INTRODUCTION TO MATHEMATICAL BIOLOGY

HOMEWORK SOLUTIONS

October 17, 2016

Exercise 5.1

Consider the dynamics

$$\frac{dN_i}{dt} = [b_i - \mu_i - cN]N_i, \quad i = 1, \dots, n,$$

and the trade-off $\mu(b) = \mu_0 + ab^2$.

(a) It is easy to check (similarly to Exercises 4.3–4.4) that natural selection maximizes the quantity

$$g(b) = b - \mu(b) = b - \mu_0 - ab^2$$

(where I already included the trade-off between b and μ. The maximum value is

$$\max_b g(b) = \max_b (b - \mu_0 - ab^2) = \frac{1 - 4a\mu_0}{4a}$$

which is attained at

$$b_i = b_{\text{opt}} = \frac{1}{2a}.$$

(b) The optimal strategy $b_i = b_{\text{opt}}$ is viable if and only if there exists a stable equilibrium of the single-strain dynamics, i.e. if and only if

$$\hat{N}_i = \frac{g(b_i)}{c} = \frac{1 - 4a\mu_0}{4ac} > 0 \Leftrightarrow 4a\mu_0 < 1. \tag{1}$$

Hence the optimal strain is actually viable if and only if condition (1) holds. (But notice that, if equation (1) does not hold, any strain has a negative growth rate $b_i - \mu_i$, so any strain goes extinct.)

Exercise 5.2

Let $x_i \in [0, 1]$ be the fraction of resources that the variant plant i allocates to self-defence. The corresponding death rate is

$$\mu_i = \mu(x_i) = \frac{\mu_0}{1 + \alpha x_i}$$

and the birth rate is

$$b_i = b(x_i) = B(1 - x_i).$$

It is easy to check (similarly to Exercises 4.3) that natural selection maximizes the quantity

$$g(x_i) = \frac{b(x_i)}{\mu(x_i)} = \frac{B}{\mu_0}(1-x_i)(1+\alpha x_i)$$

The function $g(x)$ is a downward parabola which attains its maximum at

$$\hat{x} = \frac{\alpha-1}{2\alpha}, \qquad g(\hat{x}) = \frac{B}{\mu_0}\frac{(\alpha+1)^2}{4\alpha}.$$

(a) The dynamics of the variant i in absence of any other strain is described by

$$\frac{dN_i}{dt} = b_i N_i \left(1 - \frac{N_i}{M}\right) - \mu_i N_i.$$

Hence, the equilibria are $N_i = 0$ and

$$\hat{N}_i = \frac{M(b_i - \mu_i)}{b_i} > 0 \Leftrightarrow M\left(1 - \frac{1}{g(x_i)}\right) > 0 \Leftrightarrow g(x_i) > 1$$

and, by solving the second order equation, we finally get

$$\begin{aligned} g(x_i) > 1 &\Leftrightarrow (1-x_i)(1+\alpha x_i) > \frac{\mu_0}{B} \\ &\Leftrightarrow -\alpha x_i^2 + x_i(\alpha-1) + 1 - \frac{\mu_0}{B} > 0 \\ &\Leftrightarrow x_{\min} < x_i < x_{\max} \end{aligned}$$

where

$$x_{\min} = \frac{\alpha - 1 - \sqrt{(1+\alpha)^2 - 4\alpha\mu_0/B}}{2\alpha}, \qquad x_{\max} = \frac{\alpha - 1 + \sqrt{(1+\alpha)^2 - 4\alpha\mu_0/B}}{2\alpha}.$$

The set of viable strategies is

$$X = \begin{cases} [0,1] \cap (x_{\min}, x_{\max}) & \text{if } \Delta := (1+\alpha)^2 - 4\alpha\mu_0/B > 0 \\ \emptyset & \text{if } \Delta \le 0. \end{cases}$$

(b) Natural selection maximizes the $g(x_i)$, subject to the constrains from point (a), i.e., x_{opt} is such that

$$g(x_{\text{opt}}) = \max_{x \in X} g(x).$$

If $\Delta \le 0$, there is no viable strategy. If $\Delta > 0$, then we check if the maximum $\hat{x} = \frac{\alpha-1}{2\alpha}$ lies in $[0,1]$:

$$\begin{aligned} \hat{x} &= \frac{\alpha-1}{2\alpha} < 1 \quad \text{for all } \alpha > 0 \text{ and} \\ \hat{x} &= \frac{\alpha-1}{2\alpha} > 0 \Leftrightarrow \alpha > 1. \end{aligned}$$

Hence, the optimal value is

$$x_{\text{opt}} = \begin{cases} \hat{x} = \frac{\alpha-1}{2\alpha} & \text{if } \Delta > 0 \text{ and } \alpha > 1 \\ 0 & \text{if } \Delta > 0 \text{ and } \alpha \le 1. \end{cases}$$

(If α is small, then the contribution of the energy for self-defense x_i is anyway very small, so the plant should not waste its energy in it, and instead it should concentrate all the energy into reproduction.)

(c) Investigate how X and x_{opt} change with μ_0, the baseline rate of mortality.

$$\Delta > 0 \Leftrightarrow (1+\alpha)^2 - 4\alpha\mu_0/B > 0 \Leftrightarrow \mu_0 < \frac{B(1+\alpha)^2}{4\alpha}$$

We conclude that viable strategies exist only if μ_0 is sufficiently small. If the baseline rate of mortality μ_0 is too large, all the strains go extinct, independently of the birth rate b.

Exercise 5.3

The equation for the continuous-time dynamics during one year is described by the equation

$$\frac{dn}{d\tau} = -\mu_0\left(1 + \frac{n}{\mu_0/c}\right)n, \quad n(0) = BN_t,$$

which has the same form of the logistic equation studied in Exercise 2.1 with

$$r_0 = -\mu_0, \quad K = -\frac{\mu_0}{c}$$

(notice that this is not exactly the logistic equation because r_0 is negative!) The explicit solution for $\tau \geq 0$ is

$$\begin{aligned} n(\tau) &= \frac{KN_0}{N_0(1-e^{-r_0\tau}) + Ke^{-r_0\tau}} \\ &= \frac{-\frac{\mu_0}{c}BN_t}{BN_t(1-e^{\mu_0\tau}) - \frac{\mu_0}{c}e^{\mu_0\tau}} \end{aligned}$$

Hence, at the end of the year ($\tau = 1$) we obtain

$$N_{t+1} = n(1) = \frac{\mu_0 BN_t}{cB(e^{\mu_0}-1)N_t + \mu_0 e^{\mu_0}} = \frac{\lambda N_t}{1+\alpha N_t}$$

with

$$\lambda = Be^{-\mu_0}, \qquad \alpha = \frac{cB}{\mu_0}\frac{e^{\mu_0}-1}{e^{\mu_0}}$$

Exercise 5.4

It is a straightforward application of the variation of constants formula for linear ODEs (you can directly obtain it by using a multiplicative factor $e^{-\beta t}$ and integrating both sides of the equation).

Exercise 5.5

(a) Let N_s, N_b be the number of medicine molecules in the stomach and in the blood, respectively. Then, the dynamics is described by

$$\begin{aligned} \frac{dN_s}{dt} &= -\alpha N_s \\ \frac{dN_b}{dt} &= +\alpha N_s - \beta N_b \end{aligned}$$

Let now $s(t) = N_s(t)/V_s$ and $b(t) = N_b(t)/V_b$ be the density of medicine in the stomach and in the blood. From the previous system, we obtain the equations for the densities

$$\frac{ds}{dt} = \frac{1}{V_s}\frac{dN_s}{dt} = -\alpha s$$
$$\frac{db}{dt} = \frac{1}{V_b}\frac{dN_b}{dt} = +\alpha\frac{V_s}{V_b}s - \beta b$$

(b) Let $s(0) = s_0$ be the initial concentration of medicine in the stomach. Then, the first equation gives

$$s(t) = s_0 e^{-\alpha t}$$

and, by plugging it into the second equation and by exploiting the variation of constants formula for linear ODEs (assuming that $b(0) = 0,$), we get

$$\begin{aligned} b(t) &= \int_0^t e^{-b(t-s)}\alpha\frac{V_s}{V_b}s_0 e^{-\alpha s}ds \\ &= \alpha\frac{V_s}{V_b}s_0 e^{-bt}\int_0^t e^{(b-\alpha)s}ds \\ &= \frac{\alpha}{b-\alpha}\frac{V_s}{V_b}s_0(e^{-\alpha t} - e^{-bt}) \end{aligned}$$

Notice that $b(t)$ is positive for $t \geq 0$ for any value of α, b, and it is vanishing for $t \to \infty$. Moreover, the concentration of the medicine in the blood $b(t)$ increases until it reaches its maximum and then decreases again.

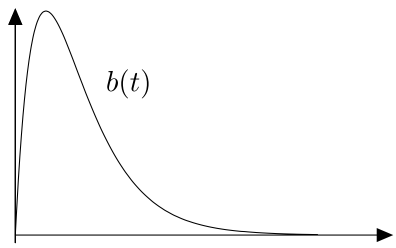

Figure 1: Qualitative plot of $b(t)$.