# Introduction to Mathematical Biology
# Exercises 11.1-11.5

11.1. *The paradox of enrichment.* Consider the Rosenzweig-MacArthur predator-prey model,

$$\begin{aligned} \frac{dN}{dt} &= rN(1 - N/K) - \frac{\beta NP}{1 + \beta TN} \\ \frac{dP}{dt} &= \left[\frac{\gamma\beta N}{1 + \beta TN} - \delta\right] P \end{aligned} \tag{1}$$

and suppose we improve the environment for the prey such that its intrinsic growth rate, $r$, and carrying capacity, $K$, increases.

(a) Show that the equilibrium density of the prey remains the same, and only the equilibrium density of the predator increases.
(b) Show that increasing $K$ can destabilize the equilibrium, and find the value of $K$ where the Hopf bifurcation occurs.

If the positive equilibrium is unstable and the system settles on a wide limit cycle, then the prey density regularly comes near zero, which runs the risk of extinction in not (fully) deterministic systems. Hence the improvement of prey population growth can lead to the extinction of the prey. This effect is called the paradox of enrichment.

11.2. *Orbits of the Lotka-Volterra predator-prey model.* Eliminating time in the Lotka-Volterra predator-prey model

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

we obtain a single differential equation that describes the orbits,

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

Solve this equation to show that the orbits are the contour lines given by $\Phi(N, P) = const$ where

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

$\Phi(N, P)$ is a *constant of motion*. Recall that models with a constant of motion are degenerate (a small change in the model will change the dynamics qualitatively, so that a constant of motion would no longer exist). If you have any software at hand that can draw contour lines, draw some of the orbits of the Lotka-Volterra predator-prey model.

11.3. *Time averages in the Lotka-Volterra predator-prey model.* The Lotka-Volterra model in (2) has the positive equilibrium $(\hat{N}, \hat{P}) = (\frac{\delta}{\gamma\beta}, \frac{r}{\beta})$, but this equilibrium is not asymptotically stable; the system settles on one of the neutral cycles obtained in the previous exercise. Show that even though the densities keep oscillating as the system cycles, the average density equals the equilibrium density, i.e.,

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

where $T$ is the length of a cycle. Note that this equality is specific to the Lotka-Volterra model, in other models the time average along a periodic orbit does not equal to the equilibrium density. *Hint:* write ODEs for $\ln N$ and $\ln P$; use that after $T$ time, the system must get back to the initial point.

11.4. *Competition with an Allee-effect.* The following model assumes Lotka-Volterra competition for species 2, but the *per capita* growth rate of species 1 is a nonlinear function of $N_1$ due to an Allee effect in the birth rate:

$$\begin{aligned}
\frac{dN_1}{dt} &= \left(\frac{\beta N_1}{\alpha + N_1} - (\delta_1 + a_{11}N_1 + a_{12}N_2)\right)N_1 \\
\frac{dN_2}{dt} &= \big(b - (\delta_2 + a_{21}N_1 + a_{22}N_2)\big)N_2
\end{aligned}$$

Perform a bifurcation analysis of this model with respect to $b$, the (constant) birth rate of species 2. *Hint:* it can be useful to sketch the zero-growth isoclines on the phase plane as a start.

11.5. *Global stability of the coexistence equilibrium in the Lotka-Volterra competition model with two species.* Consider the Lotka-Volterra competition model with two species of consumers,

$$\begin{aligned}
\frac{dN_1}{dt} &= (\rho_1 - a_{11}N_1 - a_{12}N_2)N_1 \\
\frac{dN_2}{dt} &= (\rho_2 - a_{21}N_1 - a_{22}N_2)N_2
\end{aligned}$$

and with parameters such that there is an interior equilibrium $(\hat{N}_1, \hat{N}_2) \in \operatorname{int} \mathbb{R}^2_+$.

(a) Show that

$$Q(N_1, N_2) = a_{11}a_{21}(N_1 - \hat{N}_1)^2 + 2a_{12}a_{21}(N_1 - \hat{N}_1)(N_2 - \hat{N}_2) + a_{12}a_{22}(N_2 - \hat{N}_2)^2$$

is a strict Lyapunov-function on int $\mathbb{R}^2_+$ provided that $a_{12}a_{21} > 0$, and that this guarantees the global asymptotic stability of $(\hat{N}_1, \hat{N}_2)$ in the coexistence case of $a_{21}/a_{11} < \rho_2/\rho_1 < a_{22}/a_{12}$. (*Hint:* One must use that $(\hat{N}_1, \hat{N}_2)$ is the equilibrium, but to avoid a hopeless mess, don't substitute the values of $(\hat{N}_1, \hat{N}_2)$ as expressed by the parameters!)

(b) Investigate the global stability of $(\hat{N}_1, \hat{N}_2)$ in the special case when $a_{12}a_{21} = 0$.