Math3506, 2014. Model solutions

Qu1

(a) This is a predator-prey model. There are intraspecifc competition terms $-bx^2, -fy^2$. ex is the predator per capita growth from consuming prey x and $-cy$ is the per capita reduction in prey x due to consumption by predator y. The carrying capacity for x is a/b and for y is 0.

(b) Steady states are $(0,0)$, $(a/b, 0)$ and any interior steady state solves

$$a - bx - cy = 0, \quad -d + ex - fy = 0.$$

Solving we get

$$(x^*, y^*) = \frac{1}{bf + ce}(fa + cd, ea - bd),$$

so we require $ae > bd$ for an interior steady state to exist.
For stability, we find the stability matrix

$$M = \begin{pmatrix} (a - bx - cy) - bx & -cx \\ ey & (-d + ex - fy) - fy \end{pmatrix}.$$

At $(0,0)$ we have

$$M = \begin{pmatrix} a & 0 \\ 0 & -d \end{pmatrix},$$

which has eigenvalues $a, -d$ hence $(0,0)$ is a saddle. At $(a/b, 0)$ we have

$$M = \begin{pmatrix} -a & -ac/b \\ 0 & -d + ea/b \end{pmatrix},$$

which has eigenvalues which are opposite sign when $ae > bd$ and then $(a/b, 0)$ is a saddle. If $ae < bd$ then $(a/b, 0)$ is stable. At the interior steady state (x^*, y^*) we have

$$M = \begin{pmatrix} -bx^* & -cx^* \\ ey^* & -fy^* \end{pmatrix}.$$

Thus $\lambda_1 + \lambda_2 = -bx^* - fy^* < 0$ and $\lambda_1 \lambda_2 = x^* y^* (bf + ce) > 0$ when the interior steady state exists. Hence both eigenvalues have negative real part and the interior steady state is locally stable when it exists.

(c) See fig 1

(d) When $b = 0$ and $f = 0$ the system reduces to the Lotka-Volterra predator prey model in which all trajectories are periodic.

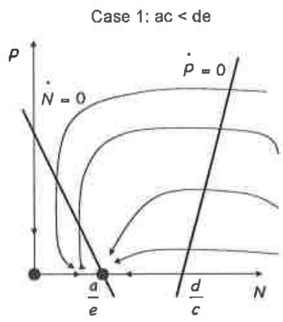


Figure 1: Qu 1 part . $ae < bd$

Qu2

(a) N_1 is the prey, N_2 is the predator.

(b) Hyperbolic response curve, asymptoting at γ. γ is the maximum feeding rate of the predator.

(c) If $N_2 = 0$, $N_1 = 0$ and $N_1 = K$. If $N_2 > 0$ then $N_1 = \mu/\sigma$ and $\phi(N_1, N_2) = \rho N_1(1 - N_1/K)$ which gives

$$\rho N_1(1 - N_1/K) = \frac{\gamma N_1 N_2}{A + N_1}$$

which gives $N_2 = \frac{\rho}{\gamma K}(A + \frac{\mu}{\sigma})(K - \frac{\mu}{\sigma})$. Hence the steady states are $(N_1, N_2) = (0,0)$, $(K, 0)$ and when $\mu < \sigma K$ a 3rd and interior $(\frac{\mu}{\sigma}, \frac{\rho}{\gamma K}(A + \frac{\mu}{\sigma})(K - \frac{\mu}{\sigma}))$.

(c)

$$J = \begin{pmatrix} -\frac{N_2\gamma}{A+N_1} + \frac{N_1 N_2 \gamma}{(A+N_1)^2} - \frac{N_1\rho}{K} + \left(1 - \frac{N_1}{K}\right)\rho & -\frac{N_1\gamma}{A+N_1} \\ N_2\sigma & N_1\sigma - \mu \end{pmatrix}$$

Thus $J(0,0) = \text{diag}(\rho, -\mu)$ so $(0,0)$ is a saddle. $J(K,0) = \begin{pmatrix} -\rho & -\frac{K\gamma}{A+K} \\ 0 & K\sigma - \mu \end{pmatrix}$ so that $(K, 0)$ is a stable node for $\mu > \sigma K$ and a saddle for $\mu < \sigma K$. When

$\mu < \sigma K$ the interior steady state (N_1^*, N_2^*) has

$$J(N_1^*, N_2^*) = \begin{pmatrix} \frac{\mu\rho((K-A)\sigma-2\mu)}{K\sigma(\mu+A\sigma)} & -\frac{\gamma\mu}{\mu+A\sigma} \\ \frac{\rho(\mu+A\sigma)(K\sigma-\mu)}{K\gamma\sigma} & 0 \end{pmatrix}.$$

We have $\det J(N_1^*, N_2^*) = \mu\rho\left(1-\frac{\mu}{K\sigma}\right) > 0$ since $\mu < \sigma K$. The stability of (N_1^*, N_2^*) is thus determined by $\text{trace}J(N_1^*, N_2^*) = \frac{\mu\rho((K-A)\sigma-2\mu)}{K\sigma(\mu+A\sigma)}$. For $(K-A)\sigma - 2\mu < 0$ (N_1^*, N_2^*) is locally stable, and for $(K-A)\sigma - 2\mu > 0$ (N_1^*, N_2^*) is unstable.

(d) If $K\sigma < 2\mu$ then the trace is always negative and hence (N_1^*, N_2^*) locally stable. A limit cycle can therefore occur only if $K\sigma > 2\mu$. The critical value at which it occurs is $A_c = \frac{K\sigma-2\mu}{\sigma}$. As A decreases from just greater than A_c to just less than A_c a stable limit cycle appears around the interior steady state. (students are not required to verify all Hopf conditions).

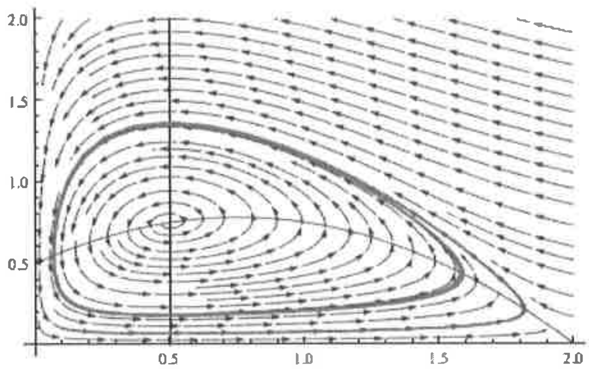
(e) 

Figure 2: Qu 2 part (e).

Qu3

(a) x^* must satisfy $x^* = f(x^*)$. x^* is locally asymptotically stable when $|f'(x^*)| < 1$.

(b) Real and non-negative solutions to $x^* = f(x^*)$ are now $x^* = 0$ and when $r > 1$, a second $x^* = (r-1)^{\frac{1}{3}}$.

$$f'(x) = \frac{r}{x^3+1} - \frac{3rx^3}{(x^3+1)^2} = \frac{r-2rx^3}{(x^3+1)^2}.$$

Thus $f'(0) = r$ so that $x^* = 0$ is locally stable for $r < 1$ and unstable for $r > 1$. For $r > 1$ we have

$$f'((r-1)^{\frac{1}{3}}) = \frac{r-2(r-1)r}{r^2} = \frac{3}{r} - 2 < 1 \text{ for } r > 1.$$

Hence $x^* = (r-1)^{\frac{1}{3}}$ is locally stable when it exists.

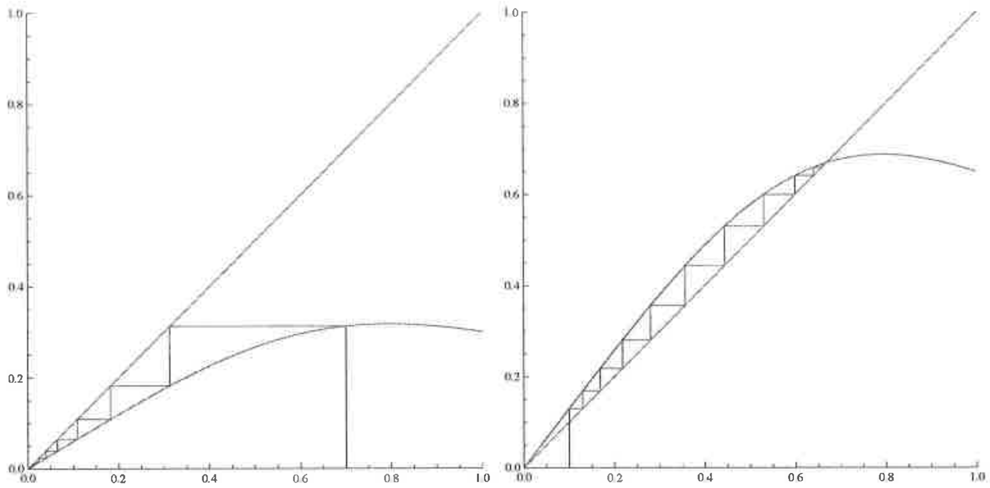


Figure 3: Q3 part b. Left $r < 1$, right $r > 1$

(c) We now have $x_{t+1} = \frac{rx_t}{1+x^3} - x_t$. Then new steady states are $x^* = 0$ and $x^* = (\frac{r-2}{2})^{\frac{1}{3}}$ when $r > 2$. At $x^* = (\frac{r-2}{2})^{\frac{1}{3}}$ we have

$$f'(x^*) = \frac{r - 2rx^3}{(x^3+1)^2} - 1 = \frac{r - (r-2)r}{(\frac{r-2}{2}+1)^2} - 1 = -5 + \frac{12}{r}.$$

Notice that for $r > 3$ we have $f'(x^*) < -1$ and so a stable 2-cycle appears around x^* as r increases through $r = 3$. Thus for $r \in (2, 3)$, $x^* = 0$ is unstable, $x^* = (\frac{r-2}{2})^{\frac{1}{3}}$ locally stable, but for $r > 3$ $x^* = (\frac{r-2}{2})^{\frac{1}{3}}$ becomes unstable and a stable 2-cycle appears.

Qu4

(a)

$$L = \begin{pmatrix} f_1 & f_2 & f_3 & \cdots & f_{n-1} & f_n \\ p_1 & 0 & 0 & \cdots & 0 & 0 \\ 0 & p_2 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \cdots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & p_{n-1} & 0 \end{pmatrix}.$$

(Here $f_k = p_0 b_k$ is the expected number of offspring per adult of age k that survive from birth to age 1).

(b) Characteristic polynomial reads $c(\lambda) = \det(L - \lambda I)$. We find the characteristic polynomial ϕ_n whose roots are the eigenvalues of L_n:

$$\phi_n(\lambda) = |L_n - \lambda I_n|.$$

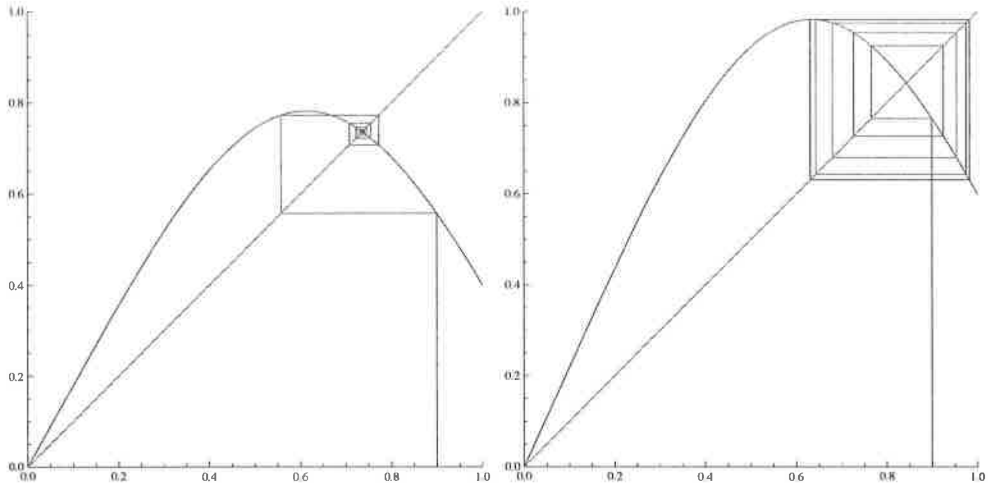


Figure 4: Q3 part c. Left $r < 3$, right $r > 3$

Thus

$$\phi_n(\lambda) = \begin{vmatrix} f_1 - \lambda & f_2 & f_3 & \cdots & f_n \\ p_1 & -\lambda & 0 & \cdots & 0 \\ 0 & p_2 & -\lambda & \cdots & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & \cdots & 0 & p_{n-1} & -\lambda \end{vmatrix}$$

Expand via the last column:

$$\phi_n(\lambda) = (-1)^{n-1} f_n \begin{vmatrix} p_1 & -\lambda & 0 & \cdots & 0 \\ 0 & p_2 & -\lambda & \cdots & 0 \\ \vdots & \vdots & \vdots & \vdots & -\lambda \\ 0 & \cdots & \cdots & \cdots & p_{n-1} \end{vmatrix} + (-\lambda) \begin{vmatrix} f_1 - \lambda & f_2 & f_3 & \cdots & f_{n-1} \\ p_1 & -\lambda & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & \cdots & 0 & p_{n-2} & -\lambda \end{vmatrix}$$

Hence, letting $l_k = p_0 p_1 \cdots p_{k-1}$ be the probability of survival to age k (from birth),

$$\begin{aligned} \phi_n(\lambda) &= (-1)^{n-1}(p_0 p_1 \cdots p_{n-1}) b_n - \lambda \phi_{n-1} \\ &= (-1)^{n-1} l_n b_n - \lambda \phi_{n-1} \\ &= (-1)^{n-1} l_n b_n - \lambda((-1)^{n-2} l_{n-1} b_{n-1} - \lambda \phi_{n-2}) \\ &= (-1)^{n-1}(l_n b_n + \lambda l_{n-1} b_{n-1}) + \lambda^2 \phi_{n-2} \\ &= (-1)^{n-1}(l_n b_n + \lambda l_{n-1} b_{n-1}) + \lambda^2((-1)^{n-3} l_{n-2} b_{n-2} - \lambda \phi_{n-3}) \\ &= (-1)^{n-1}(l_n b_n + \lambda l_{n-1} b_{n-1} + \lambda^2 l_{n-2} b_{n-2}) + \lambda^3 \phi_{n-3} \end{aligned}$$

Continuing we obtain:

$$\phi_n(\lambda) = (-1)^{n-1}\left\{\sum_{r=0}^{n-2} b_{n-r}l_{n-r}\lambda^r + \lambda^{n-1}\phi_1\right\}$$

But $\phi_1(\lambda) = f_1 - \lambda = b_1 l_1 - \lambda$ and hence

$$\phi_n(\lambda) = (-1)^{n-1}\left\{\sum_{r=0}^{n-2} b_{n-r}l_{n-r}\lambda^r + \lambda^{n-1}(b_1 l_1 - \lambda)\right\}$$

giving finally

$$\phi_n(\lambda) = (-1)^{n-1}\lambda^n\left\{\sum_{r=0}^{n-1} b_{n-r}l_{n-r}\lambda^{r-n} - 1\right\} = (-1)^{n-1}\lambda^n\left\{\sum_{k=1}^{n} b_k l_k \lambda^{-k} - 1\right\}$$

The non-zero eigenvalues of the Leslie matrix thus satisfy the **Euler-Lotka equation**

$$\sum_{k=1}^{\infty}\frac{b_k l_k}{\lambda^k} = 1.$$

(Note that we can sum to infinity as each $l_k = 0$ for $k > n$.)

(c) We now have $f_k = 0$ for $k = 1, \ldots, n-1$. Thus $\lambda^n = b\ell_n$ which gives $\lambda = (bl_n)^{1/n}\exp(\frac{2\pi k}{n})$ for $k = 0, 1, \ldots, n-1$.

$$N(t+n) = L^{t+n}N(0) = \Re\{\sum_{k=0}^{n-1}\lambda_k^{t+n}\alpha_k v_k\} = \Re\{\sum_{k=0}^{n-1}\lambda_k^t\alpha_k v_k\} = \omega N(t).$$

When we look at the age distribution $\mathbf{X}$ we are left with $\mathbf{X}$ as the ratio of two periodic functions of period n, i.e. a periodic function of period n.

(d) The population will die out if $bl_n = bp_0p_1\cdots p_{n-1} < 1$, i.e. $b_{critical} = (p_0p_1\cdots p_{n-1})^{-1}$.

Qu5

(a)

$$\int_0^{N(t)}\frac{dN}{N(1-N/K)} = \int_0^t r\,dt = rt$$

$$\int_0^{N(t)}\frac{dN}{N(1-N/K)} = \int_0^{N(t)}\frac{1}{N} + \frac{1}{K-N}\,dN = \log\frac{(K-N_0)N(t)}{N_0(K-N(t))}$$

$$\Rightarrow e^{rt} = \frac{(K-N_0)N(t)}{N_0(K-N(t))}.$$

$$\Rightarrow N(t) = \frac{N_0}{\frac{N_0}{K} + (1-\frac{N_0}{K})e^{-rt}}$$

(b) With $d\tau = \rho(t)\,dt$ we have $\tau = \int_0^t \rho(s)\,ds$. This gives

$$N(t) = \frac{N_0}{\frac{N_0}{K} + (1 - \frac{N_0}{K})e^{-r\tau(t)}} = \frac{N_0}{\frac{N_0}{K} + (1 - \frac{N_0}{K})e^{-r\int_0^t \rho(s)\,ds}}$$

But ρ periodic, period T. Set $t = nT + s$ then $\int_0^t \rho(s)\,ds = nRT + \int_0^s \rho(u)\,du$ which gives the desired result.

(c) When (i) $R > 0$, $N(t) \to K$, (ii) $R < 0$, $N(t) \to 0$.

(d) When $R = 0$, $N(t)$ is periodic with period T (when bounded!). If (i) $N_0 < K$ then $N(t)$ remains bounded for all t, but if (ii) $N_0 > K$ then it is possible for $N(t)$ to become unbounded on $[0, T]$.