MATHEMATICAL MODELLING

HOMEWORK SOLUTIONS

October 7, 2015

Exercise 10

(a) Population dynamics

$$
\begin{array}{llllll}
 & \text{prey dyn} & \text{exp.predation} & \text{unexp.predation} & \text{exp.forgetting} & \text{death} \\
\dfrac{dX}{dt} = & g(X) & -\beta_e X Y_e & -\beta_u X Y_u & & \\
\dfrac{dY_e}{dt} = & & & +\beta_u X Y_u & -\gamma Y_e & -\delta Y_e \\
\dfrac{dY_u}{dt} = & & +p\beta_e X Y_e & -(1-p)\beta_u X Y_u & +\gamma Y_e & -\delta Y_u
\end{array}
$$

The equation for the total density of predators $Y := Y_e + Y_u$ is

$$\frac{dY}{dt} = p\beta_e X Y_e + p\beta_u X Y_u - \delta Y.$$

(b) Tips for the scaling: since I want the transitions between experienced and unexperienced to be fast, I start by imposing high rates for the corresponding i-transitions $(\beta_e, \beta_u, \gamma)$; then, I scale the other parameters/variables to obtain the desired fast/slow equations.

Let $\varepsilon > 0$ be a small scaling parameter. Scale parameters and variables using the following scaling

$$\frac{\gamma}{\varepsilon}, \quad \frac{\beta_e}{\varepsilon}, \quad \frac{\beta_u}{\varepsilon}, \quad \varepsilon p, \quad \varepsilon Y_u, \quad \varepsilon Y_e \quad \text{(and therefore } \varepsilon Y\text{)} \tag{1}$$

and we obtain the following equations for the fast-slow dynamics

$$
\begin{aligned}
\frac{dX}{dt} &= g(X) - \beta_e X Y_e - \beta_u X Y_u && \text{(slow)} \\
\frac{dY}{dt} &= p\beta_e X Y_e + p\beta_u X Y_u - \delta Y && \text{(slow)} \\
\frac{dY_e}{dt} &= \tfrac{\beta_u}{\varepsilon} X Y_u - \tfrac{\gamma}{\varepsilon} Y_e - \delta Y_e && \text{(fast)} \\
\frac{dY_u}{dt} &= p\beta_e X Y_e - \tfrac{(1-\varepsilon p)\beta_u}{\varepsilon} X Y_u + \tfrac{\gamma}{\varepsilon} Y_e - \delta Y_u && \text{(fast)}
\end{aligned}
$$

(c) We write $Y_u = Y - Y_e$ and introduce the fast time $\tau := t/\varepsilon$. For fixed X and Y, in the limit $\varepsilon \to 0$, the equation for the fast dynamics

$$\frac{dY_e}{d\tau} = \beta_u XY - (\beta_u X + \gamma)Y_e.$$

The quasi-equilibrium is

$$\overline{Y}_e(X,Y) = \frac{\beta_u XY}{\beta_u X + \gamma} \tag{2}$$

and it is easy to check that the equilibrium is stable. At quasi-equilibrium, $q = \frac{\beta_u X}{\beta_u X+\gamma}$ is the fraction of the predator population that is experienced.

(d-e) The equations for the slow dynamics are

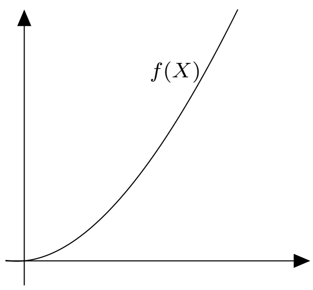
$$\frac{dX}{dt} = g(X) - (\beta_e - \beta_u)X\overline{Y}_e - \beta_u XY = g(X) - \frac{\beta_e X + \gamma}{\beta_u X + \gamma}\beta_u XY \tag{3}$$

$$\frac{dY}{dt} = \frac{\beta_e X + \gamma}{\beta_u X + \gamma} p\beta_u XY - \delta Y, \tag{4}$$

From (3) we conclude that the functional response to predation is

$$f(X) = \frac{\beta_e X + \gamma}{\beta_u X + \gamma}\beta_u X.$$

Observe that, for $X \geq 0$, the functional response explodes to infinity as X increases.



Assume $g(X)$ is logistic, i.e.

$$g(X) = rX\left(1 - \frac{X}{K}\right).$$

Observe that this is a Gause model with $f(X)$, $g(X)$ defined as before. The equilibria are $(0,0)$, $(K,0)$, and $(\overline{X}, \overline{Y})$, satisfying

$$p\beta_e\beta_u\overline{X}^2 + (p\gamma - \delta)\beta_u\overline{X} - \delta\gamma = 0$$

and

$$\overline{Y} = \frac{r}{\beta_u\overline{X}}\left(1 - \frac{\overline{X}}{K}\right)\frac{\beta_u\overline{X} + \gamma}{\beta_e\overline{X} + \gamma}.$$

As seen in the lectures, the stability of $(\overline{X}, \overline{Y})$ is determined by the slope of the X-isocline in $\overline{X}$. The X-isocline is

$$\frac{g(X)}{f(X)} = \frac{r}{\beta_u}\left(1 - \frac{X}{K}\right)\frac{\beta_u X + \gamma}{\beta_e X + \gamma}$$

and

$$\frac{d}{dt}\left(\frac{g(X)}{f(X)}\right) = -\frac{r}{\beta_u K}\frac{\beta_u X + \gamma}{\beta_e X + \gamma} - \frac{r\gamma}{\beta_u}\left(1 - \frac{X}{K}\right)\frac{\beta_e - \beta_u}{(\beta_e X + \gamma)^2}$$

which is negative for all $0 < X < K$. Therefore, we conclude that $(\overline{X}, \overline{Y})$ is a stable equilibrium of the slow predator-prey dynamics.

(f) To obtain a Holling type III functional response, we need to include a mechanisms of "saturation", so that the functional response is bonded even when the prey density is very high. For instance, this can be obtained by including handling time in the model.

Let $\boxed{Y_h}$ be a handling predator. We modify the i-level processes in the following way

$$\begin{aligned}
\boxed{X} + \boxed{Y_e} &\xrightarrow{\beta_e} \boxed{Y_h} \\
\boxed{X} + \boxed{Y_u} &\xrightarrow{\beta_u} \boxed{Y_h} \\
\boxed{Y_h} &\xrightarrow{(1-p)\lambda} \boxed{Y_e} \\
\boxed{Y_h} &\xrightarrow{p\lambda} \boxed{Y_e} + \boxed{Y_u} \\
\boxed{Y_e} &\xrightarrow{\gamma} \boxed{Y_u} \\
\boxed{Y_j} &\xrightarrow{\delta} \text{dead} \qquad j = e, u, h
\end{aligned}$$

Exercise 11

Note that fast processes are described by large rates, so we make use of a small scaling parameter $\varepsilon > 0$.

(a) Denote $\boxed{Y_s}$ a single searching predator, $\boxed{Y_p}$ a pair of interacting predator individuals.

$$\begin{aligned}
\boxed{Y_s} + \boxed{Y_s} &\xrightarrow{\alpha/\varepsilon} \boxed{Y_p} \\
\boxed{Y_p} &\xrightarrow{\mu/\varepsilon} 2\,\boxed{Y_s} \\
\boxed{X} + \boxed{Y_s} &\xrightarrow{(1-p)\beta} \boxed{Y_s} \\
\boxed{X} + \boxed{Y_s} &\xrightarrow{p\beta} 2\,\boxed{Y_s} \\
\boxed{Y_s} &\xrightarrow{\delta} \text{dead} \\
\boxed{Y_p} &\xrightarrow{2\delta} \boxed{Y_s}
\end{aligned}$$

The population densities are described by

$$\begin{aligned}
\frac{dX}{dt} &= g(X) - \beta X Y_s \\
\frac{dY_s}{dt} &= -\frac{\alpha}{\varepsilon} Y_s^2 + 2\frac{\mu}{\varepsilon} Y_p + p\beta X Y_s - \delta Y_s + 2\delta Y_p \\
\frac{dY_p}{dt} &= \frac{\alpha}{2\varepsilon} Y_s^2 - \frac{\mu}{\varepsilon} Y_p - 2\delta Y_p
\end{aligned}$$

Introduce the total density of predators, $Y = Y_s + 2Y_p$. This is a slow variable. Consider the system

$$\begin{aligned}
\frac{dX}{dt} &= g(X) - \beta X Y_s = g(X) - f_a(X, Y) Y \\
\frac{dY}{dt} &= p\beta X Y_s - \delta Y \\
\frac{dY_s}{dt} &= -\frac{\alpha}{\varepsilon} Y_s^2 + \frac{\mu}{\varepsilon}(Y - Y_s) + p\beta X Y_s - \delta Y_s + 2\delta(Y - Y_s)
\end{aligned}$$

The fast dynamics is

$$\frac{dY_s}{d\tau} = -\alpha Y_s^2 + \mu(Y - Y_s).$$

Denote $\overline{Y}_s(Y)$ the positive quasi-equilibrium of the fast variable Y_s,

$$\alpha Y_s^2 + \mu Y_s - \mu Y = 0 \quad \Leftrightarrow \quad \overline{Y}_s = \frac{-\mu + \sqrt{\mu^2 + 4\alpha\mu Y}}{2\alpha}$$

Then, the functional response reads

$$f_a(X, Y) = \frac{-\mu + \sqrt{\mu^2 + 4\alpha\mu Y}}{2\alpha} \frac{\beta X}{Y}$$

(b) Denote $\boxed{X_s}$ a single prey, $\boxed{X_p}$ a pair of prey individuals.

$$\begin{aligned}
\boxed{X_s} + \boxed{X_s} &\xrightarrow{\alpha/\varepsilon} \boxed{X_p} \\
\boxed{X_p} &\xrightarrow{\mu/\varepsilon} 2\,\boxed{X_s} \\
\boxed{X_s} + \boxed{Y} &\xrightarrow{(1-p)\beta} \boxed{Y} \\
\boxed{X_s} + \boxed{Y} &\xrightarrow{p\beta} 2\,\boxed{Y} \\
\boxed{Y} &\xrightarrow{\delta} \text{dead}
\end{aligned}$$

Denote $X := X_s + 2X_p$ the total prey density. The population densities are described by

$$\begin{aligned}
\frac{dX_s}{dt} &= g(X) - \frac{\alpha}{\varepsilon} X_s^2 + 2\frac{\mu}{\varepsilon} X_p - \beta X_s Y \\
\frac{dX_p}{dt} &= \frac{\alpha}{2\varepsilon} X_s^2 - \frac{\mu}{\varepsilon} X_p \\
\frac{dX}{dt} &= g(X) - \beta X_s Y = g(X) - f_b(X, Y) Y \\
\frac{dY}{dt} &= p\beta X_s Y - \delta Y
\end{aligned}$$

The first two equations describe the fast dynamics and they can simplified by taking $X_s = X - 2X_p$. The quasi-equilibrium $\overline{X}_p(X, Y)$ satisfies

$$0 = \frac{\alpha}{2}(X - 2\overline{X}_p)^2 - \mu \overline{X}_p = 2\alpha \overline{X}_p^2 - (2\alpha X + \mu)\,\overline{X}_p + \frac{\alpha X^2}{2}$$

$$\overline{X}_p(X) = \frac{2\alpha X + \mu - \sqrt{\mu^2 + 4\alpha\mu X}}{4\alpha}$$

(note that $2X_p < X$). Then, the functional response to predation is

$$f_b(X) = \beta \overline{X}_s = \beta(X - 2\overline{X}_p) = \beta \frac{-\mu + \sqrt{\mu^2 + 4\alpha\mu X}}{2\alpha}.$$

Note that, since the functional response depends only on the prey density X, this is a Gause model.

(c) Denote $\boxed{X_s}$ a single prey, $\boxed{Y_s}$ a single predator, $\boxed{P}$ a prey-predator pair (note that it is important to consider the pair as a whole, because each individual in the pair depends on its specific mate). We consider predator mortality at rate δ, but we neglect prey natural mortality.

$$\begin{aligned}
\boxed{X_s} + \boxed{Y_s} &\xrightarrow{\alpha/\varepsilon} \boxed{P} \\
\boxed{P} &\xrightarrow{\mu/\varepsilon} \boxed{X_s} + \boxed{Y_s} \\
\boxed{P} &\xrightarrow{(1-p)\beta} \boxed{Y_s} \\
\boxed{P} &\xrightarrow{p\beta} 2\,\boxed{Y_s} \\
\boxed{Y_s} &\xrightarrow{\delta} \text{dead} \\
\boxed{P} &\xrightarrow{\delta} \boxed{X_s}
\end{aligned}$$

The population densities are described by

$$\begin{aligned}
\frac{dX_s}{dt} &= g(X,Y) - \frac{\alpha}{\varepsilon}X_sY_s + \frac{\mu}{\varepsilon}P + \delta P \\
\frac{dY_s}{dt} &= -\frac{\alpha}{\varepsilon}X_sY_s + \frac{\mu}{\varepsilon}P + (1+p)\beta P - \delta Y_s \\
\frac{dP}{dt} &= \frac{\alpha}{\varepsilon}X_sY_s - \frac{\mu}{\varepsilon}P - \beta P - \delta P
\end{aligned}$$

Introduce the total prey density $X := X_s + P$ and the total predator density $Y := Y_s + P$. Then,

$$\begin{aligned}
\frac{dX}{dt} &= g(X,Y) - \beta P = g(X,Y) - f_c(X,Y)Y \\
\frac{dY}{dt} &= p\beta P - \delta Y.
\end{aligned}$$

Through the identities $X_s = X - P$ and $Y_s = Y - P$, for fixed X and Y we describe the fast dynamics with the one-dimensional ODE

$$\frac{dP}{d\tau} = \alpha(X-P)(Y-P) - \mu P = \alpha P^2 - (\alpha X + \alpha Y + \mu)P + \alpha XY.$$

The fast dynamics has a stable equilibrium

$$\overline{P}(X,Y) = \frac{\alpha X + \alpha Y + \mu - \sqrt{(\alpha X + \alpha Y + \mu)^2 - 4\alpha^2 XY}}{2\alpha}$$

Therefore, the functional response is

$$f_c(X,Y) = \frac{\beta}{Y}\overline{P}(X,Y).$$