

Exercises for the course  
**“Mathematical modeling in biology”**

Sheet 03

**Exercise 11: Immune response in Phillips’ HIV model**

Phillips’ model of HIV dynamics within the body assumes that there is no immune response to HIV. Now we want to drop this assumption. How could immune response be incorporated into the model? Extend the model in a suitable way. Explain your approach and especially motivate your choice of the rates. Draw a flow diagram to visualize the model and write down the equations. Check the model as far as possible/reasonable.

**Exercise 12: The Lotka-Volterra model of competition**

In the logistic growth model, the expected number of offspring per individual decreases linearly with the population size due to decreasing resources. Now assume there are two species competing for the same resources. Let  $x_1(t)$  and  $x_2(t)$  be the expected number of individuals of the two species at time  $t \in [0, \infty)$ . Species 1 reduces the amount of available resources which should result in a reduction of the expected number of offspring of species 2. So the per capita reproduction rate of species 2 is assumed to decrease if the population size of species 1 increases. Apart from this, we assume that the amount of available resources has no influence and is therefore not needed as a variable in the model. Similarly species 2 reduces the reproductive success of species 1. Write down assumptions on the expected number of each species and motivate your assumptions. Then write down the model equations for  $x_1$  and  $x_2$ .

**Exercise 13: Interpreting a model** Consider an epidemic outbreak of a lethal disease in which the infectious period and the incubation period of the disease are different. Denote the expected number of susceptibles at time  $t \in [0, \infty)$  by  $s(t)$ , those incubating the disease by  $b(t)$  (short for breeding), the individuals who are infectious by  $i(t)$  and those that have died by  $r(t)$ . During the epidemic the total population including all deceased is assumed to be constant, say equal to  $N$ . Suppose that those incubating the disease already infect others but the infection rate is much smaller than the infection rate of infectious individuals. Interpret the following model

$$\begin{aligned}\frac{ds(t)}{dt} &= -\gamma \frac{s(t)}{N} \left( i(t) + \rho b(t) \right) \\ \frac{db(t)}{dt} &= \gamma \frac{s(t)}{N} \left( i(t) + \rho b(t) \right) - \beta b(t) \\ \frac{di(t)}{dt} &= \beta b(t) - \delta i(t) \\ \frac{dr(t)}{dt} &= \delta i(t)\end{aligned}$$

where  $\gamma$ ,  $\rho$ ,  $\beta$  and  $\delta$  are positive constants. Draw a flow diagram to visualize the equations. What does each of the parameters measure? Read off the assumptions of the model (e.g. the death rate is the same for every infectious individual). Now suppose that in the early stages of the epidemic only a few (relative to the total population) individuals,  $b(0)$ , become infected all at the same time and then are incubating the disease. So they do not become infectious for a time of order  $1/\beta$ . During this time  $s(t) \approx N$ . Use this to solve for  $b(t)$  as a function of  $t$ .

**Exercise 14: Age structure**

Consider an age structured population. Let  $\beta(a)$  be the per capita birth rate at age  $a \in [0, \infty)$  and let  $\delta(a)$  be the per capita death rate at age  $a$ . We derived in the course a criterion on  $\beta(\cdot)$  and  $\delta(\cdot)$  when the population grows to infinity and when it decreases to zero. Use this formula to answer the following questions. Consider the following simplified situation of human beings. Assume that women only give birth between age 20 and age 50. In this time interval, the birth rate is assumed to be constantly equal to  $\gamma$ .

1. Suppose that the death rate of women is zero before age 60 and is constantly equal to  $\eta$  after that age. Under which conditions on  $\gamma$  and  $\eta$  is the population increasing and when is the population decreasing? Rephrase your answer in terms of the expected number of children. Give an interpretation why your answer is independent of  $\eta$ .
2. Now assume the death rate of women to be constantly equal to  $\varepsilon$  before age 60 and to be constantly equal to  $\eta$  after age 60. Under which conditions on  $\gamma$ ,  $\varepsilon$  and  $\eta$  is the population increasing and when is it decreasing?

**Exercise 15: Equilibria and stability** In Exercise 6 we obtained a haploid model of natural selection with mutation in continuous time. Let  $p(t)$  be the relative frequency of the selected type at time  $t \in [0, \infty)$ . This frequency satisfies

$$\frac{dp(t)}{dt} = \sigma p(t) (1 - p(t)) + \mu_0 (1 - p(t)) - \mu_1 p(t)$$

where  $\sigma$  is the selection coefficient,  $\mu_0$  is the mutation rate towards the selected type and  $\mu_1$  is the mutation rate from the selected type to the wild type. The parameters  $\sigma$ ,  $\mu_0$  and  $\mu_1$  are all assumed to be strictly positive. Calculate the equilibrium/equilibria of this model. (To check your result: If  $\mu_0 = \mu_1 = \frac{\sigma}{2}$ , then the smallest equilibrium point is  $\frac{1}{\sqrt{2}}$ .) Then check whether the equilibrium/equilibria is/are locally stable or locally unstable. Give a short explanation why your result was to be expected. Now assume that there are no mutations  $\mu_0 = 0 = \mu_1$ . Specify the equilibria and specify the stability of these equilibria (if you think of how the model should behave in that case, then you might be able to guess the answer).