INTRODUCTION TO MATHEMATICAL BIOLOGY

HOMEWORK SOLUTIONS

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Exercise 10.1

We compute the jacobian matrix in $(0,0)$:

$$J = \begin{pmatrix} r-m & m \\ m & -\mu-m \end{pmatrix}$$

Hence

$$\mathrm{tr}(J) = r - \mu - 2m, \qquad \det(J) = -r(\mu+m) + m\mu$$

The equilibrium is unstable (hence, the population is viable) if the determinant is negative or if the trace is positive, i.e., if one of these conditions holds:

$$r > \frac{m\mu}{\mu+m}$$

or

$$r > \mu + 2m.$$

Notice that

$$\mu + 2m = \frac{(\mu+2m)(\mu+m)}{\mu+m} = \frac{m\mu}{\mu+m} + \frac{\mu^2+2m\mu+2m^2}{\mu+m} > \frac{m\mu}{\mu+m},$$

hence we conclude that the population is viable if

$$r > \frac{m\mu}{\mu+m}.$$

Exercise 10.2

(a) R_0 is the expected number of offspring in a lifetime of an individual in a virgin environment. Since a juvenile becomes adult with probability $\gamma/(\mu_1+\gamma)$ and the average lifetime of an adult is $1/\mu_2$, we have

$$R_0 = \frac{\gamma}{\mu_1+\gamma}\frac{b(0)}{\mu_2} = \frac{\gamma}{\mu_1+\gamma}\frac{b_0}{\mu_2}.$$

(b) At equilibrium, $\hat{N}_1 = \mu_2\hat{N}_2/\gamma$, and

$$0 = b(\hat{N}_2) - \frac{\mu_1\mu_2}{\gamma} - \mu_2 \quad \Leftrightarrow \quad \hat{N}_2 = \frac{1}{c}(b_0 - \frac{\mu_1\mu_2}{\gamma} - \mu_2).$$

(c) We compute the jacobian matrix at equilibrium

$$J = \begin{pmatrix} -\mu_1 - \gamma & b_0 - 2c\hat{N}_2 \\ \gamma & -\mu_2 \end{pmatrix} = \begin{pmatrix} -\mu_1 - \gamma & -b_0 + 2\mu_2 \frac{\mu_1+\gamma}{\gamma} \\ \gamma & -\mu_2 \end{pmatrix}$$

$$\mathrm{tr}(J) = -\mu_1 - \mu_2 - \gamma < 0, \qquad \det(J) = b_0\gamma - \mu_1\mu_2 - \gamma\mu_2$$

hence the equilibrium $(\hat{N}_1, \hat{N}_2)$ is stable whenever it is positive, i.e. whenever

$$b_0 > \frac{\mu_1\mu_2}{\gamma} + \mu_2.$$

Exercise 10.3

The equilibrium $(\hat{x}, \hat{c})$ satisfies

$$r(\hat{c}) = f$$
$$\hat{x} = \frac{c_0 - \hat{c}}{k}$$

and it is positive if and only if $c_0 > \hat{c} = r^{-1}(f)$. The jacobian at equilibrium is

$$J = \begin{pmatrix} r(\hat{c}) - f & r'(\hat{c})\hat{x} \\ -kr(\hat{c}) & -kr'(\hat{c})\hat{x} - f \end{pmatrix} = \begin{pmatrix} 0 & r'(\hat{c})\hat{x} \\ -kf & -kr'(\hat{c})\hat{x} - f \end{pmatrix}$$

$$\mathrm{tr}(J) = -kr'(\hat{c})\hat{x} - f < 0, \qquad \det(J) = kfr'(\hat{c})\hat{x},$$

(because $r'(c) > 0$ for all c). Hence, we conclude that the equilibrium is stable whenever it is positive. To prove that it is a node, we need to verify that $\det - \mathrm{tr}^2/4 < 0$:

$$\det - \frac{\mathrm{tr}^2}{4} = kfr'(\hat{c})\hat{x} - \frac{(kr'(\hat{c})\hat{x} + f)^2}{4} = -\frac{(kr'(\hat{c})\hat{x} - f)^2}{4} < 0.$$

Exercise 10.4

(a) The equilibria are $(0, 0)$ and $(\hat{N}, \hat{T})$ satisfying

$$\hat{T} = \frac{r}{c} > 0, \qquad \hat{N} = \frac{\alpha r}{pc} > 0.$$

The jacobian at equilibrium is

$$J = \begin{pmatrix} 0 & -c\hat{N} \\ p & -\alpha \end{pmatrix}$$

$$\mathrm{tr}(J) = -\alpha < 0, \qquad \det(J) = pc\hat{N} > 0,$$

hence the positive equilibrium is always stable.
(b) The nontrivial equilibrium $(\hat{N}, \hat{T})$ is a stable focus when $\det - \mathrm{tr}^2/4 > 0$, i.e., when

$$\alpha r - \alpha^2/4 > 0 \quad \Leftrightarrow \quad \alpha < 4r,$$

hence oscillations occur when the toxin decays slowly.

(c) Assume $p, \alpha \gg r, cT$. We introduce a small parameter $\varepsilon \ll 1$ and the scaled parameters $p = \tilde{p}/\varepsilon$, $\alpha = \tilde{\alpha}/\varepsilon$. Then, by substituting and letting $\varepsilon \to 0$,

$$\frac{dN}{dt} = rN - cTN$$
$$0 = \tilde{p}N - \tilde{\alpha}T \quad \Rightarrow \quad T = \frac{\tilde{p}N}{\tilde{\alpha}}$$

and hence the dynamics of the bacteria is described by

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{\frac{r\tilde{\alpha}}{\tilde{p}c}}\right)$$

which is logistic with carrying capacity $K = \frac{r\tilde{\alpha}}{\tilde{p}c}$.

Exercise 10.5

(a) We model the reactions involving $R_U U$ and $R_U V$:

$$\frac{dx}{dt} = k_1(1 - x - y)u - k_{-1}x$$
$$\frac{dy}{dt} = k_2(1 - x - y)v - k_{-2}y$$

The quasi-equilibrium is

$$\hat{x}(u,v) = Q_1 k_{-2} k_1 u, \qquad \hat{y}(u,v) = Q_1 k_2 k_{-1} v$$

where

$$Q_1 = \frac{1}{k_2 k_{-1} v + k_{-2} k_1 u + k_{-2} k_{-1}}.$$

For the stability, we compute the jacobian:

$$J = \begin{pmatrix} -k_1 u - k_{-1} & -k_1 u \\ -k_2 v & -k_2 v - k_{-2} \end{pmatrix}$$

$$\mathrm{tr}(J) = -k_1 u - k_2 v - k_{-2} < 0,$$
$$\det(J) = (k_1 u + k_{-1})(k_2 v + k_{-2}) - k_1 k_2 uv = k_{-1}(k_2 v + k_{-2}) + k_{-2} k_1 u > 0,$$

hence the quasi-equilibrium is stable.

Analogously, we derive the system for p and q:

$$\frac{dp}{dt} = k_2(1 - p - q)u - k_{-2}p$$
$$\frac{dq}{dt} = k_1(1 - p - q)v - k_{-1}q$$

The quasi-equilibrium is

$$\hat{p}(u,v) = Q_2 k_2 k_{-1} u, \qquad \hat{q}(u,v) = Q_2 k_{-2} k_1 v$$

where

$$Q_2 = \frac{1}{k_2 k_{-1} u + k_{-2} k_1 v + k_{-2} k_{-1}}.$$

(a) The slow system is

$$\frac{du}{dt} = ax - \mu u = aQ_1 k_{-2} k_1 u - \mu u = \frac{\phi u}{1 + \alpha u + \beta v} - \mu u$$
$$\frac{dv}{dt} = aq - \mu v = aQ_2 k_{-2} k_1 v - \mu v = \frac{\phi v}{1 + \beta u + \alpha v} - \mu v$$

with

$$\phi = a\frac{k_1}{k_{-1}}, \qquad \alpha = \frac{k_1}{k_{-1}}, \qquad \beta = \frac{k_2}{k_{-2}}$$

(b) The equilibria of the slow system are $(0,0)$, $(0,\hat{v}_0)$, $(\hat{u}_0, 0)$ and $(\hat{u},\hat{v})$ such that

$$\hat{u}_0 = \hat{v}_0 = \frac{\phi - \mu}{\mu\alpha}$$

and

$$\hat{u} = \hat{v} = \frac{\phi - \mu}{\mu(\alpha + \beta)}.$$

Notice that the system admits nontrivial equilibria if and only if $\phi > \mu$.

For the stability, we compute the generic jacobian matrix:

$$J(u,v) = \begin{pmatrix} \frac{\phi(1+\alpha u+\beta v)-\alpha\phi u}{(1+\alpha u+\beta v)^2} - \mu & \frac{-\beta\phi u}{(1+\alpha u+\beta v)^2} \\ \frac{-\beta\phi v}{(1+\beta u+\alpha v)^2} & \frac{\phi(1+\beta u+\alpha v)-\alpha\phi v}{(1+\beta u+\alpha v)^2} - \mu \end{pmatrix}$$

and then we compute it at the different equilibria:

$$J(0,0) = \begin{pmatrix} \phi - \mu & 0 \\ 0 & \phi - \mu \end{pmatrix}$$
$$J(\hat{u}_0, 0) = \begin{pmatrix} \frac{-\alpha\phi\hat{u}_0}{(1+\alpha\hat{u}_0)^2} - \mu & \frac{-\beta\phi\hat{u}_0}{(1+\alpha\hat{u}_0)^2} \\ 0 & \frac{\phi}{1+\beta\hat{u}_0} - \mu \end{pmatrix}$$
$$J(0, \hat{v}_0) = \begin{pmatrix} \frac{\phi}{1+\beta\hat{v}_0} - \mu & 0 \\ \frac{-\beta\phi\hat{v}_0}{(1+\alpha\hat{v}_0)^2} & \frac{-\alpha\phi\hat{v}_0}{(1+\alpha\hat{v}_0)^2} \end{pmatrix}$$
$$J(\hat{u}_0, \hat{v}_0) = \begin{pmatrix} \frac{-\alpha\phi\hat{u}}{(1+\alpha\hat{u}+\beta\hat{v})^2} & \frac{-\beta\phi\hat{u}}{(1+\alpha\hat{u}+\beta\hat{v})^2} \\ \frac{-\beta\phi\hat{v}}{(1+\beta\hat{u}+\alpha\hat{v})^2} & \frac{-\alpha\phi\hat{v}}{(1+\beta\hat{u}+\alpha\hat{v})^2} \end{pmatrix}$$

It is easy to check that the trivial equilibrium is always unstable. The positive equilibrium $(\hat{u},\hat{v})$ is stable if $\alpha > \beta$ and in this case $(\hat{u}_0, 0)$ and $(0, \hat{v}_0)$ are unstable. Vice versa, if $\alpha < \beta$ the positive equilibrium $(\hat{u},\hat{v})$ is unstable and the equilibria $(\hat{u}_0, 0)$ and $(0, \hat{v}_0)$ are stable.

Hence, the system can actually function as a genetic switch only under the condition $\alpha < \beta$.