INTRODUCTION TO MATHEMATICAL BIOLOGY

HOMEWORK SOLUTIONS

December 12, 2016

Exercise 11.1

(a) The positive equilibrium of the system is

$$\hat{N} = \frac{\delta}{(\gamma - \delta T)\beta}$$
$$\hat{P} = \frac{\gamma}{\delta} r \hat{N}(1 - \hat{N}/K)$$

which exists positive if and only if $\gamma > \delta T$ and $\hat{N} < K$. We note that $\hat{N}$ is independent of the parameters r and K.
(b) We compute the jacobian at equilibrium:

$$J = \begin{pmatrix} \hat{N}\left(-r/K + \beta\hat{P}\frac{\beta T}{(1+\beta T\hat{N})^2}\right) & -\frac{\beta\hat{N}}{1+\beta T\hat{N}} \\ \gamma\beta\hat{P}\frac{(1+\beta T\hat{N})-\hat{N}\beta T}{(1+\beta T\hat{N})^2} & \frac{\gamma\beta\hat{N}}{(1+\beta T\hat{N})} - \delta \end{pmatrix} = \begin{pmatrix} \frac{r\hat{N}}{K}\frac{-1+\beta TK-2\beta T\hat{N}}{1+\beta T\hat{N}} & -\frac{\delta}{\gamma} \\ r\gamma\frac{K-\hat{N}}{K(1+\beta T\hat{N})} & 0 \end{pmatrix}$$

$$\operatorname{tr}(J) = \frac{r\hat{N}}{K}\frac{\beta TK - 1 - 2\beta T\hat{N}}{1+\beta T\hat{N}}, \qquad \det(J) = \delta r\frac{K-\hat{N}}{K(1+\beta T\hat{N})} > 0$$

Notice that $\operatorname{tr}(J)$ can be positive or negative according to the value of the parameters. When increasing K the value of $\hat{N}$ stays constant and the trace goes from negative to positive values, hence destabilizing the equilibrium. A necessary condition for Hopf bifurcation to occur is $\operatorname{tr}(J) = 0$. Notice that this condition is also sufficient since $\det(J) > 0$ (whenever the equilibrium exists positive). Hence, a Hopf bifurcation occurs at

$$\begin{aligned}
& \frac{r\hat{N}}{K}\frac{\beta TK - 1 - 2\beta T\hat{N}}{1+\beta T\hat{N}} = 0 \\
\Leftrightarrow\ & \beta TK - 1 - 2\beta T\hat{N} = 0 \\
\Leftrightarrow\ & \beta TK - 1 - \frac{2T\delta}{(\gamma - \delta T)} = 0 \\
\Leftrightarrow\ & K_{\text{Hopf}} = \frac{\gamma + \delta T}{\beta T(\gamma - \delta T)}
\end{aligned}$$

Exercise 11.2

Consider the Lotka–Volterra predator-prey model

$$\begin{aligned}\frac{dN}{dt} &= rN - \beta NP \\ \frac{dP}{dt} &= \gamma\beta NP - \delta P\end{aligned} \tag{2}$$

and the single differential equation

$$\frac{dP}{dN} = \frac{\gamma\beta NP - \delta P}{rN - \beta NP}$$

We solve it by separation of variables:

$$\frac{r - \beta P}{P} dP = \frac{\gamma\beta N - \delta}{N} dN$$

By integrating both sides, we get

$$\int \frac{r - \beta P}{P} dP = \int \frac{\gamma\beta N - \delta}{N} dN$$
$$\Leftrightarrow \quad r \ln P - \beta P = \gamma\beta N - \delta \ln N + c$$

where c is a constant that can be determined from the initial conditions. Hence, any orbit (N, P) is such that

$$\Phi(N, P) = r \ln P + \delta \ln N - \beta P - \gamma\beta N$$

is constant, hence every orbit lies on a contour line of $\Phi(N, P)$. By plotting the contour lines of $\Phi(N, P)$ (see Figure 1), we conclude that the solutions of the systems are periodic.

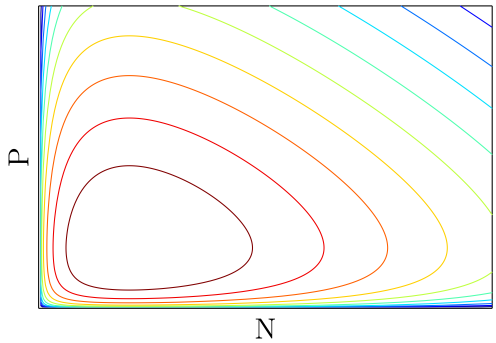

Figure 1: Contour lines of $\Phi(N, P)$, plotted with the Matlab function `contour`.

Exercise 11.3

Let $(N(t), P(t))$ be a periodic solutions of (2) with period T. Let $n(t) = \ln N(t)$, $p(t) = \ln P(t)$. Then, we can write

$$\begin{aligned}\frac{dn}{dt} &= \frac{N'}{N} = r - \beta P \\ \frac{dp}{dt} &= \frac{P'}{P} = \gamma\beta N - \delta.\end{aligned}$$

Since after T time the system goes back to the initial point, it holds

$$0 = n(T) - n(0) = \int_0^T \frac{dn}{dt}dt = \int_0^T (r - \beta P(t))dt = rT - \beta \int_0^T P(t)dt$$
$$0 = p(T) - p(0) = \int_0^T \frac{dp}{dt}dt = \int_0^T (\gamma\beta N(t) - \delta)dt = \gamma\beta \int_0^T N(t)dt - \delta T$$

From the latter equations we conclude

$$\frac{1}{T}\int_0^T N(t)dt = \frac{\delta}{\gamma\beta}$$
$$\frac{1}{T}\int_0^T P(t)dt = \frac{r}{\beta}.$$

Exercise 11.4

The zero-growth isoclines of the of the system are (see Figure 2)

$$N_1\text{-isocline: } N_1 = 0 \quad \text{or} \quad N_2 = f(N_1) := \frac{1}{a_{12}}\left[\frac{\beta N_1}{\alpha + N_1} - \delta_1 - a_{11}N_1\right]$$
$$N_2\text{-isocline: } N_2 = 0 \quad \text{or} \quad N_2 = g(N_1) := \frac{1}{a_{22}}\left[b - \delta_2 - a_{21}N_1\right].$$

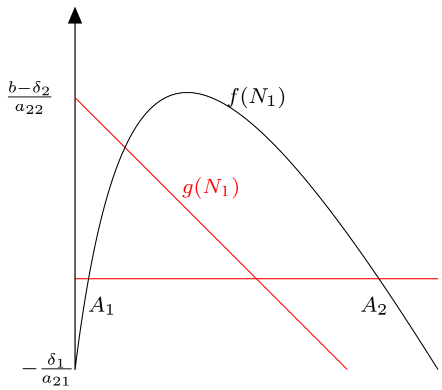

Figure 2: Qualitative shape of the isoclines of the system in the plane (N_1, N_2). Black: N_1-isocline, red: N_2-isocline. (Note that the relative position of the isoclines depends on the parameters).

Note that the N_1-isocline is independent of b and $f(N_1)$ is a concave function: if the maximum value is negative, then there is no interior equilibrium. Otherwise, if the maximum of $f(N_1)$ is positive (calculate conditions!) there are two intersections with the N_1-axis at

$$A_{1,2} = \frac{\beta - \delta_1 - \alpha a_{11} \pm \sqrt{(\beta - \delta_1 - \alpha a_{11})^2 - 4\delta_1\alpha a_{11}}}{2a_{11}}$$

(which are both positive).

The N_2-isocline is the union of the axis $N_2 = 0$ and the straight line $g(N_1)$ with negative angular coefficient $-a_{21}/a_{22}$, which intersects the N_2-axis at $(b - \delta_2)/a_{22}$ and the N_1-axis at $(b - \delta_2)/a_{21}$. Hence, increasing b does not affect the slope of the line, but it shifts the line vertically.

Therefore, we can distinguish three cases.

(i) the maximum of f is negative: there is no interior equilibrium of the system for any value of b.

(ii) the maximum of f is positive and $-a_{21}/a_{22} < f'(A_2) < 0$: the system has no interior equilibrium for $0 \le b \le b_1$ such that $(b_1 - \delta_2)/a_{21} = A_1$; one interior equilibrium for $b_1 < b \le b_2$ such that $(b_2 - \delta_2)/a_{21} = A_2$; no interior equilibrium for $b > b_2$ (two transcritical bifurcations).

(iii) the maximum of f is positive and $-a_{21}/a_{22} \ge f'(A_2)$: the system has no interior equilibrium for $0 \le b \le b_1$; one interior equilibrium for $b_1 < b \le b_2$; two interior equilibria for $b_2 \le b < b_3$ such that f and g are tangent for $b = b_3$; no interior equilibrium for $b > b_3$ (two transcritical bifurcations and one fold bifurcation of equilibria).

Exercise 11.5

Note that necessary conditions for the existence of a positive equilibrium are

$$\rho_1 a_{22} - \rho_2 a_{12} > 0, \quad \text{and} \quad \rho_2 a_{11} - \rho_1 a_{21} > 0,$$

that imply

$$a_{11}a_{22} - a_{12}a_{21} > 0. \tag{1}$$

(a) Note that $Q(\hat{N}_1, \hat{N}_2) = 0$ and

$$Q(N_1, N_2) = a_{11}a_{21}\left[\left((N_1 - \hat{N}_1) + \frac{a_{12}}{a_{11}}(N_2 - \hat{N}_2)\right)^2 + \frac{a_{12}}{a_{11}}\frac{a_{11}a_{22} - a_{12}a_{21}}{a_{11}a_{21}}(N_2 - \hat{N}_2)^2\right] > 0$$

thanks to (1).

Finally, we check that Q is decreasing along the trajectories by exploiting the fact that $(\hat{N}_1, \hat{N}_2)$ is an equilibrium and by assuming $a_{12}a_{21} > 0$:

$$\begin{aligned}
\frac{dQ}{dt} &= 2a_{21}[a_{11}(N_1 - \hat{N}_1) + a_{12}(N_2 - \hat{N}_2)]\dot{N}_1 + 2a_{12}[a_{21}(N_1 - \hat{N}_1) + a_{22}(N_2 - \hat{N}_2)]\dot{N}_2 \\
&= 2a_{21}[a_{11}N_1 + a_{12}N_2 - \rho_1](\rho_1 - a_{11}N_1 - a_{12}N_2)N_1 \\
&\qquad + 2a_{12}[a_{21}N_1 + a_{22}N_2 - \rho_2](\rho_2 - a_{21}N_1 - a_{22}N_2)N_2 \\
&= -2a_{21}(\rho_1 - a_{11}N_1 - a_{12}N_2)^2 N_1 - 2a_{12}(\rho_2 - a_{21}N_1 - a_{22}N_2)^2 N_2 < 0.
\end{aligned}$$

Hence, $Q(N_1, N_2)$ is a Lyapunov function of the system, which allows to prove the global stability of $(\hat{N}_1, \hat{N}_2)$.

(b) One possible solution.

Without loss of generality, assume that $a_{12} = 0$. The vertical line $N_1 = \rho_1/a_{11}$ consists of two orbits of the system, hence no other orbit can intersect such line. In particular, the system cannot have periodic orbits. Now, we can identify a bounded region Ω containing $(\hat{N}_1, \hat{N}_2)$ such that every orbit eventually enters Ω. Since $(\hat{N}_1, \hat{N}_2)$ is the only locally stable equilibrium and there are no periodic orbits, Poincaré–Bendixson theorem allows to conclude that $(\hat{N}_1, \hat{N}_2)$ is also globally stable.