac{r}{\alpha} > 0 \qquad \Longrightarrow N* = 0 \text{ is an } \underline{\text{unstable}} \text{ steady state.}$$

$$f'(K) = \frac{r}{\alpha} (1 - \alpha - 1)$$

$$= -r < 0 \qquad \Longrightarrow N* = K \text{ is a } \underline{\text{stable}} \text{ steady state.}$$

$$\Longrightarrow \lim_{t \to 0} N(t) = K$$

(ii) The L'Hospital's rule gives

$$\begin{split} &\lim_{\alpha \to 0} \frac{rN}{\alpha} \left[1 - \left(\frac{N}{K} \right)^{\alpha} \right] \\ &= rN \left[\frac{\frac{\partial}{\partial \mathbf{q}} \left(1 - \left(\frac{N}{K} \right)^{\alpha} \right)}{\frac{\partial}{\partial \mathbf{q}} \left(\alpha \right)} \right] \\ &= rN \left[\frac{-\left(\frac{N}{K} \right)^{\alpha} \ln \frac{N}{K}}{1} \right] \\ &= -rN \ln \frac{N}{K} \end{split}$$

The equation is:

$$\frac{dN}{dt} = -rN\ln\frac{N}{K}$$

$$\frac{1}{N}\frac{dN}{dt} = -r\ln\left(\frac{N}{K}\right)$$

$$\frac{d}{dt}\ln\left(\frac{N}{K}\right) = -r\ln\left(\frac{N}{K}\right)$$

$$\ln\frac{N}{K} = ce^{-rt}$$

$$\ln\frac{N(0)}{K} = ce^{-rt}$$

$$c = \ln\left[\frac{N(0)}{K}\right]$$

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$$N(t) = K \exp\left[\ln \frac{N(0)}{K} e^{-rt}\right]$$

$$\lim_{t \to \infty} N(t) = K \exp\left[\ln \frac{N(0)}{K} \cdot 0\right]$$

$$= Ke^{0}$$

$$= K \quad \text{as in (i)}$$

(iii) Suppose that the equation has a periodic solution with period T, i.e. N(t+T)=N(T). Then we consider the integral

$$\int_{t}^{t+T} \left(\frac{dN}{dt}^{2}\right) \ dt = \int_{t}^{t+T} f\left(N\right) \frac{dN}{dt} \ dt = \int_{N(t)}^{N(t+T)} f\left(N\right) \ dN = \int_{N(t)}^{N(t)} f\left(N\right) dN = 0$$

But the left-hand integral is positive, since $\left(\frac{dN}{dt}\right)^2$ is not identically zero, so we have a contradiction. So, the simple scalar equation $\frac{dN}{dt} = f(N)$ cannot have periodic solutions.

(i) We notice that the solution $U(z) = (1 + ae^{bz})^{-s}$ automatically satisfies the boundary conditions

$$U(\infty) = 0$$
 and $U(-\infty) = 1$

The corresponding ODE for U(z) is

$$L(U) = U'' + cU' + U(1 - U^q) = 0$$

Since the solution is translational-invariant¹, $z \to z + \text{const}$, then it is clear that a is an arbitrary constant, i.e. b and s should not depend on a. We compute:

$$\begin{split} &U'(z) = -s \frac{abe^{bz}}{(1 + ae^{bz})^{s+1}} \\ &U''(t) = -sb^2 ae^{bt} \left(1 + ae^{bz} \right)^{-s-2} \left(1 - ase^{bz} \right) \\ &L(U) = \frac{1}{(1 + ae^{bz})^{s+2}} \left[a^2 \left(s^2 b^2 - seb + 1 \right) e^{2bz} + \left(2 - scb - sb^2 \right) ae^{bz} + 1 - \left(1 + ae^{bt} \right)^{2-sq} \right] \end{split}$$

We want $L(U) \equiv 0$ for all $z \implies$ all coefficients of e^b, e^{bt} and e^{2bt} must be all 0.

$$\Rightarrow 2 - sq = 0 \qquad ,1 \text{ or } 2$$

$$2 - sq = 0 \qquad \Rightarrow sq = 2$$

$$2 - sq = 1 \qquad \Rightarrow sq = 1$$

$$2 - sq = 2 \qquad \Rightarrow sq = 0 \text{ (not possible since } s > 0, q > 0.)$$

 \implies Two possibilities: $s=\frac{1}{q}$ and $s=\frac{2}{q}$. Let

$$s = \frac{1}{q} \qquad (sq = 1)$$

$$2 - sq = 2 - 1 = 1$$

$$L(U) = (1 + ae^{bz})^{-s-2} \left[a^2 (s^2b^2 - scb + 1) e^{2bz} + (2 - scb - sb^2) ae^{bz} - ae^{bz} \right] \equiv 0$$

$$\implies sb (sb - c) + 1 = 0$$

$$2 - scb - sb^2 - 1 = 0 \qquad \Leftrightarrow 1 = sb (b + c)$$

¹Analogously an operator A on functions is said to be translation invariant with respect to a translation operator T_{δ} if the result after applying A doesn't change if the argument function is translated. More precisely it must hold that $\forall \delta Af = A\left(T_{\delta}f\right)$

$$sb\left(sb-c\right)+sb\left(b+c\right)=0$$

$$sb\left(sb+b\right)=0$$

$$sb^{2}\left(s+1\right)=0$$
 not possible, $s>0$ & $(s+1)>0$

The only remaining possibility is

$$s = \frac{2}{a} \qquad \text{or } sq = 2$$

This leads to

$$s^{2}b^{2} - scb + 1 = 0 \qquad \Longrightarrow sb(c - sb) = 1 \qquad (1)$$

$$2 - scb - sb^{2} = 0 \qquad \Longrightarrow sb(b + c) = 2 \qquad (2)$$

$$(1) \text{ and } (2) \Longrightarrow b + c = 2(c - sb)$$

$$\Longrightarrow c = b(1 + 2s)$$

$$sb[b + b(1 + 2s)] = 2 \qquad \Longrightarrow sb^{2}(2 + 2s) = 2$$

$$\Longrightarrow b = \frac{1}{\sqrt{s(s+1)}} \qquad c = \frac{1 + 2s}{\sqrt{s(s+1)}}$$

But $s = \frac{2}{q} \implies$

$$b = \frac{q}{\sqrt{2(q+2)}}$$

$$c = \frac{q+4}{\sqrt{2(2+q)}}$$

If $U(0) = \frac{1}{2}$,

$$\frac{1}{(1+a)^s} = \frac{1}{2}$$
$$(1+a)^2 = 2$$
$$1+a = 2^{1/s}$$
$$a = 2^{1/s} - 1$$
$$\Rightarrow a = \boxed{2^{q/2} - 1}$$

(ii) When q = 1, the equation is known as "Fisher-Kolmogorov" equation

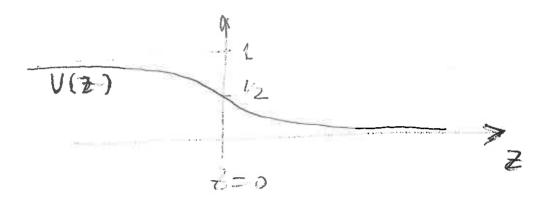
$$S = 2$$
 $b = \frac{1}{\sqrt{6}}$ $c = \frac{5}{\sqrt{6}} \approx 2.04$ $a = \sqrt{2} - 1$
$$U(z) = \frac{1}{\left[1 + (\sqrt{2} - 1)e^{z/\sqrt{6}}\right]^2}$$

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The equation describes 'geographic' spread of population that grows logistically since z=x-ct initially $(t=-\infty)$, $z=\infty$ and $U\left(\infty\right)=0$, there is no population. As it grows it spreads as a travelling wave until it reaches the 'carrying capacity' U=1 i.e $U\left(-\infty\right)=1$ that corresponds to $t=\infty$. The term $\frac{\partial^2 U}{\partial x^2}$ describes the spatial spread of the population (i.e. diffusion).



(i) Let $p_n = p$ be the equilibrium (steady) state, then

$$p = \frac{W_{AA}p^2 + W_{Aa}p(1-p)}{W_{AA}p^2 + 2W_{Aa}p(1-p) + W_{aa}(1-p)^2}$$
 or
$$W_{AA}p^3 + 2W_{Aa}p^2(1-p) + W_{aa}p(1-p)^2 = W_{AA}p^2 + W_{Aa}p(1-p)$$
$$\implies p(1-p)\left[(-W_{AA} + 2W_{Aa} - W_{aa})p + W_{aa} - W_{Aa}\right] = 0$$
$$\implies p_{(0)}^* = 0 \qquad p_{(1)}^* = 1 \qquad p_{(2)}^* = \frac{1}{1 + \frac{W_{AA} - W_{Aa}}{W_{aa} - W_{Aa}}}$$

The last one only exists if

$$\frac{W_{AA} - W_{Aa}}{W_{aa} - W_{Aa}} > 0 \qquad (0 \le p^* \le 1)$$
 if $(W_{aa} - W_{Aa}) (W_{AA} - W_{Aa}) > 0$

There are two possibilities

(a)

$$W_{AA} > W_{Aa}$$
 (homozygate advantageous)

(b)

$$W_{AA} < W_{Aa}$$
 (hetrozygate advantageous)

Denote

$$f(p) = \frac{W_{AA}p^2 + W_{Aa}p(1-p)}{W_{AA}p^2 + 2W_{Aa}p(1-p) + W_{aa}(1-p)^2}$$

$$f'(0) = \frac{W_{Aa}}{W_{aa}} \qquad f(1) = \frac{W_{Aa}}{W_{AA}} \qquad \text{(after some computation)}$$

(a)

$$f'\left(0
ight)<1$$
 $p_{\left(0\right)}^{*}=1$ and $p_{\left(1\right)}^{*}=1$ are stable $p_{\left(2\right)}^{*}$ is an unstable steady state

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(b)

$$f'(0) > 1$$
 $p_{(0)}^* = 1$ and $p_{(1)}^* = 1$ are unstable $p_{(2)}^*$ is an stable steady state

If (a) and (b) are not satisfied, then $p_{(2)}^*$ does not exist. Then only $p_{(0)}^* = 0$ and $p_{(1)}^* = 1$ exist and

(c)

$$W_{aa} < W_{Aa} < W_{AA}$$
 $\implies p_{(0)}^* = 0 \text{ unstable}$ $p_{(1)}^* = 1 \text{ stable}$

(d)

$$W_{AA} < W_{Aa} < W_{aa} \qquad \Longrightarrow p_{(0)}^* = 0 \text{ stable} \qquad p_{(1)}^* = 1 \text{ unstable}$$

(ii) If $W_{aa} = W_{Aa} = W_{AA}$ then $P_{n+1} = P_n = P_0, q_n = q_0$, i.e. if there is no relation and the mating is random the frequencies are unchanged. This is the so-called Hardy-Weinberg equilibrium.

(i)

$$f(N) = \frac{rN}{1 + bN^2}$$

$$f'(N) = \frac{r(1 + bN^2) - rN2bN}{(1 + bN^2)^2}$$

$$= r\frac{1 - bN^2}{(1 + bN^2)^2}$$

$$f'(N) = 0 \text{ if } N = \frac{1}{\sqrt{b}}$$

$$N_{max} = f\left(\frac{1}{\sqrt{b}}\right) = \frac{r}{2\sqrt{b}}$$

$$M_{min} = f\left(M_{max}\right) = \frac{2r^2}{(4 + r^2)\sqrt{b}}$$

(ii) The steady states are
$$N^*=0$$
 and
$$f'=\frac{r}{1+b(N^*)^2}$$

$$r=b\left(N^*\right)^2+f$$

$$N^*=\sqrt{\frac{r-1}{b}}(\text{ exists iff }r>1)$$

$$f'(0)=r \text{ and}$$

$$f'\left(\sqrt{\frac{r-1}{b}}\right)=r\frac{1-(r-1)}{r^2}=\frac{2-r}{r}$$

Bifurcation values:

$$f'(0) = 1 \implies r = 1$$

$$f'\left(\sqrt{\frac{r-1}{b}}\right) = 1 \implies \frac{2-r}{r} = 1 \implies 2-1 \implies r = 1$$
 if $0 < r < 1$, $N^* = 0$ is stable, $N^* = \sqrt{\frac{r-1}{b}}$ unstable if $r > 1$, $N^* = 0$ is unstable, $N^* = \sqrt{\frac{r-1}{b}}$ is stable

(iii) Usually the steady state is $N^* = \text{carrying capacity} = \frac{r-1}{b}$, r clearly has the meaning of a birth rate, and $\rightarrow b \sim \frac{1}{(\text{carrying capacity})^2}$ is a parameter related to the carrying capacity of the model.

The population becomes extinct when $N_{min} < 1$. i.e.

$$\frac{2r^2}{(4+r^2)\sqrt{b}} < 1$$

$$\sqrt{b} > \frac{2r^2}{4+r^2} = 2 - \frac{8}{r^2+4}$$
(3)

if b > 4 then

$$\sqrt{b} = 2 > 2 = \frac{8}{r^2 + 4}$$

and the above condition (3) is satisfied.

(iv)

$$\begin{split} N_t &= \sqrt{\frac{r-1}{b}} + n_t, \qquad n_t \ll 1 \\ N_t \left(1 + bN_t^2\right) &= rN_t \\ \left(\sqrt{\frac{r-1}{b}} + n_{t+1}\right) \left[1 + b\left(\sqrt{\frac{r-1}{b}} + n_{t-1}\right)^2\right] &= r\sqrt{\frac{r-1}{b}} + rn_t \\ \left(\sqrt{\frac{r-1}{b}} + n_{t+1}\right) \left[1 + b\frac{r-1}{b} + b\sqrt{\frac{r-1}{b}}n_{t-1} + bn_t^2 \atop quadratic}\right] &= r\sqrt{\frac{r-1}{b}} + rn_t \\ \left(\sqrt{\frac{r-1}{b}} + n_{t+1}\right) \left(r + 2\sqrt{b(r-1)} \; n_{t-1}\right) &= r\sqrt{\frac{r-1}{b}} + rn_t \\ r\sqrt{\frac{r-1}{b}} + rn_{t+1} + \sqrt{\frac{r-1}{b}} \; 2\sqrt{b(r-1)} \; n_{t-1} + quadratic = r\sqrt{\frac{r-1}{b}} + rn_t \\ rn_{t+1} + 2(r-1)n_{t-1} - rn_t &= 0 \implies n_{t+1} - n_t + 2\frac{r-1}{r}n_{t-1} = 0 \end{split}$$

(v) Looking for solutions $n = n_0 \lambda^t$, we have a characteristic equation

$$\lambda^{2} - \lambda + 2\frac{r-1}{r} = 0$$

$$\lambda_{1,2} = \frac{1 \pm \sqrt{1 - 8\frac{r-1}{r}}}{2},$$
if $r \to 2$, $\lambda_{1,2} = \frac{1 \pm \sqrt{1 - 4}}{2} = \frac{1 \pm i\sqrt{3}}{2}$

$$|\lambda_{1,2}| = \frac{1}{2}|1 \pm i\sqrt{3}|$$

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$$=\frac{1}{2}\sqrt{1^2+(\sqrt{3})^2}=1 \implies r=2 \text{ is a bifurcation value}.$$

$$\lambda_{1,2}=e^{(XX\pi i/3)} \implies n_t=n_0e^{\pi l/3}+\overline{n}_0e^{\pi lt/3}, ifn_0=|n_0|e^{i\gamma}$$

$$\implies n_t=|n_0|\left[e^{i(\pi t/3+\gamma)}+e^{-i(\pi 3/t+\gamma)}\right]$$

$$=2|n_0|\cos\left(\frac{\pi}{3}\ t+\gamma\right)$$

 n_0, γ are constants, real, this is a periodic solution and the period p is

$$\frac{\pi}{3} p = 2\pi$$

$$\implies p = 6$$

(i)

$$\dot{u} = a \left[u \left(1 - u \right) - \frac{uv}{1 + bu} \right] = f \left(u, v \right)$$

$$\dot{v} = v \left[\frac{bu}{1 + bu} - c \right] = g \left(u, v \right)$$

The steady states are the solution of

where

$$u^* = \frac{c}{b(1-c)}$$
 $v^* = \frac{b-c(1+b)}{b(1-c)}$

 $u^*>0$ and meaningful if $u^*=c\left(1+b\right)$, i.e. $b>\frac{c}{1-c}$

(ii)

$$egin{aligned} \mathcal{A} &= \left(egin{array}{ccc} rac{\partial f}{\partial u} & rac{\partial f}{\partial v} \\ rac{\partial f}{\partial u} & rac{\partial f}{\partial v} \end{array}
ight) \ &= \left(egin{array}{ccc} a \left(1 - 2a - rac{v}{1 + bu} + rac{uvb}{(1 + bu)^2}
ight) & -rac{au}{1 + bu} \\ & rac{bv}{1 + bu} - rac{b^2 uv}{(1 + bu)^2} & rac{bu}{1 + bu} - c \end{array}
ight) \end{aligned}$$

 $\mathcal{A}(0,0) = \begin{pmatrix} a & 0 \\ 0 & -c \end{pmatrix}$ with eigenvalues $\lambda_1 = a > 0, \ \lambda_2 = -c < 0 \implies (0,0)$ is a saddle point.

Eigenvectors $\begin{pmatrix} 0 \\ 1 \end{pmatrix}$ and $\begin{pmatrix} 1 \\ 0 \end{pmatrix}$

$$\mathcal{A}\left(1,0\right) = \left(\begin{array}{cc} -a & -\frac{a}{1+b} \\ 0 & \frac{b}{1+b} - c \end{array}\right) \implies \lambda_1 = -a < 0, \qquad \lambda_2 = \frac{b}{1+b} - c > 0$$

since
$$\lambda_2 = \frac{b - c(1+b)}{1+b} = \frac{b(1-c) - c}{1+b} > \frac{\frac{c}{1-c}(1-c) - c}{1+b} = 0$$

 \implies (1,0) is a saddle point, eigenvector $\begin{pmatrix} 1 \\ 0 \end{pmatrix}$ and $\begin{pmatrix} \frac{c(1-b)-b-a(1+b)}{a} \end{pmatrix}$, second entry is negative.

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We notice also that $a^* = \frac{c}{1-c} < 1$.

$$\mathcal{A}\left(u^{*},v^{*}
ight)=\left(egin{array}{cc} rac{ac\left[b\left(1-c
ight)-\left(c+1
ight)
ight]}{b\left(1-c
ight)} & -rac{ac}{b} \ b\left(1-c
ight)-c & 0 \end{array}
ight)$$

Characteristic equation

$$\lambda^2 = (\operatorname{tr} A) \,\lambda + \det A = 0$$

$$\lambda^2 - ac \frac{b\left(1-c\right) - \left(c+1\right)}{b\left(1-c\right)} \lambda + \frac{ac}{b} \underbrace{\left[b\left(1-c\right) - c\right]}_{\text{always positive}} = 0$$

Since $\det A > 0$, for stability, we have $\operatorname{tr} A < 0$ i.e.

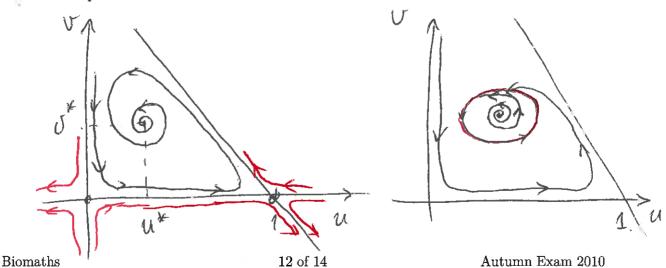
$$b < \frac{c+1}{1-c} \implies \text{if } \frac{1+c}{1-c} > b > \frac{c}{1-c}$$

the solution (u^*, v^*) exists and is stable.

(iii) If b approaches the bifurcation value $b = \frac{1+c}{1-c}$, the characteristic equation is

$$\lambda^2 + \frac{ac(1-c)}{1+c} \left[\frac{1+c}{1-c} (1-c) \right] = 0$$
$$\lambda^2 + \frac{ac(1-c)}{1+c} = 0$$

with two imaginary roots $\implies (u^*, v^*)$ becomes centre-type equilibrium. Since the other two equilbina are unstable, we expect that (u^*, v^*) is a stable limit cycle, i.e. (u, v) is approaching a stable periodic solution.



(i)

$$\left(\frac{dI}{dt}_{t=0}\right) = rI\left(0\right)\left[S\left(0\right) - \mathbf{Q}\right] > 0$$

So I is increasing if $S_0 > \emptyset$ which means an epidemic outbreak.

(ii)

$$\frac{dS}{dt} + \frac{dI}{dt} + \frac{dR}{dt} = (-rSI) + (rSI - aI) + (aI) = 0$$

$$\implies N = S + I + R = \text{const} \quad \text{(total number of population)}.$$

(iii)

$$\frac{dS}{dR} = -\frac{S}{\checkmark}$$

$$\frac{dR}{dt} = aI = a(N - S - R) = a\left(N - R - S_0e^{-R/\checkmark}\right)$$

$$R(0) = 0$$

$$\implies S = S_0e^{-R/\checkmark}$$

(iv) If
$$\frac{R}{\rho} \ll 1$$
, we have $e^{-R/\rho} \simeq 1 - \frac{R}{\rho} + \frac{1}{2} \left(\frac{R}{\rho}\right)^2$ and then
$$\frac{dR}{dt} = a \left[N - R - S_0 + \frac{S_0 R}{\rho} - \frac{S_0 R^2}{2\rho^2}\right]$$
$$\frac{dR}{dt} = a \left[N - S_0 + \left(\frac{S_0}{\rho} - 1\right)R - \frac{S_0 R^2}{2\rho^2}\right]$$
$$R(0) = 0$$

(v)

$$\frac{dR}{dt} = f(N)$$

with roots

$$R_{1,2} = \frac{-\left(\frac{S_0}{\wp} - 1\right) \pm \sqrt{\left(\frac{S_0}{\wp} - 1\right)^2 + 9\left(N - S_0\right)\frac{S_0}{2\wp^2}}}{-2\frac{S_0}{2\wp^2}}$$

The only positive one is

$$R^* = \mathcal{O}^2 rac{\sqrt{\left(rac{S_0}{\mathcal{O}}-1
ight)^2 + 2rac{S_0(NS_0)}{\mathcal{O}^2}} + \left(rac{S_0}{\mathcal{O}}-1
ight)}}{2S_0}$$

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and thus we expect $\lim_{t\to\infty}R(t)=R^*\equiv R(\infty)$. $R(\infty)$ is the number of the remainder class after the epidemic outbreak.

(vi) We have an integral of Motion $I + S - 9 \ln S = \text{const}$ i.e.

$$I = -S + \mathcal{G} \ln S + I\left(0\right) + S\left(0\right) - \mathcal{G} \ln S\left(0\right)$$

The maximum I_{max} occurs at $S=\slash\hspace{-0.1cm}p$ where $\dfrac{dI}{dt}=0$.

$$I_{ ext{max}} = X - \mathbf{p} + \mathbf{p} \ln \left(rac{arphi}{S_0}
ight)$$

Thus for initial values $I_0>0$ and $S_0>\emptyset$, the phase trajectory starts with $S>\emptyset$ and I increases from I_0 and an epidemic ensues If $S_0<\emptyset$ decreases from I_0 and an epidemic occurs. All trajectories start from the line S+I=N since initially R(0)=0.

