PRACTICAL WORK 3

The numbers in brackets before the question refer to the lecture part that the questions relate to.

The exercise on the relationship between the phase plane and time plots is very instructive to see the link between these. I would certainly recommend you try that exercise.

The bifurcation diagrams for the model with prey density dependence and the Rosenzweig-McArthur model are worth doing. You will see how you can do quite advanced analysis with this software. You will see (or have seen) the results in the lecture, but the ability to do it yourself is an important skill.

In the exercise that analysis effect of space on the dynamics of a predator-prey model this is taken much further. Have a go, but if you get stuck, I will show you what you should have seen.

(4-1) The Lotka-Volterra predator-prey model

The file `lvpp.ode` contains the code for the Lotka-Volterra predator prey model with the effects of fisheries. Plot the output of the model as time plots and in the phase plane. Also plot the isoclines (*Nullcline*). Once you have done this, in the phase plane plot, *Initialconds*, select *Mice*, click in the phase plane to pick other initial conditions. What do you see? Where is the equilibrium of the model? Is it stable? Is it unstable?

You can find out the eigenvalues by doing the following. Click on "*Sing pts*" and select "*Mouse*". Click somewhere in the window close to the equilibrium of the model. A window will pop up that ask if you want to print the eigenvalues. Answer "*YES*" and the eigenvalues will print in the terminal window (the black one). What are the eigenvalues? Are they complex? Is the real parts negative?

Now change the parameter f, which describes the fishing effort. What happens to the equilibrium? Relate this to D'Ancona's observation.

(4-2) Draw the bifurcation diagram in k for the Lotka-Volterra model with prey density dependence. Use `pp3d.ode` for this.

(4-2) The relationship between the phase plane and time plots

The predator-prey models are a nice opportunity to revisit the connection between plots of variables against time, and the phase plane. In a predator-prey model we have 2 variables, V and P, that we solve for time, t. The resulting solution lives in a 3 dimensional space as it is a sequence of points characterised by the values of V, P and t.

The file `pp3d.ode` generates the solution of a predator-prey model with a carrying capacity for the prey, and plots it in a 3d space. It also plots the phase plane, which is the projection of the 3 dimensional curve on the plane t=0, and plots a time plot of the densities of v against t, as a projection on the plane P=0. I did not plot P against time as the figure gets rather busy. If you want to see this you have to uncomment the line starting with "nplot=4" in the `pp3d.ode` file.

The see the plot, start XPP with `pp3d.ode`. Select to *Initialconds*, select *Go*. The time plot is created but does not show in the window because you need to fit in the window. You do this by selecting *Window/Zoom* and then *Fit*. The plot should now be visible. Use your mouse to click somewhere on the figure and drag it around. This will turn the figure. Move it so you can see the phase plane. Observe how the projections relate to the 3D figure.

If you want, you can change the parameters or the initial conditions. If you are ambitious you can use other models to make the same projections.

***(4-1) The constant of motion for the Lotka-Volterra model.** Show that the model :

$$\frac{dV}{dt} = V(r - \alpha P)$$
$$\frac{dP}{dt} = P(\beta V - q)$$

Has a constant of motion given by $H = \beta V - q \ln V + \alpha P - r \ln P$. To do this you need to show that *H* does not change over time for solutions of the Lotka-Volterra model. What could this be useful for?

***(4-3) Show that the equilibrium of the Lotka-Volterra model with prey density dependence is globally stable.** So far the stability of an equilibrium that you considered is local stability. If an equilibrium is locally stable, nearby solutions will converge to it. However, this doesn't say anything about solutions that are far away from the equilibrium. Sometimes it is possible to make statements about global stability, and find out that all solutions will converge to one point. I will show one way in which this can be done for the LV model with density dependence:

$$\frac{dV}{dt} = V(r(k - V) - \alpha P)$$
$$\frac{dP}{dt} = P(\beta V - q)$$

To prove global stability, follow the numbered steps. To demonstrate global stability, (1) show that the function $H = \beta V - q \ln V + \alpha P - r(k - q/\beta) \ln P$ can only decrease or stay the same over time over solutions of the Lotka-Volterra model with density dependence.

Once you have done this, you know that as time progresses the function *H* can only get smaller or stay the same. Next, (2) show that if $k > q/\beta$ the function *H* is lower bounded for positive *V* and *P* (i.e. you want to establish that the value of *H* can't forever decreases). If this is the case the function *H* will have to stop decreasing at some point. The system must therefore progress to a state where *H* doesn't change anymore and stay there forever. Next, (3) find the set of values of *V* and *P* for which the function *H* doesn't change. If this set contains a single forward invariant set, this set is globally stable. In this case (4) show that the set the set of values of *V* and *P* for which the function *H* doesn't change contains the positive equilibrium. If you have taken all these steps, you have shown that the equilibrium is globally stable.

The function *H* that you have used here is a so called Lyapunov function. It acts like an entropy function, a quantity that can never go up over time. We can makes this visible using XPP. The file `pplyapnv.ode` contains the systems of ODEs shown above, and the function H. Open the file in

XPP. First, by looking at the solutions over time, ascertain that the value of *V* and *P* can go up and down but that *H* always decreases.

Next, look at the phase plane (easiest done by closing the window and starting again). Now go through the following sequence of commands: go to *Graphics stuff*, select *Freeze* and then switch *On freeze*. This will freeze your solutions to the screen so they remain visible. Next, go to *Initialconds*, select *Mice*, click in the phase plane and draw a number of solutions, try to start close to the borders of your window. Next use ESC to stop drawing, and now click on *nUmerics*, and then *Color code* and choose *Another quantity*. When prompted, choose H for your color coding and choose *Optimize.* Use ESC to leave the *nUmerics* menu and now go to *Dir. Field/flow.* Choose *Colorize* and when asked about Grid, answer something like 100. The phase plane will colour in, and the colour that each point will take will be specified bv the function *H*. Can you see the egg shapes of the orbits of the Lotka-Volterra model without density dependence in the boundaries between the colours? Next do *Initialconds,* and *Go* once more. Your frozen orbits will reappear. Can you see how they all move from warmer to cooler colours? Over the orbits the values of *H* decreases as the orbits moves through the different coloured zones.

(4-2) Investigate the dynamics of the Rosenzweig-McArthur model. Use the file `pprmca.ode` to make a bifurcation diagram in *k.* Note that the equilibrium loses its stability for large values of k. Why is this? To get a clue, grab the curve and click through the points. Watch the circle in the bottom left corner of your screen which shows you the multipliers (here: the exponential values of the eigenvalues).

In the bifurcation diagram, use *Grab* to go to the point where the equilibrium loses stability. This has type HB. Select this point by pressing Enter once you are on it. Now click on *Run* and select *Periodic*. The little circles that you can see appearing show the maximum and minimum value of the parameter you have chosen on the limit cycle. Note that the circles are green, which indicate the limit cycle is stable. You can check this by using *Grab* and check that there are no multipliers are outside the unit circle if you click through the solution. (*(only for those with an interest in the mathematical theory behind this material). You will notice that there is one multiplier on the unit circle, and the other one is within. This is related to the Poincare return map that is used to calculate the stability of limit cycles. Can you explain why there is one multiplier on the unit circle?)

Use *Grab* to select a point where the equilibrium is stable, go back to XPP to look at the phase portrait. Now go back to auto, use *Grab* to find a value for k where the limit cycle exists. Select, go back to XPP to look at the phase portrait and compare.

(4-3) The effect of space on the dynamics of a predator-prey model. In this exercise we will study how space can change the dynamics of the Rosenzweig-McArthur model, and how spatial predator prey systems are less likely to become extinct. To do so we will use a model in which the predator and prey population inhibit two patches, between which the predators can move with rate *d* (this would apply to a system of plants and herbivores). Because the predator and prey densities can take very small values it is convenient to use a model version in which we transform the densities into its logarithmic values. This also makes the model numerically easier to study (if you wonder how to do this works, see the exercise below.) The model is in the file `pprmca2.ode`

Open `pprmca2.ode` in XPP and make a bifurcation diagram in k as you did in the previous exercise. Use *Grab* to go to the point where the equilibrium loses stability, which is indicated with HB. Select this point by pressing Enter once you are on it. Now click on *Run* and select *Periodic*. As in the previous exercise you will see circles appearing which now indicate the logarithm of maximum and minimum values. You will see that the circles are different colour: some are green and some are blue. Use *Grab* to check that for the blue circles there is at least one multiplier located outside the unit circle. Use *Grab* to select a point where the limit cycle is stable (green), go back to XPP to look at the phase portrait, you can see the limit cycle in the phase plane. Plot the logarithm of the prey values in patch 1, vs patch 2. Note that they are always the same.

Now go back to AUTO, use *Grab* to find a value for k where where the colour changes from green to blue. You will see that there are two multipliers one the unit circle, one on 1, and a second the multiplier is on the real axis at -1. Just as in the logistic map, this means that a period doubling occurs, and AUTO indicates this by the letters PD under type, in the bottom line of the screen. Use *Grab* to select one of the PD points (there are two of them) and then click *Run* and select *Doubling*. A new branch of circles will appear. Do the same for the second PD point.

Use *Grab* to select a point where the limit cycle that you have found through continuing the “doubling” is stable (green), go back to XPP to look at the phase portrait. Plot the logarithm of the prey values in patch 1, vs patch 2. Note that they are different now. Also look at the time plot: can you see that the period has doubled? Now go back to AUTO, use *Grab* to find a value for k where the limit cycle is just unstable (blue), and go back to XPP to look at the phase portrait. Run XPP for sufficiently long time (use *Initialconds*, select *Last* several times) so that the dynamics can move away from the unstable limit cycle. What happens?

Observe that in the spatial model the same solutions are possible as in the non-spatial model if the densities are the same in both patches. In the spatial model also completely new dynamics appear, in which the densities differ between patches. These spatial dynamics are different, and for the stable period 2 cycles the minimum values are not as low as in the non-spatial model.

***(4-3 advanced) Transforming a model into logarithmic values.** Show that the logistic model

$$\frac{dx}{dt} = rx(k - x)$$

Can be transformed into the system

$$\frac{dy}{dt} = r(k - e^{y})$$

By choosing y=ln(x). How should the initial condition be transformed? This transformation has the advantage that it is much easier to the study numerically for very small values. When solving differential equation models numerically very small values can cause numerical problems. The transformed model is numerically much more stable for small values. The price to pay for this is that the equilibrium x=0 cannot be studied anymore, because it is located at minus infinity.

If you want to practice this trick further, transform the Lotka-Volterra predator-prey model in new variables which represent the logarithm of the densities. Code them up for XPP and study their behaviour. This is easiest done by changing an existing file, like `lvpp.ode`, and save it under a different name.

(4-3) Investigate the dynamics of the Nicholson-Bailey model. The model is given by

$$H_{t+1} = \lambda H_t \exp(-aP_t)$$

$$P_{t+1} = H_t\left(1 - \exp(-aP_t)\right)$$

You can use the file `nb.ode`.

Calculate the equilibrium and work out what the stability of the equilibrium is.
