MAA135 Seminar 2: Population dynamics

In this seminar you will use some web-based interactive examples to explore some phenomena in mathematical modelling of population dynamics.

Before you start the interactive part of the seminar it is highly recommended that you work through the preparatory exercises below. There will be no examination of these preparatory exercises but the teacher will assume that you know the answers to them.

To start looking at and experimenting with the examples click the 'Seminar 2: Model plotter' link on Canvas. You should choose model and example according to the title of each section.

For a passing grade (G) you need to discuss the results of all tasks marked with a bullet (•) with the teacher. For pass with distinction (VG) you need to write a 1-3 page report that discusses the results of all tasks marked with a star (★) and submit it on Canvas latest 2019-05-10. If an item in a list is marked with a dash (–) then it is either a preparatory exercise or part of the description of an example. It will not be examined but it is highly recommended that you both read and consider it carefully.

Preparatory exercises

Let N and P denote the population size of the prey and predator respectively.

- In the standard Lotka-Volterra model with two species the system is expected to periodically go through four stages:

N increasing / P increasing	N increasing / P decreasing
N decreasing / P increasing	N decreasing / P decreasing

  Describe in which order these stages are expected to occur.

- By hand, draw an example of a time diagram and a phase diagram for the following situations:
  - N and P vary periodically.
  - After some time N and P approaches different constant (non-zero) values.
  - After some time the predator goes extinct and the prey population increases until it reaches its carrying capacity.
- In your hand-drawn diagrams mark the following values (if applicable): initial population, equilibrium point, stationary state.
- In class we discussed a specific word used for systems where it is very difficult to predict what will happen in the future. Do you remember this word?

The Lotka–Volterra model with 2 species and no intraspecific competition

If we denote the number of prey population by $N(t)$ and the predator population by $P(t)$ then the classical Lotka–Volterra model for the interaction between two species can be written like this:

$$\begin{cases} \dfrac{\mathrm{d}N}{\mathrm{d}t} = aN(t) - cN(t)P(t) \\ \dfrac{\mathrm{d}P}{\mathrm{d}t} = -bP(t) + dN(t)P(t) \end{cases}$$

Tasks

- Compare the time diagram and phase diagram with each other. Do they seem to be compatible? How do you move in the phase diagram?
- Calculate the equilibrium point $(N_{eq}, P_{eq}) = \left(\frac{b}{d}, \frac{a}{c}\right)$. Compare the equilibrium with the time- and phase diagram. Does it look like you have gotten a reasonable equilibrium point? What does the equilibrium point correspond to in the time diagram and in the phase diagram?
- Make a rough estimation of what the average values of the two populations would be. Compare your estimate to the equilibrium point.
- Try setting your initial values to the equilibrium point, what happens?
- Try changing one or more of the parameters and try to predict what is going to happen in the time diagram and phase diagram. Also calculate the new equilibrium if it changes.

The Lotka-Volterra model fitted to muskrat–mink data

There are three examples where the standard Lotka–Volterra model has been fitted to data for muskrat (prey) and mink (predator) in different parts of Canada[1].

The data does not directly describe the populations of the two animals but follows the same overall trends as the population.

For these three examples the standard Lotka–Volterra model does not fit well but a model with approximately right periodicity and amplitude is provided.

In one of the regions there is a significant qualitative difference in the dynamics between the two species in comparison to the other regions (hint: look at the order of the peak for the two species).

Tasks

★ Compare the three examples with each other. Describe which region that differs from the other two. Describe how this difference can be seen in the time diagram, phase diagram and in the coefficients of the fitted model. Explain why this shows that the predator-prey relationship is unlikely to be the driving force in the odd region.

The Lotka–Volterra model with 3 species and intraspecific competition

The Lotka–Volterra model can be generalized to any number of species and allow any species to compete with any other species (including themselves). If we have n species and denote their respective populations with $N_k(t)$, $k = 1, \ldots, n$ the generalized Lotka–Volterra model is given by the following system of equations:

$$\begin{cases} \dfrac{\mathrm{d}N_1}{\mathrm{d}t} = a_1 N_1(t) - \displaystyle\sum_{k=1}^{n} b_{1k} N_1(t) N_k(t) \\ \dfrac{\mathrm{d}N_2}{\mathrm{d}t} = a_2 N_2(t) - \displaystyle\sum_{k=1}^{n} b_{2k} N_2(t) N_k(t) \\ \qquad \vdots \\ \dfrac{\mathrm{d}N_n}{\mathrm{d}t} = a_n N_n(t) - \displaystyle\sum_{k=1}^{n} b_{nk} N_n(t) N_k(t) \end{cases}$$

If we interpret this system in the same way as we interpret the standard Lotka–Volterra equation then can conclude the following:

– If species number k does not need to hunt any other organisms to reproduce then $a_k > 0$.

[1] *Spatio-Temporal Patterns of Mink and Muskrat in Canada during a Quarter Century*, H. Viljugrein, O. C. Lingjaerde, N. C. Stenseth and M. S. Boyce, Journal of Animal Ecology, Vol. 70, No. 4. (2001), pp. 671-682.

- If species number k needs to hunt other organisms to reproduce then $a_k < 0$.
- If species number k competes with species number j then $b_{kj} > 0$ and $b_{kj} > 0$. Note that we can have $k = j$.
- If species number k exploits (hunts) species number j then $b_{kj} < 0$ and $b_{jk} > 0$.
- We could also imagine a symbiotic relationship between species number k and j where $b_{kj} < 0$ and $b_{jk} < 0$.

In this part of the seminar we will see four examples of how such a model can behave when we have three competing species.

Tasks

- Try Ex. 1. Look at the parameter values. Use the interpretation above to describe the relations between the three species in your own words.
- The long-term behaviour of this examples is similar to the two-species model we analysed before. What do you call this behaviour and how do we move in the phase diagram?
- Try Ex. 2. Describe the long-term behaviour of this system in your own words. How do we move in the phase diagram?
- Try Ex. 3. Try to interpret the result ecologically (hint: is this a healthy ecosystem?). Confirm that species $N3$ approaches it carrying capacity with a calculation.
- Try Ex. 4. Can you see a pattern in how the populations vary in time? If not, examine the system interval over a longer interval of time by increasing both 'Model time' and 'Plot time'. Do you know a good word for describing this kind of system?
- Try to come up with an example of a property (or a 'rule of thumb') of the system in Ex. 4 that is easy to see in the phase diagram but hard to see in the time diagram.

The Gatto model and the paradox of enrichment

The paradox of enrichment is a phenomenon that features in many different population models. It was first described[2] by M. L. Rosenzweig.

When the carrying capacity for the prey is increased (for example by increasing the food supply for the prey) this is referred to as *enriching* the system. The expected result is that an enriched system should have higher populations of both prey and predator.

The paradox of enrichment states that under certain circumstances it is possible to destabilise and even cause extinction in a system by enriching it.

Here we will discuss this phenomenon using the Gatto model (more commonly known as the MacArthur–Rosenzweig model). This model is given by the system

$$\begin{aligned} \frac{\mathrm{d}N}{\mathrm{d}t} &= \left(a - bN(t) - \frac{cP(t)}{d + N(t)}\right) N(t) \\ \frac{\mathrm{d}P}{\mathrm{d}t} &= \left(\frac{kN(t)}{d + N(t)} - m\right) P(t) \end{aligned}$$

In this model the value of $\frac{1}{b}$ can be interpreted as the carrying capacity of prey.

It can be shown[3] that when $a = c = d = 1$, and $\frac{1}{b} < 1 + 2\frac{m}{k-m}$ the system will be stable and approach a stationary value for the predators and prey. If the carrying capacity is to high the system will instead start to oscillate very rapidly.

Tasks

- ★ Confirm experimentally that $\frac{1}{b}$ corresponds to the carrying capacity (hint: choose your parameters such that the predator population cannot be sustained).

- ★ Demonstrate the paradox of enrichment for this model. Calculate where the carrying capacity is high enough to destabilise the system and show at least three examples of the systems behaviour, one that is stable, one that is near the limit and one that is unstable.

[2] *Paradox of Enrichment: Destabilization of Exploitation Ecosystems in Ecological Time*, Science, New Series, Vol. 171, No. 3969. (Jan. 29, 1971), pp. 385-387.

[3] See for example the second subsection article on *Paradox of enrichment* on Wikipedia: `https://en.wikipedia.org/wiki/Paradox_of_enrichment#Link_with_Hopf_bifurcation`