ADAPTIVE DYNAMICS 2012

SOLUTIONS TO EXERCISES 1-2

Exercise 1

Consider the Lotka-Volterra competition model:

$$\dot{n}_i = r(x_i)n_i \left(1 - \sum_{j=1}^{l} \frac{a(x_i, x_j)n_j}{k(x_i)}\right) \qquad i = 1, ..., l \tag{1}$$

where

- n_i is the population density of the strategy x_i,
- $r(x_i)$ is the intrinsic rate of increase,
- $k(x)$ is the carrying capacity,
- $a(x, y)$ is the competition kernel.

In our case, we have 2 different densities of strategies

- n for the resident with strategy x and
- m for the mutant with strategy y.

Since we set $a(x, x) = a(y, y) = 1$, we have the dynamical system

$$\begin{cases} \dot{n} = r(x)n \left(1 - \frac{n+a(x,y)m}{k(x)}\right) \\ \dot{m} = r(y)m \left(1 - \frac{m+a(y,x)n}{k(y)}\right) \end{cases} \tag{2}$$

see page 2 of the second lecture notes.

(a) Phase plane analysis

<u>How to do a phase plane analysis</u>:

- First, look at the conditions, in this case $n,\ m \geq 0$ (shaded zone)
- Draw the isoclines of $\dot{n} = 0$ and $\dot{m} = 0$.

$$\dot{m} = 0 \Leftrightarrow r(y)m \left(1 - \frac{m + a(y, x)n}{k(y)}\right) = 0$$

$$\Leftrightarrow \begin{cases} m = 0 \quad or \\ 1 - \frac{m+a(y,x)n}{k(y)} = 0 \end{cases} \qquad \Leftrightarrow \begin{cases} m = 0 \quad or \\ m = k(y) - a(y, x)n \end{cases}$$

That gives the isocline $\dot{m} = 0$.

$$\dot{n} = 0 \Leftrightarrow r(x)m \left(1 - \frac{m + a(x, y)n}{k(x)}\right) = 0$$

$$\Leftrightarrow \begin{cases} n = 0 \quad or \\ 1 - \frac{n+a(x,y)m}{k(x)} = 0 \end{cases} \qquad \Leftrightarrow \begin{cases} n = 0 \quad or \\ n = k(x) - a(x, y)m \Leftrightarrow m = \frac{n-k(x)}{a(x,y)} \end{cases}$$

- Find where they cross: that gives the equilibrium and you can see if there are different cases.
  Where do we have $\dot{m} = \dot{n} = 0$.

  $$n = 0 \Rightarrow m = k(y) \quad \text{or } m = 0$$

  gives the first equilibrium $(0, k(y))$. Also if $m = 0$ that gives $n = k(x)$.
- Draw the isoclines and look at the direction of the flow.
  We have 2 lines to draw:

  $$\begin{cases} m = k(y) - a(y,x)n & (\dot{m} = 0) \\ m = \frac{n - k(x)}{a(x,y)} & (\dot{n} = 0) \end{cases}$$

  We have 3 different cases,
  (1) $k(y) > \frac{k(x)}{a(x,y)}$
  (2) $k(y) = \frac{k(x)}{a(x,y)}$
  (3) $k(y) < \frac{k(x)}{a(x,y)}$
  Let's consider the first case $k(y) > \frac{k(x)}{a(x,y)}$:
  Remember that when the flow crosses the isocline of $\dot{n} = 0$, it can cross only vertically since $\dot{n} = 0$ so there is no speed in the n-direction. Similarly, the arrows of the direction of the flow has to be horizontal when it crosses $\dot{m} = 0$.
  To find the direction of the arrows in the region below the isocline of $\dot{n} = 0$ (red line), take a point, for example (ϵ, ϵ) and see the sign in equations (2). You find

  $$\begin{cases} \dot{n} = r(x)\epsilon \left(1 - \frac{\epsilon + a(x,y)\epsilon}{k(x)}\right) > 0 \\ \dot{m} = r(y)n \left(1 - \frac{\epsilon + a(y,x)\epsilon}{k(y)}\right) > 0 \end{cases}$$

  so the arrow points upward and that extends to the region that doesn't cross the isocline $\dot{n} = 0$. The arrows also point to the right and that extends to the region that doesn't cross the isocline $\dot{m} = 0$. Similarly, you find for the point $(k(x), \epsilon)$

  $$\begin{cases} \dot{n} = r(x)k(x) \left(1 - \frac{k(x) + a(x,y)\epsilon}{k(x)}\right) < 0 \\ \dot{m} = r(y)\epsilon \left(1 - \frac{\epsilon + a(y,x)k(x)}{k(y)}\right) \end{cases}$$

  and by assumption $k(y) > \frac{k(x)}{a(x,y)}$ therefore $\dot{m} < 0$.
- Look at the equilibrium, the intersection of the isoclines $\dot{m} = 0 = \dot{n}$ and see in which direction the arrows are going.
  - At least one arrow pointing away from the equilibrium $\Rightarrow$ not stable.
  - All the arrow 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 exercise 4 from Mathematical modeling on the following adress)

  `http://wiki.helsinki.fi/display/mathstatKurssit/Mathematical+modeling%2C+spring+201`

(*) <u>The case $k(y) > \frac{k(x)}{a(x,y)}$</u>

By looking at the figure 1,we can conclude that:

- $n = k(x)$ is an unstable equilibrium,

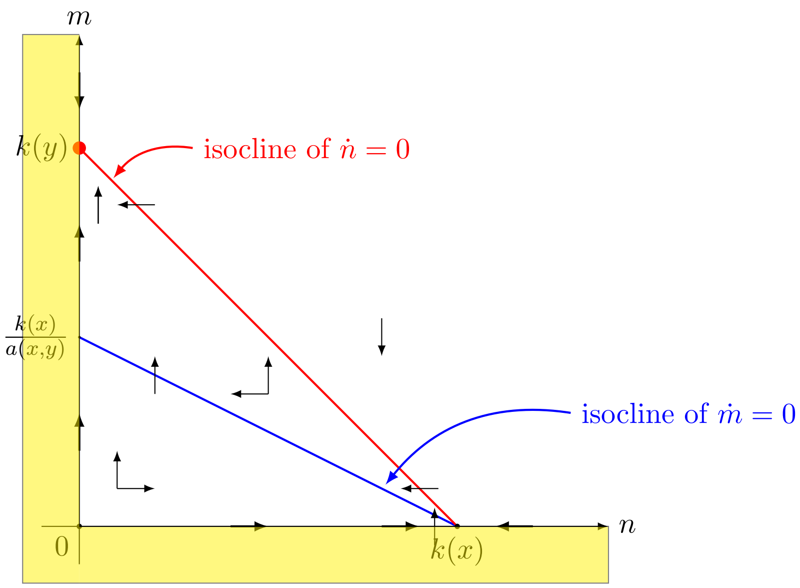


Figure 1: Isoclines in the case $k(y) > \frac{k(x)}{a(x,y)}$.

- $m = k(y)$ is a stable equilibrium,
- $(0, 0)$ is an unstable equilibrium.

This is a case of invasion and substitution.

Remark 0.1. *Notice that the plot of the arrows could be easily done using the fact that when $m = 0$ for example, the Lotka-Volterra equation becomes the logistic equation which has $n = k(x)$ as stable equilibrium and $n = 0$ as unstable equilibrium. Thus we know that the arrows point toward $k(x)$ and away from 0. That gives the orientation of the arrows in general. No need to compute at various point. Do the same for m.*

(**) The case $k(y) = \frac{k(x)}{a(x,y)}$

The whole line $\dot{n} = \dot{m} = 0$ in figure 2 is made of stable equilibrium. This is invasion and coexistence.

(***) The case $k(y) < \frac{k(x)}{a(x,y)}$

From the figure 3, we can conclude that:

- $n = k(x)$ is a stable equilibrium,
- $m = k(y)$ is an unstable equilibrium,
- $(0, 0)$ is an unstable equilibrium.

This is a case of non invasion.

(b) For this exercise where we give the conditions for invasion and substitution, non invasion and invasion and coexistence, we recall the definition of the invasion fitness.

$$S_x(y) = \lim_{\substack{m \to 0 \\ n \to k(x)}} \frac{d \log m}{dt} = \frac{\dot{m}}{m}$$

with $\dot{m} = r(y)m\left(1 - \frac{m+a(y,x)n}{k(y)}\right)$. The $m \to 0$ corresponds to the introduction of 1 mutant or very few and $n = k(x)$ is because we are at equilibrium of the resident dynamics.

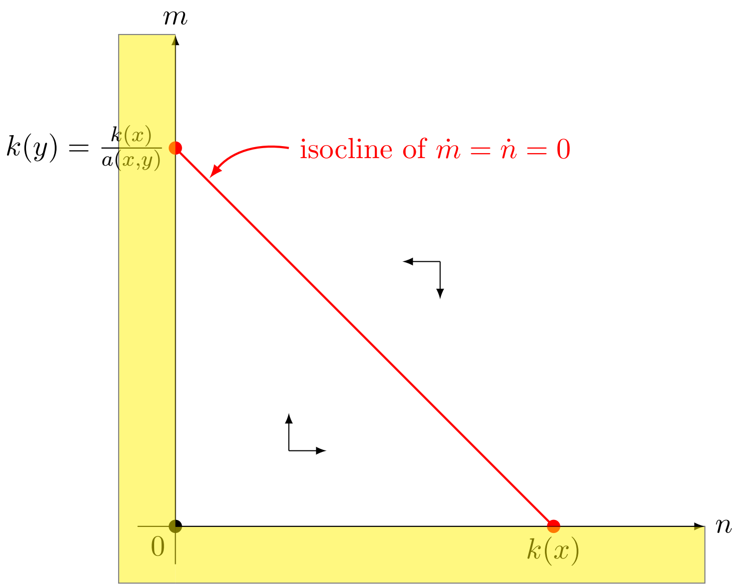


Figure 2: Isoclines in the case $k(y) = \frac{k(x)}{a(x,y)}$.

Therefore we have

$$S_x(y) = r(y)\left(1 - \frac{a(y,x)k(x)}{k(y)}\right)$$

where we usually take $r(y) = 1$ for simplicity.

Remark 0.2. *Notice that since* $S_x(y) = \lim_{\substack{m \to 0 \\ n \to k(x)}} \frac{\dot{m}}{m}$ *and* $m > 0$*,* $S_x(y)$ *and* $\dot{m}$ *have the same sign on a neighbourhood of* $(k(x), 0)$ *which gives the stability of the equilibrium.*

Conditions for

(i) Non invasion: $\frac{k(x)}{a(x,y)} > k(y)$.
That implies

$$\begin{aligned} \frac{k(x)}{a(x,y)} > k(y) &\Leftrightarrow \frac{k(y)a(x,y)}{k(y)} < 1 \\ &\Leftrightarrow r(x)\left(1 - \frac{k(y)a(x,y)}{k(y)}\right) > 0 \\ &\Leftrightarrow S_y(x) > 0 \end{aligned}$$

under the condition that $S_x(y) = 0$. Therefore

$$\begin{cases} S_x(y) = 0 \\ S_y(x) > 0 \end{cases} \Leftrightarrow \text{ Non invasion}$$

meaning that if $S_x(y) = 0$ (i.e y is neutral to invade x) and x can invade y then y can't invade x.

(ii) Invasion & substitution: $\frac{k(x)}{a(x,y)} < k(y)$.
That is equivalent to

$$r(x)\left(1 - \frac{k(y)a(x,y)}{k(y)}\right) > 0 \Leftrightarrow S_y(x) < 0$$

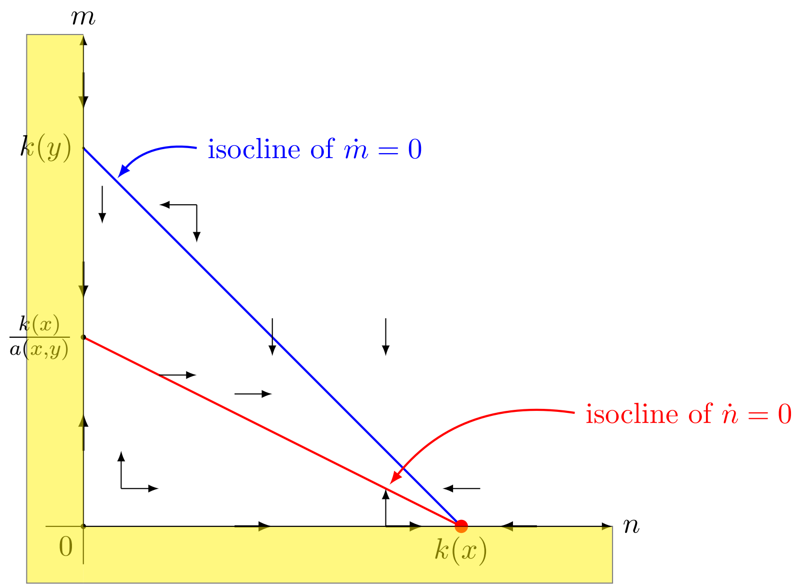


Figure 3: Isoclines in the case $k(y) < \frac{k(x)}{a(x,y)}$.

with the condition that $S_x(y) = 0$. Therefore

$$\begin{cases} S_x(y) = 0 \\ S_y(x) < 0 \end{cases} \quad \Leftrightarrow \text{ Invasion \& substitution}$$

(iii) Invasion & coexistence: $\frac{k(x)}{a(x,y)} = k(y)$.
With the condition $S_x(y) = 0$, that is equivalent to

$$\begin{cases} S_x(y) = 0 \\ S_y(x) = 0 \end{cases} \quad \Leftrightarrow \text{ Invasion \& coexistence}$$

(c) Pairwise Invadability Plot if $k(x) = e^{-x^2}$ and $a(x,y) = e^{-\alpha(x-y)^2}$ with $\alpha = 1$.
We do not assume anymore that $S_x(y) = 0$. This was only for the questions (a) and (b).
Let's compute $S_x(y)$

$$\begin{aligned} S_x(y) &= \lim_{\substack{m \to 0 \\ n \to k(x)}} \frac{\dot{m}}{m} = r(y) \left(1 - \frac{a(y,x)n + m}{k(y)}\right)\Big|_{m=0, m=k(x)} \\ &= 1 - \frac{a(y,x)k(x)}{k(y)} \quad \text{where } r(y) = 1 \\ &= 1 - \frac{e^{-(x-y)^2} e^{-x^2}}{e^{-y^2}} \\ &= 1 - e^{-2x(x-y)} \end{aligned}$$

Thus solving the equation $S_x(y) = 0$, we find the conditions

$$\begin{aligned} S_x(y) = 0 &\Leftrightarrow 1 - e^{-2x(x-y)} = 0 \\ &\Leftrightarrow -2x(x-y) = 1 \\ &\Leftrightarrow x = 0 \quad \text{or} \quad x = y \end{aligned}$$

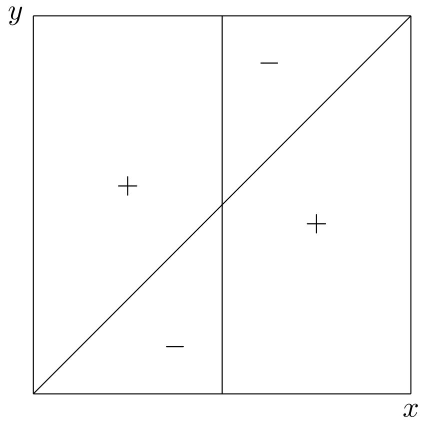


Figure 4: Sign plot of $S_x(y)$.

Then we compute $S_x(y)$ for different points (x, y) to find the sign in the different regions and we get the following plot, see figure 4

(d) Any Evolutionarily Stable Strategies (ESS)?

We recall the definition of an ESS from page 8 of the second lecture notes.

<u>Definition</u>: A strategy is evolutionarily stable if no $y \neq x$ can invade.

From the sign plot of $S_x(y)$, we can see that no $x \neq 0$ is an ESS.

If $x < 0$ then $x < y < 0$ is such that $S_x(y) > 0$ so y can invade x and
if $x < 0$ then $0 < y < x$ is such that $S_x(y) > 0$ so y can invade x.

For $x = 0$ then $S_x(y) = 0$ which we studied before. We have to look at $S_y(x)$ and use question (b). If we plot $S_y(x)$, we find

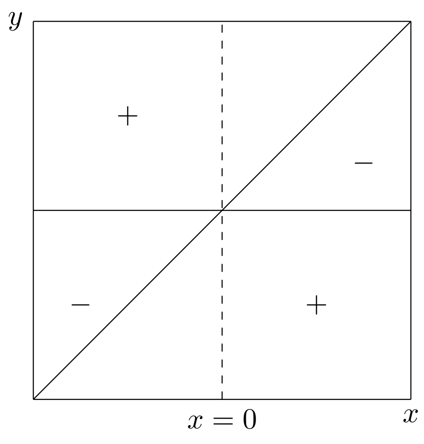


Figure 5: Sign plot of $S_y(x)$.

and we see that for $x = 0$, $S_y(x) > 0$ so there is no invasion and $x = 0$ is an ESS.

(e) Which strategies can coexist?

We superimpose the sign plots of $S_x(y)$ and $S_y(x)$. See p.8 of the second lectures notes.

Two strategies can coexist if they are in a ++ region so $x > 0$ and $y < 0$ or $x < 0$ and $y > 0$ can coexist according to figure 6

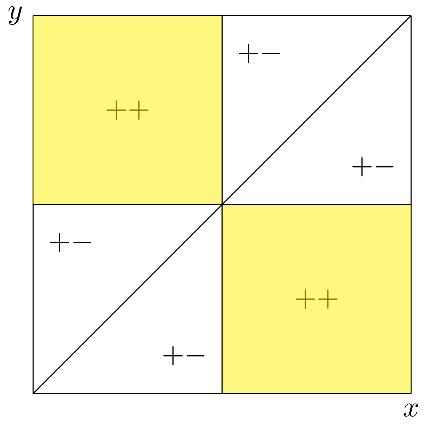


Figure 6: Superimposed sign plot.

(f) Strategy dynamics with monomorphic resident population with small mutation steps

Let $x < 0$ then by question (d), if $x < y \leq 0$ then y invades and that way, it converges to 0. Then, as we saw in question (d) again, $x = 0$ is an ESS so we remain there.

If $x > 0$ then similarily, it converges to 0 which is an ESS.

Exercise 2

Lotka Volterra competition model with $k(x) = e^{-x^2}$ and $a(x, y) = e^{-\alpha|x-y|}$, $\alpha > 0$.

(a) Pairwise invadability plot (PIP)

$$S_x(y) = \lim_{\substack{m \to 0 \\ n \to k(x)}} 1 - \frac{a(y,x)n + m}{k(y)} = 1 - \frac{a(y,x)k(x)}{k(y)}$$

with $k(x)$ and $a(y, x)$ given above so

$$S_x(y) = 1 - \frac{e^{-\alpha|x-y|}e^{-x^2}}{e^{-y^2}} = 1 - e^{-\alpha|x-y|-x^2+y^2}$$

Therefore $S_x(y) = 0$ is equivalent to the equation

$$-\alpha|x - y| - x^2 + y^2 = 0 \tag{3}$$

We have to work on 2 different cases

1. if $y \geq x$ the equation (3) becomes

$$\alpha(x - y) - x^2 + y^2 = 0 \Leftrightarrow (x - y)(\alpha - x - y) = 0$$
$$\Leftrightarrow x = y \text{ or } y = \alpha - x \quad y \geq x$$

   We look at the signs by computing $S_x(y)$ at the poimts $(x, y) = (-\alpha, 0)$ $(S_x(y) > 0)$ and $(0, 2\alpha)$ where $S_x(y) < 0$. That gives for the region $y \geq x$ the sign plot figure 7.

2. if $y \leq x$ the equation (3) becomes

$$-\alpha(x - y) - (x - y)(x + y) = 0 \Leftrightarrow (x - y)(-\alpha - x - y) = 0$$
$$\Leftrightarrow x = y \text{ or } y = -\alpha - x \quad y \leq x$$

   We look at the signs by computing $S_x(y)$ at the poimts $(x, y) = (\alpha, 0)$ $(S_x(y) > 0)$ and $(0, -2\alpha)$ where $S_x(y) < 0$. That gives for the region $y \geq x$, the sign plot, figure 8.

   Finally, the full sign plot (PIP) is given by the figure 9.

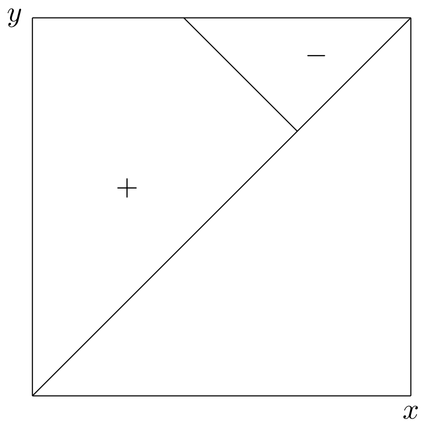


Figure 7:

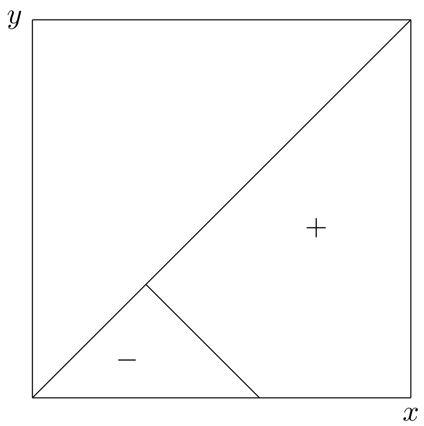


Figure 8:

(b) Dependence on α

$$\lim_{\alpha \to 0} \alpha - x = -x = \lim_{\alpha \to 0} -x - \alpha$$

(c) Evolutionarily stable strategies

From the pairwise invadability plot, figure 9, we can see that for any x, there exists a y such that $S_x(y) > 0$ so x can be invaded by y and therefore there is no ESS.

(d) Coexistence

Two strategies x and y can coexist if $S_x(y) > 0$ and $S_y(x) >$ which correpsonds on the sign plot to a region ++ on the superimposed sign plot, figure 10.

For $-\alpha - x < y < \alpha - x$ then there can be coexistence.

(e) Strategy dynamics starting with a monomorphic resident population and with small mutation steps

For any $x < -\frac{\alpha}{2}$ then any $x < y$ invades. By small steps, it converges to $x = -\frac{\alpha}{2}$. Then there can be coexistence. If you think of a plot with strategies plotted with respect to time then this looks like the plot of the case $\alpha > 1$ on p.3 of the first lecture notes. The process first slowly converges to the value $-\frac{\alpha}{2}$ and then it branches.

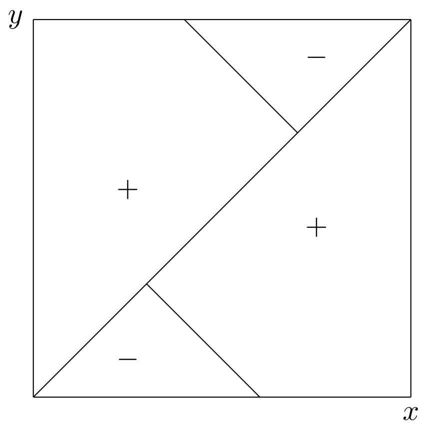
3. 

Figure 9:

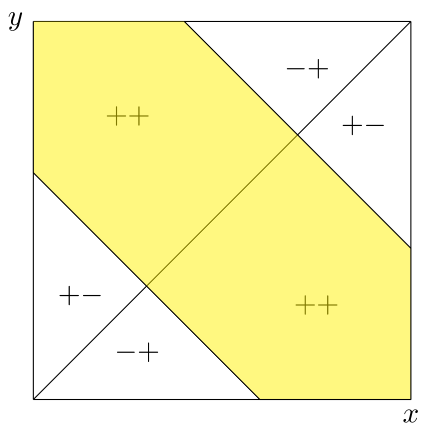


Figure 10: