Math332 Summer 2003 exam: solutions

1. *The endangered species of Cuban crocodiles Crocodylus rhombifer have a very long natural life expectancy and practically all their mortality is due to intraspecific competition. Dynamics of their population during a typical year is described by the following model:*

$$\frac{\mathrm{d}N}{\mathrm{d}t} = \begin{cases} rN - mN^2, & \text{if } 0 < t < s, \\ -mN^2, & \text{if } s < t < 1. \end{cases} \tag{1}$$

Here N is the density of the population and time t is measured from the beginning of summer. The time unit is 1 year, and $0 < s < 1$.

(a) **Question** *Explain the biological significance of the parameters s, r and m.*

Answer s: duration of the reproductive season (spring) . r: the maximal reproduction rate (birth rate in this case, as the linear death rate is zero) ; m: mortality due intraspecific competition ;

Question *What is the carrying capacity of the system for $t \in (0, s)$?*

Answer The right-hand side for this time interval can be rewritten as $rN(1 - mN/r) = rN(1 - N/K)$ where $K = r/m$.

Question *There is no linear term in the right-hand side of (1) for $t \in (s, 1)$. Suggest what biological reality is reflected by this mathematical fact.*

Answer Linear term is the difference between birth rate and death rate at small population density. Since there is no mortality except due to intraspecific competition which is absent at small population density, this difference being zero means the birth rate is also zero.

5 marks for this part

(b) **Question** *Integrate the differential equation (1) for $t \in (0, s)$ by separation of variables or otherwise, and show that*

$$N(s) = \frac{e^{rs} N(0)}{1 + mN(0)\left(e^{rs} - 1\right)/r}.$$

Answer Introducing notation $K = r/m$, we have

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

$$N = \frac{K}{1 - Ce^{-rt}},$$

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

$$N(0) = \frac{K}{1 - C}, \quad C = 1 - K/N(0),$$

$$N(t) = N(0)e^{rt} / \left[1 + mN(0)\left(e^{rt} - 1\right)/r\right] \qquad (*)$$

The requested result is obtained for $t = s$.

5 marks for this part

(c) **Question** *By considering the limit $r \to 0$ in the previous result, or by integrating the differential equation (1) for $t \in (s, 1)$ by separation of variables, or otherwise, show that*

$$N(1) = \frac{N(s)}{1 + m(1 - s)N(s)}.$$

Answer Equation (1) at $t \in (s, 1)$ differs from that at $t \in (0, s)$ by replacing r with zero. Since $\lim_{r \to 0} \frac{e^{rt}-1}{r} = t$, formula (*) in this limit becomes

$$N(t) = N(0)e^{rt} / \left[1 + mtN(0)\right].$$

With initial conditions set at time s, this gives

$$N(s + t) = N(s) / \left[1 + mtN(s)\right].$$

Using this result to predict for time $t = 1 - s$ ahead, we get

$$N(s + 1 - s) = N(1) = N(s) / \left[1 + m(1 - s)N(s)\right] \qquad (\dagger)$$

as requested.

5 marks for this part

(d) **Question** *By combining results of parts 1b and 1c, show that the long-term dynamics of the crocodile population can be described by the following discrete-time model:*

$$N_{n+1} = \frac{RN_n}{1 + aN_n}$$

where N_n is the population size in the beginning of year n. Find coefficients R, a of this discrete-time model in terms of coefficients r, m, s of the original continuous-time model (1).

Answer Substitution of (†) into (*) gives

$$N(1) = \frac{e^{rs}N(0)\left(1 + \frac{m(e^{rs}-1)}{r}N(0)\right)^{-1}}{1 + m(1 - s)N(0)e^{rs}\left(1 + \frac{m(e^{rs}-1)}{r}N(0)\right)^{-1}}$$

$$= \frac{e^{rs}N(0)}{1 + \left[m(e^{rs} - 1)/r + m(1 - s)e^{rs}\right]N(0)} = \frac{RN(0)}{1 + aN(0)}$$

where

$$R = e^{rs} \text{ and } a = m\left[(1 - s)e^{rs} + (e^{rs} - 1)/r\right]$$

Since these relationships are true for every year, we can identify $N(0)$ and $N(1)$ of the continuous model with N_n and N_{n+1} of the discrete model, respectively.

5 marks for this part

Total for this question: 20 marks

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2. *Truscott and Brindley (1994) have suggested a model describing dynamics of plankton in the North Sea. In that model, the equation for the biomass of phytoplankton (microscopic algae), in suitably chosen units, is*

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

where x is phytoplankton biomass concentration and z is the biomass concentration of the zooplankton (microscopic crustaceans) grazing on the phytoplankton. For the purposes of the present problem, z can be considered constant, r and K are constant parameters.

   (a) **Question** *Explain 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 plankton in absence of the predators. Second term: decrease of population density due to predation. Parameter r: maximal reproduction rate of the phytoplankton. Parameter K: carrying capacity of the habitat.

   Question *What is the Holling type of the predatory response of zooplankton to phytoplankton?*

   Answer This is Holling type 3 response.

   5 marks for this part

   (b) **Question** *Assume from now on that $z = 1$. 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 this model. Use this method to demonstrate that at $K = 15$ and $r = 0.4$, there are three positive equilibrium states, and roughly estimate their values.*

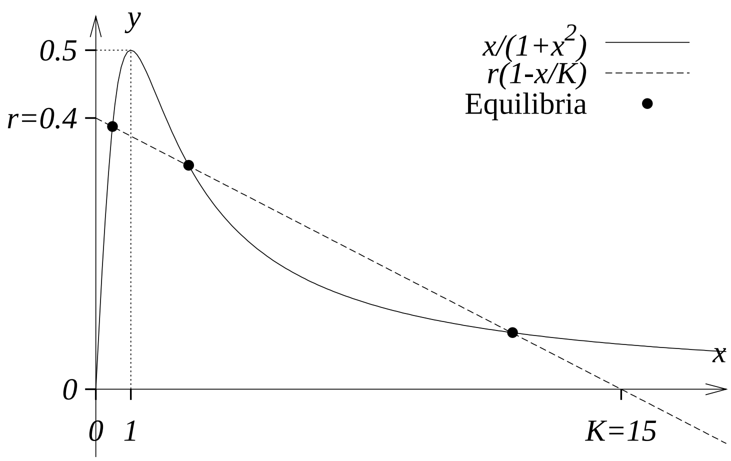
   Answer The equilibrium states in (2) are solutions of the equation

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

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

$$r(1 - x/K) = f(x)$$

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



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

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7 marks for this part

(c) **Question** *Based on the graphical method discussed in part 2b, or otherwise, derive conditions on parameters r, K 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 $y = r(1 - x/K)$ and curve $y = f(x)$, which gives the system

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

which is solved for r and K as

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

4 marks for this part

(d) **Question** *In the end of winter, the parameters of the North Sea were $r \approx 0.4$ and $K \approx 15$, and the phytoplanton density was $x \approx 0.5$. During the spring, r and K slowly increased, and phytoplankton density x slowly increased too, until the "spring bloom", i.e. a sudden increase of the phytoplankton density to a very high value ($x > 20$), occurred. Use the result of part 2c to find, to 2 significant* *figures, what were the values of the parameters r and K at that moment, if the phytoplankton density immediately before the bloom was $x = 1.05$.*

Answer As follows from the above analysis, in winter phytoplankton was in the lower stable equilibrium. The sudden onset will occur when the lower stable equilibrium ceases to exist, i.e. at a bifurcation point. The bifurcation parameters values can be found by substituting $x = 1.05$ into (*), which gives $r \approx 0.52$, $K \approx 23$.

4 marks for this part

Total for this question: 20 marks

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3. *The behaviour of a community of cowpea weevil Callosobruchus maculatus can be described by the discrete-time Hassell model:*

$$N_{t+1} = \frac{RN_t}{(1 + aN_{t-T})^b} \tag{3}$$

(a) **Question** *Explain the biological significance of the parameters R, a, b and T in this model.*

Answer R: maximal reproduction coefficient in absense of intraspecific competition. a: parameter characterising the inverse of the population size at which the intraspecific competition becomse noticeable. b: parameter characterising the severity of the intraspecific competition. T: delay of the effect of the intraspecific competition.

4 marks for this part

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

Answer

- $N = 0$, exists and feasible for all positive values of parameters.
- $N = (R^{1/b} - 1)/a$, feasible only for $R > 1$.

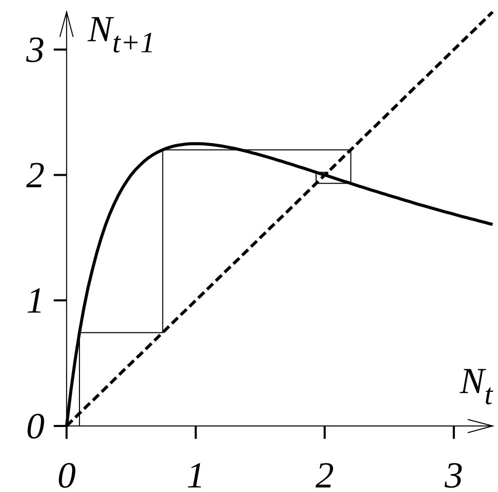
Question *In particular, specify the equilibria possible for parameter values $a = 1$, $b = 2$ and $R = 9$.*

Answer $N = 0$ and $N = (9^{1/2} - 1)/1 = 2$.

5 marks for this part

(c) **Question** *Consider the case of $T = 0$, $a = 1$, $b = 2$ and $R = 9$. Sketch a cobweb or ladder diagram for this model, 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 Cobweb diagram:



Thus the nontrivial equilibrium is oscillatory stable.

5 marks for this part

(d) **Question** *Consider the case of $T = 1$, $a = 1$, $b = 2$ and $R = 9$. 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*

$$h_{t+1} - h_t + \frac{4}{3}h_{t-1} = 0.$$

Hence show that this equilibrium is oscillatory unstable.

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

$$N_{t+1} = F(N_t, N_{t-1})$$

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

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

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

$$\frac{\partial F(N^*, N^*)}{\partial N_t} = \frac{9}{(1 + N^*)^2} = 1$$

$$\frac{\partial F(N^*, N^*)}{\partial N_{t-1}} = -\frac{2 * 9N^*}{(1 + N^*)^3} = -\frac{4}{3}$$

and therefore

$$h_{t+1} = h_t - \frac{4}{3}h_{t-1}$$

as required. Assuming solutions to this equation in the form $h_t = C\mu^t$, this gives the characteristic equation

$$\mu - 1 + \frac{4}{3}\mu^{-1} = 0$$

or, equivalently,

$$\mu^2 - \mu + \frac{4}{3} = 0$$

which has complex conjugate roots $\frac{1 \pm i\sqrt{13/3}}{2}$ with positive real part, thus oscillatory instability

6 marks for this part

Total for this question: 20 marks

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4. *The population of Kokanee salmon Oncorhynchus nerka kennerlyi living around lake Okanagan in British Columbia consists of five age groups: age 0 (eggs, larvae and fries) and 1 year old through to 4 years old fish. The fraction of the age 0 group surviving to age 1 is p_0; the fraction of the age 1 group surviving to age 2 is p_1 and the fraction of age 2 group surviving to age 3 is p_2. Half of the age 3 fish spawn at that age, producing Q eggs each in average and die after that; a fraction $p_3 < 1/2$ of age 3 fish (i.e. some of those who did not spawn) live on to age 4; the rest die without spawning. Of the age 4 fish, half spawn $2Q$ eggs each in average and die, and the other half dies without spawning, so none survive to age 5. This dynamics can be described by Leslie model*

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

where $\mathbf{N}_t = (N_t^0, \dots N_t^4)^T$ 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 fish age groups. Thus construct the Leslie transition matrix* $\mathbf{L}$.

   Answer The system:

$$\begin{aligned} N_{t+1}^0 &= 0.5QN_t^3 + QN_t^4 \\ N_{t+1}^1 &= p_0 N_t^0 \\ N_{t+1}^2 &= p_1 N_t^1 \\ N_{t+1}^3 &= p_2 N_t^2 \\ N_{t+1}^4 &= p_3 N_t^3 \end{aligned}$$

Leslie matrix is therefore

$$\mathbf{L} = \begin{bmatrix} 0 & 0 & 0 & 0.5Q & Q \\ p_0 & 0 & 0 & 0 & 0 \\ 0 & p_1 & 0 & 0 & 0 \\ 0 & & p_2 & 0 & 0 \\ 0 & 0 & 0 & p_3 & 0 \end{bmatrix}$$

4 marks for this part

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

Answer

$$P(\lambda) = \det(\mathbf{L} - \lambda\mathbf{I})$$

$$= -\lambda^5 + p_0p_1p_2(0.5Q)\lambda + p_0p_1p_2p_3Q = 0 \qquad (*)$$

Question *By considering the function $P(\lambda)/\lambda^5$ for positive λ, show that for all $p_0, \dots, p_3$ and Q positive, this polynomial always has exactly one positive root.*

Answer

$$P(\lambda)/\lambda^5 = -1 + p_0p_1p_2Q(0.5\lambda^{-4} + p_3\lambda^{-5}).$$

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

9 marks for this part

(c) **Question** *Recent years' observations have shown that $Q \approx 1000$ and that the population of fish each year is approximately $1/\sqrt{2}$ times the population the previous year. Assuming that $p_3 = 2^{-3/2}$, estimate the probability of a fish egg to survive to the mature stage (year 3).*

Answer The requested probability is a product of three factors, $p_0p_1p_2$. The characteristic equation (*) can be re-written in the form

$$p_0p_1p_2(\lambda Q/2 + p_3Q) = \lambda^5$$

Substitute here $p_3 = 2^{-3/2}$, $Q = 1000$, $\lambda = 2^{-1/2}$ and resolve for $p_0p_1p_2$, this gives

$$p_0p_1p_2 = \frac{2^{-5/2}}{2^{-1/2}Q} = \frac{1}{4000}.$$

Question *Find the stationary age distribution in terms of parameters p_0 and p_1.*

Answer The stationary age distribution vector $\mathbf{N}$ is a solution of

$$(\mathbf{L} - \lambda\mathbf{I})\mathbf{N}_* = 0,$$

and can be chosen as

$$\mathbf{N}_* = \left[\ 1,\quad \lambda^{-1}p_0,\quad \lambda^{-2}p_0p_1,\quad \lambda^{-3}p_0p_1p_2,\quad \lambda^{-4}p_0p_1p_2p_3\ \right]^T.$$

As we know that $\lambda = 2^{-1/2}$, $p_3 = 2^{-3/2}$ and $p_0p_1p_2 = 1/4000$, this reduces to

$$\mathbf{N}_* = \left[\ 1,\quad \sqrt{2}p_0,\quad 2p_0p_1,\quad \sqrt{2}/2000,\quad \sqrt{2}/4000\ \right]^T.$$

Question *In particular, determine the established ratio of numbers of 3-year-old and 4-year-old fish.*
Answer $N_*^3 : N_*^4 = 2 : 1.$.

7 marks for this part

Total for this question: 20 marks

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5. *About 40 thousand years ago, the well established existence of the European population of Homo neanderthalensis has been challenged by a new aggressive species Homo sapiens which invaded from Africa. The two species competed for mammoths and caves, and their interaction could be described by a Lotka-Volterra-Gause model*

$$\begin{aligned} \mathrm{d}N_1/\mathrm{d}t &= N_1\left(r_1 - a_1N_1 - b_{12}N_2\right) \\ \mathrm{d}N_2/\mathrm{d}t &= N_2\left(r_2 - a_2N_2 - b_{21}N_1\right) \end{aligned} \tag{5}$$

where N_1 and N_2 are densities of H. sapiens and H. neanderthalensis respectively, and the numerical values of the coefficients, in appropriate units, are $r_1 = 5$, $r_2 = 4$, $a_1 = a_2 = 2$, $b_{12} = b_{21} = 1$.

(a) **Question** *Describe the biological significance of the parameters r_j, a_j and b_{jk}.*
Answer r_j: maximal reproduction rates. a_j: intensity of the intraspecific competition within the species. b_{jk}: intensity of the interspecific competion between the species.

3 marks for this part

(b) **Question** *Assuming that the two species actually coexisted for some time, find their equilibrium densities.*
Answer Conditions of equilibrium:

$$\begin{aligned} \mathrm{d}N_1/\mathrm{d}t &= N_1(5 - 2N_1 - N_2) = 0, \\ \mathrm{d}N_2/\mathrm{d}t &= N_2(4 - N_1 - 2N_2) = 0. \end{aligned}$$

Coexistence: both N_1 and N_2 are nonzero, thus

$$\begin{aligned} 2N_1 + N_2 &= 5, \\ N_1 + 2N_2 &= 4 \end{aligned}$$

solution of which is

$$N_1^* = 2, \quad N_2^* = 1.$$

Question *By how much did this unfortunate invasion decrease the population of the Neanderthals?*

Answer In absence of *H. sapiens*, i.e. $N_1 = 0$, the Neanderthal population obeyed

$$\mathrm{d}N_2/\mathrm{d}t = N_2(4 - 2N_2) = 0.$$

with stable equilibrium $N_2 = 2$, i.e. twice larger than after the invasion.

6 marks for this part

(c) **Question** *Rewrite the model (5) for new dynamic variables x, y defined by*

$$N_1 = 2 + x, \qquad N_2 = 1 + y.$$

Find the orbit derivative of function V defined as

$$V(x, y) = x^2 + xy + y^2$$

and show that it is negatively definite in the region $\{N_1 > 0, N_2 > 0\} = \{x > -2, y > -1\}$. What does this result mean for (i) stability of the coexistence equilibrium, (ii) possibility of periodic solution in this model?

Answer

$$\begin{aligned} \mathrm{d}x/\mathrm{d}t &= -(2 + x)(2x + y) \\ \mathrm{d}y/\mathrm{d}t &= -(1 + y)(x + 2y) \end{aligned}$$

$$\frac{\mathrm{d}V}{\mathrm{d}t} = \frac{\partial V}{\partial x}\frac{\mathrm{d}x}{\mathrm{d}t} + \frac{\partial V}{\partial y}\frac{\mathrm{d}y}{\mathrm{d}t}$$

$$= -(2 + x)(2x + y)^2 - (1 + y)(x + 2y)^2$$

which is negative as long as $2 + x > 0$, $1 + y > 0$ and x and y don't vanish simultaneously, i.e. negatively definite as requested. By Lyapunov's theorem, the coexistence equilibrium is globally stable in this region, and periodic solutions are impossible.

7 marks for this part

(d) **Question** *Only a few thousand years after the invasion, H. sapiens outperformed their competitors by inventing bone needles, which allowed them to make clothes out of mammoth wool and thus significantly decreased mortality due to harsh weather conditions. Specify which parameter in the model (5) would describe that change. Assuming that that was the only factor, find out the minimal change in that parameter necessary for complete extinction of the Neanderthals.*

Answer Competition unrelated mortality is the negative contribution to the maximal reproduction rate, i.e. its decrease means increase of the coefficient r_1. At all other parameters fixed, the coexistence equilibrium now satisfies

$$\begin{aligned} 2N_1 + N_2 &= r_1, \\ N_1 + 2N_2 &= 4 \end{aligned}$$

solution of which is

$$N_1^* = \frac{4r_1 - 8}{6}, \quad N_2^* = \frac{16 - 2r_1}{6}.$$

For r_1 increasing from $r_1 = 5$, this equilibrium becomes non-feasible ($N_2 < 0$) when r_1 exceeds 8.

4 marks for this part

Total for this question: 20 marks

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6. *The tachinid fly Myiopharus doryphorae parasitises on the beetle Leptinotarsa decemlineata, which is also known as the Colorado beetle and is a ferocious pest of potato plantations. An ecologically aware potato farmer decided, rather than using insecticides, to combat the beetles by keeping a population of these useful flies. Based on his own observation of the insects, the farmer developed a variant of the Lotka-Volterra predator-prey model to describe the interaction of the two species:*

$$\begin{aligned} \frac{\mathrm{d}B}{\mathrm{d}t} &= B - B^2 - BF, \\ \frac{\mathrm{d}F}{\mathrm{d}t} &= BF - F^2. \end{aligned} \tag{6}$$

where B stands for the population of the beetles and F for the population of the flies.

(a) **Question** *Describe the biological meaning of each of the five terms in the right-hand sides of equations (6).*

Answer In the first equation: B: reproduction of the beetles, feeding on the potatos, $-B^2$: density-dependent component of mortality of beetles (intraspecific competition), $-BF$: beetles mortality due to predation by the flies, In the second equation: BF: reproduction rate of the flies due to their feeding on the beetles, $-F^2$: density-dependent mortality of flies (intraspecific competition).

5 marks for this part

(b) **Question** *Find the equilibria in this model and classify their stability.*

Answer The Jacobian of the right-hand sides:

$$J(B, F) = \frac{\partial(\dot{B}, \dot{F})}{\partial(B, f)} = \begin{bmatrix} 1 - 2B - F & -B \\ F & B - 2F \end{bmatrix}$$

The equilibria satisfy system of equations

$$B(1-B-F)=0,$$
$$F(B-F)=0.$$

Total extinction equilibrium: $B=F=0$. Its community matrix $J(0,0) = \begin{bmatrix} 1 & 0 \\ 0 & 0 \end{bmatrix}$, eigenvalues $\lambda_{1,2}=\{0,1\}$; as at least one of the eigenvalues is positive, this equilibrium is unstable.
Monopolistic survival of beetles: $B=1$, $F=0$. Its community matrix $J(1,0) = \begin{bmatrix} -1 & -1 \\ 0 & 1 \end{bmatrix}$, eigenvalues $\lambda_{1,2}$, i.e. it is a saddle point.
Monopolistic survival of flies is impossible: $B=0$ implies $F=0$.
Coexistence: if $B \neq 0$ and $F \neq 0$, then $B=F=1/2$. Its community matrix is $J(1/2,1/2) = \begin{bmatrix} -1/2 & -1/2 \\ 1/2 & -1/2 \end{bmatrix}$ with eigenvalues $\lambda_{1,2} = \frac{-1\pm i}{2}$, i.e. it is a stable focus.

Question *Thus explain why the farmer's first attempt to exterminate the beetles has failed.*

Answer There are no beetle-free equilibria in this system, and the only stable equilibrium is coexistence of beetles with the flies.

10 marks for this part

(c) **Question** *Inspired by this mathematical model, the farmer has decided that he may be more successful if he supports his useful flies with some additional food source, which would allow them to survive even in the complete absence of beetles. To reflect this change, he modified his model in the following way:*

$$\frac{\mathrm{d}B}{\mathrm{d}t} = B - B^2 - BF,$$
$$\frac{\mathrm{d}F}{\mathrm{d}t} = sF + BF - F^2,$$

where parameter s represents the additional reproduction rate of the flies due to the supplement. Find what values of s would be sufficient to get rid of the beetles by making their coexistence with the flies impossible. Verify that the beetle-free existence of the flies in that case will be stable.

Answer The modified coexistence conditions are

$$1-B-F=0,$$
$$s+B-F=0.$$

The solution is $B=\frac{1-s}{2}$, $F=\frac{1+s}{2}$. This becomes biologicaly non-feasible ($B<0$) if $s>1$.. The beetle-free state of the flies, $B=0$, is possible when simultaneously $sF + BF - F^2 = 0$ at $F \neq 0$, i.e. $F = s$. Its community matrix is $J(B, F) = \begin{bmatrix} 1-2B-F & -B \\ F & s+B-2F \end{bmatrix}$, $J(0, s) = \begin{bmatrix} 1-s & 0 \\ s & -s \end{bmatrix}$ with eigenvalues $\lambda_{1,2} = \{1-s, -s\}$ which at $s > 1$ are both real negative, and the beetle-free state is a stable node.

5 marks for this part

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*

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

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

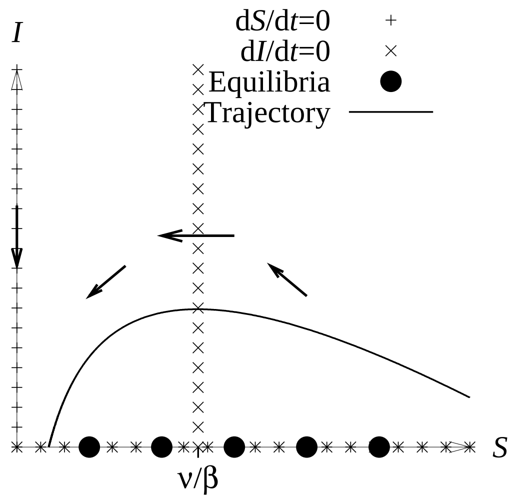
(a) **Question** *Explain the biological meaning of the terms in these equations, and what biological assumptions have been used in this model.*

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 succeptibles 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 marks for this part

(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 marks for this part

(c) **Question** *The Bombay epidemic involved only a small fraction of the city population. Substitute $S = \nu/\beta + \sigma$ into (7) and assume that $|\sigma|$ and I are small. Simplify the first equation by keeping the main term and neglecting the smaller term. Verify by substitution that the following functions are a solution to the resulting system, for arbitrary p:*

$$\sigma = -\frac{2}{\beta} p \tanh(pt); \qquad I = \frac{2}{\nu\beta} p^2 \operatorname{sech}^2(pt)$$

(remember that $(\tanh x)' = \operatorname{sech}^2 x = 1 - \tanh^2 x$*).*

Answer The suggested substitution leads to the system

$$\begin{aligned} \mathrm{d}\sigma/\mathrm{d}t &= -\nu I - \beta\sigma I \\ \mathrm{d}I/\mathrm{d}t &= \beta\sigma I \end{aligned}$$

In the first equation, the second term is much smaller than the first term because σ is assumed small; discarding that term gives

$$\begin{aligned} \mathrm{d}\sigma/\mathrm{d}t &= -\nu I \\ \mathrm{d}I/\mathrm{d}t &= \beta\sigma I. \end{aligned}$$

Substitution of the given solution gives: $\dot{\sigma} = -\frac{2}{\beta}p^2 \operatorname{sech}^2(pt) = -\nu I$, and $-\nu I = -\frac{2}{\beta}p^2 \operatorname{sech}^2(pt) = \dot{\sigma}$, thus the first equation is satisfied. Similarly, $\dot{I} = \frac{2}{\nu\beta}p^2 \left(1 - \tanh^2(pt)\right)' = -\frac{2}{\nu\beta}p^2 (2\tanh pt)(p \operatorname{sech}^2 pt) = -\frac{2}{\nu\beta}p^3 \tanh pt \operatorname{sech}^2 pt$, and $\beta\sigma I = \beta\left(-\frac{2}{\beta}p\right)\left(\frac{2}{\nu\beta}p^2\right)\tanh pt \operatorname{sech}^2 pt = -\frac{4}{\nu\beta}p^3 \tanh pt \operatorname{sech}^2 pt = \dot{I}$ and the second equation is satisfied.

4 marks for this part

(d) **Question** *The number of deaths per week in the Bombay epidemic can be approximately described by the following dependence:*

$$800 \ \mathrm{sech}^2(0.2t),$$

where time is measured from the middle of the epidemic. Using the analytical solution discussed in part 7c, what information about the parameters of the model can be deduced from these statistical data?

Answer As the majority of cases of plague are lethal, the number of deaths is approximately the same as the rate of removal, i.e. νI. The analytical solution gives for it $\nu I = \frac{2}{\beta} p^2 \,\mathrm{sech}^2\, pt$. Comparing this with the statistics, we find that $p = 0.2$ and $\beta = 2p^2/800 = 10^{-4}$.

4 marks for this part

Total for this question: 20 marks
