Math332 January 2006 exam: solutions

1. *Saccharomyces cerevisiae is one of the most commercialized species of bakers yeast. The dynamics of yeast population in a bioreactor with constant supply of nutrients can be approximately described by the Verhulst equation*

$$\frac{\mathrm{d}N}{\mathrm{d}t} = rN(1 - N/K), \tag{1}$$

where $N(t)$ is the yeast biomass at time t.

(a) **Question** *Explain the biological significance of the parameters r and K.*

Answer r: the maximal, low-density reproduction rate ; K: the carrying capacity of the habitat, i.e. the bioreactor ;

Question *How will parameters r, K change if the volume of the bioreactor is increased tenfold, with the same composition of supplied nutrients?*

Answer The reproduction rate at low densities, r, depends on nutrients composition so it would not change. The carrying capacity K represents stationary biomass, so would increase tenfold.

[4]

(b) **Question** *Integrate the differential equation (1) by separation of variables or otherwise, and show that*

$$N(t) = \frac{e^{rt}N(0)}{1 + N(0)\left(e^{rt} - 1\right)/K}.$$

Answer Separating variables, we have

$$\int \frac{1}{N(1 - N/K)}\mathrm{d}N = \int r\mathrm{d}t, \qquad \ln\left|\frac{N-K}{N}\right| = -rt + C_1, \qquad N = \frac{K}{1 + C_2e^{-rt}},$$

for the general solution, or with account of the initial condition,

$$N(0) = \frac{K}{1 + C_2}, \qquad C_2 = K/N(0) - 1, \qquad N(t) = N(0)e^{rt}/\left[1 + N(0)\left(e^{rt} - 1\right)/K\right] \tag{$*$}$$

as requested.

[5]

(c) **Question** *Deduce from the result of part 1(b) the dependence of $N(t+\tau)$ on $N(t)$ for $\tau > 0$.*

Answer Formula (*) is valid for any t; let us replace it with τ:

$$N(\tau) = N(0)e^{r\tau}/\left[1 + (N(0)/K)\left(e^{r\tau} - 1\right)\right].$$

Since the differential equation does not depend on time explicitly, a solution shifted in time by a constant is another solution, thus

$$N(t+\tau) = N(t)e^{r\tau}/\left[1 + (N(t)/K)\left(e^{r\tau} - 1\right)\right],$$

which is the requested dependence.

Question *Show that the mapping $N(t) \to N(t+\tau)$ is described by a Hassell equation*

$$N(t+\tau) = \frac{RN(t)}{(1 + aN(t))^b}$$

and find the values of R, a and b in this equation in terms of the parameters r and K of the continuous-time model and the time interval τ.

Answer By inspection,

$$R = e^{r\tau}, \quad a = (e^{r\tau} - 1)/K, \quad b = 1.$$

[5]

(d) **Question** *The yeast biomass is harvested at discrete time intervals τ. The process is cyclic, i.e. the harvest H is equal to the increase of the population during one such interval, $H = N(t+\tau) - N(t)$. Using your previous results or otherwise, find the maximal harvest H achievable at fixed r, K and τ, and the value of $N(t)$ which will yield this maximum*

Answer From the previous part, we have $N_{t+\tau} = RN_t/(1 + aN_t)$, where $R = e^{r\tau}$ and $a = (e^{r\tau} - 1)/K$. Hence we have

$$H(N_t) = N_{t+\tau} - N_t = N_t\left(\frac{R}{1 + aN_t} - 1\right).$$

Differentiation gives

$$\frac{\partial H(N)}{\partial N} = \frac{R}{(1 + aN)^2} - 1 = 0.$$

Since this derivative is monotonically decreasing for $N > 0$, the only zero of this derivative, achieved at $N = \boxed{N_{cr} = (R^{1/2} - 1)/a}$ is the global maximum for $N > 0$, and the value of this maximum is $\boxed{H_{\max} = H(N_{cr}) = (R^{1/2} - 1)^2/a = (R - 2\sqrt{R} + 1)/a}$.

[6]

Total for this question: 20 marks

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2. *The model of outbreaks of spruce budworm Choristoneura fumiferana suggested by Ludwig (1978) can be written in the form*

$$\frac{\mathrm{d}x}{\mathrm{d}t} = rx\left(1 - \frac{x}{K}\right) - \frac{x^2 z}{x^2 + 1} \tag{2}$$

where x is budworm population density, z is the density of the population of birds preying on the budworms and r and K are constant parameters.

(a) **Question** *Explain the biological significance of the two terms in the right-hand side of this equation, and of the parameters r and K.*

Answer First term: the Verhulst dynamics of the budworms in absence of the predators. Second term: decrease of population density due to predation. Parameter r: maximal reproduction rate of the budworm population. Parameter K: carrying capacity of the habitat.

Question *What is the Holling type of the predatory response of birds to the budworms?*

Answer This is Holling type 3 response.

[5]

(b) **Question** *Draw carefully the graph of the function $y = f(x) = x/(x^2 + 1)$ in the range $x \in [0, 15]$. Explain how it can be used to find graphically the equilibrium values of x in the above model, for given values of r, z and K? Use this method to demonstrate that at $K = 15$, $r = 1$ and $z = 2.5$, there are three positive equilibrium states, and roughly estimate their values.*

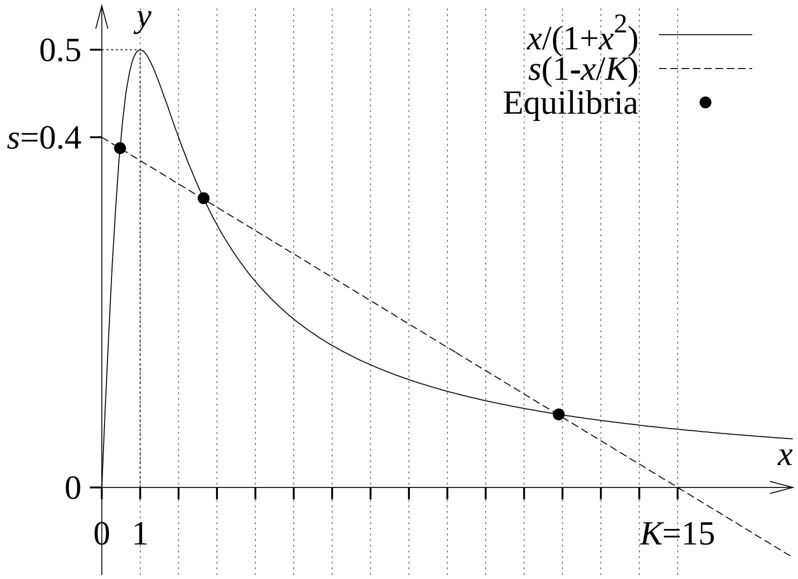
Answer The equilibrium states in (2) are solutions of the equation

$$rx(1 - x/K) - z\frac{x^2}{1 + x^2} = 0$$

which has a trivial solution $x = 0$ and the nontrivial solutions satisfy

$$\frac{r}{z}\left(1 - \frac{x}{K}\right) = f(x)$$

where $f(x)$ is the function defined in the question. Thus solutions can be found as intersections of the graph of this function, $y = f(x)$, with the line $y = s(1 - x/K)$, where $s = r/z$:



From this graph for the given K and r we have equilibria at $P \approx 0.5, 2.5$ and 12.

.

[7]

(c) **Question** *Based on the graphical method discussed in part 2(b), or otherwise, derive conditions on parameters K, r, z and x for the bifurcation of double equilibria in this model. Solve these conditions for r and K as explicit functions of the double equilibrium position x.*

Answer Double equilibrium corresponds to tangency of the straight line $y = s(1 - x/K)$, where $s = r/z$, and curve $y = f(x)$, which gives the system

$$s - \frac{s}{K}x = \frac{x}{x^2+1},$$
$$-\frac{s}{K} = f'(x) = \frac{1-x^2}{(x^2+1)^2}$$

which is solved for s and K as

$$s = \frac{r}{z} = \frac{2x^3}{(1+x^2)^2},$$
$$K = \frac{2x^3}{(x^2-1)} \qquad (*)$$

[4]

(d) **Question** *For the specified values of parameters, $r = 1$, $K = 15$, $z = 2.5$, the budworm population was in an equilibrium with $x > 10$. This attracted more birds to the infested forest, which resulted in a gradual decline of the budworm density. When the budworm density decreased to $x \approx 7.4$, a collapse happened, i.e. a sudden decrease of the budworm density to a very low value $x < 1$. Use the result of part 2(c) to find, to 2 significant figures, what was the density of bird population at that moment.*

Answer As follows from the above analysis, the budworm population was in the higher "outbreak" stable equilibrium. The sudden decline will occur when the higher stable equilibrium ceases to exist, i.e. at a bifurcation point. The bifurcation parameters values can be found by substituting $x = 7.4$ into (*), which gives $s \approx 0.26$ and $z = r/s \approx 3.8$.

[4]

Total for this question: 20 marks

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3. *One of the most famous "feral" cat colonies lives in the Colosseum in Rome. An ecologist visiting Rome as a tourist has observed that females in that colony often help their daughters to raise their kittens. She has conjectured that dynamics of that population can be modelled using an appropriate modification of the discrete-time Ricker model:*

$$N_{t+1} = RN_t \exp\left(-aN_t + bN_{t-T}\right) \qquad (3)$$

where $N_t \geq 0$ is the size of the population of female cats of the reproductive age at time t measured in generations, and $T \geq 0$ and $a > b > 0$ are constant parameters, $t, T \in \mathbb{Z}$.

(a) **Question** *Suggest an interpretation of the biological significance of the parameters R, a and b.*

Answer R: low-density reproduction coefficient . a: parameter characterising the severity of the intraspecific competition. b: parameter characterising the positive contribution of the older cats in raising the young.

Question *What should be the value of parameter T, if cats only help to raise their grandchildren but do not care about more distant generations?*

Answer Todays grandmothers have been mothers one generation ago, so their number at time t is proportiona, subject to survival, to N_{t-1}. Thus $T = 1$.

[4]

(b) **Question** *Find any nonzero equilibria in this model and the ranges of parameter values at which they exist and are biologically feasible.*

Answer The only equilibrium is $N = \ln(R)/(a-b) = N^*$. Since $a > b$, it is feasible only for $R > 1$.

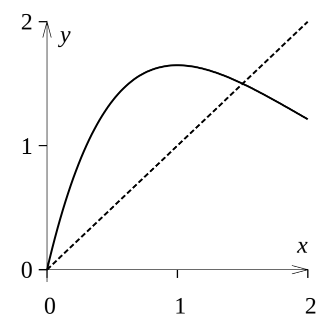
Question *Investigate their stability.*

Answer For $T = 0$, the right-hand side is $F(N_t) = RN_t \exp(-(a-b)N_t)$. We have $F'(N) = R(1-(a-b)N)\exp(-(a-b)N)$ and $F'(N^*) = 1 - \ln(R)$. Stability corresponds to $F'(N^*) \in (-1, 1)$ which requires $R \in (1, e^2)$. It is monotonic if $F'(N^*) > 0$ which requires $R < e$.

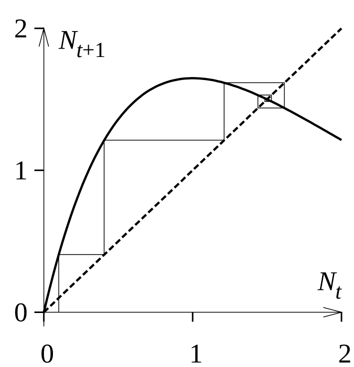
[7]

(c) **Question**

Consider the case of $T = 0$, $a = 2$, $b = 1$ and $R = e^{3/2}$. Using the graphs of functions $y = x\exp(\frac{3}{2} - x)$ and $y = x$ shown on the right, sketch a cobweb/stepladder diagram for model (3), with the initial condition $x_0 = 0.1$. Deduce from it whether or not the nontrivial equilibrium in this model is stable. Is this equilibrium monotonic or oscillatory?



Answer



Thus the nontrivial equilibrium is oscillatory (sign-alternating) stable.

[3]

(d) **Question** *Consider the case of $T = 1$, $a = 2$, $b = 1$ and $R = e^{3/2}$. Using the substitution $N_t = N^* + h_t$, where N^* is the nontrivial equilibrium, and $|h_t|$ is small, verify that the behaviour of the system close to this equilibrium is described by*

$$h_{t+1} + 2h_t - \frac{3}{2}h_{t-1} = 0.$$

Hence conclude, whether the grandmothers' contribution has stabilizing or destabilizing effect on this population's dynamics.

Answer Considering equation (3) at $T = 1$ as

$$N_{t+1} = F(N_t, N_{t-1}) = [F(p,q)]_{p=N_t, q=N_{t-1}}$$

and using linear approximation of F in both its arguments, we obtain

$$N^* + h_t = F(N^*, N^*) + \frac{\partial F}{\partial p}(N^*, N^*)h_t + \frac{\partial F}{\partial q}(N^*, N^*)h_{t-1}$$

Take into account that $N^* = F(N^*, N^*)$ for equilibrium, and calculating the partial derivatives of F,

$$\frac{\partial F(N^*, N^*)}{\partial p} = [(1-ap)\exp(-ap+bq)R]_{p=q=N^*} = -2$$

$$\frac{\partial F(N^*, N^*)}{\partial q} = [Rpb\exp(-ap+bq)]_{p=q=N^*} = \frac{3}{2}$$

and therefore

$$h_{t+1} = -h_t + \frac{3}{2}h_{t-1}$$

as required. Assuming solutions to this equation in the form $h_t = \mathrm{Re}\,(C\mu^t)$, this gives the characteristic equation

$$\mu + 2 - \frac{3}{2}\mu^{-1} = 0$$

or, equivalently,

$$\mu^2 + 2\mu - \frac{3}{2} = 0$$

One of its roots $-1-\sqrt{5/2} < -1$, so this equilibrium has sign-alternating instability, as opposed to the sign-alternating stability of the similar model without delay. Thus the delayed contribution has a destabilizing effect.

[6]

Total for this question: 20 marks

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4. *The spotted knapweed Centaurea biebersteinii, whose natural habitat stretches from Central Europe to Western Siberia, is now a serious problem weed in North America where it was accidentally introduced in 1880s. The population of plants consists of seeds (age group 0), seedlings (age group 1), young adults (age group 2), medium adults (age group 3) and old adults (age group 4). Each year,*
   - *a fraction $B_0 \in (0,1)$ of seeds remain in the soil, and a fraction $P_0 \in (0,1)$ germinates into seedlings,*
   - *a fraction $P \in (0,1)$ of seedlings become young adults,*
   - *the same fraction P of young adults become medium adults,*
   - *the same fraction P of medium adults become old adults,*
   - *young, medium and old adults each produce $B > 0$ seeds on average; seedlings do not produce any seeds. The dynamics of this population can be described by Leslie model*

$$\mathbf{N}_{t+1} = \mathbf{L}\mathbf{N}_t \tag{4}$$

where $\mathbf{N}_t = (N_t^0, \ldots N_t^4)^T$ is the column-vector describing the population in year t, and N_t^j is the size of the j-th age group at that year.

(a) **Question** *Write down the system of discrete time evolution equations for the plant age groups. Thus construct the Leslie transition matrix* $\mathbf{L}$.

Answer The system:

$$\begin{aligned}
N_{t+1}^0 &= B_0 N_t^0 + BN_t^2 + BN_t^3 + BN_t^4 \\
N_{t+1}^1 &= P_0 N_t^0 \\
N_{t+1}^2 &= PN_t^1 \\
N_{t+1}^3 &= PN_t^2 \\
N_{t+1}^4 &= PN_t^3
\end{aligned}$$

Leslie matrix is therefore

$$\mathbf{L} = \begin{bmatrix} B_0 & 0 & B & B & B \\ P_0 & 0 & 0 & 0 & 0 \\ 0 & P & 0 & 0 & 0 \\ 0 & 0 & P & 0 & 0 \\ 0 & 0 & 0 & P & 0 \end{bmatrix}$$

[4]

(b) **Question** *Find the characteristic polynomial $p(\mu)$ for $\mathbf{L}$.*

Answer

$$\begin{aligned} p(\mu) &= \det(\mathbf{L} - \mu\mathbf{I}) \\ &= -\mu^5 + B_0\mu^4 + P_0PB\mu^2 + P_0P^2B\mu + P_0P^3B \end{aligned}$$

Question *By considering the function $f(\mu) = p(\mu)/\mu^5$ for positive μ, show that for $P_0 > 0$, $B_0 > 0$, $P > 0$ and $B > 0$, this polynomial always has exactly one positive root.*

Answer

$$f(\mu) = p(\mu)/\mu^5 = -1 + B_0/\mu + BP_0P/\mu^3 + BP_0P^2/\mu^4 + BP_0P^3/\mu^5.$$

For $\mu \to +0$, we have $f(\mu) \to +\infty$, i.e. is positive. For $\mu \to +\infty$, this function approaches -1, i.e. is negative. As $f(\mu)$ is continuous, it must have at least one zero in the interval $(0, +\infty)$. This function is monotonically decreasing, thus it may have only one zero.

[7]

(c) **Question** *Observations have shown that an unchecked population of spotted knapweed increases by 25% each year. Assuming that $P_0 = B_0 = 1/4$ and $P = 1/2$, estimate, to 1 decimal place, the average value B of seeds produced by an adult plant.*

Answer Resolving equation $p(\mu) = 0$ with respect to the unknown B, we get

$$B = \frac{(\mu - B_0)\mu^4}{P_0P(\mu^2 + P\mu + P^2)} \tag{$*$}$$

For given values of parameters, including $\mu = 1.25$, this gives value $B \approx 8.0$.

[5]

(d) **Question** *Two species of seed head flies, Urophora affinis and U. quadrifasciata, are well-established on spotted knapweed. The larvae of these species reduce seed production by 50% by feeding on spotted knapweed seed heads. Determine if using these flies would alone be an effective method of biocontrol of the knapweed population, for the values of parameters specified in part 4(c).*

Answer To stop the growth of the knapweed, we need $\mu < 1$. Note that function $B_* = B(\mu)$ defined by equation (*) is motonically increasing as long as $\mu > B_0$ (can be checked by differentiation). So to provide $\mu < 1$, we need $B < B_*(1) \approx 3.4$. This is smaller than 50% of the unchecked number of seeds $B \approx 8.0$, thus only a 50% reduction of seeds caused by *Urophora* flies is insufficient and would not stop the growth of the weed.

[4]

Total for this question: 20 marks

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5. *The snowshoe hare Lepus americanus is nearly the only prey of the Canadian lynx Lynx lynx. Their population dynamics are so closely linked that they exhibit stable synchronous oscillations with the period of several years, evidence of which can be seen in the records of pelts obtained by Hudson Bay company. Consider a modification of the Lotka-Volterra model describing the dynamics of the two populations:*

$$\begin{aligned} \mathrm{d}H/\mathrm{d}t &= H\left(a - \alpha L^2\right) \\ \mathrm{d}L/\mathrm{d}t &= L\left(-b + \beta H^2\right) \end{aligned} \tag{5}$$

where H is the hare population size, L is the lynx population size, both estimated by thousands of pelts obtained, time t is measured in years, and a, b, α, β are positive coefficients.

(a) **Question** *Describe the biological significance of the parameters a, α, b and β.*

Answer a: reproduction rate of hare in absence of predators. α: coefficient describing decrease of hare reproduction rate due to predation. b: decline rate of lynx in absence of prey . β: coefficient describing increase of lynx reproduction rate due to availability of prey.

[4]

(b) **Question** *Find all biologically feasible equilibria in this model and classify their stability in the linear approximation.*

Answer Equilibria satisfy the system of algebraic equations $H(a-\alpha L^2)=0$, $L(b-\beta H^2)=0$, which has only two solutions for non-negative populations: $(H,L)=(0,0)$ and $(H,L)=(H^*,L^*)=(\sqrt{b/\beta},\sqrt{a/\alpha})$. The Jacobian of the right-hand sides is

$$J(H,L)=\frac{\partial(\dot H,\dot L)}{\partial(H,L)}=\begin{bmatrix} a-\alpha L^2 & -2\alpha HL \\ 2\beta HL & -b+\beta H^2 \end{bmatrix}.$$

For the trivial equilibrium, the community matrix is $A_0=J(0,0)=\begin{bmatrix} a & 0 \\ 0 & -b \end{bmatrix}$, so the eigenvalues are $\lambda_1=-a<0$, $\lambda_2=b>0$ and this is a <u>saddle point</u> (unstable) . For the coexistence equilibrium, the community matrix is $A_1=J(H^*,L^*)=\begin{bmatrix} 0 & -2\sqrt{ab\alpha/\beta} \\ 2\sqrt{ab\beta/\alpha} & 0 \end{bmatrix}$. It has two purely imaginary eigenvalues $\lambda_{1,2}=\pm i\omega$ where $\omega=2\sqrt{ab}$, so this equilibrium is oscillatory. Since $\mathrm{Re}\,(\lambda_{1,2})=0$, its stability is <u>not decided by linear approximation</u>.

[5]

(c) **Question** *Find the orbit derivative of function V defined as*

$$V(H,L)=\frac{\alpha}{2}L^2-a\ln(L)+\frac{\beta}{2}H^2-b\ln(H)$$

and show that this derivative is identically zero for all solutions of (5).

Answer

$$\begin{aligned}\frac{\mathrm{d}V}{\mathrm{d}t}&=\frac{\partial V}{\partial H}\frac{\mathrm{d}H}{\mathrm{d}t}+\frac{\partial V}{\partial L}\frac{\mathrm{d}L}{\mathrm{d}t}\\ &=\left(\beta H-\frac{b}{H}\right)H(a-\alpha L^2)+\left(\alpha L-\frac{a}{L}\right)(-b+\beta H^2)\\ &=0\end{aligned}$$

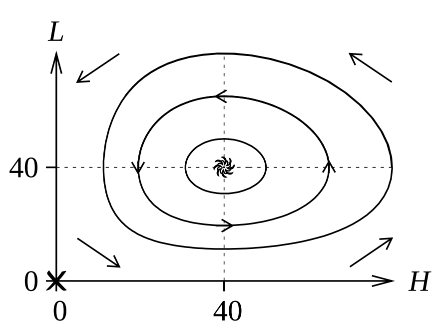
Question *What does this result mean for (i) possibility of periodic solution in this model, (ii) asymptotic stability of the coexistence equilibrium, (iii) its Lyapunov stability.*

Answer Since $\mathrm{d}V/\mathrm{d}t=0$, trajectories of (5) with positive intial conditions are (parts of) isolines $V(H,L)=$ const. As $V\to+\infty$ for $H,L\to+0$ and $H,L\to+\infty$, all such isolines are bounded curves, and none of them can approach either equilibrium. Thus any solutions starting at $H>0$, $L>0$, $(H,L)\neq(H^*,L^*)$ is a periodic solution. Therefore, (H^*,L^*) can not be asymptotically stable, but it is Lyapunov stable.

[6]

(d) **Question** *Using your results, estimate, to 1 significant figure, the average sizes of the two populations and the period of their mutual oscillations for $a=b=0.32$ and $\alpha=\beta=2\times10^{-4}$. Sketch the phase portrait of the system at these parameters, by designating on the (H,L) plane the equilibria, the null-clines $\dot H=0$ and $\dot L=0$ and a few typical trajectories.*

Answer



$H^*=L^*=\sqrt{a/\alpha}=\sqrt{b/\beta}=40$ (thousand pelts), and $T=2\pi/\omega=\pi/\sqrt{ab}\approx10$ (years). Phase portrait shown on the left.

[5]

Total for this question: 20 marks

6. *The accidental release of cats to Amsterdam Island in the southern Indian Ocean has considerably increased ecological pressure on endemic bird species. Eradication of cats has been considered. However the plan raised concerns that such eradication will lead to an increase of the island's population of rats, which are prey to cats but predators to birds, and thus make the birds' situation worse. In 1999, Courchamp et al. constructed a mathematical model of the ecosystem, which in a simplified form can be represented in a Lotka-Volterra-Gause form,*

$$\begin{aligned}\frac{\mathrm{d}B}{\mathrm{d}t} &= B(\alpha - \beta B - \gamma R - \delta C)\\ \frac{\mathrm{d}R}{\mathrm{d}t} &= R(\epsilon + \zeta B - \eta R - \theta C)\\ \frac{\mathrm{d}C}{\mathrm{d}t} &= C(\kappa + \lambda B + \mu R - \nu C).\end{aligned} \tag{6}$$

where all constant coefficients $\alpha \dots \nu$ are assumed positive.

(a) **Question** *Explain how, based on the signs of the terms in the right-hand sides, one can deduce that B describes the population of birds, R describes the population of rats and C describes the population of cats.*

Answer In the equation for B, both interspecies competition terms are negative thus this is prey to two other species, i.e. birds . In the equation for C, both interspecies competition terms are positive thus this is the top predator, i.e. cats . Thus R is population of rats.

[3]

(b) **Question** *From now on, assume $\alpha = 3$, $\epsilon = \theta = \nu = 4$, $\kappa = 2$, and all other coefficients $= 1$. Show that $R = B = C = 1$ is an equilibrium*

Answer Substitution of the values into (6) gives:

$$\begin{aligned}\frac{\mathrm{d}B}{\mathrm{d}t} &= 1 \times (3 - 1 - 1 - 1) = 0,\\ \frac{\mathrm{d}R}{\mathrm{d}t} &= 1 \times (4 + 1 - 1 - 4) = 0,\\ \frac{\mathrm{d}C}{\mathrm{d}t} &= 1 \times (2 + 1 + 1 - 4) = 0,\end{aligned}$$

so the equations are satisfied.

Question *Investigate its stability.* Hint: one of the eigenvalues is equal to -1.

Answer The community matrix of the equilibrium is

$$\mathbf{A} = \left[\frac{\partial(\dot{B}, \dot{R}, \dot{C})}{\partial(B, R, C)}\right]_{R=B=C=1} = \begin{bmatrix} -\beta B & -\gamma B & -\delta B \\ \zeta R & -\eta R & -\theta R \\ \lambda C & \mu C & -\nu C \end{bmatrix} = \begin{bmatrix} -1 & -1 & -1 \\ 1 & -1 & -4 \\ 1 & 1 & -4 \end{bmatrix}$$

The characteristic equation is

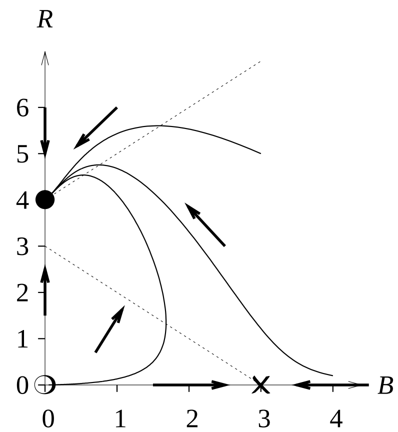
$$\chi(\Lambda) = \det \mathbf{A} - \Lambda \mathbf{I} = -\Lambda^3 - 6\Lambda^2 - 15\Lambda - 10 = 0.$$

This factorizes to $\chi(\Lambda) = -(\Lambda + 1)(\Lambda^2 + 5\Lambda + 10)$, thus apart from the given eigenvalue $\Lambda_1 = -1$, we have two eigenvalues $\Lambda_{2,3} = \frac{-5 \pm i\sqrt{15}}{2}$. Thus the equilibrium is oscillatory stable.

[6]

(c) **Question** *Consider the model at the values of parameters specified in the previous part, in the absence of cats, $C = 0$. On the phase plane (B, R), sketch the phase portrait by drawing the null-clines, finding equilibria, designating the crude directions of trajectories in parts of the phase plane separated by null-clines and sketching some typical trajectories.*

Answer



The birds+rats system, at given parameters, is

$$\frac{\mathrm{d}B}{\mathrm{d}t} = B(3-B-R)$$
$$\frac{\mathrm{d}R}{\mathrm{d}t} = R(4+B-R)$$

The $\dot{B}=0$ (vertical) isoclines are $B=0$ and $B+R=3$; below $B+R=3$ trajectories go to the right, above it to the left. The $\dot{R}=0$ (horizontal) isoclines are $R=0$ and $R=B+4$; below $R=B+4$ trajectories go up, above it they go down. Thus in the positive quadrant there are three equilibria, $(B,R)=(0,0)$, $(3,0)$ and $(0,4)$. By analysing possible behaviour of trajectories, one can see that $(0,0)$ is unstable node, $(3,0)$ is a saddle point and $(0,4)$ is stable node.

[8]

(d) **Question** *Give the interpretation of your results in parts 6(b) and 6(c) in terms of benefits and damages to the bird population.*

Answer Part 6b showed that in presence of cats, a coexistence equilibrium of all three populations is possible. Part 6c showed that in absebce of cats, coexistence between birds and rats is not possible, and the only outcome, at nonzero initial population of birds and rats, is monopolistic survival of rats.

Question *In reality, after all consideration, the plan to eradicate cats has been abandoned. Would this be a correct decision if the system was described by equations 6 with the specified values of parameters?*

Answer Assuming that the purpose was preservation of the endemic birds, the decision was correct, since eradication of cats would lead to extinction of birds, and with cats at least some population of birds would stay.

[3]

Total for this question: 20 marks

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7. *To describe Bombay plague epidemic of 1905-6, Kermack and McKendrick (1927) have suggested the following model*

$$\begin{aligned}\mathrm{d}S/\mathrm{d}t &= -\beta SI \\ \mathrm{d}I/\mathrm{d}t &= \beta SI - \nu I\end{aligned} \tag{7}$$

where S is the number of susceptible, I the number of infective individuals of the population, and β and ν are non-negative parameters.

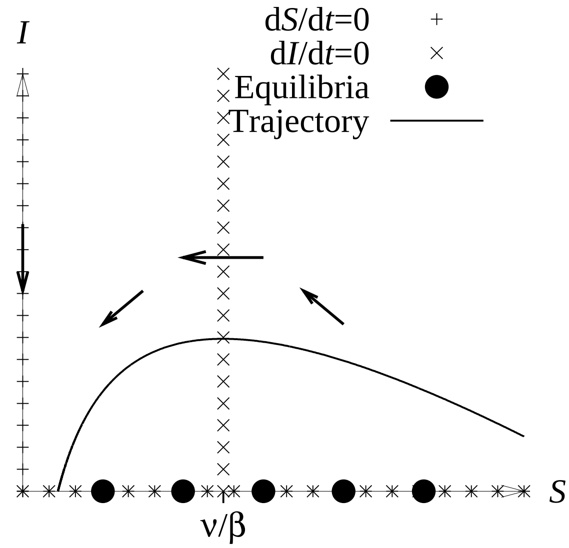
(a) **Question** *Explain the biological meaning of the terms in these equations, and what biological assumptions have been used in this model.*

Answer Terms: βSI — the rate of transmission of the disease νI — rate of removal . Assumptions:
— Rate of transmission is proportional to the rate of encounter of susceptibles and infectives, meeting at random.
— Removals of individuals are independent events with certain probabilities per capita per unit of time.
— The removed individuals never return to the epidemics, e.g. die or acquire permanent immunity. — All vital dymamics (number of births and disease-unrelated mortalities) neglected.

[6]

(b) **Question** *Perform the phase-plane analysis of the model (7): draw the null-clines, indicate equilibria, show the general direction of trajectories in different parts of the phase plane, and sketch a typical trajectory representing an epidemic.*

Answer Null clines:
— $\dot{S}=0$: two lines, $S=0$ and $I=0$
— $\dot{I}=0$: two lines, $S=\nu/\beta$ and $I=0$
Equilibria: the two sets of null-clines have the whole line $I=0$, and only that line, as an intersection, thus this whole line consists of equilibria. General direction of trajectories: since $\dot{S}<0$, all trajectories move leftwards, since $\dot{I}=\beta I(S-\frac{\nu}{\beta})$, trajectories go up where $S>\nu/\beta$ and down where $S<\nu/\beta$. Phase portrait:



[6]

(c) **Question** *Consider function $V(S,I) = I + S - \frac{\nu}{\beta}\ln(S)$. Calculate its orbit derivative due to system (7).*

Answer

Question *Thus show that any trajectory of (7) satisfies equation $I = \frac{\nu}{\beta}\ln(S) - S + \text{const}$.*

Answer

Question *Deduce from here an equation, relating the population S_0 before an epidemic and population S_∞ after the epidemic.*

Answer $\frac{\nu}{\beta}\ln(S_0) - S_0 = \frac{\nu}{\beta}\ln(S_\infty) - S_\infty$

Question *Prove that S is a Lyapunov function of (7), and state what this means for the possibility of periodic solutions in this model.*

Answer $\dot{S} \leq 0$ by the first evolution equation. The set where $\dot{S} = 0$ is only $\{I = 0\} \cup \{S = 0\}$. Thus periodic solutions are impossible.

[5]

(d) **Question** *There was an outbreak of plague in the village of Eyam in England from 1665 to 1666. The village sealed itself off when the plague was discovered. In the epidemic, the population of the village decreased from 350 to 83. Assume that the mortality rate for infectives was approximately 1/day. Estimate from these data the value of the coefficient β in (7).*

Answer In the beginning and in the end of epidemic, $I = \frac{\nu}{\beta}\ln(S_0) - S_0 + V = \frac{\nu}{\beta}\ln(S_\infty) - S_\infty + V = 0$, thus $\nu/\beta = (S_0 - S_\infty)/(\ln(S_0) - \ln(S_\infty)$. The mortality rate is the value of ν. Thus $\beta = \nu(\ln(S_0) - \ln(S_\infty)/((S_0 - S_\infty) \approx 0.005$.

[3]

Total for this question: 20 marks