MATHEMATICAL MODELLING

HOMEWORK SOLUTIONS

October 14, 2015

Exercise 12

This is an example of juvenile-juvenile interference competition.

Within-season dynamics. Let x_n be the number of adults at the beginning of season n, and let $\boxed{U}$ and $\boxed{V}$ denote adult and juvenile individuals, respectively. I assume that juveniles die only due to competition (no natural death within the season) and use the rate 2γ instead of γ (for simplicity of notation).

$$\boxed{U} \xrightarrow{\beta} \boxed{V} + \boxed{U}$$
$$\boxed{V} + \boxed{V} \xrightarrow{2\gamma} \boxed{V}$$

The within-season dynamics is described by

$$\begin{cases} \frac{dU}{dt} = 0 & U(0) = x_n \\ \frac{dV}{dt} = \beta U - \gamma V^2 & V(0) = 0 \end{cases}$$

The first equation gives $U(t) = x_n$ for all $t \in [0, 1]$. We can solve the second equation by separation of variables

$$\int_0^{V_n(t)} \frac{dV}{\beta x_n - \gamma V^2} = \int_0^t dt \tag{1}$$

For the left-hand side we now use the integration formula

$$\int \frac{dx}{1 - x^2} = \frac{1}{2} \log \left| \frac{1 + x}{1 - x} \right| + c.$$

Therefore,

$$\int_0^{V_n(t)} \frac{dV}{\beta x_n - \gamma V^2} = \frac{1}{\sqrt{\beta x_n \gamma}} \int_0^{V_n(t)} \frac{\sqrt{\frac{\gamma}{\beta x_n}} dV}{1 - (\sqrt{\frac{\gamma}{\beta x_n}} V)^2} = \frac{1}{2\sqrt{\beta x_n \gamma}} \log \left| \frac{1 + \sqrt{\frac{\gamma}{\beta x_n}} V_n(t)}{1 - \sqrt{\frac{\gamma}{\beta x_n}} V_n(t)} \right|$$

Assume $\sqrt{\frac{\gamma}{\beta x_n}} V_n(t) < 1$. We plug into (1) and obtain

$$1 + \sqrt{\frac{\gamma}{\beta x_n}} V_n(t) = e^{2\sqrt{\beta x_n \gamma}\, t} \left(1 - \sqrt{\frac{\gamma}{\beta x_n}} V_n(t) \right)$$
$$(e^{2\sqrt{\beta x_n \gamma}\, t} + 1) \sqrt{\frac{\gamma}{\beta x_n}} V_n(t) = e^{2\sqrt{\beta x_n \gamma}\, t} - 1$$
$$V_n(t) = \frac{e^{2\sqrt{\beta x_n \gamma}\, t} - 1}{e^{2\sqrt{\beta x_n \gamma}\, t} + 1} \sqrt{\frac{\beta x_n}{\gamma}}$$

Note that $V_n(0) = 0$ and $\sqrt{\frac{\gamma}{\beta x_n}} V_n(t) < 1$ for all $t \geq 0$, therefore we do not need to consider the case opposite case ($\sqrt{\frac{\gamma}{\beta x_n}} V_n(t) > 1$).

Between-season dynamics. Let σ denote the fraction of juveniles that survive from one season to the next and become adults. Therefore,

$$x_{n+1} = \sigma V_n(1) = \sigma \frac{e^{2\sqrt{\beta\gamma x_n}} - 1}{e^{2\sqrt{\beta\gamma x_n}} + 1} \sqrt{\frac{\beta x_n}{\gamma}} =: f(x_n).$$

Equilibria and stability. The equilibria are $x = 0$ and $\bar{x}$ such that

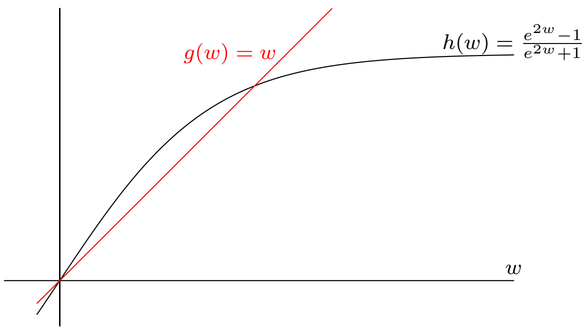
$$\bar{x} = \sigma \frac{e^{2\sqrt{\beta\gamma\bar{x}}} - 1}{e^{2\sqrt{\beta\gamma\bar{x}}} + 1} \sqrt{\frac{\beta\bar{x}}{\gamma}} \quad \Leftrightarrow \quad \sqrt{\beta\gamma\bar{x}} = \beta\sigma \frac{e^{2\sqrt{\beta\gamma\bar{x}}} - 1}{e^{2\sqrt{\beta\gamma\bar{x}}} + 1} \tag{2}$$

In order to check if there exist a positive $\bar{x}$ satisfying (2), we check if the two curves $g(w) = w$ and $h(w) = \beta\sigma\frac{e^{2w}-1}{e^{2w}+1}$ have a positive intersection (see picture). This is equivalent to check that $h(w)$ has a derivative greater than 1 in 0.

$$h'(0) = \beta\sigma \frac{2e^{2w}(e^{2w}+1) - 2e^{2w}(e^{2w}-1)}{(e^{2w}+1)^2}\Big|_{w=0} = \beta\sigma$$

Therefore,

$$\exists \bar{x} > 0 \Leftrightarrow \beta\sigma > 1.$$



The function $f(x_n)$ has a similar shape to the graph of $h(w)$ (but with no horizontal asymptote). Therefore, if a positive equilibrium exist, it is easy to verify its stability by using the cobweb method.

Exercise 13

Consider the Ricker model

$$x_{n+1} = a x_n e^{-b x_n}. \tag{3}$$

The equilibrium condition is

$$1 = a e^{-b\bar{x}}, \tag{4}$$

and we have seen in the lecture that the stability of $\bar{x}$ depends only on the coefficient a. Consider now the two different derivations.

Adult-juvenile competition with reproductive burst. In class we solved explicitly the within-season dynamics and found

$$v_n(t) = \beta x_n e^{-\gamma x_n t}.$$

Assume that the season length is T. Then, the between-season dynamics is given by (3) with

$$a = \sigma\beta, \qquad b = \gamma T.$$

From the equilibrium condition (4) we observe that the value of $\bar{x}$ depends on the season length T (the higher is T, the smaller is the equilibrium density $\bar{x}$). Instead, since a does not depend on T, the stability of $\bar{x}$ is also independent of T.

Site occupancy with scramble competition. The within-season dynamics gives

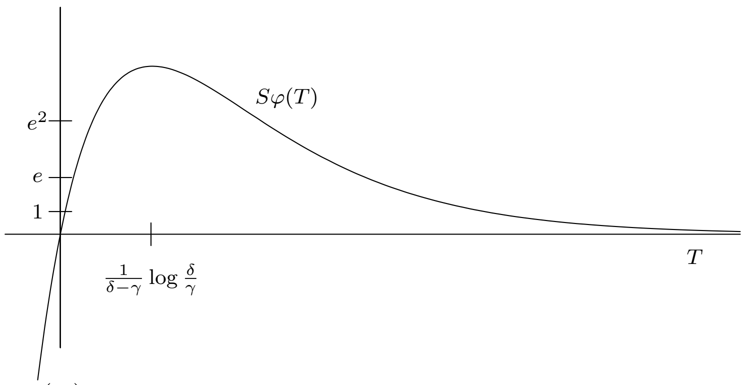
$$v_n(t) = \frac{e^{-\delta t} - e^{-\gamma t}}{\gamma - \delta}\beta x_n.$$

Denote S the density of sites and define $\varphi(T) := \sigma\beta\frac{e^{-\delta T} - e^{-\gamma T}}{\gamma - \delta}$. When we consider scramble competition, we get the Ricker model (3) with

$$a = S\varphi(T), \qquad b = \varphi(T).$$

The equilibrium $\bar{x}$ is defined by (4). Its existence and stability depend on the coefficient a. In particular, we distinguish the following cases

no positive equilibrium	$\Leftrightarrow$	$0 < a \leq 1$	$\Leftrightarrow$	$S\varphi(T) \leq 1$
$\bar{x}$ monotonically stable	$\Leftrightarrow$	$1 < a < e$	$\Leftrightarrow$	$1 < S\varphi(T) < e$
$\bar{x}$ oscillatory stable	$\Leftrightarrow$	$e < a < e^2$	$\Leftrightarrow$	$e < S\varphi(T) < e^2$
$\bar{x}$ oscillatory unstable	$\Leftrightarrow$	$a > e^2$	$\Leftrightarrow$	$S\varphi(T) > e^2$



We observe that $\varphi(T)$ is increasing up to

$$\hat{T} = \frac{1}{\delta - \gamma}\log\frac{\delta}{\gamma}$$

and then it decreases to zero. Assume all the parameters except T are fixed, so the shape of $\varphi(T)$ is well determined. The threshold values $1, e, e^2$ are in the vertical axis.

Therefore, increasing T but remaining below $\hat{T}$ makes it easier to *destabilize* the equilibrium. Instead, when we consider $T > \hat{T}$ and we increase T further and further, we observe the following changes:

$\bar{x}$ unstable $\rightarrow$ $\bar{x}$ oscillatory stable $\rightarrow$ $\bar{x}$ monotonically stable $\rightarrow$ $x = 0$ is stable (extinction).

Note that, for some parameter values, it might hold $S\varphi(T) < e^2$ for all T. In this case the positive equilibrium is always stable when it exists.

Exercise 14

Within-season dynamics. From the i-processes (to simplify the notation, I introduce $\eta = \nu/2$), we get the equations

$$\begin{cases} \frac{dU}{dt} = -\mu U - \eta U^2, & U(0) = x_n \\ \frac{dV}{dt} = -\delta V - \gamma UV, & V(0) = \beta x_n \end{cases} \tag{5}$$

Note that the reproductive burst is translated into the initial condition for V.

We solve the first equation by separation of variables,

$$\int_{x_n}^{U_n(t)} \frac{dU}{U(\mu + \eta U)} = -\int_0^t dt. \tag{6}$$

To solve the left-hand side, we observe that

$$\frac{1}{U(\mu + \eta U)} = \frac{A}{U} + \frac{B}{\mu + \eta U} \quad \Leftrightarrow \quad A = \frac{1}{\mu}, \quad B = -\eta A = -\frac{\eta}{\mu}$$

and therefore

$$\begin{aligned} \int_{x_n}^{U_n(t)} \frac{dU}{U(\mu + \eta U)} &= \frac{1}{\mu}\left[\int_{x_n}^{U_n(t)} \frac{dU}{U} - \int_{x_n}^{U_n(t)} \frac{\eta dU}{\mu + \eta U}\right] \\ &= \frac{1}{\mu}\left[\log U_n(t) - \log x_n - \log(\mu + \eta U_n(t)) + \log(\mu + \eta x_n)\right] \\ &= \frac{1}{\mu}\log\left(\frac{(\mu + \eta x_n)U_n(t)}{x_n(\mu + \eta U_n(t))}\right) \end{aligned}$$

We are now ready to solve (6):

$$\frac{1}{\mu}\log\left(\frac{(\mu + \eta x_n)U_n(t)}{x_n(\mu + \eta U_n(t))}\right) = -t$$

$$U_n(t, x_n) = \frac{\mu x_n e^{-\mu t}}{\mu + \eta x_n - \eta x_n e^{-\mu t}}. \tag{7}$$

We now solve the second equation in (5), again by separation of variables,

$$\int_{\beta x_n}^{V_n(t)} \frac{dV}{V} = -\int_0^t (\delta + \gamma U_n(s, x_n))ds$$

from which we get

$$V_n(t) = \beta x_n e^{-\delta t} e^{-\gamma \int_0^t U_n(s, x_n)ds}$$

Between-season dynamics. Assume that a proportion σ of juveniles survive to the next season and become adults. The we get the discrete-time equation

$$\begin{aligned} x_{n+1} &= \sigma V_n(1) = \sigma\beta x_n e^{-\delta} e^{-\gamma \int_0^1 U_n(s,x_n)ds} \\ &= \frac{\sigma\beta x_n}{\mu} e^{-\delta} \left(\mu + \eta x_n - \eta x_n e^{-\mu}\right)^{-\gamma/\eta} =: f(x_n) \end{aligned}$$

(this is obtained by calculating $\int U_n(t,x_n)dt = \frac{1}{\eta}\log\left|\mu + \eta x_n - \eta x_n e^{-\mu t}\right|$).

We now study graphically the existence and stability of a positive equilibrium $\bar{x}$. The function f is plotted in the picture. A positive equilibrium $\bar{x}$ exists if and only if $f'(0) < 1$. We calculate

$$f'(0) = \frac{\sigma\beta}{\mu} e^{-\delta} \left(\mu + \eta x - \eta x e^{-\mu}\right)^{-\gamma/\eta} \Big|_{x=0} = \sigma\beta e^{-\delta}\mu^{-\gamma/\delta - 1}.$$

Therefore,

$$\exists \bar{x} > 0 \Leftrightarrow \sigma\beta e^{-\delta}\mu^{-\gamma/\delta-1} < 1.$$

If this is the case, by analysing the graph by the cobweb method, it is easy to convince yourself that the positive equilibrium $\bar{x}$ is unstable.