

Question 1. Make a model (10 points)

Make a simple biological model for the number of worker-bees in a colony living in and around a beehive. The model should describe the basic biology. Workers bring honey to the hive, and it is safe to assume that there are sufficient flowers in the neighborhood such that the daily amount of honey that is brought to the hive is proportional to the number of worker bees. Workers consume part of the honey that is present in the hive, they have a death rate that decreases when they consume sufficient honey, and they are born from larvae produced by the queen. Assume that there always is a single queen staying within the hive, and also consuming part of the honey in the hive. The daily number of larvae she produces is limited by the amount of honey she consumes (until some maximum). Larvae also consume honey and mature into worker bees at a rate that also depends on their daily consumption. Write a natural model for the amount of honey, H , the number of workers, W , and the number of larvae L in the colony. For simplicity assume that the daily consumption rate of larvae, workers and the queen is the same.

$$\frac{dH}{dt} = aW - cH(W + L + 1), \quad \frac{dL}{dt} = \frac{eH}{h_e + H} - \frac{mLH}{h_m + H}, \quad \frac{dW}{dt} = \frac{mLH}{h_m + H} - \frac{dW}{1 + H/h_d},$$

Question 2: Boerlijst et al., PLOS ONE 2013. (5 points)

Why do they only observe an early warning signal in the time series of the juveniles? Make sure you use the terms eigenvalue and eigenvector. Use no more than 100 words.

At the saddle-node bifurcation a single eigenvalue becomes zero. The eigenvector associated with this eigenvalue is most pointing in the direction of the juveniles. So it is largely the recovery of the juveniles that becomes slow. Actually the real part of other eigenvalues decreases when the bifurcation is approached. Hence the recovery of adults and predators becomes faster.

Question 3: Huisman & Weissing, Nature 1999. (5 points)

Explain why in Eq (2) each resource declines proportional to the summed growth rates of all consumers. Make sure you explain the meaning of the c_{ji} term in your answer. Use no more than 100 words.

When a consumer cell produces a new cell by division, which occurs at a rate $\mu_i R()$, the new cell consumes the amount of resource that is contained in such a cell. c_{ji} is the amount of resource j contained in cell of species i .

Question 4: Berngruber et al., PLOS Pathogens 2013. (5 points)

Explain the contribution of Fig. 4 to the take home message of the paper. No more than 100 words.

The figure compares the peak level predictions of the model and the outcome of experiments for infections starting at a low initial value (1%), intermediate (10%), or at a high initial prevalence. The peak ratio of virulent over non-virulent free virus is higher than that of virulent over non-virulent provirus, and these ratios decline with the initial prevalence. These observations (circles) agree with the model predictions (crosses). Thus virulent viruses do better at a low prevalence.