Problem sheet 4

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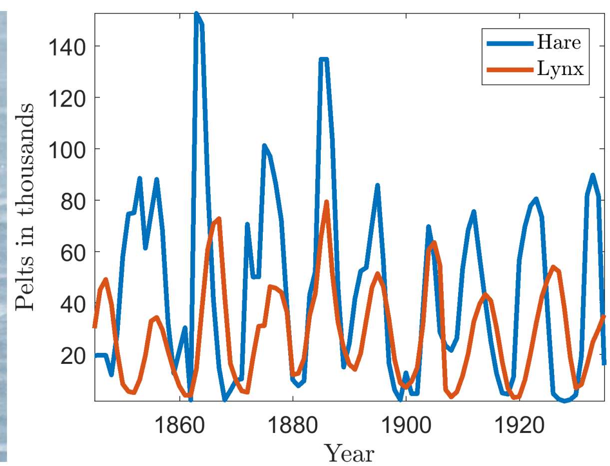
1 Lotka-Volterra equations

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

(a)



(b)

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

we consider a 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

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

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.

[1] 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.

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:

$$\dot{u} = u - uv, \tag{2}$$
$$\dot{v} = \alpha(uv - v), \tag{3}$$

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 α. Note, that you are not required to show that $[L]$ and $[H]$ have the right dimension and α 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

$$\frac{\mathrm{d}u}{\mathrm{d}v} = \frac{\dot{u}}{\dot{v}}. \tag{4}$$

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

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

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

1.1 Answers

1.1.1

The populations oscillate. A rise in prey comes before a rise in predator. Other sensible comments are allowed.

1.1.2

(a) Prey does not die naturally, a prey death rate could be included.

(b) Predator and prey do not need partners to reproduce, such reproduction equations could be included.

(c) Predation is a one to one transference, usually more prey are needed to produce enough energy to provide a new predator generation. Instead of producing two lynx we could rewrite the predation equation to give $1 + \epsilon$ predators.

(d) Other assumptions and fixes are available.

1.1.3

$$\dot{H} = k_1 H - k_2 HL, \tag{6}$$
$$\dot{L} = k_2 HL - k_3 L. \tag{7}$$

1.1.4

Let $H = [H]u$, $L = [L]v$, $t = [t]\tau$, the appropriate scales are then:

$$[H] = \frac{k_3}{k_2}, \quad [L] = \frac{k_1}{k_2}, \quad [t] = \frac{1}{k_1} \tag{8}$$

and $\alpha = k_3/k_1$.

1.1.5

The steady states are $(0, 0)$ and $(1, 1)$.

1.1.6

The Jacobian of the system is

$$J(u,v) = \begin{bmatrix} 1-v & -u \\ \alpha v & \alpha(u-1) \end{bmatrix}. \tag{9}$$

For (0,0)

$$J(0,0) = \begin{bmatrix} 1 & 0 \\ 0 & -\alpha \end{bmatrix}, \tag{10}$$

the eigenvalues are, thus, $\lambda = 1 > 0$ and $-\alpha < 0$. Hence, (0,0) is a saddle point.

For (1,1)

$$J(0,0) = \begin{bmatrix} 0 & -1 \\ \alpha & 0 \end{bmatrix}, \tag{11}$$

the eigenvalues are, thus, $\lambda = \pm\sqrt{-\alpha}$, which are purely imaginary. Hence (1,1) is a centre.

1.1.7

$$\frac{\mathrm{d}u}{\mathrm{d}v} = \frac{u\,(1-v)}{\alpha v\,(u-1)} \tag{12}$$

which can reformulated to be

$$\int_{u_0}^{u} \frac{\alpha(u-1)}{u}\,\mathrm{d}u = \int_{v_0}^{v} \frac{1-v}{v}\,\mathrm{d}v, \tag{13}$$

from which we can derive

$$\alpha(u - \log(u)) - \alpha(u_0 - \log(u_0)) = (\log(v) - v) - (\log(v_0) - v_0), \tag{14}$$

which can be rearranged to be

$$\alpha(u - \log(u)) + v - \log(v) = \alpha(u_0 - \log(u_0)) + v_0 - \log(v_0). \tag{15}$$

Exponentiating both sides of the equation we get

$$e^{u\alpha}u^{-\alpha}e^{v}v^{-1} = e^{\alpha(u_0-\log(u_0))+v_0-\log(v_0)}, \tag{16}$$

which can finally be rearranged to produce

$$\left(\frac{e^v}{v}\right)\left(\frac{e^u}{u}\right)^{\alpha} = e^C, \tag{17}$$

where $C = \alpha(u_0 - \log(u_0)) + v_0 - \log(v_0)$.

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)?

2.1 Answers

2.1.1

The simulations can be seen in Figure 2. Different initial conditions cause the trajectory to be on different parallel oscillatory trajectories. The trajectories are exactly matched by the curves given by equation (17). Larger initial conditions have a longer period.

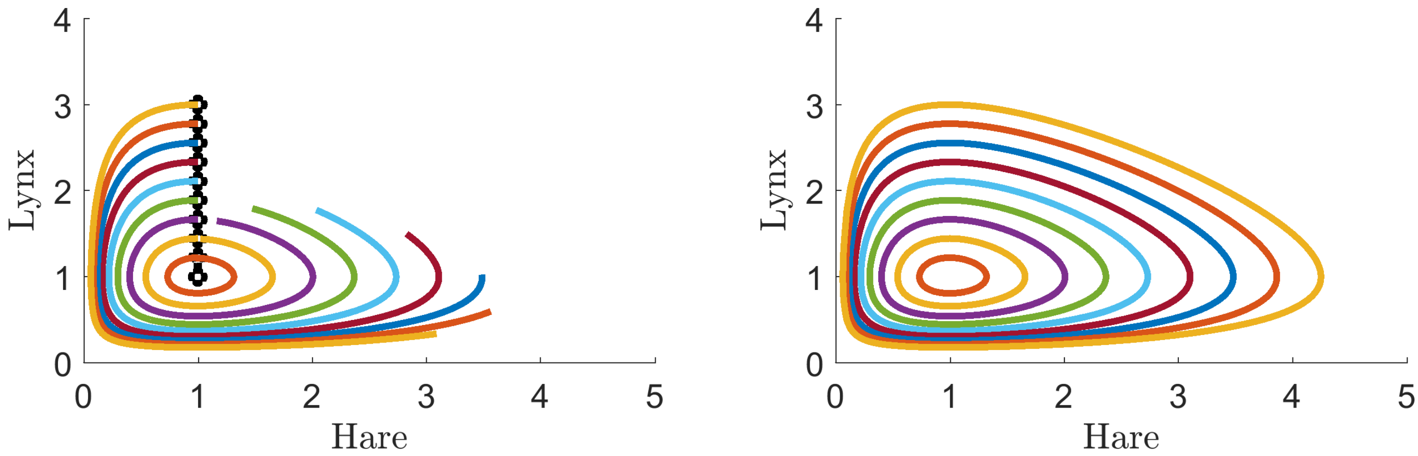


Figure 2: Left: simulation of equations (2) and (3). The black points illustrate the initial condition, the trajectories are spiralling anticlockwise. Right: Simulation of equation (17) with the same initial conditions as in the left image.

2.1.2

The simulations in Figure 2 exactly match the linearised stability solution suggesting that (1,1) is a centre. However, the simulations illustrate that this is a global phenomenon, in that all trajectories periodically oscillate around (1,1).

2.1.3

The time course simulation in Figure 3 illustrate that the trajectories do have similar traits of periodic oscillations and that growth in the lynx population lags behind growth in the hare population.

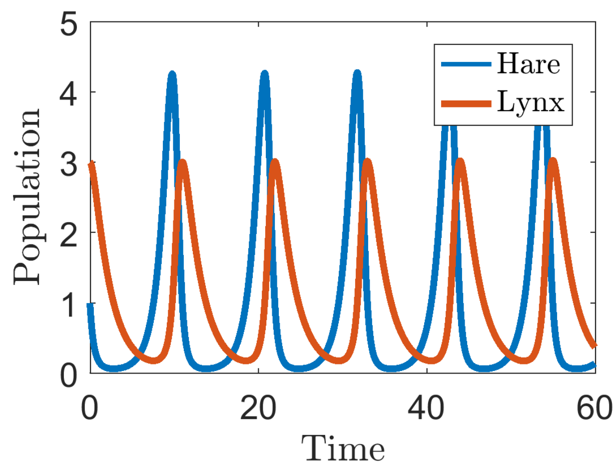


Figure 3: Left: simulation of equations (2) and (3).

3 Bifurcations

Consider the following set of equations which model the interactions of two populations N_1 and N_2:

$$\dot{N}_1 = r_1 N_1 \left(1 - \frac{N_1}{K_1 + b_{12} N_2}\right), \tag{18}$$

$$\dot{N}_2 = r_2 N_2 \left(1 - \frac{N_2}{K_2 + b_{21} N_1}\right). \tag{19}$$

1. What dynamics are occurring between the 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 α_{12}, α_{21} and ρ.

3. Show that the system has four steady states:
$$(0,0), \quad (0,1), \quad (1,0), \quad (\bar{u}_1, \bar{u}_2), \tag{20}$$
where
$$\bar{u}_1 = \frac{1+\alpha_{12}}{1-\alpha_{12}\alpha_{21}}, \quad \bar{u}_2 = \frac{1+\alpha_{21}}{1-\alpha_{12}\alpha_{21}}. \tag{21}$$
What restrictions (if any) do we need to place of 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.

3.1 Answers

3.1.1

An increase in N_1 causes and increase in the steady state of N_2, thus, we have mutualism. Namely the population both cause each other to grow.

3.1.2

The equations simplify to:
$$\dot{u}_1 = u_1\left(1 - \frac{u_1}{1+\alpha_{12}u_2}\right), \tag{22}$$
$$\dot{u}_2 = \rho u_2\left(1 - \frac{u_2}{1+\alpha_{21}u_1}\right). \tag{23}$$

3.1.3

Setting $\dot{u}_1 = \dot{u}_2 = 0$ provides the given steady states. Note that we need $\alpha_{12}\alpha_{21} > 1$ for $(\bar{u}_1, \bar{u}_2)$ to make sense as a positive steady state, since we are dealing with populations.

3.1.4

The Jacobian is
$$J(u_1,u_2) = \begin{bmatrix} 1 - \frac{2u_1}{1+\alpha_{12}u_2} & \frac{au_1^2}{(1+\alpha_{12}u_2)^2} \\ \frac{\rho u_2^2}{(1+\alpha_{21}u_1)^2} & \rho - \frac{2\rho u_2}{1+\alpha_{21}u_1} \end{bmatrix}, \tag{24}$$
and so
$$J(0,0) = \begin{bmatrix} 1 & 0 \\ 0 & \rho \end{bmatrix}, \tag{25}$$
meaning that $(0,0)$ is an unstable node.
$$J(0,1) = \begin{bmatrix} 1 & 0 \\ a\rho & -\rho \end{bmatrix}, \tag{26}$$
meaning that $(0,1)$ is a saddle.
$$J(1,0) = \begin{bmatrix} -1 & a \\ 0 & \rho \end{bmatrix}, \tag{27}$$
meaning that $(1,0)$ is a saddle.
$$J(\bar{u}_1,\bar{u}_2) = \begin{bmatrix} -1 & \alpha_{12} \\ \rho\alpha_{21} & -\rho \end{bmatrix}. \tag{28}$$
Calculating the eigenvalues, λ, of $J(\bar{u}_1,\bar{u}_2)$ we find that
$$\lambda^2 + \underbrace{(1+\rho)}_{>0}\lambda + \underbrace{\rho(1-\alpha_{12}\alpha_{21})}_{>0} = 0. \tag{29}$$

Since the coefficient of λ and the constant term are positive (equally the trace and determinant of $J(\hat{u}_1, \hat{u}_2)$ are negative and positive, respectively), then $(\bar{u}_1, \bar{u}_2)$ is stable whenever it exists.

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

$$\dot{u} = u - uv, \tag{30}$$
$$\dot{v} = b(uv - v) - bv^2. \tag{31}$$

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?

4.1 Answer

4.1.1

The steady states are $(0,0)$, $(0,-1)$ and $(2,1)$.

4.1.2

The Jacobian is

$$J(u,v) = \begin{bmatrix} 1-v & -u \\ bv & b(u-1-2v) \end{bmatrix}, \tag{32}$$

so,

$$J(0,0) = \begin{bmatrix} 1 & 0 \\ 0 & -b \end{bmatrix}, \tag{33}$$

meaning that (0,0) is a saddle point.

$$J(2,1) = \begin{bmatrix} 0 & -2 \\ b & -b \end{bmatrix}. \tag{34}$$

The eigenvalues satisfy

$$\lambda^2 + b\lambda + 2b = 0, \qquad \implies \lambda_\pm = \frac{-b \pm \sqrt{b(b-8)}}{2}. \tag{35}$$

For $0 \leq b < 8$ $\lambda_\pm$ is complex and the real part is negative, so we have a stable spiral. For $b \geq 8$ $\lambda_- < \lambda_+ < 0$ and so we have a stable node.

4.1.3

In the basic Lotka-Volterra case, all trajectories are closed, periodic orbits. In the case of predator competition the non-zero steady state is always stable.

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:

$$\dot{x} = \sigma(y - x), \tag{36}$$
$$\dot{y} = x(\rho - z) - y, \tag{37}$$
$$\dot{z} = xy - \beta z. \tag{38}$$

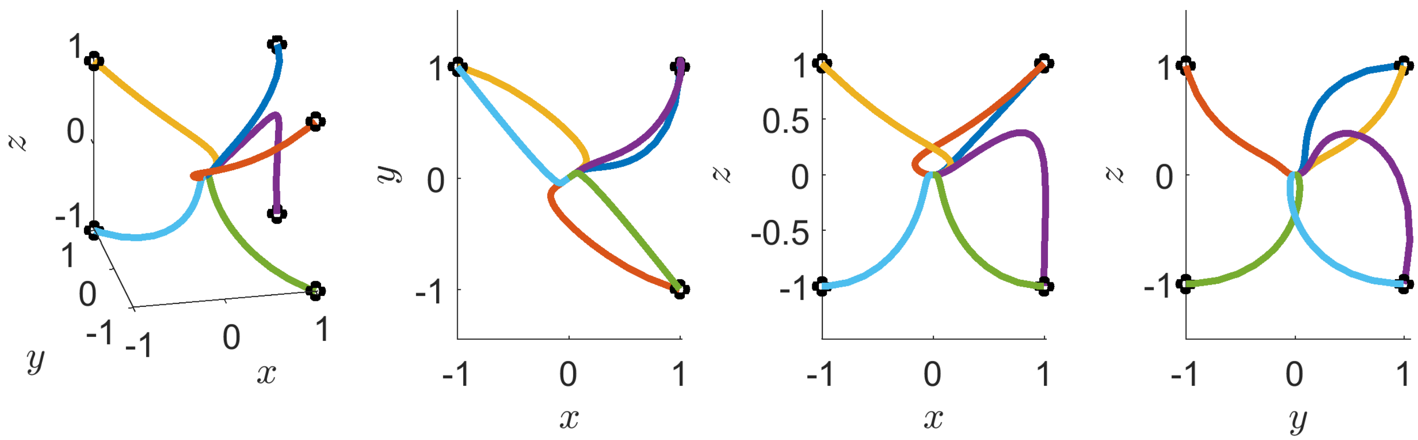
The equations relate the properties of a two-dimensional fluid layer uniformly warmed from below and cooled from above. In particular, the equations describe the rate of change of three quantities with respect to time: x is proportional to the rate of convection; y is proportional to the horizontal temperature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

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

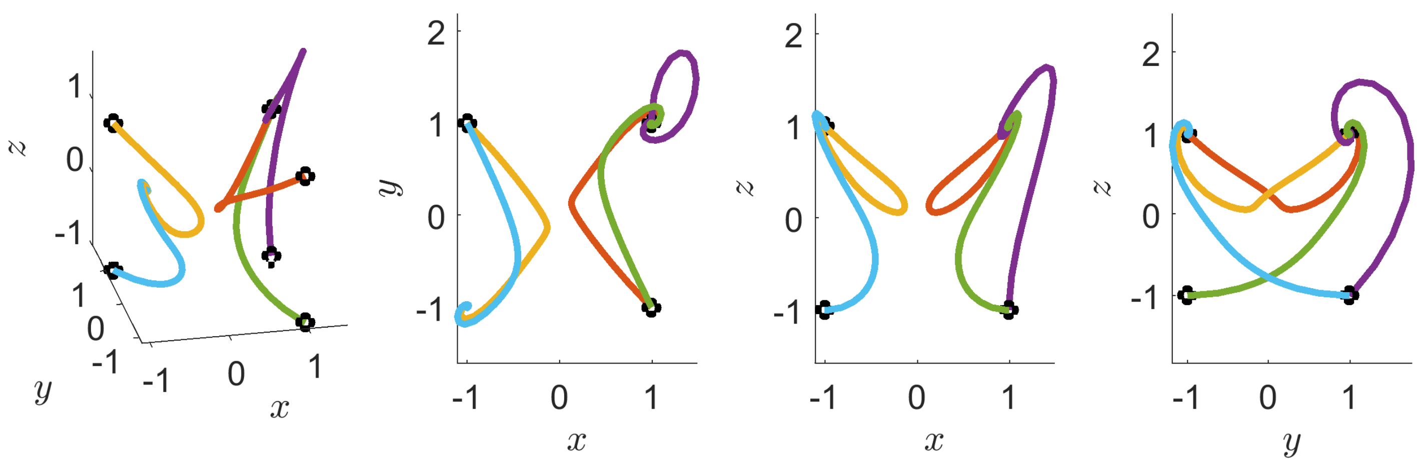
1. What are the steady states, noting dependencies of ρ?
2. Characterise the stability of the zero steady state only, noting dependencies of ρ. Note that you will have to find the eigenvalues of a 3×3 matrix. Substituting in the values of the steady state will help you. The non-zero steady states are always either stable nodes or stable spirals when they exist.
3. Simulations for $\rho > 1$ and $\rho < 1$ are illustrated in Figure 4. 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 5.



(a) $\rho = 0.5$



(b) $\rho = 2$

Figure 4: Simulating the Lorenz equations with $\sigma = 1$, $\beta = 1$ and ρ 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.

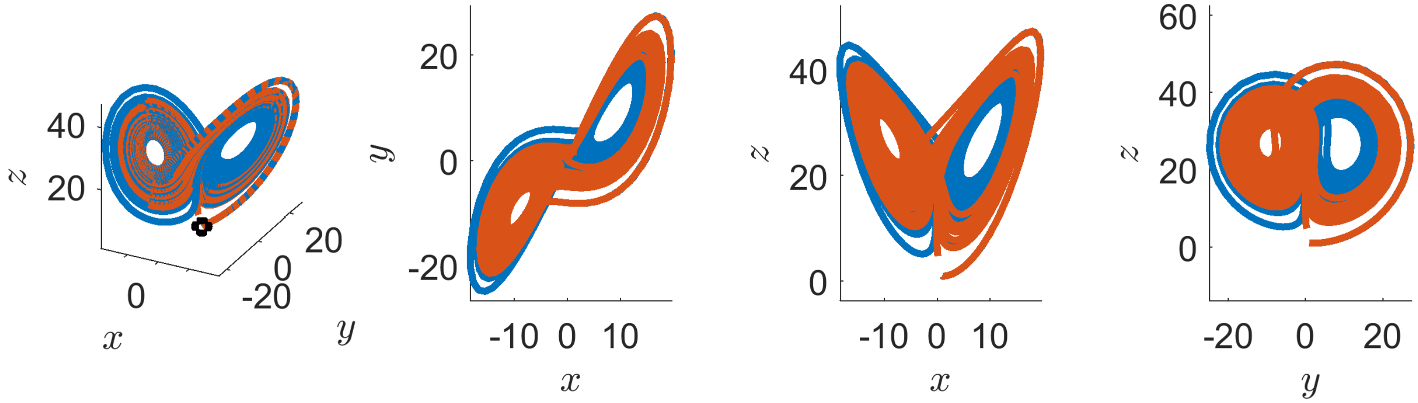
5.1 Answers

5.1.1

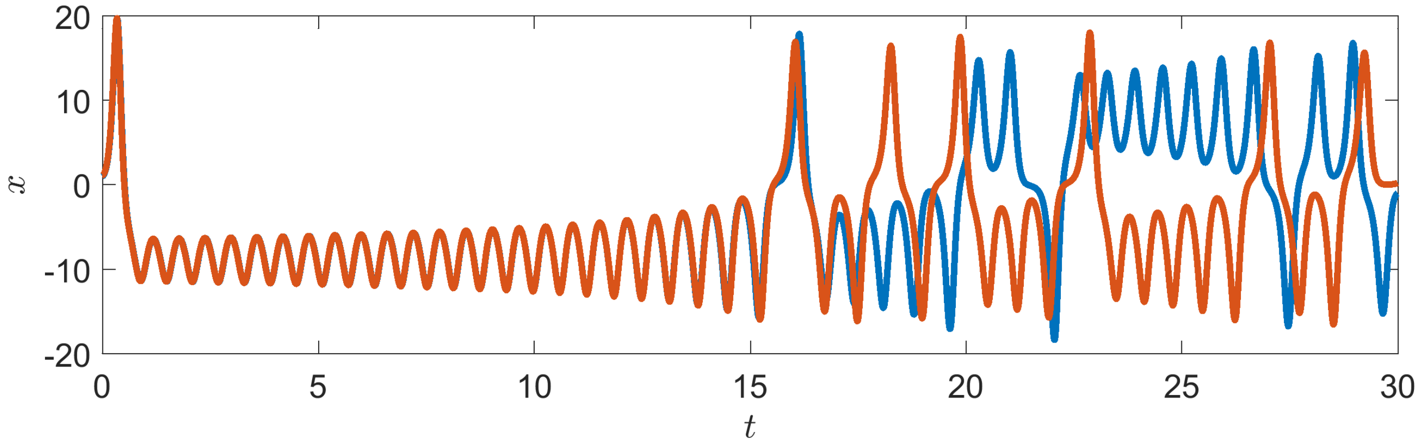
There are three steady states:

$$(0, 0, 0), \quad (\pm\sqrt{\rho - 1}, \pm\sqrt{\rho - 1}, \rho - 1). \tag{39}$$

and we note that we need $\rho > 1$ for the non-zero states to exist.



(a)



(b)

Figure 5: 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.

5.1.2

The Jacobian is

$$J(x, y, z) = \begin{bmatrix} -1 & 1 & 0 \\ r - z & -1 & -x \\ y & x & -1 \end{bmatrix}. \tag{40}$$

$$J(0, 0, 0) = \begin{bmatrix} -1 & 1 & 0 \\ \rho & -1 & 0 \\ 0 & 0 & -1 \end{bmatrix}, \tag{41}$$

thus, the eigenvalues satisfy the equation

$$(-1 - \lambda)((-1 - \lambda)^2 - \rho) = 0, \quad \implies \lambda_{-1} = -1, \quad \lambda_{\pm} = -1 \pm \sqrt{\rho}. \tag{42}$$

Hence, $(0, 0, 0)$ is stable if $0 < \rho < 1$ and unstable if $\rho > 1$.

5.1.3

The simulations in Figure 4 show that when $0 < \rho < 1$ the steady state always tends to the origin. However, for $\rho > 1$, the trajectory tends to one of the non-zero steady states depending on the initial condition.

5.1.4 EXTENSION 1

The stability of the $(\pm\sqrt{\rho-1}, \pm\sqrt{\rho-1}, \rho-1)$ states are both the same. Here, we will illustrate how to extract the eigenvalues of $(\sqrt{\rho-1}, \sqrt{\rho-1}, \rho-1)$, the negative case is similar.

$$J(\sqrt{\rho-1}, \sqrt{\rho-1}, \rho-1) = \begin{bmatrix} -1 & 1 & 0 \\ 1 & -1 & -\sqrt{\rho-1} \\ \sqrt{\rho-1} & \sqrt{\rho-1} & -1 \end{bmatrix}, \tag{43}$$

thus, the eigenvalues satisfy the equation

$$\begin{aligned} 0 &= (-1-\lambda)((-1-\lambda)^2 + (\rho-1)) - ((-1-\lambda) + (\rho-1)), & (44)\\ &= \lambda^3 + 3\lambda^2 + (1+\rho)\lambda + 2(\rho-1), & (45)\\ &= (\lambda+2)(\lambda^2+\lambda+\rho-1). & (46)\\ & & (47) \end{aligned}$$

Hence,

$$\lambda_{-2} = -2, \quad \lambda_{\pm} = \frac{-1 \pm \sqrt{5-4\rho}}{2}, \tag{48}$$

and all eigenvalues have negative real part whenever $\rho > 1$.

5.1.5 EXTENSION 2

In the case that $\sigma = 10$, $\rho = 28$ and $\beta = 3$ the eigenvalues relating to $(0,0,0)$ are

$$\lambda_1 \approx -22.8, \quad \lambda_2 \approx 11.8 \quad \lambda_3 = -3. \tag{49}$$

So the state is unstable. The non-zero steady states are $(\pm 9, \pm 9, 27)$, the accompanying eigenvalues are

$$\lambda_1 \approx -14.1, \quad \lambda_2 \approx 0.04 + 10.7I \quad \lambda_3 = 0.04 - 10.7I. \tag{50}$$

Thus, these states are also unstable. Normally, when all steady steady states are unstable we would expect the trajectory to tend to infinity along one of the coordinates, creating a singularity. However, the trajectories in these simulations are always bounded, thus, they cannot escape to infinity. Equally, they can not oscillate around one of the critical point because otherwise it would be a centre and not unstable. Thus, something more complicated must be occurring. Namely, chaos!