# Introduction to Mathematical Biology
# Exercises 5.1-5.5

5.1 *Optimal birth rate.* Consider a logistic population with strains that differ in their birth and death rates,

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

where $N = \sum_{i=1}^{n} N_i$ is total population size, and the coefficient $c$, which measures how fast the per capita growth rate decreases with population size, is the same for each strain. (This is the case if density dependence comes from aggressive interactions between the individuals, see exercise 2.2.) The birth and death rates are traded off; for the sake of illustration, assume that the trade-off function is $\mu(b) = \mu_0 + ab^2$ (where $\mu_0, a$ are positive constants).

(a) Find the optimal birth rate.
(b) May it happen that the optimal strain is not viable?

5.2 *Selection in the site-limited plant population model.* Suppose that variants of a plant species compete for living sites according to the continuous-time dynamics

$$\frac{dN_i}{dt} = b_i N_i \left(1 - \frac{N}{M}\right) - \mu_i N_i \quad \text{for } i = 1, ..., n$$

where $N = \sum_{i=1}^{n} N_i$ is total population size, $M$ is the number of sites, and $b_i$ and $\mu_i$ are the birth and death rates of variant $i$, respectively. A living site provides a fixed amount of resources to be used per unit of time, and the birth rate and the death rate of the plant depend on how much of this resource the plant uses for producing seeds and for self-defence (e.g. producing chemical defence against phytophagous insects). Let thus $x_i \in [0, 1]$ denote the fraction of resources allocated to self-defence. Assume that the death rate decreases with self-defence according to $\mu_i = \mu(x_i) = \mu_0/(1 + \alpha x_i)$, where $\mu_0$ is the death rate when the plant has no self-defence and $\mu_0/(1 + \alpha)$ is the minimum death rate, obtained when the plant uses all resources for self-defence ($x = 1$). (Note that the particular form of the function $x \mapsto \mu(x)$ is assumed as an example, and has not been derived from any underlying biology.) The fraction of resource not used for self-defence, $1 - x_i$, is used to produce seeds. We assume that seed production is proportional to the amount of resource used for seeds, i.e., $b_i = b(x_i) = B \cdot (1 - x_i)$, where $B$ is the number of seeds produced when all resources are used for reproduction.

(a) Determine the set of viable strategies (i.e., the set $X \subseteq [0, 1]$ such that a plant with strategy $x_i \in X$ is able to maintain a positive equilibrium population size in absence of any other variant).
(b) Determine the optimal strategy $x_{opt}$.
(c) Investigate how $X$ and $x_{opt}$ change with $\mu_0$, the baseline rate of mortality.

5.3 *Discrete birth events with continuous death.* Many insects reproduce only once, at a specific time point in the year, and die immediately after reproduction. Let us census the population immediately before reproduction, when $N_t$ parents are present in year $t$, and they produce a total of $BN_t$ offspring. The offspring need to survive a full year's time to become parents themselves. Throughout the year (for time $0 \le \tau \le 1$), the number of offspring $n(\tau)$ follows a continuous-time dynamics with death only, where we assume a linearly density-dependent death rate $\mu(n) = \mu_0 + cn$ with positive constants $\mu_0, c$. We thus arrive at the mixed discrete-continuous time model

$$n(0) = BN_t, \quad \frac{dn}{d\tau} = -(\mu_0 + cn)n \text{ for } 0 \le \tau \le 1, \quad N_{t+1} = n(1)$$

Prove that the discrete-time map $N_t \mapsto N_{t+1}$ is given by the Beverton-Holt model

$$N_{t+1} = \frac{\lambda N_t}{1 + \alpha N_t}$$

and express the new parameters $\lambda, \alpha$ with $B, \mu_0, c$. (*Hint:* recall exercise 2.1 to spare work. The present exercise follows the original derivation by Beverton and Holt.)

5.4 *Poisson distribution.* In the lecture, we derived the differential equations

$$\begin{aligned}
\frac{dP_0}{dt} &= -\beta P_0 \\
\frac{dP_1}{dt} &= \beta P_0 - \beta P_1 \\
&\vdots \\
\frac{dP_{i+1}}{dt} &= \beta P_i - \beta P_{i+1} \\
&\vdots
\end{aligned}$$

for the probabilities of a Poisson process. To fill in the one step we did not do in detail, show that the solution for $P_{i+1}(t)$ is

$$P_{i+1}(t) = P_{i+1}(0)e^{-\beta t} + \int_0^t e^{-\beta(t-\tau)} \beta P_i(\tau) d\tau$$

where, for the Poisson process, $P_{i+1}(0) = 0$ and therefore the first term vanishes.

5.5 *Sequential decay.* When a medicine tablet is taken orally, the medicine is first absorbed from the stomach into the blood at a positive rate $\alpha$ such that any given molecule in the stomach has a probability $\alpha \cdot dt$ to be absorbed in $dt$ time, and the medicine is then removed from the blood by the kidneys and/or by the liver at a positive rate $\beta$ such that any given molecule in the blood is removed with probability $\beta \cdot dt$ in $dt$ time. Let $s(t)$ denote the concentration (=mass/volume) of the medicine in the stomach (where $t$ is the time since taking the medicine and $s(0) = s_0$ is given by the mass of the tablet divided with the volume of the stomach), and let $b(t)$ be the concentration in the blood ($b(0) = 0$)). The medicine is effective while it is in the blood, hence we are interested in how the blood concentration $b(t)$ changes with time.

(a) Construct a model for how the *number* of medicine molecules (or equivalently the mass of the medicine) changes in the stomach and in the blood. Recall that the number of molecules equals the concentration times the volume of the stomach ($V_s$) and of the blood ($V_b$), respectively. Use this to rewrite the model for the concentrations and show that these obey the ODEs

$$\begin{aligned} \frac{ds}{dt} &= -\alpha s(t) \\ \frac{db}{dt} &= \alpha \frac{V_s}{V_b} s(t) - \beta b(t) \end{aligned}$$

(b) Solve this system for $b(t)$, plot the solution, and interpret the shape of the function $t \mapsto b(t)$. Show that $b(t)$ is nonnegative and finite for every (biologically sensible) choice of the parameters so that the result is biologically meaningful. (*Hint:* use the previous exercise to spare work.)