MTH1003 Mathematical Modelling

Group project III: Population Dynamics

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Introduction

In this project, we studied the dynamics of the populations of two different species of squirrels, reds and greys, which inhabit the same ecosystem and compete for resources. We modelled the populations, represented by r(t) and g(t) with suitably scaled units, using a Lotka - Volterra model and used a variety of numerical and analytical methods to analyse the behaviour of the species under different conditions.

1 Conservation

1.1 Classification of equilibrium points

To start with, we model the populations of red and grey squirrels using the Lotka- Volterra model;

$$\dot{r} = r(1-g), \quad \dot{g} = g(2-r). \tag{1}$$

By setting both derivatives equal to 0 and solving the equations simultaneously, we found that this system has 2 equilibrium points; (0,0) and (2,1). To classify these equilibrium points we consider the Jacobian matrix, A for this system;

$$A = \begin{pmatrix} \dot{r}_r & \dot{r}_g \\ \dot{g}_r & \dot{g}_g \end{pmatrix} = \begin{pmatrix} 1-g & -r \\ -g & 2-r \end{pmatrix}$$

At the point (0,0):

$$A = \begin{pmatrix} 1 & 0 \\ 0 & 2 \end{pmatrix}$$

The eigenvalues of this matrix are 1 and 2. As both eigenvalues are real and positive, we can classify the equilibrium point at (0,0) as an unstable improper node.

At the point (2,1):

$$A = \begin{pmatrix} 0 & -2 \\ -1 & 0 \end{pmatrix}$$

The eigenvalues of this matrix are -2 and 2. As both eigenvalues are real but have opposite signs, the equilibrium point at (2,1) is a saddle, and therefore unstable.

1.2 Conserved quantity

In order to find a conserved quantity for this system, we considered dg/dr and integrated to produce a constant function.

$$\frac{dg}{dr} = \frac{\dot{g}}{\dot{r}} = \frac{g(2-r)}{r(1-g)}$$

$$\frac{dg}{dr}\frac{(1-g)}{g} = \frac{2-r}{r}$$

$$\int \frac{(1-g)}{g}\frac{dg}{dr}\,dr = \int \frac{2-r}{r}\,dr$$

$$log(g) - g = 2log(r) - r + C$$

$$e^{r-g+C} = \frac{r^2}{g}$$

$$e^C = \frac{r^2}{g}e^{g-r}$$

$$\frac{r^2}{g}e^{g-r} = B$$

For C and B constants.

Since B is a constant, the function C(r,g) = $\frac{r^2}{g}e^{g-r}$ is constant for all r, g. Hence the function C(r,g) is conserved in the system.

1.3 Time Stepping

We can use the forward Euler time integration scheme to approximate a solution for this system using a time step of 0.1.

We can graph C(t) for this numerical solution and observe that for the first five units of time, C stays relatively constant. In the last unit of time, C deviates significantly.

We are aiming to get a solution that does a better job at conserving C; so we attempt another version of this time step with a smaller value of $\Delta(t)$, $\Delta(t) = 0.01$. We notice the smaller the value $\Delta(t)$ is, the more constant C stays. The goal is to have a C that has a relative change less than 0.001 at the final time, so choosing $\Delta(t) = 0.005$ suffices to achieve this.

Figures 1 and 2 contain the plots showing $\Delta(t) = 0.1$ and $\Delta(t) = 0.005$ respectively. Equilibrium points (0,0) and (2,1) are shown on the plots.

The relative change of C is approx. 1.3; i.e., by the end of the time interval, the C value has more than doubled. However, up until roughly t = 5, the C value stays constant and only increases in the last interval of time. Thus, C is mostly conserved for most of the trajectory but not at the end.

The slope field has a bifurcation at (2,1). For our trajectory to end up on the correct side of this bifurcation, we need a very small-time step; i.e., 0.005. Simply using a time step of 0.1 results in the trajectory ending up on the wrong side.

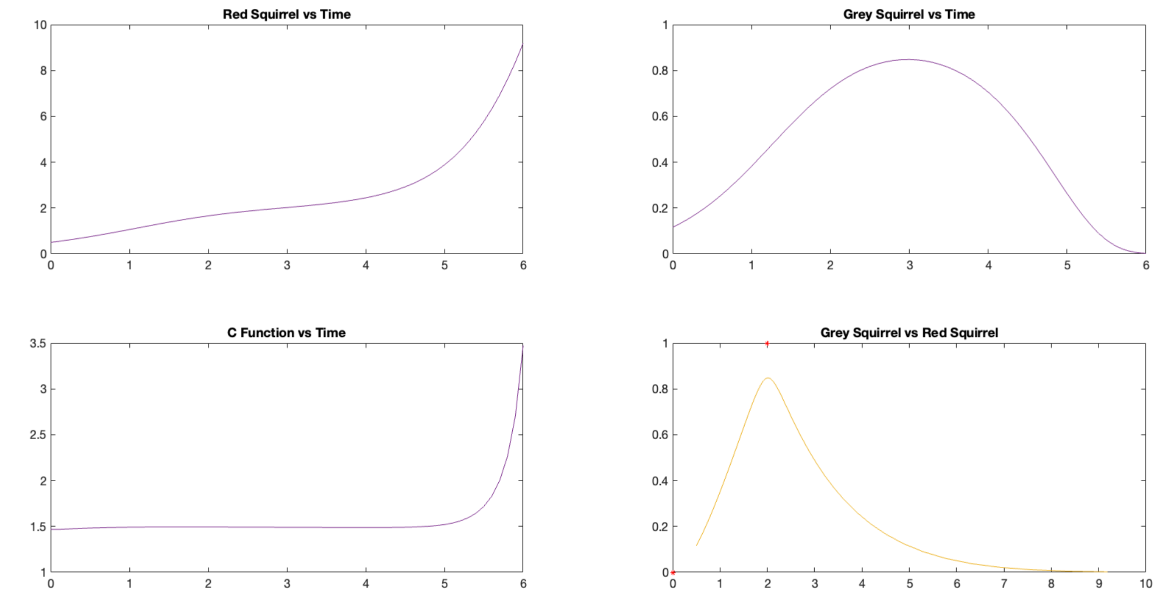

Figure 1: Graph showing time stepping when $\Delta(t) = 0.1$

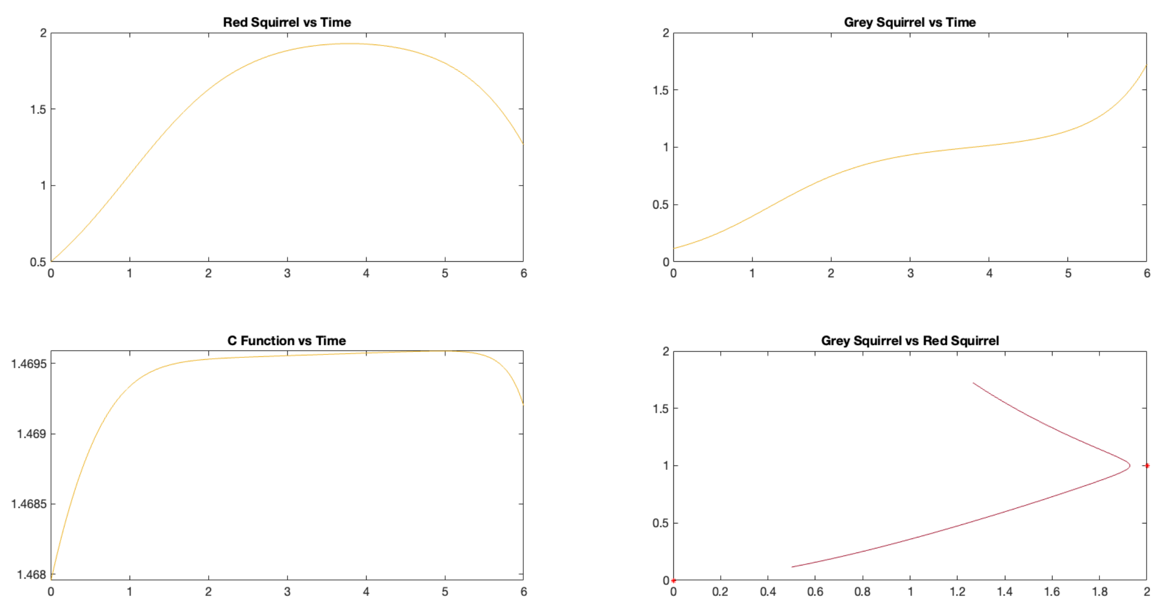

Figure 2: Graph showing time stepping when $\Delta(t) = 0.005$

2 Stable and unstable manifolds

We consider the equilibrium point (2, 1) and we try to find its manifolds.

By finding the eigenvalues of A at (2, 1), we calculated that the direction the unstable manifold leaves the saddle to be $\begin{pmatrix} \sqrt{2} \\ -1 \end{pmatrix}$ and the direction the stable manifold leaves the saddle is $\begin{pmatrix} \sqrt{2} \\ 1 \end{pmatrix}$.

By choosing the point (2.01, 0.99) and running the time-stepping code, the line we plotted numerically leaves the equilibrium point (2, 1). The same event occurs when we choose the point (1.99, 1.01). We chose these points because they are close to the saddle and in the direction of the vector we calculated. The curve we get for the unstable manifold is shown in blue on Figure 3. It seems to agree with linear stability theory.

To estimate the stable manifold, we chose the points (2.01, 1.01) and (1.99, 0.99). We made this work by making our code step 'back in time', and the curves we obtained are shown in green on Figure 3. This agrees with the linear stability analysis once again as the general direction of the stable manifold which we found by hand.

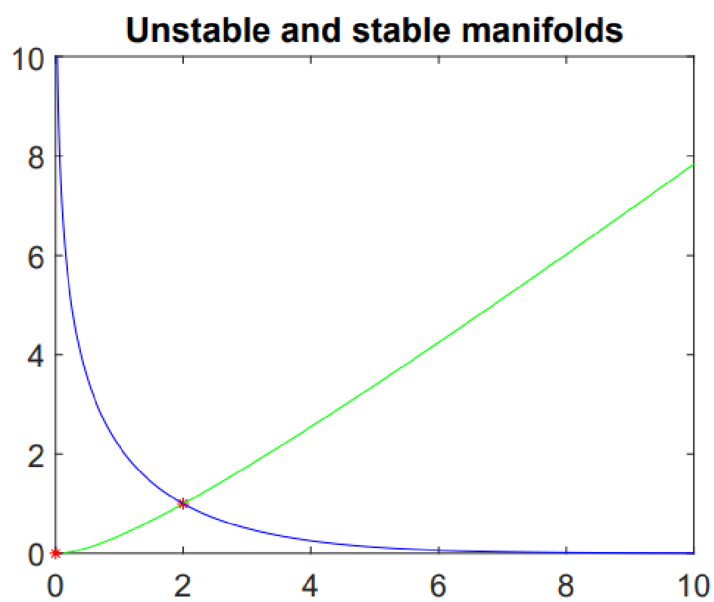

Figure 3: Numerical representation of the unstable and stable manifolds

3 Nullclines and equilibria

We now consider the extended Lotka–Volterra model for red and grey squirrels;

$$\dot{r} = r(1 - r - g), \quad \dot{g} = g(a - r - bg), \tag{2}$$

with a = 2 and b = 3

Nullclines are curves on which the first derivative of r and g equals zero. When $\dot{r} = 0$ motion is purely in the g-direction (vertical) and when $\dot{g} = 0$ motion is purely in the r-direction (horizontal) The r and g nullclines of this system can be found by setting (2) to zero, which produces the following four equations:

r = 0 or r = 1 − g and g = 0 or r = 2 - 3g

Equilibrium points are where $\dot{r}$ nullclines intersect $\dot{g}$ nullclines. By solving the equations simultaneously, we found there were four equilibrium points; (0,0), (0,2/3), (1,0), (1/2,1/2). These are shown in Figure 4.

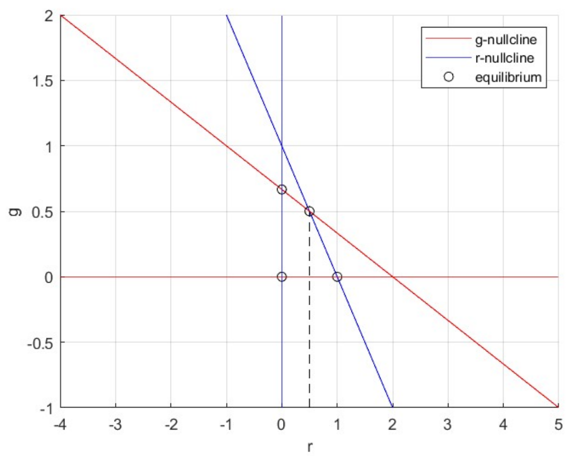

Figure 4: A graph of the nullclines of the system, with their equilibrium points indicated by circles.

We linearise the system by calculating the Jacobian matrix which is a matrix of first order partial derivatives of the system.

$$A = \begin{pmatrix} \dot{r_r} & \dot{r_g} \\ \dot{g_r} & \dot{g_g} \end{pmatrix} = \begin{pmatrix} 1 - 2r - g & -r \\ -g & 2 - r - 6g \end{pmatrix}$$

Finding eigenvalues: We use the Jacobian matrix at the corresponding equilibrium point and can use the following equation det | A - λI| = 0

At the point (0,0):

$$A = \begin{pmatrix} 1 & 0 \\ 0 & 2 \end{pmatrix}$$

λ = 1, 2 The eigenvalues are different real and positive and hence can be classified as an unstable improper node.

At the point (0, 2/3):

$$A = \begin{pmatrix} 1/3 & 0 \\ -2/3 & -2 \end{pmatrix}$$

λ = -2, $\frac{1}{3}$ Both the eigenvalues are real but have opposite signs and hence can be classified as a saddle which is therefore unstable.

At the point (1,0):

$$A = \begin{pmatrix} -1 & -1 \\ 0 & 1 \end{pmatrix}$$

λ = -1, 1 Both the eigenvalues are real but have opposite signs and hence can be classified as a saddle which is therefore unstable.

At the point (1/2, 1/2):

$$A = \begin{pmatrix} -1/2 & -1/2 \\ -1/2 & -3/2 \end{pmatrix}$$

$\lambda = \frac{1}{2}(-2-\sqrt{2})$, $\frac{1}{2}(\sqrt{2}$ - 2) The eigenvalues are different, real and negative and hence can be classified as a stable improper node.

4 Ecosystem management

4.1 The effect of decreasing the parameter b

Using the extended Lotka- Volterra model (2), initially the parameters a and b are 2 and 3 respectively. Notably, the system has a stable equilibrium point at (0.5, 0.5). The determinant-trace diagram in Figure 5 shows that this point (represented by the square) is a stable improper node.

We model the effect of environmental change by decreasing the parameter b. Figure 5 shows how the model behaves as you start to decrease b. It shows that the stable equilibrium point moves towards the vertical axis, implying that the stable equilibrium will occur when the population of red squirrels is small in comparison to the population of greys.

Eventually, as parameter b approaches 2, the stable equilibrium reaches the axis as shown in Figure 5, which means that the system is only stable when the population of red squirrels is zero. We can see in the determinant-trace diagram the square is on the axis between a saddle and a node. Hence below the critical value of b = 2, the point becomes a saddle which is unstable and therefore the stable equilibrium of co-existing reds and greys ceases to exist.

4.2 Changing the parameter a

In order to offset the effect of decreasing the parameter b, ecosystem managers can alter conditions to change the value of the parameter a. As shown in Figure 6, decreasing the value of a, creates a stable equilibrium of co-existing reds and greys which had ceased to exist as b was decreased. As the value of a approaches 1.5, the system has a stable equilibrium with roughly equal populations of reds and greys as shown in Figure 6. However, if they decrease the value of a below 1.5, the population of greys at which the stable equilibrium occurs will be very small in comparison to the population of reds. As shown in Figure 7, when the value of a approaches 1, the stable equilibrium of co-existing reds and greys ceases to exist.

We saw that with the parameter b equal to 2, the ecosystem managers will be able to alter the conditions to change the value of a in a way which will result in restoring the stable equilibrium. However, if the value of b is less than or equal to 1, the stable equilibrium could only occur if the populations had a negative value, which is not possible. Hence, if the value of b is below 1, the ecosystem managers are unable to save the system. Figure 8 shows an example of a system with b = 0.5, we can see from the phase plane plot that all the trajectories are all tending towards infinity parallel to the grey axis. This means that the population of grey squirrels would increase exponentially whilst the red squirrels would die out no matter what environmental changes were made.

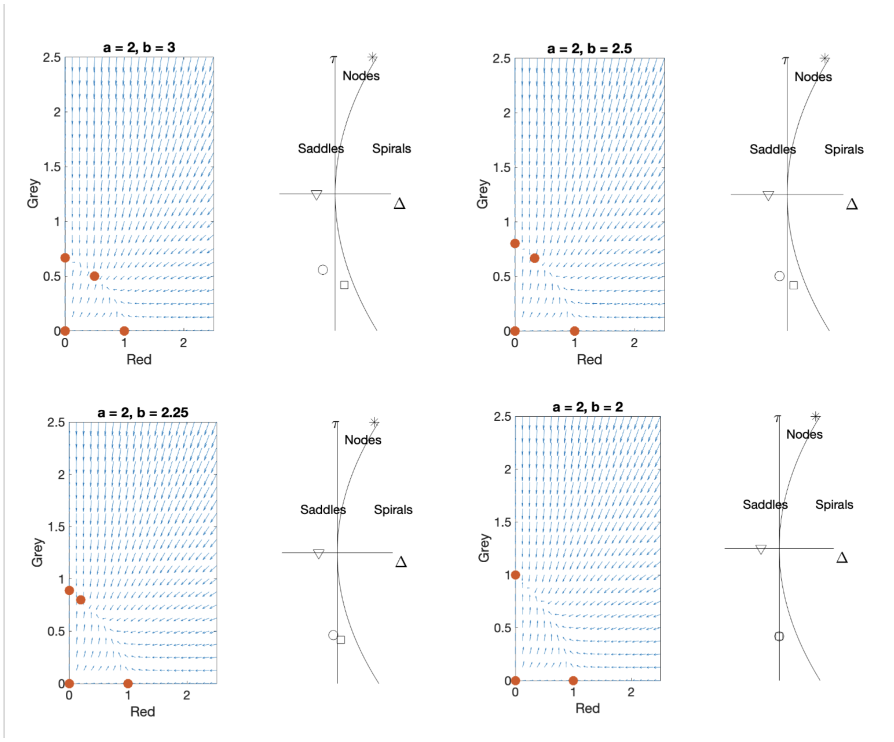

Figure 5: Phase plane plots and determinant-trace diagrams as the parameter b decreases, with parameter a = 2

5 Red and grey squirrels in the real world

5.1 Background

Red squirrels have lived in the UK for around 10,000 years and are our native species of squirrel. Grey squirrels were brought from North America in the 1800s. Greys compete for food, habitat, and resources much more successfully than reds, and therefore both species cannot coexist in the long term. [1] Red squirrels also live throughout Ireland, western Europe, Russia, Mongolia, and northwest China. [2]

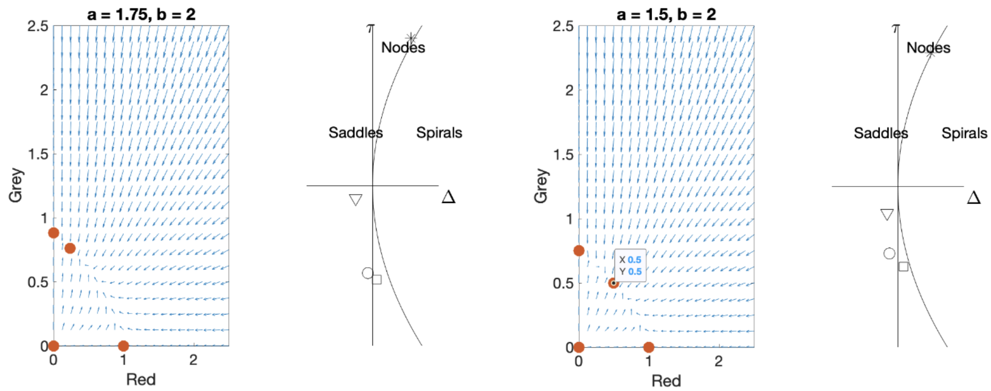

Figure 6: Phase plane plots and determinant-trace diagrams as the parameter a decreases, with parameter b = 2

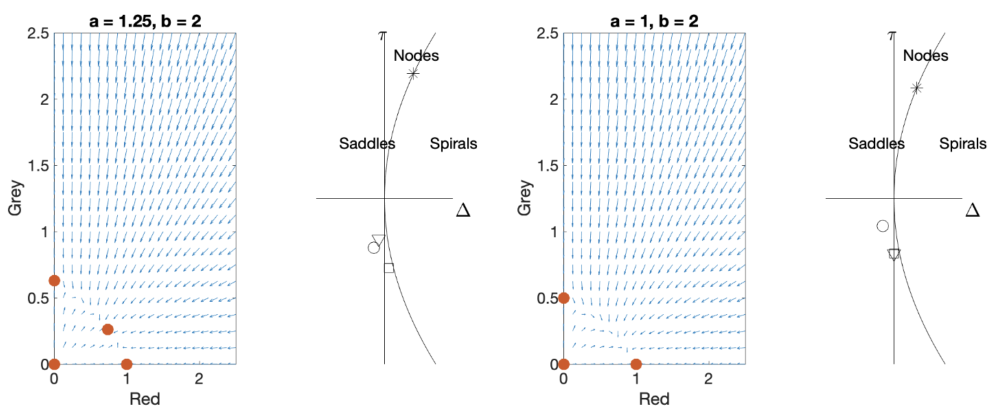

Figure 7: Phase plane plots and determinant-trace diagrams as the parameter a is decreased beyond 1.5, keeping b = 2

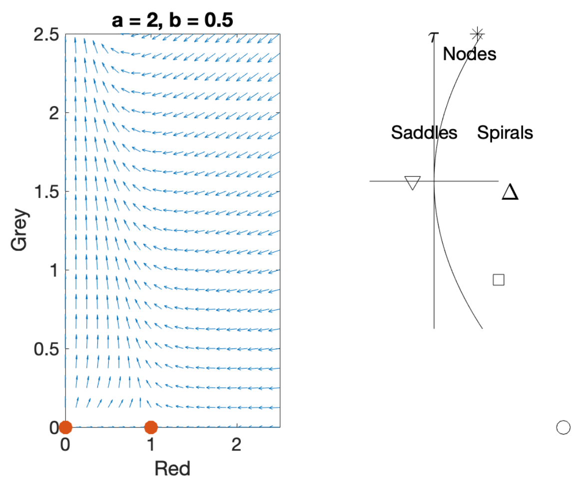

Figure 8: Phase plane plots and determinant-trace diagrams with the parameters a = 2, b = 0.5

5.2 Factors omitted from the model

A real-world factor not included in our Lotka-Volterra model is the impact of Squirrelpox Virus (SQPV). SQPV is carried by grey squirrels, without affecting their health, however often kills red squirrels. Once infected, red squirrels are unable to see or feed properly, leading them to die of starvation or dehydration. [1] Considering the effect of squirrel pox on red squirrels, we could improve the model by adding a parameter before the g variable in the $\dot{r}$ equation, to reflect the virus's harm to reds, and lack thereof to greys.

Another important real-world factor is loss of habitat, especially over the last century. Land development can separate areas of woodland inhabited by red squirrels, leading to isolated areas unable to sustain wildlife effectively. This is made worse as grey squirrels already compete more successfully for habitat, a now limited resource, forcing red squirrels into other areas where it's more difficult to survive. [1] The Lotka- Volterra model can't take into account unpredictable events like sudden loss of habitat which would have huge impacts on the squirrel populations, especially the reds.

Environmentalists are working to keep the density of grey squirrels low in certain areas, to aid the survival of red squirrels. One example is The Wildlife Trusts, who manage red squirrel habitats and control grey squirrels in areas where red squirrels are at risk of extinction. [1]

Another example is The Woodland Trust, who work to develop long-term conservation strategies to encourage reds and deter greys. These include monitoring and controlling grey squirrels, helping landowners to improve habitats for squirrels, and planting trees to reconnect areas of woodland. They are also supporting research by The University of Exeter into how pine martens can help to control numbers of grey squirrels, and therefore help restore red squirrel populations. [2]

The aid given by such organisations could be represented by the changing of the parameter a in section 4, i.e. artificially controlling the baseline exponential growth of grey squirrels in certain areas.

A final factor is pine martens, a predator that targets grey squirrels over red squirrels. As red squirrels are native to the UK, they evolved alongside pine martens for thousands of years, meaning they are less affected than greys, who have been in the UK for less than 200 years. In some areas, pine marten populations are seen to be growing, consequently, these areas see a decline in grey squirrels, which is good for reds. [3] Adding in a factor to account for a predator, such as pine martens that affect one competitor more than the other, would improve the population model.

6 Bibliography

[1] Wildlife Trusts: Red squirrels. Retrieved March 15, 2023 from

https://www.wildlifetrusts.org/saving-species/red-squirrels

[2] Woodland Trust: Red Squirrel Facts. Retrieved March 15, 2023 from

https://www.woodlandtrust.org.uk/blog/2018/11/red-squirrel-facts/

[3] Forestry England: The return of pine martens to England's forests. Retrieved March 17, 2023 from

https://www.forestryengland.uk/blog/the-return-pine-martens-englands-forests

7 Appendix

7.1 Section 1 - Conservation

```
clear

% Derivative function of red squirrel and grey squirrel and a function for
% C

DR = @(r,g) r*(1-g) ;

DG = @(r,g) g*(2-r) ;

CF = @(r,g) (((r^2)/g)*exp(g-r)) ;

% Initial conditions for squirrels and c function

r(1) = 0.5 ;
g(1) = 0.116 ;
t(1) = 0 ;
c(1) = CF(r(1),g(1)) ;

% Size of time step

DT = 0.1    ;  % Make DT = 0.005 to achieve a cChange < 0.001

% Ending time and number of steps

tstop = 6    ;

nstop = round(tstop/DT);


% Forward Euler Time Integration Scheme


for n = 1:nstop

    % step
    t(n+1) = t(n) + DT;
    r(n+1) = r(n) + DT*DR(r(n),g(n)) ;
    g(n+1) = g(n) + DT*DG(r(n),g(n)) ;
    c(n+1) = CF(r(n),g(n))    ;

      subplot(2,2,1)
    plot(t,r)
    title('Red Squirrel vs Time','Fontsize',16)
    set(gca,'Fontsize',16)
    hold on

    subplot(2,2,2)
    plot(t,g)
    title('Grey Squirrel vs Time','Fontsize',16)
    set(gca,'Fontsize',16)
    hold on

     subplot(2,2,3)
```

```
    plot(t,c)
    title('C Function vs Time','Fontsize',16)
    set(gca,'Fontsize',16)
    hold on

      subplot(2,2,4)
    plot(r,g)
    title('Grey Squirrel vs Red Squirrel','Fontsize',16)
    set(gca,'Fontsize',16)
    hold on

    plot(0,0,"r*")  ;

    plot(2,1,"r*")  ;

end

% Relative change of C

cChange = abs((c(nstop+1)-c(1))/c(1))   ;

disp(cChange)
```

7.2 Section 2 - Stable and unstable manifolds

```
% Finding manifolds for Q2

% Direction of unstable manifold: (sqrt2 , -1)
% Unstable manifold in blue
% Direction of stable manifold: (sqrt2 , 1)
% Stable manifold in green
clear

DR = @(r,g) r*(1-g) ;
DG = @(r,g) g*(2-r) ;
CF = @(r,g) (((r^2)/g)*exp(g-r)) ;

% Stable manifold below (2,1)
r(1) = 1.99 ;
g(1) = 0.99 ;
t(1) = 0 ;

DT = 0.005  ;
tstop = 6   ;
nstop = round(tstop/DT);

for n = 1:nstop

    t(n+1) = t(n) + DT;
    r(n+1) = r(n) - DT*DR(r(n),g(n)) ;
    g(n+1) = g(n) - DT*DG(r(n),g(n)) ;

end
plot(r,g,"g")
xlim([0 10])
ylim([0 10])
title('Unstable and stable manifolds','Fontsize',16)
set(gca,'Fontsize',16)
hold on
```

```
plot(0,0,"r*")  ;
plot(2,1,"r*")  ;

% Stable manifold above (2,1)
r(1) = 2.01 ;
g(1) = 1.01 ;

for n = 1:nstop

    r(n+1) = r(n) - DT*DR(r(n),g(n)) ;
    g(n+1) = g(n) - DT*DG(r(n),g(n)) ;

end
plot(r,g,"g")
xlim([0 10])
ylim([0 10])
hold on
% Unstable manifold below (2,1)
r(1) = 2.01 ;
g(1) = 0.99 ;

for n = 1:nstop

    r(n+1) = r(n) + DT*DR(r(n),g(n)) ;
    g(n+1) = g(n) + DT*DG(r(n),g(n)) ;

end
plot(r,g,"b")
xlim([0 10])
ylim([0 10])
hold on

% Unstable manifold above (2,1)
r(1) = 1.99 ;
g(1) = 1.01 ;

for n = 1:nstop

    r(n+1) = r(n) + DT*DR(r(n),g(n)) ;
    g(n+1) = g(n) + DT*DG(r(n),g(n)) ;

end
plot(r,g,"b")
xlim([0 10])
ylim([0 10])
hold on
```

7.3 Section 3 - Nullclines and equilibria

```
% Q3
clear, clc, close all
N=1000000;
g_lim = linspace(-1,2,N);

% r and g nullcline equations
r_null = @ (g) 1-g ;
g_null = @ (g) 2-3*g ;
```

```
for i = 1:N
r_p(i) = r_null(g_lim(i)) ;
g_p(i) = g_null(g_lim(i)) ;
end

% labelling axes and plotting nullclines
figure(1)
hold on
yline(0,'r')
xline(0,'b')
plot(r_p,g_lim,'b')
plot(g_p, g_lim, 'r')
xlabel('r')
ylabel('g')

% Finding equilibrium points
grid on
equ_1 = @ (g) g_null(g) - r_null(g) ;
eq1 = fzero(equ_1,0.5) ;
eq2 = fzero(g_null, 0.6) ;
eq3 = fzero(r_null,1) ;

% creating legends and indicating where the equilibrium points are
plot(0.5,eq1,'ok',[0.5,0.5],[-1,0.5],'k--')
plot(0,eq2,'ok')
plot(eq3,0,'ok')
plot(0,0,'ok')
legend('g-nullcline','r-nullcline','','','equilibrium')
```

7.4 Section 4 - Ecosystem management

```
function [ rdot, gdot ] = bifurcation_F( r, g, a )
%F rdot and gdot for red and grey squirell model when b = 2

rdot = r*(1 - r - g);
gdot = g*(a - r - 2 * g);

end
```

```
% Plot equilibria and phse plane flow
% for a Lotka-Volterra species competition model

% Assume parameter b is set by calling script

subplot(1,2,1)

% Number of arrows in each direction
npt = 21;

% Set region to plot
% Whole region of interest
rmin = 0; rmax = 2.5;
gmin = 0; gmax = 2.5;
% Zoom on (0,1)
%rmin = 0.0; rmax = 0.2;
%gmin = 0.9; gmax = 1.1;
% Zoom on (2,0)
%rmin = 1.9; rmax = 2.1;
%gmin = 0.0; gmax = 0.2;
```

```
% Zoom on stable node
%ne = numel(ex);
%rc = er(ne); gc = eg(ne);
%rmin = rc-0.1; rmax = rc+0.1;
%gmin = gc-0.1; gmax = gc+0.1;
rr = linspace(rmin,rmax,npt);
gg = linspace(gmin,gmax,npt);

% Compute phase plane ‘velocities’
for j = 1:npt
    for i = 1:npt
        [rdot,gdot] = bifurcation_F(rr(i),gg(j), a);
        % Scale the arrows - this is a bit empirical
        norm = sqrt(rdot*rdot+gdot*gdot);
        norm = norm^0.8;
        vr(i,j) = rdot/norm;
        vg(i,j) = gdot/norm;
    end
end


% Plot phase plane ‘velocities’
quiver(rr,gg,vr',vg')
axis([rmin,rmax,gmin,gmax])
set(gca,'FontSize',16)
title(['a = 2, b = 2.25'])
xlabel('Red')
ylabel('Grey')
hold on

% Mark equilibrium points on the quiver plot
scatter(er,eg,150,'filled')
hold off
```

```
% Plot a series of phase plane diagrams
% and delta-tau diagrams for a Lotka-Volterra
% species competition model

clear
% set b = 2
b = 2.25;

% Symbols for plotting equilibria
psyms = ['k*';'kv';'ko';'ks'];

% Plot axes for delta-tau diagram
subplot(1,2,2)
hold off
r = [-3,3]; g = [0,0];
plot(r,g,'k')
hold on
r = [0,0]; g = [-3,3];
plot(r,g,'k')
g = -3:0.02:3; r = g.*g/4;
plot(r,g,'k')
axis off
text(3.1,-0.2,'\Delta','FontSize',20)
text(-0.3,3,'\tau','FontSize',20)
text(-2,1,'Saddles','FontSize',16)
```

```
text(2,1,'Spirals','FontSize',16)
text(0.4,2.6,'Nodes','FontSize',16)

% Loopover values of the parameter b
for a = 2:-0.02:2

    % Equilibrium points - we worked these out by hand
    clear er eg
    % (0,0)
    er(1) = 0.0;
    eg(1) = 0.0;
    % (1,0)
    er(2) = 1.0;
    eg(2) = 0.0;
    % (0,a/b)
    er(3) = 0.0;
    eg(3) = a/b;
    % ((b - a)/(b - 1),(a - 1)/(b - 1))
    er(4) = (b - a)/(b - 1);
    eg(4) = (a - 1)/(b - 1);
end

    % Plot equilibrium points and phase plane velocities
    bifurcation_plotpp

    % Evaluate determinant and trace of Jacobian matrix
    % at each equilibrium point and plot; use a different
    % symbol for each one
    for ie = 1:numel(er)
        r = er(ie); g = eg(ie);
        A = [1 - 2*r - g,  -r;                ...
                        -g,  a - r - 2*b*g ];
        delta = det(A);
        tau = trace(A);
        subplot(1,2,2)
        ps = psyms(ie,:);
        plot([delta],[tau],ps,'Markersize',12)
    end
```