Population Dynamics

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Abstract

This article gives an overview about techniques that are being used in the modelling of population dynamics. The first part deals with discrete population models that are suitable for species that reproduce in certain intervals and have no overlap between the successive generations. Also the stability of discrete and continuous models is examined. The second part of this work exemplifies a predator prey relationship on the Lotka Voltera System and on example data of the lynx and the snowshoe hare.

1 Introduction

Modelling the dynamics of Populations is a common tool widely used in ecology. As other types of modelling it serves in testing hypotheses about mechanisms involved in the regulation of the population size. There are different approaches in modelling populations, not only because there are many different kinds of populations, and therefore also reproduction strategies. We can describe the growth of a bacteria population in an unbound medium for example by the Malthusian growth model [1], which is a simple exponential growth model. Here the population size at time point t relates in an exponential manner to the start population with a certain growth rate r ($B_t = B_{t_0} e^{rt}$). A major drawback of this model is, that we assume the growth of the bacteria to be continuous which is not true. But for large populations this effect can be neglected. A more precise model could take the discrete steps that occur when a single cell divides into account.

2 Discrete Population Models

2.1 Introduction

This section will deal with models that are discrete in their time steps. This section is mainly based on the book of Murray [2]. Discrete time steps means that the population number at time point t_{i+1} is a function of the population at time point t_i ($N_{t_{i+1}} = f(N_{t_i})$), where $t_{i+1} - t_i$ is the time step. To emphasise that this formula always has a steady state at point 0, we can also write $N_{t_{i+1}} = N_{t_i} F(N_{t_i})$. The formulas given above are also called difference equations, because they show the difference between two successive generations.

These difference equations or discrete models are justified for species that reproduce in certain intervals and have no overlap between the successive generations (e.g. salmon, snowdrops or *Octopus Vulgaris*). In general these difference

equations are too hard to be solved analytically, but as for ODE models we can extract some information about the dynamics without an analytical solution.

2.2 Example: Fibonacci Sequnce

One example of a difference equation is the Fibonacci sequence which occurs in an astonishing number of phenomena in nature as in architecture or art. The Fibonacci sequence was introduced by Leonardo of Pisa (1180s-1250), who considered the growth of a hypothetical rabbit population. In this hypothetical population the rabbits never die and reproduce in a certain interval (e.g one month). The rabbits need one interval to mature and each pair of mature rabbits produces one new pair each month. This means that the number of pairs at time point t is the number of rabbits in the previous time point (cause these rabbits do not die) plus the number of rabbits that was there two time steps before (the number of rabbits that are mating for the first time). Written in a formula this is $R_{t+1} = R_t + R_{t-1}$. This growth is depicted in figure 2.2
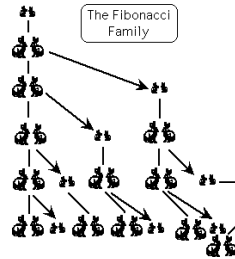

Figure 1: Fibonacci growth of a rabbit population.

If we look at the ratio of two successive Fibonacci numbers, we can see that they converge at the golden ratio $(\frac{\sqrt{(5)}-1}{2})$, which gives a ratio where the ratio of a sum of two quantities to the larger part equals the ratio of the larger part to the smaller part. Figure 2.2 shows among others the Parthenon in which the top part relates to the bottom part in a golden ratio. If we multiply the golden ratio with 360 degrees we will get out 222.5. Therefore $137.5 = 360 - 222.5$ can be called the golden angle. This golden angle occurs in some plants when the angles of the branches are projected to a two dimensional surface.

As mentioned beforehand, the Fibonacci sequence can be found quite often in nature. For example the number of spirals in a lot of plants (e.g. sunflowers, cauliflower or pine cones) are Fibonacci numbers, and the number of spirals in clockwise and counterclockwise direction are successive Fibonacci numbers. Figure 2.2 shows some examples where the Fibonacci sequence occurs in nature or in architecture.

2.3 Analysis of Difference Equations

A Difference equation has the form $N_{t_{i+1}} = f(N_t)$. This formula has a steady state where $N_t = f(N_t)$. If we plot N_t against N_{t+1}, the steady states are the intersections of the bisection of the axis and the curve f. This graphical representation gives also an intuitive way of illustrating the propagation of the
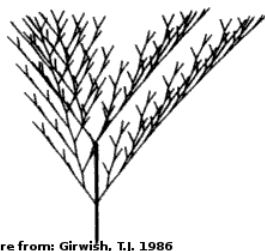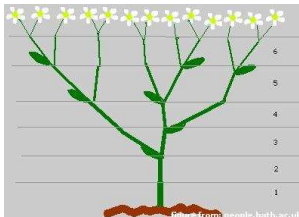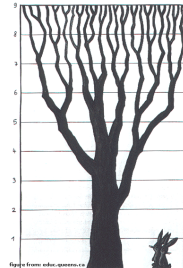
Figure 2: Examples for the Fibonacci sequence in nature and architecture. LU: Nautilus shell which forms a Fibonacci spiral, where the sketched rectangles are related by the golden ratio. MU: Parthenon in Athens where the different structures are related by the golden ratio. It was build before the golden ratio was discovered in mathematics. RU: Pine cone where the number of spirals are Fibonacci numbers. LD: Tree branching with golden angle. MD: The number of branches on each level is a Fibonacci number. RD: Same as in MD

system which is called cobwebbing. If we start with an initial population N_0 the population at the next time point will be $f(N_t)$. Therefore we project this value to the x-axis and start again. This procedure is shown in figure 2.3
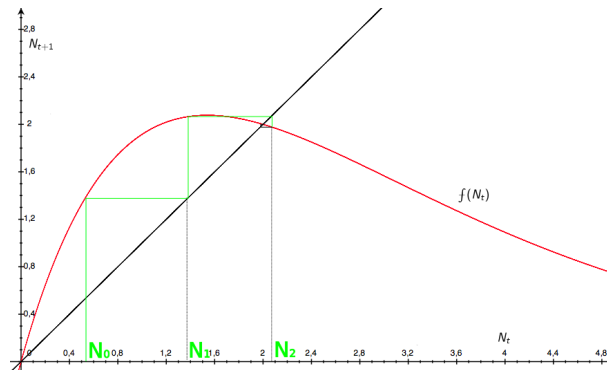

Figure 3: Example of cobwebbing. From the starting value N_0 the population is projected by the propagation function f to the next time point N_1.

As already mentioned, steady states of the system are the intersections of the axis bisection and the propagation function f. A system is in steady state if it does not change over time. Steady states can be stable or unstable. A stable steady state will fall back to its original state if perturbed a little. In contrast an unstable steady state will leave the steady state if perturbed a little. Therefore the system will never stay in an unstable steady state in reality, since small perturbations occur all the time.

Mathematically the stability of a steady state is determined by the value of the derivative of the propagation function f in steady state. In our discrete case the absolute value of the derivative has to be smaller than 1 in order have a stable steady state. If the absolute value of the derivative is greater than one the steady state is unstable. If we move on from the one dimensional case to higher dimensions we can describe linear systems by a matrix equation $x_{t+1} = Ax_t$ where A is a square matrix which has as many rows as x. In this case the solution of the systems reads $x_t = A^t x_0$. It is clear that this equation will grow unbounded if A has an eigenvalue with absolute value greater than 1. So in the multidimensional case all eigenvalues of the system in steady state have to have an absolute value smaller than 1 for the system to be stable.

Similar conditions hold for the continuous case. A linear ordinary differential equation (ODE) can be written as $\frac{dx}{dt} = Ax$. Here the solution is $x(t) = x_0 \exp(tA)$, where exp is the matrix exponential function, which can not be easily computed. The region of stability of the exponential function is the negative complex half plane. Therefore all eigenvalues of A have to have a negative real part for the system to be stable.

3   Continuous Population Models

Difference equation models are suitable for populations that have no overlap between the successive generations. But species where the generations overlap

(e.g humans) can to some extend be modelled by ODE models. In ODE population models the discrete event of the birth is simplified by continuous ODE equations. This can be justified by considering large population numbers. In the ODE model the rate of change of the population is determined by a function of the population size and the time point $\frac{dS}{dt} = f(S,t)$.

3.1 Predator-Prey Models: Lotka-Volterra Systems

A simple ODE system is a Lotka-Volterra System for predator prey relations. It reads:

$$\frac{dN}{dt} = N(a - bP)$$
$$\frac{dP}{dt} = P(cN - d)$$

where N are the number of preys and P are the number of predators. a is the growth rate of the prey, b is the negative effect of the predator on the prey, c is the benefit the prey gives to the predator and d is the decay rate of the predator. It can be seen that the prey grows unbounded in an exponential manner in the absence of the predator. Likewise the predator decreases exponentially without the benefit it gets from the prey. Figure 3.1 shows a simulation result of this system as a plot over time and a phase diagram. Notice that the direction in the phase diagram is counterclockwise. This means that the prey increases first which then leads to an increase of the predator.
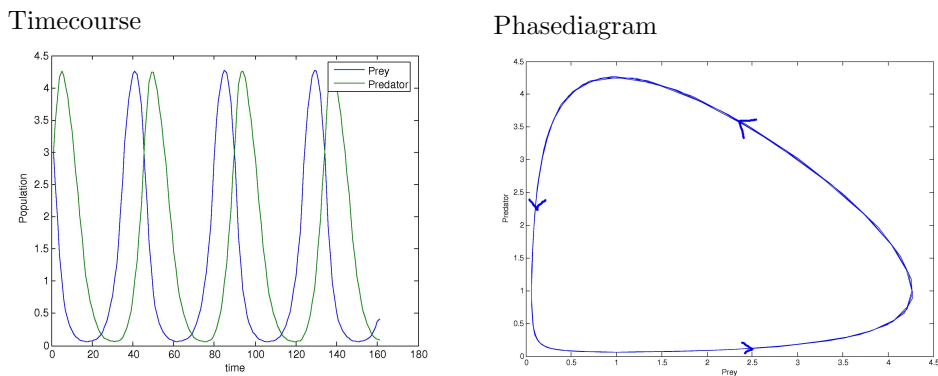

Figure 4: Simulation of the Lotka Volterra System. Left: Plot of populations over time. Right: Phase diagram

3.2 Example: Lynx - Snowhoe Hare

An example for a predator prey relationship is the Canadian lynx and the snowshoe hare. Interestingly these animals have both been hunted by a company from 1845 - 1930, which kept records about the number of caught animals. If we assume now that this company caught a fixed proportion of the animals
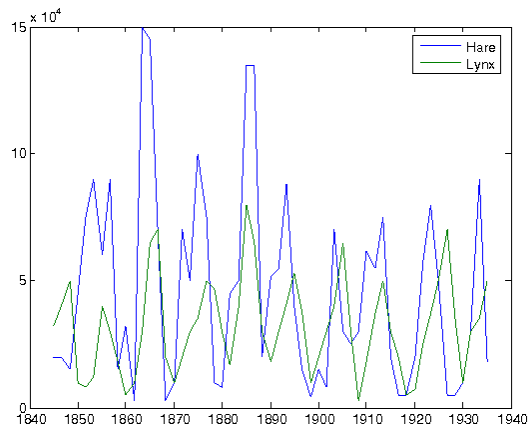
Figure 5: Catch records for lynx and snowshoe hare of the Hudson Bay Company from 1845 to 1930

in the habitat, we can examine the predator prey relationship between these animals. The number of caught animals over the years is shown in figure 3.2

At first this looks quite convincing: The two species seem to oscillate and their amplitudes are shifted. But if we plot the years 1875 until 1905 into a phase diagram as shown in figure 3.2 we see an inconsistency. We see that first the lynx increases and afterwards the hare increases, before the lynx decreases again. This would mean that the hare is hunting the lynx.

There have been several attempts to explain this data, but none has been satisfactory. One explanation would be if the hare would carry a disease killing the lynx. This could be possible, but no such disease is known. Another proposal was that the hunting is the disease, cause if the humans would hunt preferably the lynx and just hunt for the hare if no lynx is available, this could lead to a relation as shown here. But it has to be mentioned that this strange relation where the hare seems to be hunting the lynx occurs only for the years 1875 until 1905 and the data is also not very precise. So another possibility is that the data is just incorrect in this time interval.

References

[1] Simon Baumberg. *Population Genetics of Bacteria.* Cambridge University Press, 1995.

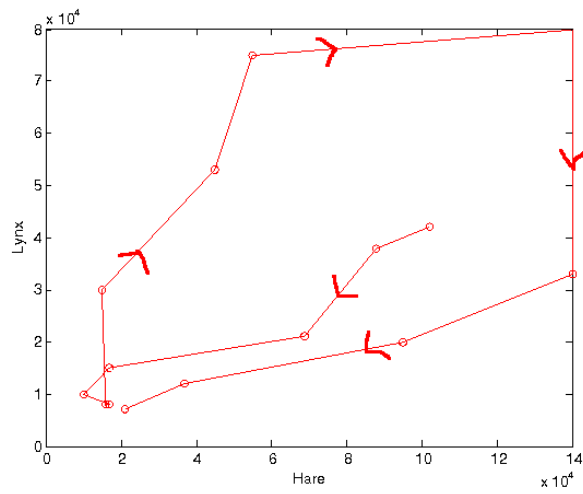[2] J.D. Murray. *Mathematical Biology I, 3rd Edition.* Springer, 2002.

Figure 6: Phase diagram of the hare-lynx relation in the years 1875 to 1905