MATHEMATICAL MODELING 2013

SOLUTIONS TO EXERCISES 4-6

Exercise 4

$$\begin{cases} \frac{dx}{dt} = \varphi - \alpha x - \beta xy \\ \frac{dy}{dt} = \gamma xy - \delta y \end{cases} \tag{1}$$

A resource-consumer model with a constant resource influx φ.

i-states

- X: resource (prey)
- Y: consumer (predator).

i-processes

$$\begin{aligned} \text{Influx: } & \emptyset \xrightarrow{\varphi} X & (A) \\ \text{Death: } & X \xrightarrow{\alpha} \dagger & (B) \\ & Y \xrightarrow{\delta} \dagger & (C) \\ \text{Capture of a prey: } & X + Y \xrightarrow{\beta-\gamma} Y & (D) \\ \text{Capture of a prey and reproduction: } & X + Y \xrightarrow{\gamma} 2Y & (E) \end{aligned}$$

with the assumption $0 < \gamma \leq \beta$.

It is also possible to exchange equations (D) and (E) with

$$\begin{aligned} \text{Capture of a prey: } & X + Y \xrightarrow{\beta-\frac{\gamma}{n}} Y & (D*) \\ \text{Capture of a prey and reproduction: } & X + Y \xrightarrow{\frac{\gamma}{n}} (n+1)Y & (E*) \end{aligned}$$

These i-processes describe the equations (1).

Phase analysis for the system

(a) solve the equations

$$\begin{cases} \dot{x} = 0 \\ \dot{y} = 0 \end{cases}$$

The first equation gives

$$\dot{x} = 0 \Leftrightarrow y = \frac{\varphi}{\beta x} - \frac{\alpha}{\beta} \tag{2}$$

and the second one gives

$$\dot{y} = 0 \Leftrightarrow y = 0 \text{ or } x = \frac{\delta}{\gamma}$$

(b) draw the isoclines

First of all, note that we want to interpret this system biologically and therefore we look at the positive quadrant ($x \geq 0$ and $y \geq 0$).

Next, try to find the x for which $y = 0$ in equation (2), to see if there is an intersection between the curve generated by equation (2) and $x = \frac{\delta}{\gamma}$.

$$y = 0 \Leftrightarrow x = \frac{\varphi}{\alpha}$$

Therefore, we have 2 different cases to consider: $\frac{\varphi}{\alpha} \leq \frac{\delta}{\gamma}$ and $\frac{\varphi}{\alpha} > \frac{\delta}{\gamma}$.

(*) The case $\frac{\varphi}{\alpha} \leq \frac{\delta}{\gamma}$

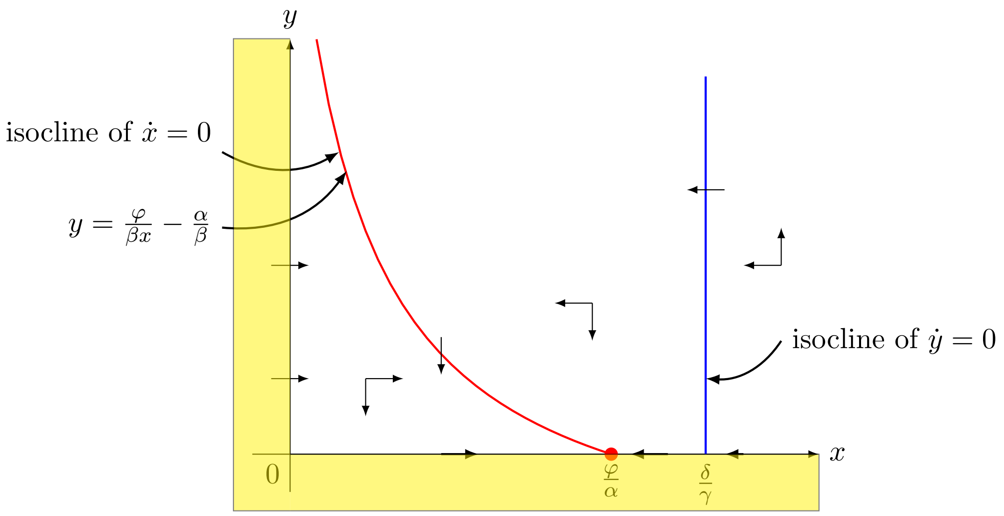

Figure 1: Isoclines in the case $\frac{\varphi}{\alpha} \leq \frac{\delta}{\gamma}$.

Remark 0.1. *How to draw and use the graph:*

- *First, look at the conditions, in this case $x, \ y \geq 0$ (shaded zone)*
- *Draw the isoclines of $\dot{x} = 0$ and $\dot{y} = 0$.*
- *Find where they cross: that gives the equilibrium and you can see if there are different cases.*
- *Look at the direction of the flow.*
  Remember that when the flow crosses the isocline of $\dot{x} = 0$, it can cross only vertically since $\dot{x} = 0$ so there is no speed in the x-direction. Similarly, the arrow of the direction of the flow has to be horizontal when it crosses $\dot{y} = 0$.
  To find the direction of the arrows in the region below the isocline of $\dot{x} = 0$ (red line), take the point $(0, 0)$ and use the equations (1) to find the sign of $\dot{x}$.
  We find $\dot{x} = \varphi > 0$ (arrow to the right) but that point doesn't work for $\dot{y}$.
  Take another point, for example (ϵ, ϵ) and you find $\dot{y} = \gamma\epsilon^2 - \delta\epsilon < 0$ so the arrow points downward and that extends to the region that doesn't cross the isocline $\dot{y} = 0$.
- *Look at the equilibrium, the intersection of the isoclines $\dot{y} = 0 = \dot{x}$ and see in which direction the arrows are going.*
  - At least one arrow pointing away from the equilibrium $\Rightarrow$ not stable.
  - All the arrows pointing toward the equilibrium $\Rightarrow$ stable.
  - Damn!! It's turning around the equilibrium $\Rightarrow$ need some further study to know. We have to look at the eigenvalues of the Jacobi matrix. (See the case $\frac{\varphi}{\alpha} > \frac{\delta}{\gamma}$)

We see that the point $(\frac{\varphi}{\alpha}, 0)$ is a stable equilibrium. It is an equilibrium because it is the intersection of $y = \frac{\varphi}{\beta x} - \frac{\alpha}{\beta}$ and $y = 0$. Therefore $\dot{x} = 0$ and $\dot{y} = 0$ and $(x, y) = (\frac{\varphi}{\alpha}, 0)$. It is stable because all the arrows are pointing toward the equilibrium.

(**) The case $\frac{\varphi}{\alpha} > \frac{\delta}{\gamma}$

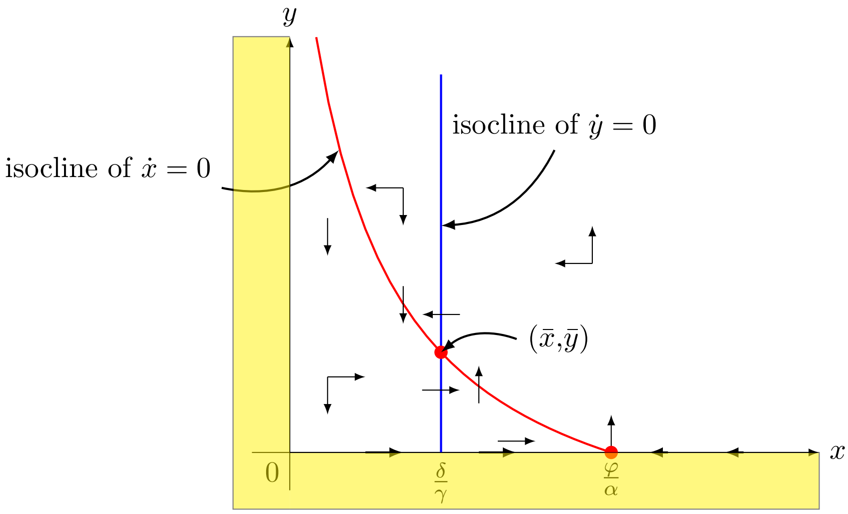

Figure 2: Isoclines in the case $\frac{\varphi}{\alpha} > \frac{\delta}{\gamma}$.

Remark 0.2. *There are 2 equilibria:*

$$(\frac{\varphi}{\alpha}, 0) \text{ and } (\bar{x}, \bar{y}) = (\frac{\delta}{\gamma}, \frac{\varphi\gamma}{\beta\delta + \gamma\alpha})$$

We see that an arrow is going away from the equilibrium $(\frac{\varphi}{\alpha}, 0)$ so it's an unstable equilibrium.

For $(\bar{x}, \bar{y})$, we see that the arrows indicate a rotative movement around the equilibrium. Therefore, we need to look at the local stabililty.

We compute the Jacobi-matrix of the system

$$\begin{cases} f_1(x, y) = \varphi - \alpha x - \beta xy \\ f_2(x, y) = \gamma xy - \delta y \end{cases}$$

which is

$$A = \begin{pmatrix} \frac{\partial f_1}{\partial x} & \frac{\partial f_1}{\partial y} \\ \frac{\partial f_2}{\partial x} & \frac{\partial f_2}{\partial y} \end{pmatrix} = \begin{pmatrix} -\alpha - \beta\bar{y} & -\beta\bar{x} \\ \gamma\bar{y} & \gamma\bar{x} - \delta \end{pmatrix} = \begin{pmatrix} -\alpha - \beta\bar{y} & -\beta\bar{x} \\ \gamma\bar{y} & 0 \end{pmatrix}$$

where the last equality stands because $\bar{x} = \frac{\delta}{\gamma}$

So as to know the sign of the real part of the eigenvalues, we simply look at the trace and the determinant.

Remark 0.3. *The characteristic polynomial is with eigenvalues λ_1 and λ_2 (which can be the same):*

$$\begin{aligned} \det(A - \lambda I) &= (\lambda - \lambda_1)(\lambda - \lambda_2) \\ &= \lambda^2 - \lambda(\lambda_1 + \lambda_2) + \lambda_1\lambda_2 \\ &= \lambda^2 - \lambda tr(A) + \det(A) \end{aligned}$$

so if

- $\det(A) > 0$ *then both eigenvalues have the same sign*
  - $tr(A) > 0$ *then* $\lambda_1 > 0$ *and* $\lambda_2 > 0$ *and it's unstable (source)*
  - $tr(A) < 0$ *then* $\lambda_1 < 0$ *and* $\lambda_2 < 0$ *and it's stable (sink)*
- $\det(A) < 0$ *then the eigenvalues have opposite sign (saddle point).*

In this case,

$$\det(A) = \gamma\bar{y}\beta\bar{x} > 0$$

so we know that the eigenvalues have the same sign.

Now, we turn to the trace

$$\text{tr}(A) = -\alpha - \beta\bar{y} < 0$$

Therefore, the eigenvalues are both negative and the equilibrium is stable.

Exercise 5

In the exercises we presented a method with minimized equations. You can also model the dynamics of the larvae with at least two parasitoid eggs explicitly. This is how it is done:

1. i-states
   - B: Butterfly (adult),
   - P: Parasitoid (adult),
   - L_0: Larva without parasitoid egg,
   - L_1: Larva with 1 parasitoid egg,
   - L_2: Larva with at least 2 parasitoid eggs.
2. i-processes

Actions from the butterfly

butterfly produces an egg: $$B \xrightarrow{\alpha} B + L_0 \quad (1)$$

Actions from the parasitoid

parasitoid lies its egg inside a larva without eggs: $$P + L_0 \xrightarrow{\beta_0} P + L_1 \quad (2)$$

parasitoid lies its egg inside a larva with 1 egg: $$P + L_1 \xrightarrow{\beta_1} P + L_2 \quad (3)$$

parasitoid lies its egg inside a larva with at least 2 eggs: $$P + L_2 \xrightarrow{\beta_2} P + L_2 \quad (4)$$

Actions from the larva

larva (without egg) becomes a butterfly: $$L_0 \xrightarrow{\gamma_0} B \quad (5)$$

larva with 1 egg becomes a parasitoid: $$L_1 \xrightarrow{\gamma_1} P \quad (6)$$

larva with at least 2 eggs (and the eggs) die: $$L_2 \xrightarrow{\gamma_2} \dagger \quad (7)$$

Death

Butterfly: $$B \xrightarrow{\delta_B} \dagger \quad (8)$$

Parasitoid: $$P \xrightarrow{\delta_P} \dagger \quad (9)$$

Larva without egg: $$L_0 \xrightarrow{\delta_0} \dagger \quad (10)$$

Larva with 1 egg: $$L_1 \xrightarrow{\delta_1} \dagger \quad (11)$$

Larva with ≥ 2 eggs: $$L_2 \xrightarrow{\delta_2} \dagger \quad (12)$$

3. p-equations

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)
$\frac{db}{dt} =$					$+\gamma_0 l_0$			$-\delta_B b$				
$\frac{dp}{dt} =$						$+\gamma_1 l_1$			$-\delta_P p$			
$\frac{dl_0}{dt} =$	$+\alpha b$	$-\beta_0 p l_0$			$-\gamma_0 l_0$					$-\delta_0 l_0$		
$\frac{dl_1}{dt} =$		$+\beta_0 p l_0$	$-\beta_1 p l_1$			$-\gamma_1 l_1$					$-\delta_1 l_1$	
$\frac{dl_2}{dt} =$			$+\beta_1 p l_1$				$-\gamma_2 l_2$					$-\delta_2 l_2$

To present it in a denser way

$$\frac{db}{dt} = \gamma_0 l_0 - \delta_B b$$
$$\frac{dp}{dt} = \gamma_1 l_1 - \delta_P p$$
$$\frac{dl_0}{dt} = \alpha b - (\beta_0 p - \gamma_0 - \delta_0) l_0$$
$$\frac{dl_1}{dt} = \beta_0 p l_0 - (\beta_1 p + \gamma_1 + \delta_1) l_1$$
$$\frac{dl_2}{dt} = \beta_1 p l_1 - (\gamma_2 + \delta_2) l_2$$

Exercise 6

Consider the model

$$\begin{cases} \frac{dx}{dt} &= \beta(n_0 - x)y - \mu x \qquad \text{(site owner)} \\ \frac{dy}{dt} &= -\beta(n_0 - x)y + \alpha x - \nu y \quad \text{(free indiv.)} \end{cases} \tag{3}$$

Let us use time-scale separation to split the system into two one-dimensional equations.

Assumptions: $x, n_0 \ll y$

1. Introduce a small dimensionless parameter ϵ and define

$$x^* = \frac{x}{\epsilon} \text{ and } n_0^* = \frac{n_0}{\epsilon}$$

so that x^* and n_0^* are the same order as y.

We have

$$x = \epsilon x^*, \quad n_0 = \epsilon n_0^* \text{ and } \frac{dx}{dt} = \epsilon \frac{dx^*}{dt}$$

2. Rewrite the system (3) in terms of x^*, n_0^* and y. This gives

$$\begin{cases} \frac{dx}{dt} = \epsilon \frac{dx^*}{dt} = \beta\epsilon(n_0^* - x^*)y - \mu\epsilon x^* \qquad \text{(site owner)} \\ \qquad\qquad \frac{dy}{dt} = -\beta\epsilon(n_0^* - x^*)y + \alpha\epsilon x^* - \nu y \qquad \text{(free indiv.)} \end{cases} \tag{4}$$

3. Take the limit as $\epsilon \to 0$ in the system (4)

$$\begin{cases} \frac{dx^*}{dt} &= \beta(n_0^* - x^*)y - \mu x^* \qquad \text{(fast)} \\ \frac{dy}{dt} &= -\nu y \qquad \text{(slow)} \end{cases}$$

Problem, the second equation should be $\frac{dy}{dt} = 0$ to really split the problem into two one-dimensional equations but if we consider that the rate of death for Y (i.e the individual without territory) is very small compared to the rate of death for individuals with territory then that solves our problem.

Try to find an example of that.

Additional condition:
$\nu \ll \mu$ then we write $\nu = \epsilon\nu^*$ and $\frac{dy}{dt} = -\nu y = -\epsilon\nu^* y \to 0$.

That implies y is evolving slowly and x is evolving fast. Therefore, on a short time scale, we can consider $y = y(0)$ as constant. Now that we have our one-dimensional system, let us consider the equation $\frac{dx^*}{dt} = \beta(n_0^* - x^*)y - \mu x^*$ where n_0^* is constant too. That gives

$$\frac{dx^*}{dt} + (\beta y(0) + \mu)x^* = \beta n_0^* y(0) \tag{5}$$

This is a linear differential equation of first order of the form $\dot{x^*} + ax^* = b$ which has as solution

$$\begin{cases} x^*(t) & = Ce^{-at} + \frac{b}{a} \\ & = Ce^{-(\beta y(0)+\mu)t} + \frac{\beta n_0^* y(0)}{\beta y(0)+\mu} \end{cases}$$

The constant can be determined using the condition at the origin, $x^*(0) = x_0^*$

$$x^*(0) = C + \frac{\beta n_0^* y(0)}{\beta y(0) + \mu}$$

The most important is that $x^*(t)$ converges to a constant as $n \to \infty$, the equilibrium.

$$\lim_{t\to\infty} x^*(t) = \frac{\beta n_0^* y(0)}{\beta y(0) + \mu} = \bar{x^*}$$

An easier way to find the equilibrium is simply by saying that $\frac{dx^*}{dt} = 0$ in (5) and derive that $\bar{x^*} = \frac{\beta n_0^* y(0)}{\beta y(0)+\mu}$.

A graphical interpretation is given in figure 3

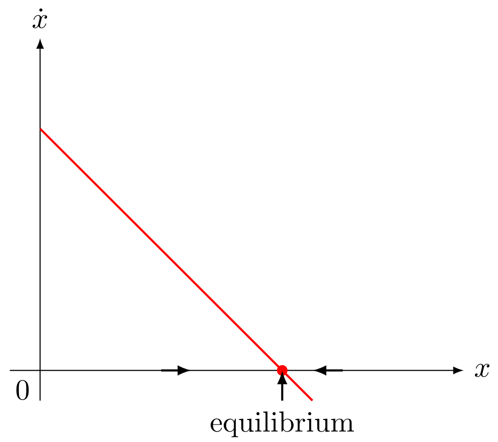

Figure 3: Graphical way to find the equilibrium $\bar{x^*}$.

We've just solved the equation for the fast process. We turn now to the equation of the slow one. Ee introduce the slow time $t^* = \epsilon t$ so $\frac{d}{dt} = \epsilon\frac{d}{dt^*}$. The system of equations (4) gives

$$\begin{cases} \frac{dx^*}{dt} = \epsilon \frac{dx^*}{dt^*} = \beta(n_0^* - x^*)y - \mu x^* & \text{(fast)} \\ \frac{dy}{dt} = \epsilon \frac{dy}{dt^*} = -\beta\epsilon(n_0^* - x^*)y + \alpha\epsilon x^* - \epsilon\nu^* y & \text{(slow)} \end{cases} \tag{6}$$

Let $\epsilon \to 0$, then the system of equations (6) becomes

$$\begin{cases} 0 = \beta(n_0^* - x^*)y - \mu x^* & \text{(fast)} \\ \frac{dy}{dt^*} = -\beta(n_0^* - x^*)y + \alpha x^* - \nu y & \text{(slow)} \end{cases} \tag{7}$$

The first equation resembles the equilibrium equation of the fast dynamics (except that $y(t^*)$ can vary) and therefore gives

$$x^*(t^*) = \frac{\beta n_0^* y(t^*)}{\mu + \beta y(t^*)}$$

If we introduce it in the second equation of (7), then, we find

$$\begin{aligned} \frac{dy}{dt^*} &= -\beta n_0^* y + \beta x^* y + \alpha x^* - \nu^* y \\ &= -\beta n_0^* y + \beta \frac{\beta n_0^* y(t^*)}{\mu + \beta y(t^*)} y + \alpha \frac{\beta n_0^* y(t^*)}{\mu + \beta y(t^*)} - \nu^* y \\ &= \frac{1}{\beta y + \mu} y \left(-\beta\nu^* y + (\alpha\beta n_0^* - \beta n_0^* - \mu\nu^*)\right) \end{aligned}$$

Hence, $\frac{dy}{dt^*} = 0$ if and only if $y = 0$ or $y = \frac{\alpha\beta n_0^* - \beta n_0^* \mu - \mu\nu^*}{\beta\nu^*}$.
We see that there are 2 cases: $\alpha\beta n_0^* - \beta n_0^* \mu - \mu\nu^* > 0$ and $\alpha\beta n_0^* - \beta n_0^* \mu - \mu\nu^* \leq 0$

(a) case $\alpha\beta n_0^* - \beta n_0^* \mu - \mu\nu^* > 0$

y	0		$\bar{y}$	
$\frac{dy}{dt^*}$	$-$	$+$		$-$
y	$\longleftarrow$	$\longrightarrow$		$\longleftarrow$

Thus 0 is an unstable equilibrium (it's a source) and $\bar{y}$ is a stable equilibrium (it's a sink).

(b) case $\alpha\beta n_0^* - \beta n_0^* \mu - \mu\nu^* < 0$

y	$\bar{y}$		0	
$\frac{dy}{dt^*}$	$-$	$+$		$-$
y	$\longleftarrow$	$\longrightarrow$		$\longleftarrow$

Thus $\bar{y}$ is an unstable equilibrium (it's a source) and 0 is a stable equilibrium (it's a sink). Remember that $y \geq 0$ so the solution $\bar{y} < 0$ is not relevant in our problem.

(c) last case $\alpha\beta n_0^* - \beta n_0^* \mu - \mu\nu^* = 0$ then

$$\frac{dy}{dt^*} = \frac{-\beta\nu^* y^2}{\beta y + \mu}$$

y	$\bar{y} = 0$	
$\frac{dy}{dt^*}$	$-$	$-$
y	$\longleftarrow$	$\longleftarrow$

$\bar{y} = 0$ shouldn't be a stable equilibrium but since we have the condition $y \geq 0$, it is indeed a stable equilibrium.