

# Problem sheet 4

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## 1 Lotka-Volterra equations

Data on the number of Canadian lynx and snowshoe hair pelts traded were collected by the Hudson Bay trading company<sup>1</sup>. The data are presented in Figure 1(b) and has been used as a proxy for population data. In this question we consider a

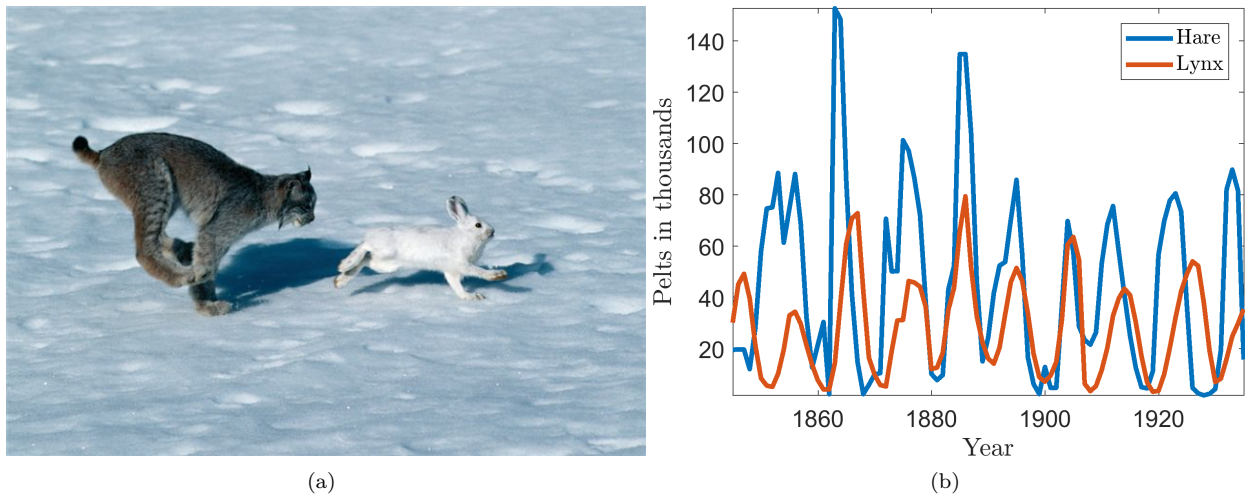


Figure 1: (a) Lynx and hare in action. (b) Number of pelts recorded over time.

mathematical model that has been suggested to describe the features seen in the data. Specifically, it is a predator-prey interaction model called the Lotka-Volterra model. Let  $L$  be the lynx population and  $H$  be the hare population. The interaction equations are

$$\underbrace{H \xrightarrow{k_1} 2H}_{\text{Hares reproduce}}, \quad \underbrace{H + L \xrightarrow{k_2} 2L}_{\text{Lynx reproduce through predation}}, \quad \underbrace{L \xrightarrow{k_3} \emptyset}_{\text{Lynx die out}}. \quad (1)$$

1. Describe two features seen in the population data of Figure 1(b).
2. Name two troubling assumptions behind the Lotka-Volterra interaction equations and suggest how they could be fixed.
3. Write down the ODEs representing the interaction system.
4. Let  $u$  and  $v$  be non-dimensional variables of the hare and lynx, respectively. Non-dimensionalise the system to produce a system of the form:

$$\dot{u} = u - uv, \quad (2)$$

$$\dot{v} = \alpha(uv - v), \quad (3)$$

<sup>1</sup>Caution about the data: I have not been able to verify this data, but this is the data (or rather the graph) that is always cited. This particular set of data came from scanning in the graph from Odum's "Fundamentals of Ecology", p. 191 which is often cited. Odum says that his graph is taken from MacLulich's "Fluctuations in the numbers of varying hare", 1937, which is not widely available. Some authors caution that this data is actually a composition of several time series, and should probably not be analysed as a whole, and that some of the lynx data was actually missing. It is said that the data was collected from Hudson's Bay historical records, and does not reflect animal populations, but rather the number of pelts turned in for trading (a large number of which came from Native Americans- mentioned because there were some medical outbreaks during these years which could account for skewed data). The data are presented here with these cautions.

where the time derivative is with respect to some non-dimensionalised time.

Provide the dimensional scales of the population (i.e.  $[L]$ ,  $[H]$  and  $[t]$ ) as well as the definition of  $\alpha$ . Note, that you are not required to show that  $[L]$  and  $[H]$  have the right dimension and  $\alpha$  is dimensionless, but it is a good way to check your working.

5. What are the steady states?
6. What is the linear stability of the states?
7. Consider

$$\frac{du}{dv} = \frac{\dot{u}}{\dot{v}}. \quad (4)$$

Show that equation (4) can be directly integrated to show that the populations must satisfy the constraint

$$\left(\frac{e^v}{v}\right) \left(\frac{e^u}{u}\right)^\alpha = e^C, \quad (5)$$

where  $C$  is a constant of integration that depends on the initial conditions, which you should specify explicitly. (Hint: rearrange  $du/dv$  such that one side contains all  $u$  terms and the other contains all  $v$  terms).

## 2 Computer simulation

Let  $\alpha = 1/2$  and simulate equations (2) and (3). Plot the results in the  $(u, v)$  plane along with equation (5). Note you will have to choose appropriate initial conditions, specify  $C$  in terms of these initial conditions and use an implicit plotting algorithm such as `fimplicit` in MatLab.

1. Vary the initial conditions, what do you notice?
2. Do your discoveries accord with the results from question 1?
3. Now consider the plot of  $(t, u)$  and  $(t, v)$ . Do the simulated curves match the data seen in Figure 1(b)?

## 3 Bifurcations

Consider the following set of equations which model the interactions of two populations  $N_1$  and  $N_2$ , where  $r_1, r_2, K_1, K_2, b_{12}$  and  $b_{21}$  are non-negative:

$$\dot{N}_1 = r_1 N_1 \left(1 - \frac{N_1}{K_1 + b_{12} N_2}\right), \quad (6)$$

$$\dot{N}_2 = r_2 N_2 \left(1 - \frac{N_2}{K_2 + b_{21} N_1}\right). \quad (7)$$

1. What is the biological interpretation of the dynamics occurring between species  $N_1$  and  $N_2$ ?  
 Hint 1: by the symmetry of  $N_1$  and  $N_2$  in the equations whatever  $N_1$  is doing to  $N_2$ ,  $N_2$  is doing to  $N_1$ . This means that the dynamics could be mutual creation (mutualism) or mutual destruction (competition).  
 Hint 2: Compare the above equations to regular logistic curve  $\dot{u} = ru(1 - u/K)$ . What happens if we increase or decrease  $K$ ? Thus, what influence does increasing or decreasing  $N_1$  have on  $N_2$ ?
2. Use  $N_1 = K_1 u_1$ ,  $N_2 = K_2 u_2$ ,  $t = \tau/r_1$  to non-dimensionalise the equations. Define  $\rho = r_2/r_1$ ,  $\alpha_{12} = b_{12}K_2/K_1$  and  $\alpha_{21} = b_{21}K_1/K_2$ . Rewrite the system parameters in terms of  $\alpha_{12}$ ,  $\alpha_{21}$  and  $\rho$ .
3. Show that the system has four steady states:

$$(0, 0), \quad (0, 1), \quad (1, 0), \quad (\bar{u}_1, \bar{u}_2), \quad (8)$$

where

$$\bar{u}_1 = \frac{1 + \alpha_{12}}{1 - \alpha_{12}\alpha_{21}}, \quad \bar{u}_2 = \frac{1 + \alpha_{21}}{1 - \alpha_{12}\alpha_{21}}. \quad (9)$$

What restrictions (if any) do we need to place on the steady states?

4. Determine the linear stability of the steady states. Taking care to note any bifurcation conditions and how they relate to the restrictions on the steady state existence.

## Exam revision

### 4 Predator competition

One of the assumptions in the Lotka-Volterra equation is that the predation effect is proportional to both the predator and prey population. However, as the number of prey increases the competition between predators will increase, thus, we consider the adapted equations

$$\dot{u} = u - uv, \quad (10)$$

$$\dot{v} = b(uv - v) - bv^2, \quad (11)$$

where  $b > 0$ .

1. What are the steady states of the system?
2. Characterise the stability of the valid steady states, noting any dependences on the parameter  $b$ .
3. How does predator competition change the outcome of the situation, compared to the basic Lotka-Volterra equation shown in question 1?

### 5 The Lorenz equations

In 1963, Edward Lorenz developed a simplified mathematical model for atmospheric convection. The model is a system of three ordinary differential equations now known as the Lorenz equations:

$$\dot{x} = \sigma(y - x), \quad (12)$$

$$\dot{y} = x(\rho - z) - y, \quad (13)$$

$$\dot{z} = xy - \beta z. \quad (14)$$

The equations relate the properties of a two-dimensional fluid layer uniformly warmed from below and cooled from above. In particular, the equations describe the rate of change of three quantities with respect to time:  $x$  is proportional to the rate of convection;  $y$  is proportional to the horizontal temperature variation;  $z$  is proportional to the vertical temperature variation. The constants  $\sigma$ ,  $\rho$ , and  $\beta$  are system parameters proportional to the Prandtl number, Rayleigh number, and certain physical dimensions of the layer itself.

For simplicity, let  $\sigma = \beta = 1$ .

1. What are the steady states, noting dependencies of  $\rho$ ?
2. Characterise the stability of the zero steady state only, noting dependencies of  $\rho$ . Note that you will have to find the eigenvalues of a  $3 \times 3$  matrix. Substituting in the values of the steady state will help you. The non-zero steady states are always either stable nodes or stable spirals when they exist.
3. Simulations for  $\rho > 1$  and  $\rho < 1$  are illustrated in Figure 2. Do these accord with your findings?

EXTENSION 1: If you are brave enough calculate the eigenvalues corresponding to the non-zero steady states and show that they always have negative real part when  $\rho > 1$ , but they may be complex.

EXTENSION 2: If you are even braver rerun the analysis with variables  $\sigma = 10$ ,  $\rho = 28$  and  $\beta = 3$ . This causes the system to act chaotically. Categorise the steady states in this case. What happens? An image of the chaotic trajectory can be seen in Figure 3.

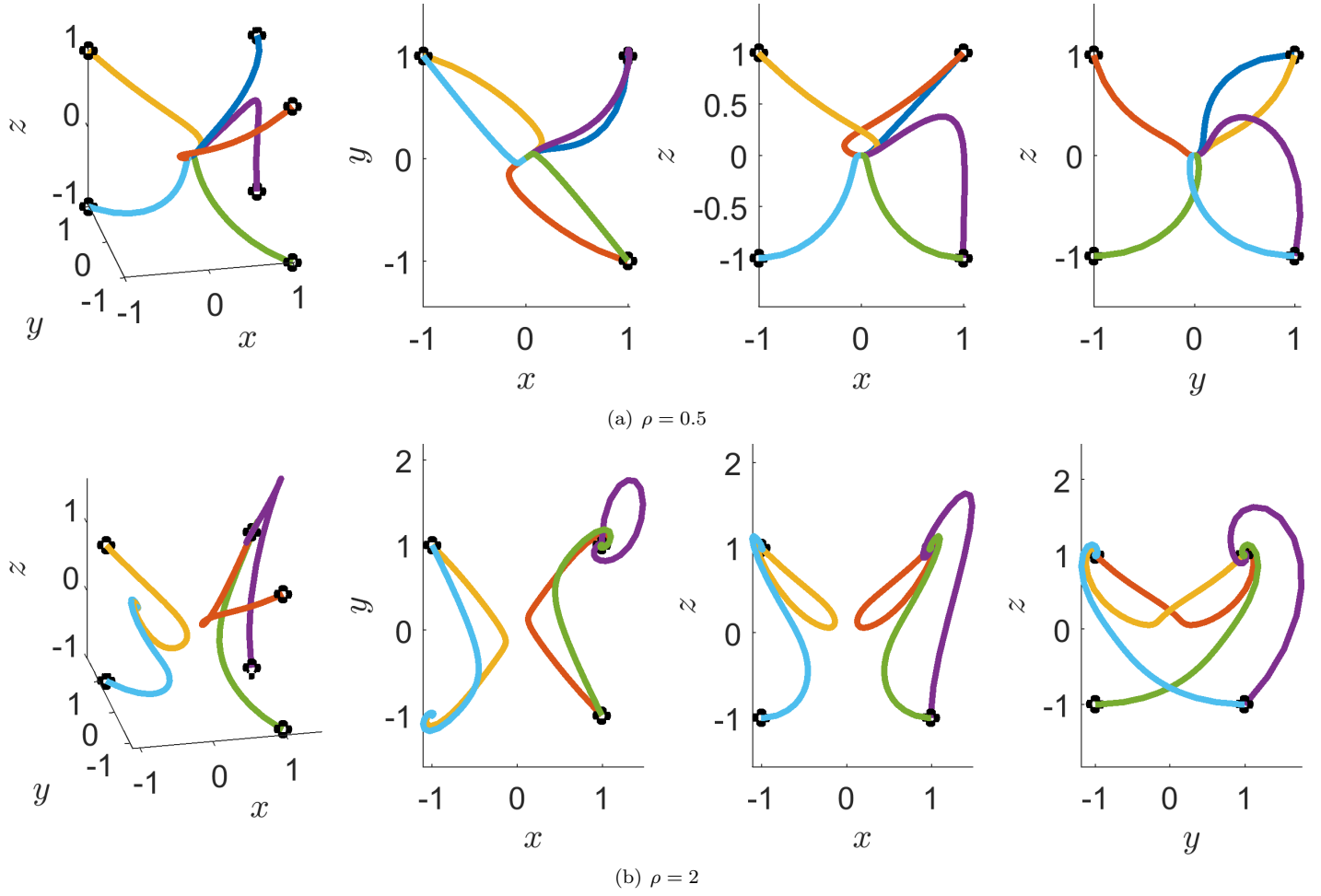


Figure 2: Simulating the Lorenz equations with  $\sigma = 1$ ,  $\beta = 1$  and  $\rho$  given beneath each figure, for a variety of initial conditions. The black circles indicate the initial conditions. On the left is the full, three-dimensional realisation, whilst the rest of the plots in the row are the  $(x, y)$ ,  $(x, z)$  and  $(y, z)$  projections.

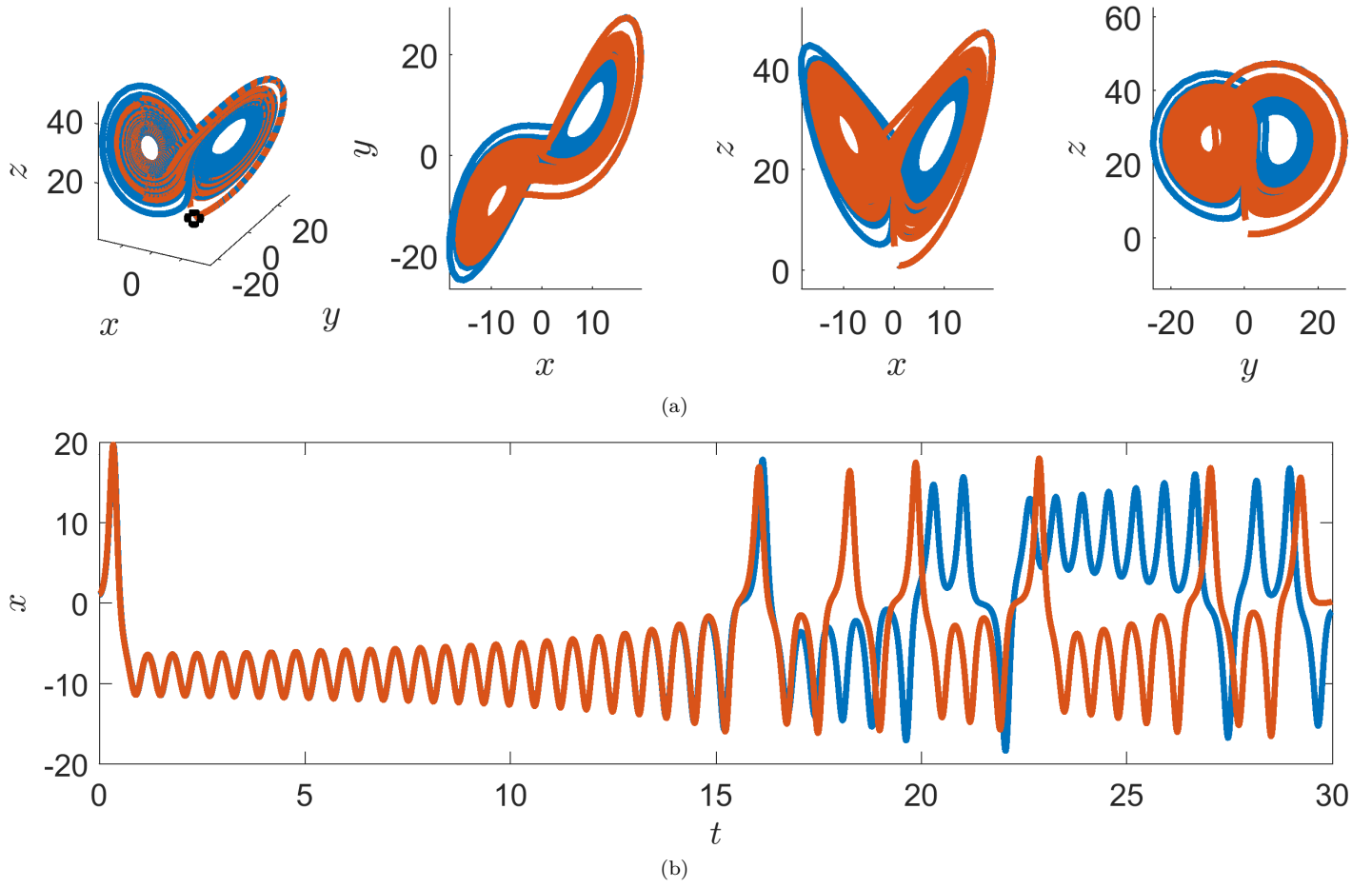


Figure 3: Simulating the Lorenz equations with  $\sigma = 10$ ,  $\beta = 3$  and  $\rho = 28$  for two initial conditions that start very close together. Top: the black circles indicate the initial conditions. On the left is the full, three-dimensional realisation, whilst the rest of the plots in the row are the  $(x, y)$ ,  $(x, z)$  and  $(y, z)$  projections. Bottom: time series of  $x$ , where we observe the two trajectories diverging.