MATHEMATICAL MODELLING

HOMEWORK SOLUTIONS

October 28, 2015

Exercise 15

Host larvae are produced at a constant per capita rate α during the season instead of a single reproductive burst. The adult host density is constant (equal to x_n) during the season.

(a) Within-season dynamics

$$\begin{cases} \dfrac{dv_0(t)}{dt} = \alpha x_n - \beta y_n v_0(t), & v_0(0) = 0 \\ \dfrac{dv_1(t)}{dt} = +\beta y_n v_0(t), & v_1(0) = 0 \end{cases}$$

The solution of the system is (solution of a linear ODE by variation of constants)

$$v_0(t) = \int_0^t e^{-\beta y_n (t-s)} \alpha x_n ds = \frac{\alpha x_n}{\beta y_n}\left(1 - e^{-\beta y_n t}\right)$$
$$v_1(t) = \alpha x_n \int_0^t \left(1 - e^{-\beta y_n s}\right) ds = \alpha x_n \left(t - \frac{1 - e^{-\beta y_n t}}{\beta y_n}\right)$$

(b) Between-season dynamics

$$\begin{cases} x_{n+1} = v_0(1) = \frac{\alpha x_n}{\beta y_n}\left(1 - e^{-\beta y_n}\right) \\ y_{n+1} = v_1(1) = \frac{\alpha x_n}{\beta y_n}\left(\beta y_n - 1 + e^{-\beta y_n}\right) \end{cases} \tag{1}$$

(c) Positive equilibrium $(\overline{x}, \overline{y})$ must satisfy

$$\begin{cases} \overline{x} = \frac{\alpha \overline{x}}{\beta \overline{y}}\left(1 - e^{-\beta \overline{y}}\right) \\ \overline{y} = \frac{\alpha \overline{x}}{\beta \overline{y}}\left(\beta \overline{y} - 1 + e^{-\beta \overline{y}}\right) \end{cases}$$

and, by simplifying, we get the equations

$$\begin{cases} \overline{y} = \frac{\alpha}{\beta}\left(1 - e^{-\beta \overline{y}}\right) \\ \overline{y} = (\alpha - 1)\overline{x} \end{cases}$$

By studying graphically the first equation, we observe that it admits a positive solution if and only if the derivative with respect to y of the function $h(y) := \frac{\alpha}{\beta}\left(1 - e^{-\beta y}\right)$ in 0 is greater than 1, if and only if $\alpha > 1$. Under the same condition, we can also invert the second equation.

Therefore, we conclude that system (1) admits a positive equilibrium $(\overline{x}, \overline{y})$ if and only if $\alpha > 1$, and in this case it is given by the equations

$$\begin{cases} \overline{y} = \frac{\alpha}{\beta}\left(1 - e^{-\beta\overline{y}}\right) \\ \overline{x} = \frac{\overline{y}}{\alpha - 1} \end{cases} \tag{2}$$

(d) Stability of $(\overline{x}, \overline{y})$. Since this is a planar system, we cannot use a graphical method like the cobweb method in one dimension. Therefore, we need to use local stability analysis. Consider system (1) and define f, g such that

$$f(x,y) = \frac{\alpha x}{\beta y}\left(1 - e^{-\beta y}\right)$$
$$g(x,y) = \frac{\alpha x}{\beta y}\left(\beta y - 1 + e^{-\beta y}\right)$$

The jacobian at the equilibrium $(\overline{x}, \overline{y})$ is given by

$$J = \begin{pmatrix} \frac{\partial f}{\partial x} & \frac{\partial f}{\partial y} \\ \frac{\partial g}{\partial x} & \frac{\partial g}{\partial y} \end{pmatrix}_{(\overline{x}, \overline{y})} = \begin{pmatrix} \frac{\alpha}{\beta y}\left(1 - e^{-\beta y}\right) & \alpha x \frac{\beta y e^{-\beta y} - 1 + e^{-\beta y}}{\beta y^2} \\ \frac{\alpha}{\beta y}\left(\beta y - 1 + e^{-\beta y}\right) & \alpha x \frac{-\beta y e^{-\beta y} + 1 - e^{-\beta y}}{\beta y^2} \end{pmatrix}_{(\overline{x}, \overline{y})}$$

and, by using the equilibrium conditions (2), we can simplify

$$J = \begin{pmatrix} 1 & 1 - \beta\overline{x} \\ \alpha - 1 & -1 + \beta\overline{x} \end{pmatrix}$$

In order to apply the stability criterion for discrete planar systems (*triangle of stability*, see picture below) we compute trace and determinant:

$$\operatorname{tr}(J) = \beta\overline{x} > 0$$
$$\det(J) = \alpha(\beta\overline{x} - 1)$$

The equilibrium is stable if and only if $(\operatorname{tr}(J), \det(J))$ lies inside the *triangle of stability*. Since $\operatorname{tr}(J) > 0$, this is true if and only if

$$\begin{cases} \operatorname{tr}(J) < 2 \\ \det(J) > \operatorname{tr}(J) - 1 \end{cases} \Leftrightarrow \begin{cases} \beta\overline{x} < 2 \\ \alpha(\beta\overline{x} - 1) > \beta\overline{x} - 1 \end{cases}$$

$$\Leftrightarrow \begin{cases} 0 < \beta\overline{x} < 1 \\ \alpha < 1 \end{cases} \text{NO!} \quad \text{or} \quad \begin{cases} 1 < \beta\overline{x} < 2 \\ \alpha > 1 \end{cases} \text{ok}$$

Therefore, we conclude that a positive equilibrium $(\overline{x}, \overline{y})$ exists if and only if $\alpha > 1$, and it is stable if, moreover, $1 < \beta\overline{x} < 2$.

Exercise 16

Reproductive burst at the beginning of the season. Adult hosts cannibalise on their larvae (density-dependent interaction with rate γ). For simplicity, I write the complete analysis of the model in which adults cannibalise only on non-parasitized larvae. The case of adult cannibalising also on parasitized larvae was shown in the exercise class.

(a) Within-season dynamics

$$\begin{cases} \dfrac{dv_0(t)}{dt} = -\beta y_n v_0(t) - \gamma x_n v_0(t), & v_0(0) = \alpha x_n \\ \dfrac{dv_1(t)}{dt} = +\beta y_n v_0(t), & v_1(0) = 0 \end{cases}$$

The solution of the linear system is

$$v_0(t) = \alpha x_n e^{-(\beta y_n + \gamma x_n)t}$$
$$v_1(t) = \alpha x_n \left(1 - e^{-(\beta y_n + \gamma x_n)t}\right)$$

Remark 1. Assuming, instead, that adult cannibalise also on parasitized larvae, the within-season dynamics reads

$$\begin{cases} \dfrac{dv_0(t)}{dt} = -\beta y_n v_0(t) - \gamma x_n v_0(t), & v_0(0) = \alpha x_n \\ \dfrac{dv_1(t)}{dt} = +\beta y_n v_0(t) - \gamma x_n v_1(t), & v_1(0) = 0 \end{cases}$$

and the analysis follows the same steps, maybe with a little more difficult calculations.

(b) Between-season dynamics

$$\begin{cases} x_{n+1} = v_0(1) = \alpha x_n e^{-\beta y_n - \gamma x_n} =: f(x_n, y_n) \\ y_{n+1} = v_1(1) = \alpha x_n \left(1 - e^{-\beta y_n - \gamma x_n}\right) =: g(x_n, y_n) \end{cases} \tag{3}$$

Assume $x_n \to \infty$. Then $f(x_n, y_n) \to 0$, contradiction. Therefore x_n is bounded. Since $y_n < \alpha x_n$ for any value of x_n, y_n is also bounded.

(c) Positive equilibrium $(\overline{x}, \overline{y})$ must satisfy

$$\begin{cases} 1 = \alpha e^{-\beta \overline{y} - \gamma \overline{x}} \\ \overline{y} = \alpha \overline{x} \left(1 - e^{-\beta \overline{y} - \gamma \overline{x}}\right) = (\alpha - 1)\overline{x} \end{cases}$$

A positive equilibrium exists if $\alpha > 1$ and if there exists a positive solution to the equation

$$1 = \alpha e^{-(\beta(\alpha-1)+\gamma)\overline{x}}$$

When $\alpha > 1$, the right-hand side is a decreasing exponential, the equation admits a positive solution and we can calculate the equilibrium explicitly:

$$\overline{x} = \frac{\log \alpha}{\beta(\alpha - 1) + \gamma} \tag{4}$$
$$\overline{y} = \frac{(\alpha - 1)\log \alpha}{\beta(\alpha - 1) + \gamma} \tag{5}$$

(d) Stability of $(\overline{x},\overline{y})$. The jacobian at the equilibrium $(\overline{x},\overline{y})$ (simplified using the equilibrium conditions for $\overline{x}$, $\overline{y}$) is

$$J = \begin{pmatrix} \alpha e^{-\beta\overline{y}-\gamma\overline{x}}(1-\gamma\overline{x}) & -\alpha\beta\overline{x}e^{-\beta\overline{y}-\gamma\overline{x}} \\ \alpha-\alpha e^{-\beta\overline{y}-\gamma\overline{x}}(1-\gamma\overline{x}) & \alpha\beta\overline{x}e^{-\beta\overline{y}-\gamma\overline{x}} \end{pmatrix} = \begin{pmatrix} 1-\gamma\overline{x} & -\beta\overline{x} \\ \alpha-1+\gamma\overline{x} & \beta\overline{x} \end{pmatrix}$$

$$\mathrm{tr}(J) = 1-\gamma\overline{x}+\beta\overline{x}$$
$$\det(J) = \alpha\beta\overline{x} > 0$$

The equilibrium is stable if and only if $(\mathrm{tr}(J),\det(J))$ lies inside the *triangle of stability*, if and only if

$$\begin{cases} -1 < \det(J) < 1 \\ \det(J) > \mathrm{tr}(J)-1 \\ \det(J) > -\mathrm{tr}(J)-1 \end{cases} \Leftrightarrow \begin{cases} \frac{\gamma}{\beta} > \alpha\log\alpha-\alpha+1 \\ (\alpha-1)\beta > -\gamma & \text{always true for } \alpha>1 \\ ((\alpha+1)\beta-\gamma)\overline{x} > -2 \end{cases}$$

$$\Leftrightarrow \begin{cases} \frac{\gamma}{\beta} > \alpha\log\alpha-\alpha+1 \\ (\alpha+1-\frac{\gamma}{\beta})\log\alpha > -2(\alpha-1+\frac{\gamma}{\beta}) \end{cases} \Leftrightarrow \begin{cases} \frac{\gamma}{\beta} > \alpha\log\alpha-\alpha+1 \\ \frac{\gamma}{\beta}(2-\log\alpha) > 2-\log\alpha-\alpha(2+\log\alpha) \end{cases}$$

$$\Leftrightarrow \begin{cases} \log\alpha < 2 \\ \frac{\gamma}{\beta} > \alpha\log\alpha-\alpha+1 \\ \frac{\gamma}{\beta} > 1-\alpha\frac{2+\log\alpha}{2-\log\alpha} \end{cases} \quad \text{or} \quad \begin{cases} \log\alpha > 2 \\ \frac{\gamma}{\beta} > \alpha\log\alpha-\alpha+1 \\ \frac{\gamma}{\beta} < 1+\alpha\frac{2+\log\alpha}{\log\alpha-2} \end{cases}$$

In conclusion: the positive equilibrium $(\overline{x},\overline{y})$ exists (given by (4)–(5)) if and only if $\alpha > 1$; the positive equilibrium is stable if, moreover,

$$\begin{cases} 1<\alpha<e^2 \\ \frac{\gamma}{\beta} > \max\left\{\alpha\log\alpha-\alpha+1, 1+\alpha\frac{2+\log\alpha}{\log\alpha-2}\right\} \end{cases} \quad \text{or} \quad \begin{cases} e^2<\alpha<e^4 \\ \alpha\log\alpha-\alpha+1 < \frac{\gamma}{\beta} < 1+\alpha\frac{2+\log\alpha}{\log\alpha-2} \end{cases}$$

Note that the condition $\alpha < e^4$ comes from requiring that: $\alpha\log\alpha-\alpha+1 < 1+\alpha\frac{2+\log\alpha}{\log\alpha-2}$.