Elgersburg Summer School, March 2014
Mathematical Biology
Exercise Sheet 1– Introductory questions

(1) Let N_t denote the abundance of females of a certain population at time $t \in \mathbb{N}_0$. The population dynamics are affected by competition within the population as follows. The population is modelled over an area of $n \in \mathbb{N}$ patches. At each time–step $t \in \mathbb{N}_0$, the population is randomly distributed across the n patches and whenever more than one individual share the same patch, competition occurs. In *contest*, one individual always survives, whereas for *scramble*, there are no survivors. After competition the survivors go on to reproduce $\lambda \in \mathbb{N}$ new individuals, which gives the population of competitors for the next generation.

(i) Write a `Matlab` (or other language) script to model both the contest and scramble experiments over some time period $\{0, 1, 2, \ldots, T\}$ for $T \in \mathbb{N}$. The code should take the parameters $N^0 := N(0)$, λ and n as inputs. Plot both N_t against t and N_{t+1} against N_t. Add the time–averages

$$A_t := \frac{1}{t+1} \sum_{j=0}^{t} N_j \,,$$

to your first plot. What qualitative trends do you observe?

(ii) Here we consider deriving a model for the above dynamics by appealing to a probabilistic approach. For fixed $t \in \mathbb{N}_0$ and for $m \in \{1, 2 \ldots, n\}$, let X_m denote the random variable describing the number of smarties in patch m at time–step t. Each random variable X_m takes values in $\{0, 1, 2, \ldots, N_t\}$. We assume that the random variables are IID so that random dispersal implies that the expected value of X_m is $\frac{N_t}{n}$. If we assume that X_m is a Poisson distribution, then

$$\mathbb{P}(X_m = k) = \frac{(\frac{N_t}{n})^k \mathrm{e}^{\frac{-N_t}{n}}}{k!}, \quad k \in \mathbb{N}_0 \,.$$

(a) Using the above assumptions (plus any others you clearly state) derive the model

$$N_{t+1} = \lambda n \left(1 - \mathrm{e}^{\frac{-N_t}{n}}\right), \quad t \in \mathbb{N}_0 \,, \tag{1}$$

for the population subject to the contest competition law.

(b) Similarly, show that the population subject to the scramble competition law can be modelled as

$$N_{t+1} = \lambda N_t \mathrm{e}^{\frac{-N_t}{n}}, \quad t \in \mathbb{N}_0 \,. \tag{2}$$

(c) What assumptions are made in deriving the above models?

(d) Compare the results of the models (1) and (2) with your experimental models.

(iii) Another approach to modelling the population is to try and fit a model to data. Two possible models for the contest competition law are

$$N_{t+1} = b(N_t)^a, \quad t \in \mathbb{N}_0 \,, \tag{3}$$

or

$$N_{t+1} = \frac{kN_t}{v + N_t}, \quad t \in \mathbb{N}_0 \,, \tag{4}$$

where the positive parameters a, b, k and v are to be determined.

(a) For $a, b, k, v > 0$ sketch graphs of the functions

$$f_1(x) = bx^a, \quad f_2(x) = \frac{kx}{v+x}, \quad x \geq 0.$$

(b) Using your experimental results estimate the values of a, k and v by fitting straight lines through your data. [Hint: There are simple transforms of N_t that make this task much easier.] You can use `Matlab` or `R` (or other language) linear regression functions if you wish.

(c) With your values of a, k and v, how do the results of the models (3) and (4) compare with both your experimental results and the model (1)?

(2) The population u_t of a certain species is modelled by the difference equation

$$u_{t+1} = \frac{au_t^2}{b^2 + u_t^2}, \quad a > 0, \quad t \in \mathbb{N}_0\,.$$

Determine the equilibria. Construct a cobweb map in the specific case when

$$a^2 > 4b^2.$$

(3) The population density of a species at time t is denoted by N_t and its dynamics is governed by the discrete-time model equation

$$N_{t+1} = f(N_t) := N_t \exp\left[r\left(1 - \frac{N_t}{K}\right)\right], \quad t \in \mathbb{N}_0\,.$$

Here r and K are positive constants.

(i) Determine the steady states and their corresponding eigenvalues. Show that as r is varied, a bifurcation occurs at $r = 2$.

(ii) In the case $r > 1$, sketch $N_{t+1} = f(N_t)$ and show, graphically or otherwise, that for large t the population oscillates between a maximum population given by $N_M = f(K/r)$ and a minimum population given by $N_m = f\left[f(K/r)\right]$.

(iii) In the case that N_t represents actual population size, so that the species becomes extinct if $N_t < 1$ for some $t \geq 1$, show that if $r > 1$ then the species here may become extinct if the carrying capacity

$$K < r \exp\left[1 + e^{r-1} - 2r\right].$$

(4) (i) Verify that

$$N(t) = \frac{KN_0e^{rt}}{K - N_0 + N_0e^{rt}}, \quad t \in \mathbb{R}_+\,,$$

is the solution of the logistic equation:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right), \qquad N(0) = N_0 > 0\,.$$

(ii) For fixed $\tau > 0$ and $n \in \mathbb{N}_0$ show that $x_n := N(n\tau)$ satisfies:

$$x_{n+1} = \frac{bx_n}{1 + cx_n}$$

where

$$b = e^{r\tau} \quad \text{and} \quad c = \frac{e^{r\tau} - 1}{K}\,.$$

(iii) Let $y_n = \frac{1}{x_n}$. Show that

$$y_{n+1} = \frac{1}{b} y_n + \frac{c}{b} \,.$$

(iv) Solve for y_n and so verify that

$$\lim_{n\to\infty} x_n = \frac{b-1}{c} = K \,.$$

(5) A model for two interacting populations N_1 and N_2 is given by

$$\frac{dN_1}{dt} = 2N_1 \left[1 - \frac{N_1}{3} + \frac{N_2}{3}\right] , \qquad \frac{dN_2}{dt} = 3N_2 \left[1 - N_2 + \frac{N_1}{2}\right] , \quad t \in \mathbb{R}_+ \,. \tag{5}$$

(i) Does (5) model a predator–prey interaction, competitive interaction or mutualistic interaction?

(ii) Find the equilibria of (5).

(iii) Find the community matrix for each equilibrium and determine its linear stability.

(iv) Sketch a plausible phase portrait for the system.

(6) Consider the following model for the reaction dynamics of two substrates u and v:

$$\frac{du}{dt} = a - bu + \frac{u^2}{v} =: f(u,v) \,, \quad \frac{dv}{dt} = u^2 - v =: g(u,v) \,, \quad t \in \mathbb{R}_+ \,. \tag{6}$$

The biological interpretation of this model is that u activates v through the term u^2. In other words, an increase of u leads to enhanced production of v. The term $\frac{1}{v}$ shows a negative feedback by v on the production of u. Such feedback is known as inhibition. So here u activates v and v inhibits u. These are similar ideas to those we used in describing competitive and mutualistic interactions of populations.

(i) Find the equilibria of (6).

(ii) Linearise (6) around each equilibrium and determine its linear stability.

(7) One basic enzymatic reaction, first proposed by Michaelis and Menten [1] involves a substrate S reacting with an enzyme E to form a complex C which in turn is converted to a product P and the enzyme itself.

We write this as

$$\mathrm{S} + \mathrm{E} \underset{k_{-1}}{\overset{k_1}{\rightleftharpoons}} \mathrm{C} \overset{k_2}{\longrightarrow} P + E \,, \tag{7}$$

where the k_js are referred to as rate constants.

The Law of Mass Action states that the rate of reaction is proportional to the product of the concentrations of the reactants. Let c, e, p and s denoting the concentrations of C, E, P and S respectively.

(i) Demonstrate that the dynamics (7) give rise to the system of ODEs

$$\left.\begin{aligned} \frac{ds}{dt} &= -k_1 se + k_{-1}c \,, & \frac{de}{dt} &= -k_1 se + k_{-1}c + k_2 c \,, \\ \frac{dc}{dt} &= k_1 se - k_{-1}c - k_2 c \,, & \frac{dp}{dt} &= k_2 c \,, \end{aligned}\right\} \quad t \in \mathbb{R}_+ \,. \tag{8}$$

[Hint: Consult [2, Section 1.A] for guidance if you are stuck].

References

[1] L. Michaelis and M. L. Menten, “Die kinetik der invertinwirkung,” *Biochem. z*, vol. 49, no. 352, pp. 333–369, 1913.

[2] E. D. Sontag, “Structure and stability of certain chemical networks and applications to the kinetic proofreading model of t-cell receptor signal transduction,” *Automatic Control, IEEE Transactions on*, vol. 46, no. 7, pp. 1028–1047, 2001.