BIOU9PC: Population and Community Ecology
Lab Practical week 8: Predation

3 November 2016

Objective

The purpose of this practical is for you to interact with simple Lotka-Volterra predator-prey models. In so doing, you will

1. Understand the linkages between ecological processes and their representations in models
2. Experience how changes in parameter values and starting conditions affect dynamics and outcomes
3. Understand the necessary conditions for the stable coexistence of predators and prey.

Introduction

Mathematical models provide an abstraction of nature. They allow us to make predictions about the behaviour of natural systems without time-consuming experiments or observation. These predictions can then be tested against reality to evaluate the realism of the model, and to determine the conditions under which the model fails to predict observations. These discrepancies are always interesting, because they indicate that unexpected phenomena are occurring.

In the 1920's, Alfred Lotka and Vito Volterra independently developed mathematical theory to model interactions between predators (P) and prey (N). In the simplest model, the prey population grows exponentially. This means that (in the absence of predation) it increases by a constant proportion (r) in every unit of time. Eventually, the universe would be filled with Prey (again, in the absence of predation). We represent the **change in the prey population per unit time** (dN/dt) as

$$dN/dt = rN \qquad \text{(Equation 1)}$$

We include predation in the following way:

$$dN/dt = rN-aNP \qquad \text{(Equation 2)}$$

where a indicates the rate of ingestion. Remember that 'd' means simply 'change'. In other words, how many prey does each predator consume per unit time? a is multiplied by both N and P, because the rate of predation will increase if either predators (P) or prey (N) are common.

The predator population, on the other hand, will decrease in the absence of prey

$$dP/dt = -dP \qquad \text{(Equation 3)}$$

where d is the per-capita mortality rate of predators. In other words, what is the probability that a single predator will die in any unit of time? Predation (i.e., consuming prey items) allows new predators to be born:

$$dP/dt = abNP-dP \qquad \text{(Equation 4)}$$

b is the 'assimilation efficiency'. In other words, how many predators are produced for each prey consumed? For foxes eating rabbits, b may be much less than 1, whereas for fly maggots eating rabbits, it may greatly exceed 1.

Question: Will *a* be greater in the fox-rabbit system or in the maggot-rabbit system?

Equations 2 and 4 together constitute Model 1: the simplest possible predator prey system. Models 2 and 3 build upon model 1 to include more biological realism in prey dynamics. In today's practical, no changes are made to the predator dynamics, though this is certainly possible.

Model 2 adds a **carrying capacity** (K) to the prey population, indicating that, in the absence of predation, its population would not grow to infinity but rather would be limited by the availability of some (unspecified) resource.

`dN/dt = rN(1-N/K)-aNP` (Equation 5)

When population sizes become very small, it becomes difficult to find a mate, and keep watch for approaching predators. The decrease in population growth rate at small population sizes is known as an **Allée effect**. Model 3 incorporates an Allee effect by adding a lower limit (f) to the prey population.

`dN/dt = r(N-f)(1-N/K)-aNP` (Equation 6)

Approach

Begin by opening the script "practical 8.r" in Rstudio. The script consists of the three predator-prey models described above. The code that actually performs the simulation is in the script "Practical 8 functions.r". You're welcome to explore this script, but there's no need to do so.

Your task is to manipulate the three models and make observations on the resulting dynamics. In lab, I encourage you to work with your neighbours. The practical report (see below) is to be completed individually.

1. The first step to analyse each model is to establish model parameters. I have provided you with a starting set of values. You can, and should, manipulate them. Note that the models can be quite sensitive to the parameter values. Change them by SMALL amounts (1-10%). Even small changes may have dramatic effects on the outcome of the models. RECORD the initial values that I provide, so that you can return to them if you have problems later.
2. Run model 1 using the function calc1(). This function returns a list with four elements:
    a. '*predictions*': at each time step, what is the population size for predators (P) and prey (N)?
    b. '*phase_plane*': For many different combinations of N and P, how will they change when we advance a single time step?
    c. '*equilibria*': Equilibrium population sizes for N and P, i.e. N* and P*.

d. '*N_init*' and '*P_init*': Initial population sizes. In the first model, you will set the initial population sizes for N and P. Setting population sizes that are very different from the equilibrium population sizes (N* and P*) will lead to instability. In models 2 & 3, initial population sizes will be set for you.

3. Plot up the results from model 1 using the function plot1(). Figure 1 illustrates some of the important outputs of the model.

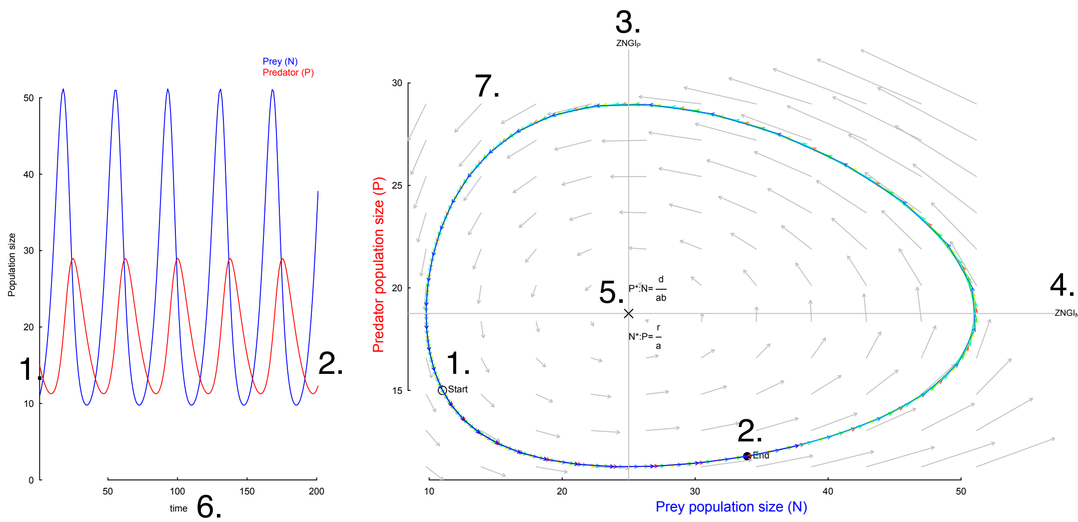

Figure 1. Example graphical output from Model 1. There are many things to notice in this figure: The phase-plane diagram (right) contains far more information than does the trajectory plot (left).

1. Initial population sizes are indicated in both the trajectories and in the phase-plane diagram. Population trends are shown in the trajectory plot as blue and red curves (for N and P, respectively). In the phase-plane diagram, they are shown as a single rainbow-colored curve. Note that, in Model 1, the population cycle steadily, so the trajectory is over-printed in the phase-plane diagram.
2. Final population sizes are also indicated in both the trajectory plot and in the phase-plane.
3. $ZNGI_P$: The Zero Net Growth Isocline for Predators. Along this line, $dP/dt = 0$. In other words, the predator population size will neither increase nor decrease when there are this many prey. Right of this line, P increases. Left of this line, P decreases (Do you know why?).
4. $ZNGI_N$: the prey population size will neither increase nor decrease when there are this many predators. In other words, along this line, $dN/dt = 0$. Above this line, N decreases. Below this line, N increases. (Do you know why?)
5. The equilibrium occurs where $ZNGI_N$ crosses $ZNGI_P$. Notice that, in this example, the equilibrium state *is never reached*. Stable limit cycles are characteristic of the simplest Lotka-Volterra predator-prey models. Note also that if the ZNGIs do not cross in the area of the graph where both Predator and Prey have positive population sizes, there can be no stable equilibrium.

6. Time is shown explicitly in the trajectory figure, but is implicit in the phase-plane diagram.
7. Each of these small grey arrows indicates how the predator and prey populations would change if they began with these values.

Assignment

Answer the following questions using your own words. Some, but not all, require figures to illustrate your answers. Answers should be concise and accurate. Do not just write everything you know. Though you may work with your classmates on this lab, each student is to write up their report independently. Turn in this assignment using Turnitin by **Monday November 7 at noon.** Indicate your identity only with your student number.

1. One at a time, increase each of the parameters of Model 1 by 10% (i.e., multiply them by 1.1). How do these changes affect the equilibrium population sizes and the amplitude of population oscillations? One parameter affects both N* and P*. Which one, and why? Which parameter(s) control(s) the frequency of population oscillations? (Frequency is indicated by the number of time steps between subsequent peaks in population size).

2. In Model 1, do the predators and prey population trajectories follow sigmoidal curves? In other words, are the population trajectories symmetrical sine waves? Do the peaks and troughs occur simultaneously? If not, describe why not, and how they differ.

3. Extinctions occur in Lotka-Volterra models if any of the parameters is very large or very small. Using Model 2, determine a set of parameters that leads to the extinction of predators first, and another set that leads to the extinction of prey first. Explain why these extinctions occur. What happens to the predator when the prey goes extinct? What happens to the prey when the predator goes extinct?

4. Model 2 introduces a carrying capacity (K) to the prey population, simulating the effect of a limiting resource for the prey. Set the parameters in Model 1 such that stable oscillations are achieved. Use those same parameters in Model 2. Then vary K, using values of 100, 100, 10000, infinity (hint: use ‘Inf’). How and why does varying the carrying capacity affect community dynamics?

5. Notice that $ZNGI_N$ in Model 3 is curved. How does the stability of the model differ when the equilibrium population size occurs at the top of this curve, to the left and to the right? (hint: adjust *d*). In other words, how and why do shifts in $ZNGI_P$ affect stability?

6. Using the model of your choice, find a set of parameters that allows for a a stable equilibrium with a greater population size of predators than prey. Show the parameters and graphical output. What biological circumstance does your model capture?