Problem sheet 5

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1 Squirrels

Figure 1: Squirrels do not like each other.

Grey, G, and red, R, squirrel populations undergo the following interactions:

- Grey squirrels are born at a rate proportional to their population, where the proportionality constant is b_1.
- Red squirrels are born at a rate proportional to their population, where the proportionality constant is b_2.
- Both squirrel populations compete internally with members of their own population (*i.e.* grey compete with grey and red compete with red, respectively). Namely, whenever two members of the same population interact one of the members is suppressed. The constant of proportionality is d_1 for the grey squirrels and d_2 for the red squirrels.
- The squirrels also compete across species. Namely, a grey and a red squirrel interaction can lead to a reduction in red squirrels, or a reduction in grey squirrels. The rate of proportionality for the reduction of grey squirrels is c_1, whilst the rate of proportionality for the reduction of red squirrels is c_2.

1. Write down the interaction equations specified by the above description.

   Hint: You should create six equations over all and they should be symmetric in G and R (*i.e.* if you swap G and R the dynamics should be the same).

2. Show that the interaction equations lead to the following ODEs

$$\dot{G} = b_1 G - d_1 G^2 - c_1 RG, \quad (1)$$
$$\dot{R} = b_2 R - d_2 R^2 - c_2 RG. \quad (2)$$

3. What are the dimensions of b_1, b_2, d_1, d_2, c_1 and c_2 in terms of density and time?
4. Non-dimensionalise the system to produce the following equations

$$\frac{\mathrm{d}u}{\mathrm{d}\tau} = u(1 - u - \alpha_{12}v), \tag{3}$$

$$\frac{\mathrm{d}v}{\mathrm{d}\tau} = \rho v(1 - v - \alpha_{21}u). \tag{4}$$

   Specify the population scales and the time scales and show that the scales have the appropriate dimensions.
5. What are the parameter groupings ρ, α_{12} and α_{21} in terms of b_1, b_2, d_1, d_2, c_1 and c_2? Show that ρ, α_{12} and α_{21} are dimensionless.
6. Find all steady states of the system, noting any parameter dependencies that need to be satisfied for the steady state to exist.
7. Calculate the stability of the trivial steady states. Namely, those in which one of the populations is zero, noting parameter dependencies of the stability criterion.

   Calculating the stability of the fourth steady state,

$$(u_s, v_s) = \frac{1}{1 - \alpha_{12}\alpha_{21}}(1 - \alpha_{12}, 1 - \alpha_{21}), \tag{5}$$

   leads to a complicated eigenvalue calculation and we will use curve sketching in the next question to consider the stability of this steady state.

   Hint: you should find there are four cases:

   (a) $\alpha_{12} < 1$ and $\alpha_{21} < 1$;
   (b) $\alpha_{12} < 1$ and $\alpha_{21} > 1$;
   (c) $\alpha_{12} > 1$ and $\alpha_{21} < 1$;
   (d) $\alpha_{12} > 1$ and $\alpha_{21} > 1$.
8. Sketch the (u, v) phase plane in each of the cases (a)-(d). You should include: the nullclines; annotations regarding the signs of $\mathrm{d}u/\mathrm{d}\tau$ and $\mathrm{d}v/\mathrm{d}\tau$ in each region delineated by the nullclines; accompanying directional arrows in each region; directional arrows on the nullclines; and, finally, trajectories illustrating the expected evolution with initial conditions taken from each region.

   Use these sketches to determine the stability of (u_s, v_s), when it exists.
9. Describe what happens to the grey and red squirrels in each of the cases (a)-(d).

1.1 Answers

1.1.1

$$G \underset{d_1}{\overset{b_1}{\rightleftarrows}} 2G, \quad G + R \xrightarrow{c_1} R. \tag{6}$$

$$R \underset{d_2}{\overset{b_2}{\rightleftarrows}} 2R, \quad G + R \xrightarrow{c_2} G. \tag{7}$$

1.1.2

Using the Law of Mass Action on the interactions equations shown in answer 1.1.1 we get the given equations.

1.1.3

$\dim(b_1) = \dim(b_2) = 1/\text{time}$.
$\dim(d_1) = \dim(d_2) = \dim(c_1) = \dim(c_2) = 1/(\text{time}\times\text{density})$.

1.1.4

Using $G = [G]u$, $R = [R]v$ and $t = [t]\tau$ we find that $[G] = b_1/d_1$, $[R] = b_2/d_2$, both of which have dimensions of density and $[t] = 1/b_1$, which has dimensions of time.

1.1.5

Subsequently, $\rho = b_2/b_1$, $\alpha_{12} = c_1 b_2/(d_2 b_1)$ and $\alpha_{21} = c_2 b_1/(d_1 b_2)$, which can all be seen to be dimensionless.

1.1.6

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

$$(u_s, v_s) = \frac{1}{1-\alpha_{12}\alpha_{21}}(1-\alpha_{12}, 1-\alpha_{21}). \tag{8}$$

We note that for (u_s, v_s) to exist then either $\alpha_{12}, \alpha_{21} < 1$ or $\alpha_{12}, \alpha_{21} > 1$.

1.1.7

The Jacobian of the system is

$$J(u,v) = \begin{bmatrix} 1-2u-\alpha_{12}v & -\alpha_{12}u \\ -\rho\alpha_{21}v & \rho\left(1-2v-\alpha_{21}u\right) \end{bmatrix}. \tag{9}$$

Thus,

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

The eigenvalues are the diagonal elements, which are both positive. Hence (0,0) is an unstable node.

$$J(1,0) = \begin{bmatrix} -1 & -\alpha_{12} \\ 0 & \rho(1-\alpha_{21}) \end{bmatrix}. \tag{11}$$

The eigenvalues are the diagonal elements. Hence, (1,0) is a stable node if $\alpha_{21} > 1$ and a saddle point if $\alpha_{21} < 1$.

$$J(0,1) = \begin{bmatrix} 1-\alpha_{12} & 0 \\ -\rho\alpha_{21} & -\rho \end{bmatrix}. \tag{12}$$

The eigenvalues are the diagonal elements. Hence, (0,1) is a stable node if $\alpha_{12} > 1$ and a saddle point if $\alpha_{12} < 1$.

In summary (0,0) always exists and is always unstable, (1,0) and (0,1) always exist but their stability depends on $(\alpha_{12}, \alpha_{21})$ and, finally, existence and stability of (u_s, v_s) depends on $(\alpha_{12}, \alpha_{21})$. Specifically,

(a) when $\alpha_{12} < 1$ and $\alpha_{21} < 1$ (1,0) is unstable, (0,1) is unstable and (u_s, v_s) exists, stability to be considered in the next question.

(b) when $\alpha_{12} < 1$ and $\alpha_{21} > 1$ (1,0) is stable, (0,1) is unstable and (u_s, v_s) does not exist.

(c) when $\alpha_{12} > 1$ and $\alpha_{21} < 1$ (1,0) is unstable, (0,1) is stable and (u_s, v_s) does not exist.

(d) when $\alpha_{12} > 1$ and $\alpha_{21} > 1$ (1,0) is stable, (0,1) is stable and (u_s, v_s) exists, stability to be considered in the next question.

1.1.8

From the bottom left sketch of Figure 2 we see that when $\alpha_{12}, \alpha_{21} > 1$ (u_s, v_s) is unstable, specifically, it is a saddle point. Equally, the bottom right sketch of Figure 2 shows that when $\alpha_{12}, \alpha_{21} < 1$ (u_s, v_s) is stable.

1.1.9

In this model we see four possible outcomes. In three of these cases only one of the populations survives and exists at the expense of the other, *i.e.* the red squirrel population survives, but the grey squirrel population dies out. Only in the case that $\alpha_{12}, \alpha_{21} < 1$ are both populations able to live together. In ecology this concept is called competitive exclusion. It suggests that two species competing for exactly the same resources cannot stably coexist. One of the two competitors will always have an ever so slight advantage over the other that leads to extinction of the second competitor in the long run (or evolution into distinct ecological niches).

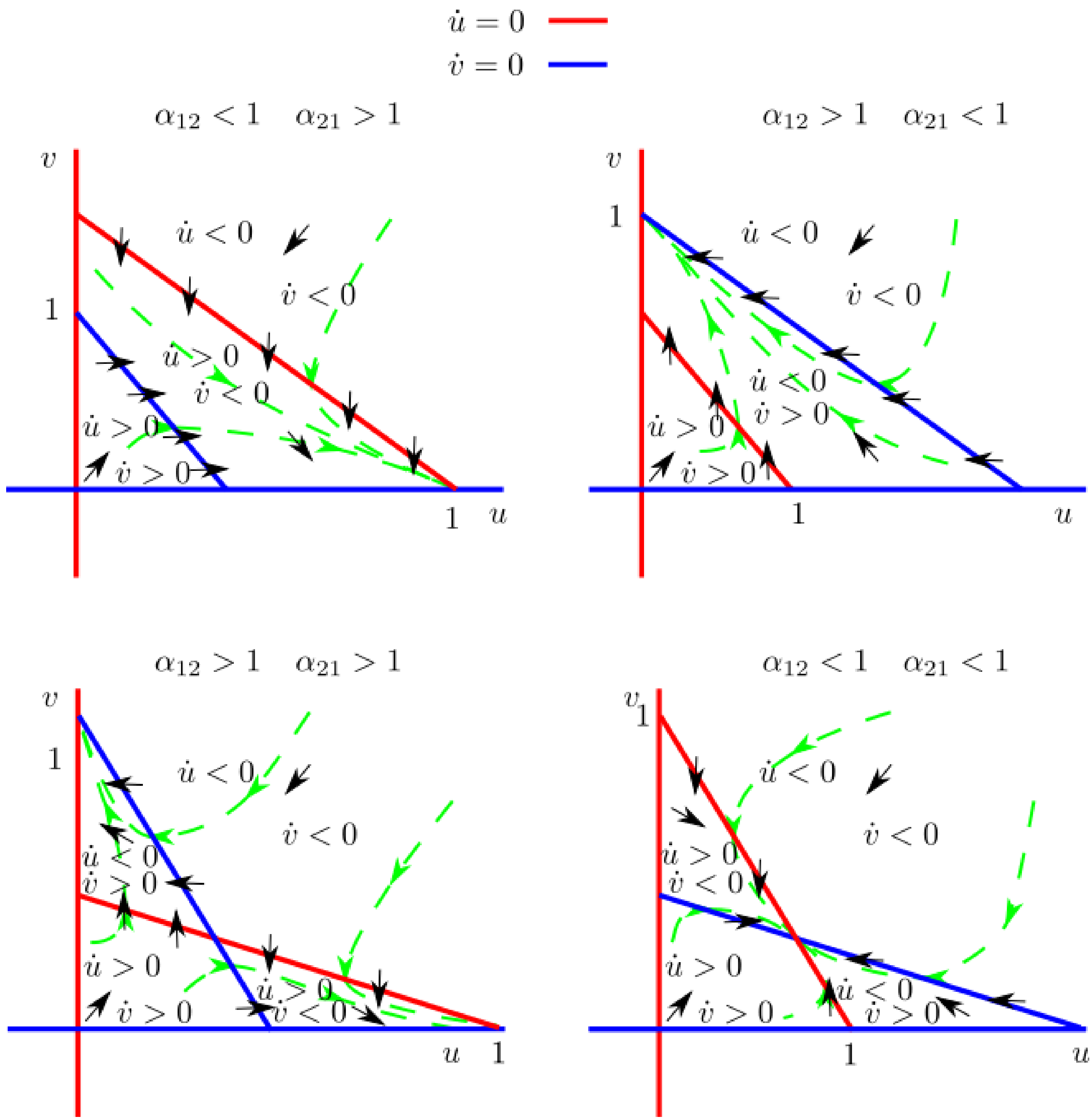

Figure 2: Phase planes in all possible configurations.

2 Fitzhugh-Nagumo

In 1952 Alan Hodgkin and Andrew Huxley developed the first quantitative model of the propagation of an electrical signal along a squid giant axon. They received the 1963 Nobel Prize in Physiology or Medicine for this work. Fitzhugh and Nagumo simplified this work and showed how the essentials of the excitable process could be distilled into a simpler model, which is analytically tractable.

Let v be membrane voltage potential (note this can go negative) and let n be the cellular recovery variable. The non-dimensional equation controlling voltage spikes in a nerve are given by

$$\epsilon\dot{v} = v(0.5 - v)(v - 1) - n, \tag{13}$$
$$\dot{n} = v - \gamma n, \tag{14}$$

where γ and ϵ are positive.

1. Derive the steady states noting any parameter restrictions.
2. Assume $\gamma < 16$, characterise the stability of any steady states that exist.
3. Draw, with as much detail as possible, the (v, n) phase diagrams in the $\gamma < 16$ case.

2.1 Answers

2.1.1

The steady states are $(0, 0)$ and (v_s, n_s), where $n_s = v_s/\gamma$ and

$$v_s = \frac{3\gamma \pm \sqrt{\gamma^2 - 16\gamma}}{4\gamma}. \tag{15}$$

The steady states (v_s, n_s) only exist when $\gamma > 16$.

2.1.2

The Jacobian is

$$J(v, n) = \begin{bmatrix} \frac{6v-6v^2-1}{2\epsilon} & -\frac{1}{\epsilon} \\ 1 & -\gamma \end{bmatrix}. \tag{16}$$

In the case of $\gamma < 16$ only $(0, 0)$ exist and, so,

$$J(0, 0) = \begin{bmatrix} -\frac{1}{2\epsilon} & -\frac{1}{\epsilon} \\ 1 & -\gamma \end{bmatrix}. \tag{17}$$

The trace of J is negative, whilst the determinant is positive, therefore, $(0, 0)$ is stable.

2.1.3

The $\gamma < 16$ phase plane is shown in Figure 3. Since $1/\gamma$ is the gradient of the n nullcline increasing γ corresponds to lowering the n nullcline. Thus, in the case that $\gamma > 16$ the line will cut the cubic three times. Further, in this case, the phase plane will suggest that the two extreme steady states are stable, but the middle one is unstable.

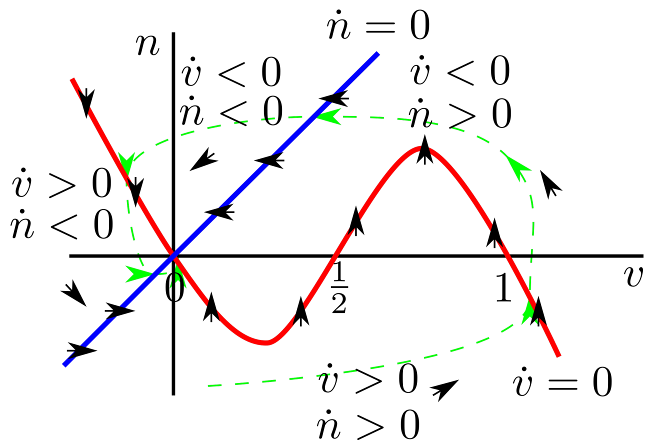

Figure 3: Phase planes, directions and possible trajectory.

3 Computer simulation

Simulate equations (13) and (14) with parameters $\gamma = 2$ and $\epsilon = 0.001$. Specifically, plot the trajectories in the (v, n) space along with the nullclines. Further, initialise the trajectories near the $(0, 0)$ steady state but with negative v initially. Hint: for this simulation you will have to use a 'stiff' solver. Matlab's standard solver is `ode23s`.

1. What happens to the trajectories (see Figure 4)?
2. Why is this weird?
3. What happens when you increase γ?
4. Suppose we have a trajectory that starts at the origin and we increase γ past 16 and then lower it again. Could this model exhibit hysteresis?

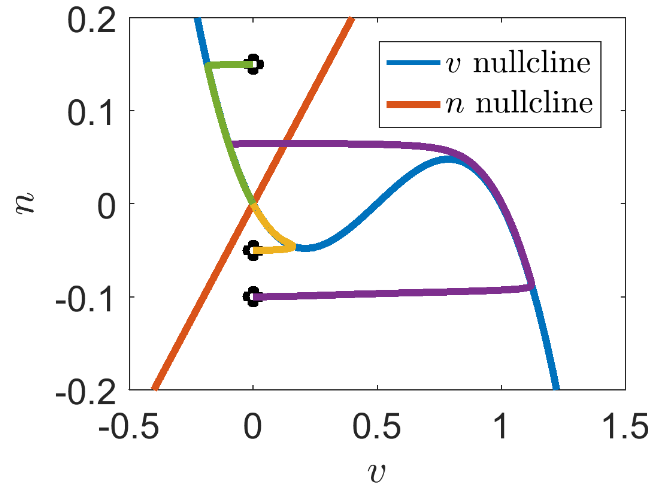

Figure 4: Simulation of equations (13) and (14) with parameters $\gamma = 2$ and $\epsilon = 0.001$.

3.1 Answers

3.1.1

Trajectories with a small perturbation head back to zero. If the perturbation sends v negative enough then the trajectory takes a long excursion towards the v nullcline before heading back to (0,0).

3.1.2

Even though (0,0) is stable the trajectory takes a long time to get there. This is called a relaxation trajectory.

3.1.3

The trajectories with initial conditions below the minimum of the cubic head towards the higher steady, rather than head back to (0,0).

3.1.4

This model does not exhibit hysteresis since the lower steady state never disappears, thus, if the trajectory starts there it stays there, regardless the change in γ.

Exam revision

4 Damped pendulum

The equation of a damped pendulum is

$$\ddot{\theta} + \underbrace{\eta\dot{\theta}}_{\text{Energy loss due to air resistance}} + k\sin(\theta) = 0, \tag{18}$$

where k and η are positive constants.

1. Write the second order differential equation (18) as two first order ODEs.
2. Identify the steady states of your two variable system, noting any parameter dependencies.
3. Characterise the stability of the steady states, noting any parameter dependencies.
4. Draw the phase diagram of the system in the $(\theta, \dot{\theta})$ plane. Include nullclines, trajectory directions, stability information of the steady states and draw a number of trajectories to illustrate potential dynamics.

4.1 Answers

4.1.1

Let $v = \dot{\theta}$ then

$$\dot{\theta} = v, \tag{19}$$
$$\dot{v} = -\eta v - k\sin(\theta). \tag{20}$$

4.1.2

The steady states are $(0, n\pi)$, where n is an integer.

4.1.3

The Jacobian is

$$J(\theta, v) = \begin{bmatrix} 0 & 1 \\ -k\cos(\theta) & -\eta \end{bmatrix}. \tag{21}$$

Thus,

$$J(n\pi, 0) = \begin{bmatrix} 0 & 1 \\ -k(-1)^n & -\eta \end{bmatrix}. \tag{22}$$

The eigenvalues are

$$\lambda(n)_\pm = \frac{-\eta \pm \sqrt{\eta^2 - 4k(-1)^n}}{2}. \tag{23}$$

Thus if n is even then $Re(\lambda(n)_\pm) < 0$ and the steady state is stable. Note that it is either a node or a spiral depending on how large the damping, η, is. Namely, large damping makes the point a stable node, whilst small damping will provide a stable spiral. This coincides with our physical intuition, namely, if there is little damping the pendulum will continue to oscillate.

Alternatively, if n is odd $\lambda_- < 0 < \lambda_+$, thus, we have a saddle.

4.1.4

5 Similar systems

Consider the two following systems:

$$\dot{u}_1 = u_2, \tag{24}$$
$$\dot{u}_2 = -u_1, \tag{25}$$

and

$$\dot{v}_1 = v_1 v_2, \tag{26}$$
$$\dot{v}_2 = -v_1^2. \tag{27}$$

1. Show that the quantities of $u_1^2 + u_2^2$ and $v_1^2 + v_2^2$ are conserved across their respective systems. What does this mean?
2. Illustrate the differences between the two systems by calculating the steady states, characterising their stability and drawing the phase planes with as much information as possible.

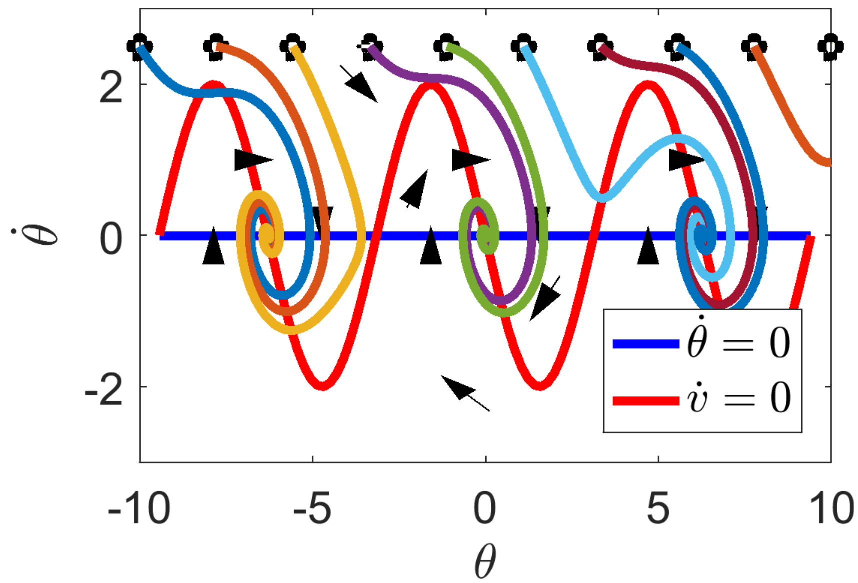

Figure 5: Phase plane of the damped pendulum equations with $\eta = 0.5$ and $k = 1$.

5.1 Answers

5.1.1

There are two ways to show that the squared sum of each set of variables is constant. Firstly, we could differentiate the sum with respect to time and substitute in the ODEs, *i.e.*

$$\frac{\mathrm{d}}{\mathrm{d}t}(u_1^2 + u_2^2) = 2u_1\dot{u}_1 + 2u_2\dot{u}_2 = 2u_1u_2 - 2u_2u_1 = 0. \tag{28}$$

Since the derivative is zero, the integral must be a constant with respect to time.

Alternatively, we can divide one equation by the other and integrate the resulting equation,

$$\frac{\dot{v}_1}{\dot{v}_2} = \frac{\mathrm{d}v_1}{\mathrm{d}v_2} = -\frac{v_2}{v_1}. \tag{29}$$

Separating the derivative we find that

$$\int_0^{v_1} v_1' \, \mathrm{d}v_1' = -\int_0^{v_2} v_2' \, \mathrm{d}v_2', \tag{30}$$

namely $v_1^2 + v_2^2 =$constant.

This means that however u_1 and u_2, or v_1 and v_2 evolve, they must always satisfy the equation of a circle, which will be determined by the initial conditions. Thus, the trajectories of (u_1, u_2) and (v_1, v_2) prescribe circles.

5.1.2

In each case (0,0) is a steady state. In the second case $(0, v)$ is also a steady state for all values of v. The Jacobian for each case is

$$J(u_1, u_2) = \left[\begin{array}{cc} 0 & 1 \\ -1 & 0 \end{array}\right], \tag{31}$$

and

$$J(v_1, v_2) = \left[\begin{array}{cc} v_2 & v_1 \\ -2v_1 & 0 \end{array}\right]. \tag{32}$$

In the first case the eigenvalues of (0,0) are $\pm I$, thus, it is a centre. In the second case J the eigenvalues of $(0, v)$ are 0 and v. Thus, if $v > 0$ the state is unstable and if $v \leq 0$ the stability cannot be determined through linearisation as 0 is an eigenvalue. However, we know that (v_1, v_2) must always lie on a circle and from equation (27) we can see that v_2 is always decreasing. The minimum value it can obtain is at the bottom of the circle $v_1^2 + v_2^2 =$constant$= v_1(0)^2 + v_2(0)^2$ (where we are specifying that the constant depends on the initial condition), *i.e.* when $v_1 = 0$, which causes the system to stop evolving. Thus, all trajectories will evolve to $(0, v_2)$, where $v_2 = -\sqrt{v_1(0)^2 + v_2(0)^2}$.