SysMIC Mini Project: Predator Prey Dynamics

Report

by

Matthew Ho Wai Chin
Division of Biosciences
University College London

January, 2016

Abstract

The relationship between the Canadian lynx and snowshoe hare is a classic example in the study of predator-prey dynamics. This is because the two populations fluctuate in a characteristic cyclic manner over time, making such interaction rather predictable. In this report we present a Lotka-Volterra model based on the predator-prey relationship between the two species. The model and simulations are all implemented in MATLAB. Parameter values are estimated using the central difference derivative method and the resulting cyclic behaviour mimics that exhibited by the raw data. Parametric and stability analyses have revealed the limitations of the model and that it should only be applied to simple, relatively isolated systems. For more complex systems, logistic assumptions can be employed and this will be a trade off between realism and mathematical simplicity.

Table of Contents

1 Biological system

The interaction between predator and prey is of great interest to ecologists. Studying it can reveal information useful to conserving endangered species, pest control and improve our understanding of prey-predator dynamics in shaping community structures.

The biological example presented here is an ecological system that represents the relationship between the Canadian Lynx (predator) and Snowshoe Hare (prey). The experimental data presented here are based on the annual harvest of lynx and hare pelts from 1900 to 1920 by Hudson Bay Company in the northern regions of Canada.

Year	Hare	Lynx
1900	30000	4000
1901	47200	6100
1902	70200	9800
1903	77400	35200
1904	36300	59400
1905	20600	41700
1906	18100	19000
1907	21400	13000
1908	22000	8300
1909	25400	9100
1910	27100	7400
1911	40300	8000
1912	57000	12300
1913	76600	19500
1914	52300	45700
1915	19500	51100
1916	11200	29700
1917	7600	15800
1918	14600	9700
1919	16200	10100
1920	24700	8600

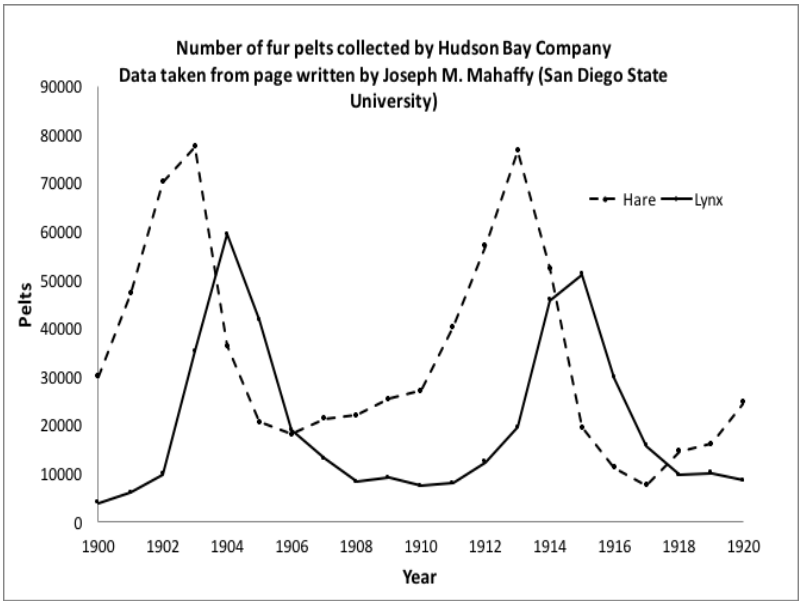

Figure 1. Raw data collected by Hudson Bay Company.

Figure 1 shows that the interaction between lynx and hare during that period of time was cyclic with a period of roughly 10 years. Also, the lynx population always peaked slightly after the hare population. The lag in population response to the changes that occured in the other species was likely due to the fact that it took time for the species to gather enough energy and reproduce. Interestingly, the cycles attracted substantial attention in the field as many ecologists had traditionally expected systems to be in equilibrium in nature.(Krebs et al. 2001)

2 Model: Lotka-Volterra

2.1 Derivation

One of the first models to describe predator-prey interaction is the Lotka-Volterra model, which was independently developed by Lotka and Volterra in the 1920s. The model describes the interaction by considering three effects – prey reproduction, predation and predator death. These processes are conceptually similar to chemical reactions by mass action. For example, a higher number of prey in the environment will lead to a higher rate of prey reproduction. This proportional relationship is analogous to how a chemical reaction becomes more likely as the number of reactant molecules in the same volume of space increases. Predation and predator death can also be modelled in a similar way. For predator death, the higher the number of predators, the more likely there is competition for food and an increase in death. The only thing that sets predation apart is that it is a bilinear relationship (predation is directly proportional to both prey and predator populations). To model these "reactions", one can start with the following:

Model

$$X \xrightarrow{k_1} 2X$$

$$X + Y \xrightarrow{k_2} 2Y$$

$$Y \xrightarrow{k_3} \emptyset$$

Here X represents a member of the prey species and Y a predator.

Here k_1, k_2 and k_3 are rate constants where k_1 = prey reproduction rate, k_2 = predation rate and k_3 = predator death rate.

From these three reactions, a stoichiometry matrix, **S**, and a rate vector, **h**, can be formed (derivations are detailed in SysMIC module 1 notes, section 2.2). Multiplying **S** and **h** gives a system of 2 first-order, nonlinear ordinary differential equations (ODEs), which form the Lotka-Volterra model.

$$\frac{dX}{dt} = k_1X - \ k_2XY$$

$$\frac{dY}{dt} = k_2XY - \ k_3Y$$

The model has been encoded in MATLAB as a function (section 3.1) that takes in parameter values for k_1, k_2 and k_3 from the simulation code (m file in section 3.2). The ecological example discussed here is the interaction between the Canadian Lynx and Snowshoe Hare and so X is renamed "Hare" and Y "Lynx" in the code.

2.2 Assumptions and Justifications

The model assumes the following:

1. Predator conversion efficiency is 100% - all of the prey energy is assimilated by the predator and turned into new predators. In other words, it only takes 1 hare for a lynx to gather enough energy to reproduce, giving 1 new lynx. This is why the predator reproduction rate is the same as the prey death/killing rate = k_2.
2. The regulation of population growth and size of the prey depends entirely on capture and consumption by the predator, hence "$-k_2XY$". This excludes any other environmental factors that might threaten the existence of the prey species, such as natural disasters or human intervention (e.g. destruction of their natural habitats).
3. The regulation of population growth and size of the predator depends entirely on the abundance of the prey, hence "k_2XY". In our context, this means the Snowshoe Hare is the sole food source of the Lynx.
4. There is an unlimited food supply for the prey.

It should be noted that these assumptions are an oversimplification of the real situation in nature and may lead to unrealistic models in some ecological contexts. This is because many other natural and artificial factors play a critical role in determining the time evolution of species populations – climate, geographical location, natural disasters and multiple species (instead of only two in our model) may contribute to various extents.

However, some systems do come close to the situation described by the assumptions. These systems tend to be isolated with predation as the sole population regulator, hence environmental factors do not have as great an influence. An example of such system is the lynx-hare interaction in northern Canada, where the hare has an ample food supply and the lynx heavily relies on snowshoe hares as a food source.

By capturing these dominant factors for our system of interest and minimising difficult-to-calculate parameters such as climate, we argue that these assumptions are reasonable for the model.

2.3 Parameter fitting

Parameter values (k_1, k_2 and k_3) for the ODEs are needed in order to run the simulation. The central difference method is employed to estimate the values such that the model mimics the raw data obtained by Hudson Bay Company. The central difference is chosen as it has a higher accuracy than asymmetrical approximation schemes (forward difference and backward difference).(Jain & Sheng 2010) To implement this approach, the ODEs are first forced into the form y = mx + c, where y and x are variables, m is the slope and c is the y-intercept:

Prey:	Predator:
$\frac{dX}{dt} = k_1X - k_2XY$	$\frac{dY}{dt} = k_2XY - k_3Y$
$\frac{1}{X}\frac{dX}{dt} = k_1 - k_2Y$	$\frac{1}{Y}\frac{dY}{dt} = k_2X - k_3$

By treating $\frac{1}{X}\frac{dX}{dt}$ as the "y" in "y = mx + c", k_2 becomes the slope and k_1 becomes the y-intercept. Similarly for $\frac{1}{Y}\frac{dY}{dt}$, k_2 is the slope and k_3 is the y-intercept.

Using central difference approximation, the first order derivative $\frac{dX}{dt}$ becomes $\frac{X(t+h)-X(t-h)}{2h}$, where h = 1 as the data were collected on an annual basis. Due to the fact that this approximation method requires data from the year before (t + h) and after (t – h) the sampling point, the calculation is carried out for each year only from 1901 to 1919 inclusive. This has been encoded within a for-loop in the simulation code (section 3.2: model parameter estimation).

Linear regression is performed on $\frac{1}{Y(t)}\frac{Y(t+h)-Y(t-h)}{2}$ $\left(\text{which is } \frac{Hare\ population\ growth\ rate}{Hare\ population}\right)$ versus X (Hare population) using MATLAB's inbuilt function `polyfit`, yielding the slope (k_2) and the y-intercept (k_3). `polyval` is also included in the code as an option for graphical visualisation (figure 2). The same procedure can be repeated for $\frac{1}{X(t)}\frac{X(t+h)-X(t-h)}{2}$ to obtain k_1. The estimated parameter values are then fed into the model for simulation.

The estimated parameters using central difference derivative approximation are k_1 = 0.4732, k_2 = 0.0234 and k_3 = 0.7646. (see section 4 for simulations)

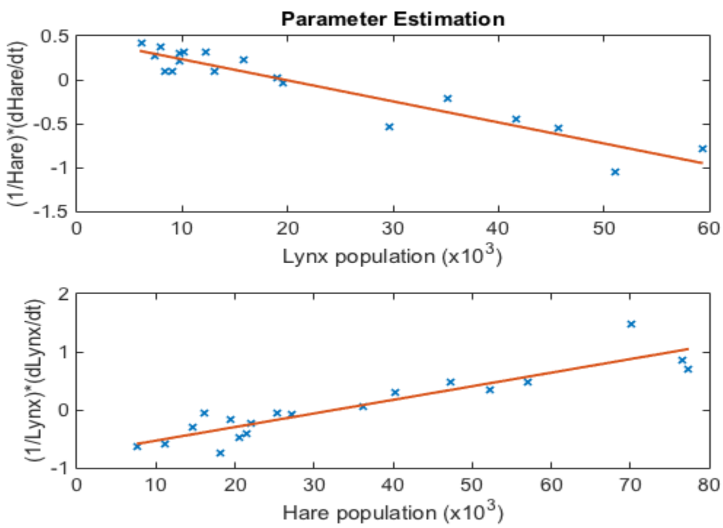

Figure 2. Plots to visualise the linear regression implemented to estimate the parameter values.

3 Code listings

3.1 Model code

```
function dx = lotka_volterra(t,x)
% Function to simulate a 3-parameter Lotka-Volterra model with
% exponential growth assumption

% Inputs:
%   t - time: unused variable as the first derivatives in the system
%       are time independent
%   x - vector containing populations of predator x(1) and prey x(2)
% Output:
%   dx - rate of change of the populations

%-------------- Grant access to global parameters--------------%
% k1 = prey birth rate
% k2 = predation/predator reproduction rate
% k3 = predator death rate
global k1 k2 k3

%------------------ ODEs ------------------%
% Definition of the ODEs
% x(1) = Number of hares
% x(2) = Number of lynx

% define ODEs
dx = [0;0];
dx(1) = k1 * x(1) - k2 * x(1) * x(2);
dx(2) = k2 * x(1) * x(2) - k3 * x(2);

end
```

3.2 Simulation code for parameter fitting and stability analysis

```
clear all, close all

%% Import Hudson Bay Company's data

[~, ~, raw] =
xlsread('/Users/matthew/Documents/MATLAB/SysMIC/Mini_project/Fur_Pel
ts_1900_to_1920.xlsx','Fur Pelts (1900 to 1920)');
raw = raw(2:end,:);

% Create output variable
data = reshape([raw{:}],size(raw));

% Allocate imported array to column variable names
Year = data(:,1);
Hare = data(:,2)/1000;
Lynx = data(:,3)/1000;

% Clear temporary variables
clearvars data raw;

%% Model parameter estimation

%------------------ Estimating k1 -----------------%
for i=1:19
    Y(i) = (1/Hare(i+1))*(Hare(i+2)-Hare(i))/2;
    X(i) = Lynx(i+1);
end

% q(2) = k1
q = polyfit(X,Y,1); % calculate linear regression
Yfit = polyval(q,X);

figure('Color',[1 1 1]), subplot(2,1,1)
plot(X,Y,'x','LineWidth',2), hold on
plot(X,Yfit,'LineWidth',2)
ylabel('(1/Hare)*(dHare/dt)')
xlabel('Lynx population (x10^3)'),
title('Parameter Estimation')
set(gca, 'FontName', 'Arial','FontSize', 14)

%------------- Estimating k2 and k3 -------------%
for i=1:19
    Y(i) = (1/Lynx(i+1))*(Lynx(i+2)-Lynx(i))/2;
    X(i) = Hare(i+1);
end

% p(1) = k2, p(2) = k3
p = polyfit(X,Y,1); % calculate linear regression
Yfit = polyval(p,X);

subplot(2,1,2)
plot(X,Y,'x','LineWidth',2), hold on
plot(X,Yfit,'LineWidth',2)
```

```
ylabel('(1/Lynx)*(dLynx/dt)')
xlabel('Hare population (x10^3)'),
set(gca, 'FontName', 'Arial','FontSize', 14)

%% Model simulation

global k1 k2 k3

% Set parameter values
k1 = abs(q(2));         % hare birth rate
k2 = abs(p(1));         % predation/reproduction rate
k3 = abs(p(2));         % lynx death rate

Timespan=[1900 1920];   % define simulation time range
InPop = [30 4];         % define initial populations
[t,x] = ode45(@lotka_volterra, Timespan, InPop);
figure('Color',[1 1 1])
plot(t,x,'LineWidth',2), hold on
% Overlay Hudson Bay Company's data
plot(Year,Hare,'o','Color','b','LineWidth',2), hold on
plot(Year,Lynx,'x','Color','r','LineWidth',2)
ylabel('Population (x10^3)'), xlabel('Year')
legend('Hare (model)','Lynx (model)','Hare (raw)','Lynx (raw)')
title('Lynx-Hare Dynamics: Parameter Fitting')
set(gca, 'FontName', 'Arial','FontSize', 14)

%-------------- Steady state and perturbation -------------------%

% For steady state, dx(1)/dt = 0 and dx(2)/dt = 0
    %   The following will need to be satisfied:
    %   number of prey at equilibrium (n_Prey) = k3/k2
    %   number of predators (n_Predator) = k1/k2

% Set equilibrium populations
n_Prey = k3/k2;
n_Predator = k1/k2;

% Run using n_Prey and n_Predator as initial populations
figure('Color',[1 1 1]);
[t,x] = ode45(@lotka_volterra, Timespan, [n_Prey n_Predator]);
subplot(2,2,1)
plot(t,x,'LineWidth',2); ylim([0 50])
ylabel('Population (x10^3)'), xlabel('Year')
legend('Hare (model)','Lynx (model)')
title('Steady State')
set(gca, 'FontName', 'Arial','FontSize', 14)

% n_Prey+10, n_Predator
[t,x] = ode45(@lotka_volterra, Timespan, [n_Prey+10 n_Predator]);
subplot(2,2,2)
plot(t,x,'LineWidth',2); ylim([0 50])
title('Prey+10, Predator');
ylabel('Population (x10^3)'), xlabel('Year')
legend('Hare (model)','Lynx (model)')
set(gca, 'FontName', 'Arial','FontSize', 14)
```

```
% n_Prey, n_Predator+10
[t,x] = ode45(@lotka_volterra, Timespan, [n_Prey n_Predator+10]);
subplot(2,2,3)
plot(t,x,'LineWidth',2); ylim([0 50])
title('Prey, Predator+10');
ylabel('Population (x10^3)'), xlabel('Year')
legend('Hare (model)','Lynx (model)')
set(gca, 'FontName', 'Arial','FontSize', 14)

% n_Prey+10, n_Predator+10
[t,x] = ode45(@lotka_volterra, Timespan, [n_Prey+10 n_Predator+10]);
subplot(2,2,4)
plot(t,x,'LineWidth',2); ylim([0 50])
title('Prey+10, Predator+10');
ylabel('Population (x10^3)'), xlabel('Year')
legend('Hare (model)','Lynx (model)')
set(gca, 'FontName', 'Arial','FontSize', 14)

%-------- gradual increase in prey population ----------%
figure('Color',[1 1 1]);

% n_Prey+5
[t,x] = ode45(@lotka_volterra, Timespan, [n_Prey+10 n_Predator]);
subplot(3,2,1)
plot(t,x,'LineWidth',2);
ylabel('Population (x10^3)'), xlabel('Year')
legend('Hare (model)','Lynx (model)')
title('Prey+10')
set(gca, 'FontName', 'Arial','FontSize', 14)

% n_Prey+100
[t,x] = ode45(@lotka_volterra, Timespan, [n_Prey+100 n_Predator]);
subplot(3,2,3)
plot(t,x,'LineWidth',2);
ylabel('Population (x10^3)'), xlabel('Year')
legend('Hare (model)','Lynx (model)')
title('Prey+100')
set(gca, 'FontName', 'Arial','FontSize', 14)

% n_Prey+1000
[t,x] = ode45(@lotka_volterra, Timespan, [n_Prey+1000 n_Predator]);
subplot(3,2,5)
plot(t,x,'LineWidth',2);
ylabel('Population (x10^3)'), xlabel('Year')
legend('Hare (model)','Lynx (model)')
title('Prey+1000')
set(gca, 'FontName', 'Arial','FontSize', 14)

%-------- gradual increase in predator population ----------%

% n_Predator+10
[t,x] = ode45(@lotka_volterra, Timespan, [n_Prey n_Predator+10]);
subplot(3,2,2)
plot(t,x,'LineWidth',2);
ylabel('Population (x10^3)'), xlabel('Year')
legend('Hare (model)','Lynx (model)')
```

```
title('Predator+10')
set(gca, 'FontName', 'Arial','FontSize', 14)

% n_Predator+100
[t,x] = ode45(@lotka_volterra, Timespan, [n_Prey n_Predator+100]);
subplot(3,2,4)
plot(t,x,'LineWidth',2);
ylabel('Population (x10^3)'), xlabel('Year')
legend('Hare (model)','Lynx (model)')
title('Predator+100')
set(gca, 'FontName', 'Arial','FontSize', 14)

% n_Predator+1000
[t,x] = ode45(@lotka_volterra, Timespan, [n_Prey n_Predator+1000]);
subplot(3,2,6)
plot(t,x,'LineWidth',2);
ylabel('Population (x10^3)'), xlabel('Year')
legend('Hare (model)','Lynx (model)')
title('Predator+1000')
set(gca, 'FontName', 'Arial','FontSize', 14)
```

3.3 Model that accepts externally specified parameters

```
function dx = lotka_volterra_param(t,x,param)
% Function to simulate a 3-parameter Lotka-Volterra model with
% exponential growth assumption

% Inputs:
%   t - time: unused variable as the first derivatives in the system
%       are time independent
%   x - vector containing populations of predator x(1) and prey x(2)
%   param - vector containing parameters k1, k2 and k3
% Output:
%   dx - rate of change of the populations

k1=param(1); k2=param(2); k3=param(3);

%------------------ ODEs ------------------%
% Definition of the ODEs
% x(1) = Number of hares
% x(2) = Number of lynx

% define ODEs
dx = [0;0];
dx(1) = k1 * x(1) - k2 * x(1) * x(2);
dx(2) = k2 * x(1) * x(2) - k3 * x(2);

end
```

3.4 Prey/predator-only and parameter-response simulations

```
clear all, close all

%% Model simulation

% define original parameters
k1 = 0.47;
k2 = 0.02;
k3 = 0.76;

param = [k1 k2 k3;
         k1*2 k2 k3;
         k1*4 k2 k3;
         k1 k2 k3;
         k1 k2*2 k3;
         k1 k2*4 k3;
         k1 k2 k3;
         k1 k2 k3*2;
         k1 k2 k3*4];    % define different sets of input parameters
Timespan=[0 50];         % define simulation time range
InPop = [50 50];         % define initial populations

% parameter-response simulations
figure('Color',[1 1 1])
for i=1:length(param)
    [t,x] = ode45(@lotka_volterra_param, Timespan, InPop, [],
param(i,:));
    subplot(3,3,i)
    plot(t,x,'LineWidth',2); ylabel('Population'), xlabel('Time')
    title(['k1=',num2str(param(i,1)),', k2=',num2str(param(i,2)),...
           ', k3=',num2str(param(i,3))]);
    legend('Hare (model)','Lynx (model)')
    set(gca, 'FontName', 'Arial','FontSize', 14)
end

% predator-only and prey-only simulations
InPop = [0  50;
         50 0];

figure('Color',[1 1 1])
for i=1:length(InPop)
    [t,x] = ode45(@lotka_volterra_param, Timespan, InPop(i,:), [],
param(1,:));
    subplot(2,1,i)
    plot(t,x,'LineWidth',2); ylabel('Population'), xlabel('Time')
    legend('Hare (model)','Lynx (model)')
    set(gca, 'FontName', 'Arial','FontSize', 14)
end
```

4 Extended discussion

4.1 Comparison with experimental data

Using the parameter values from section 2.3 the following simulation result is obtained:

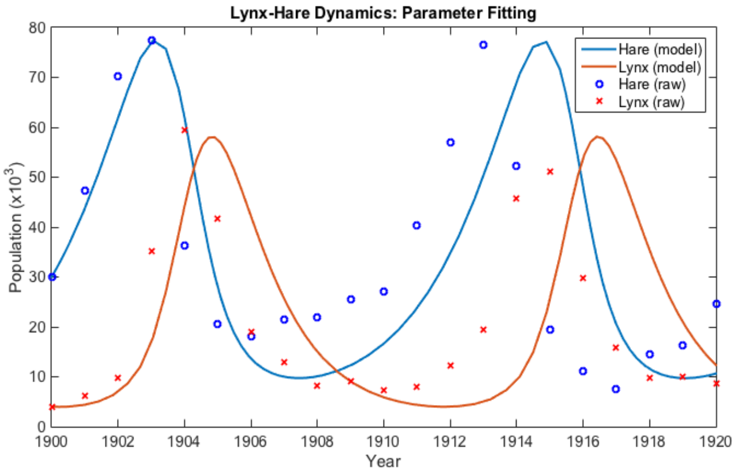

Figure 3. Simulation of hare-lynx dynamics compared with real population trends (1900-20)

The simulation reveals a cyclic behaviour (stable oscillation) for both the hare and lynx populations, with the lynx lagging behind (hence peaking after) the hare. This is expected as the populations are limited by each other in the model. Overlaying experimental data with the modelled dynamics reveals that both have a cyclic pattern with more or less the same period. However, the simulated dynamics are slightly out of phase with their raw counterparts, which is due to the fact that the parameters are only approximate values.

4.2 Steady state and stability

The steady state of the system refers to the situation when both population growth rates are equal to zero: $\frac{dX}{dt} = 0$, $\frac{dY}{dt} = 0$. At steady state, the populations of hare and lynx will be in equilibrium. To calculate the equilibrium populations, the differential equations can first be rearranged in the following way:

$$\frac{dX}{dt} = 0$$

$$k_1X - k_2XY = 0$$

$$k_1X = k_2XY$$

$$Y = equilibrium\ lynx\ population = \frac{k_1}{k_2}$$

$$\frac{dY}{dt} = 0$$

$$k_2XY - k_3Y = 0$$

$$k_2XY = k_3Y$$

$$X = equilibrium\ hare\ population = \frac{k_3}{k_2}$$

Substituting the aforementioned parameter values, the populations at steady state are:

Lynx population = $\frac{k_1}{k_2} = \frac{0.4732}{0.0234}$ = 20, hare population = $\frac{k_3}{k_2} = \frac{0.7646}{0.0234}$ = 33 (note: values are multiplied by 1000 in the plots for a more realistic picture). The system's steady state can then be obtained by setting the equilibrium population values as the initial populations in the simulation (Figure 4i). To test how the system behaves beyond its steady state, initial prey and predator populations were perturbed individually and simultaneously by a small amount to get the dynamics in Figure 4 ii, iii and iv.

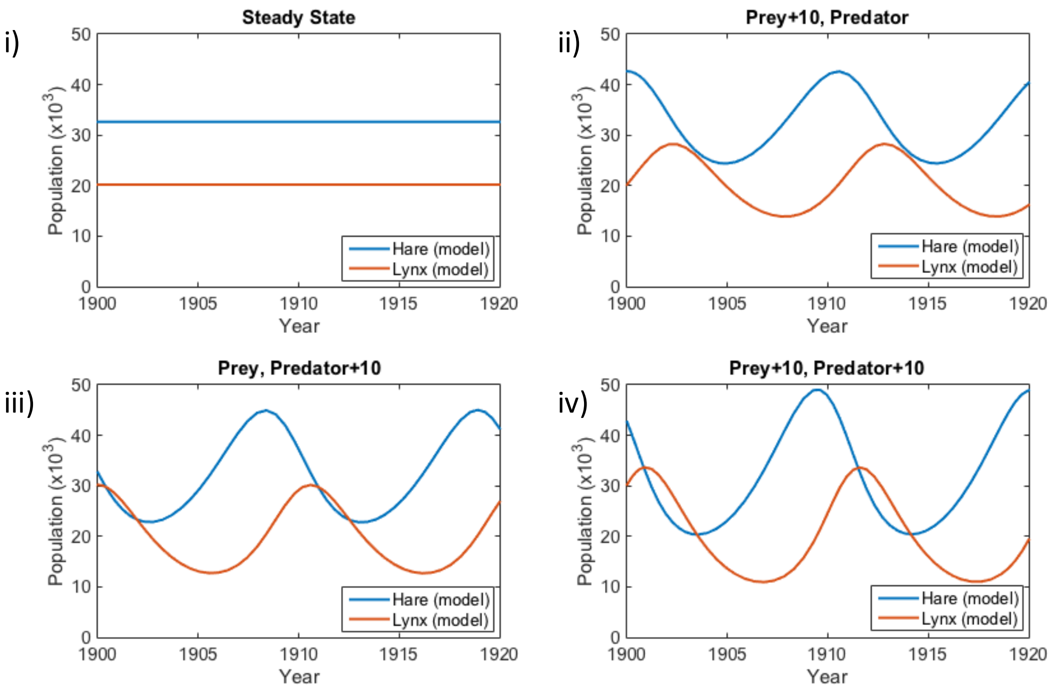

Figure 4. i) Steady state simulation, ii) Perturbation by increasing initial prey population, iii) Perturbation by increasing initial predator population, iv) Perturbation by increasing both initial populations.

As expected of a steady state, figure 4i shows no oscillation and the population of the hare remains above that of the lynx, reflecting a food pyramid-like community structure similar to that observed in nature.

In all perturbations tested, the model is able to retain the cyclic behaviour with the same period of 11 years. Increasing both initial populations by an equal amount has resulted in larger amplitudes in both species compared to increasing only one of the two. Nevertheless, the ratio of prey amplitude to predator amplitude tends to stay at around 1.26 (x10^3) for all perturbations, similar to that shown by the experimental data.

Now that we know perturbing either species will result in similar dynamics, we can test how the magnitude of perturbation affects the model's behaviour. In the simulation code, the initial prey and predator populations are both perturbed by gradually adding 10, 100 and 1000, which give the results in figure 5.

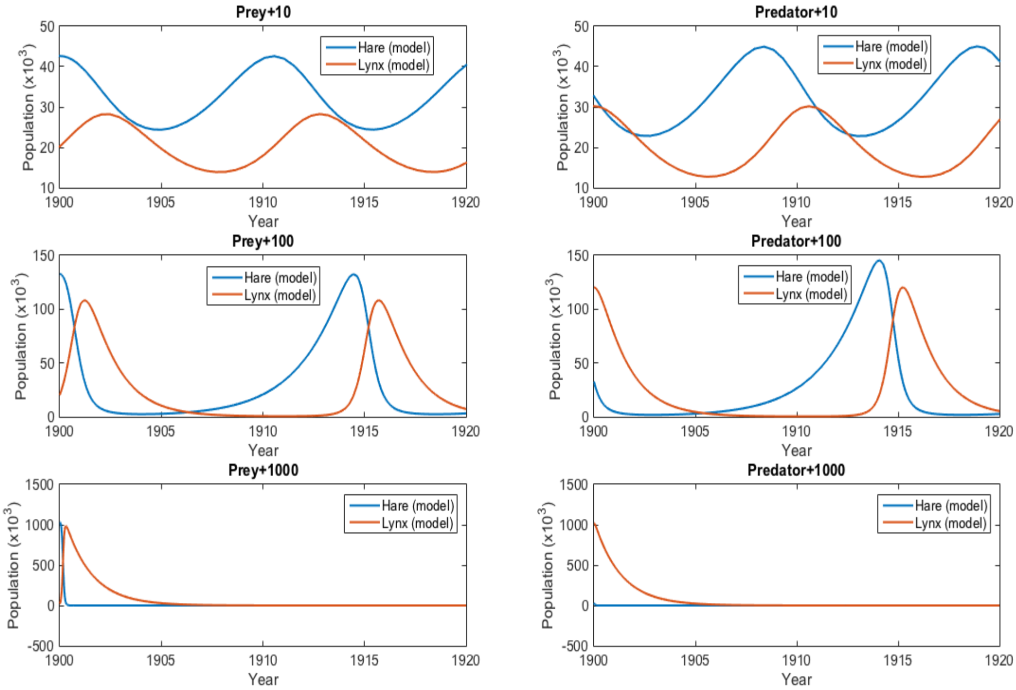

Figure 5. Perturbation by gradual increase of initial populations.

Figure 5 shows that the initial populations determine the amplitude of oscillations in a proportional manner. The lag in response also increases with the population value. When perturbation = 1000 is added the populations crash to zero. Hence, there exists a point where the oscillations of the system become unstable, whose likelihood increases as the starting populations get further away from the stable point.

4.3 Absence of prey/predator

An interesting aspect to explore is how the system will behave in the absence of the prey or predator (see code in section 3.4):

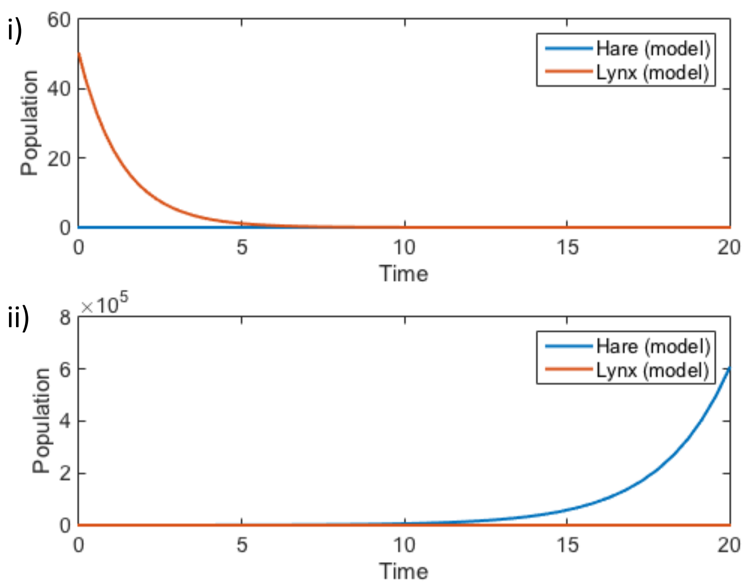

Figure 6. i) Predator (Lynx)-only response, ii) Prey (Hare)-only response

Figure 6i shows that without the hare, the lynx population experiences an exponential decay. Similarly, in 6ii, the hare population increases exponentially in the absence of lynx. These exponential relationships are actually obvious in the differential equations per se.

In the absence of prey, the expression for predator population growth rate becomes: $\frac{dY}{dt} = -\ k_3 Y$, where $-\ k_3 Y$ causes the exponential decay.

In the absence of predator, the expression for prey population growth rate becomes: $\frac{dX}{dt} = k_1 X$, where $k_1 X$ gives the exponential increase.

In the natural world, the exponential increase is highly unrealistic as no population can increase indefinitely within a space- and resource-limited habitat that is, at the same time, prone to numerous other environmental influences. Also, the model does not take into account the possibility that, in the absence of prey, the predator may switch diet and target another species for food. The exponential responses, therefore, can be considered as one of the major limitations of the model.

4.4 Effect of parameters on model behaviour

In order to test the effect k_1, k_2 and k_3 have on the system, a simulation that takes in different combinations of parameter values can be carried out. The code in section 3.4 can take in multiple sets of parameter values in the form of a matrix. Each parameter is and successively doubled while keeping the other two values constant such that the contribution of individual parameters on the system's behaviour can be tested:

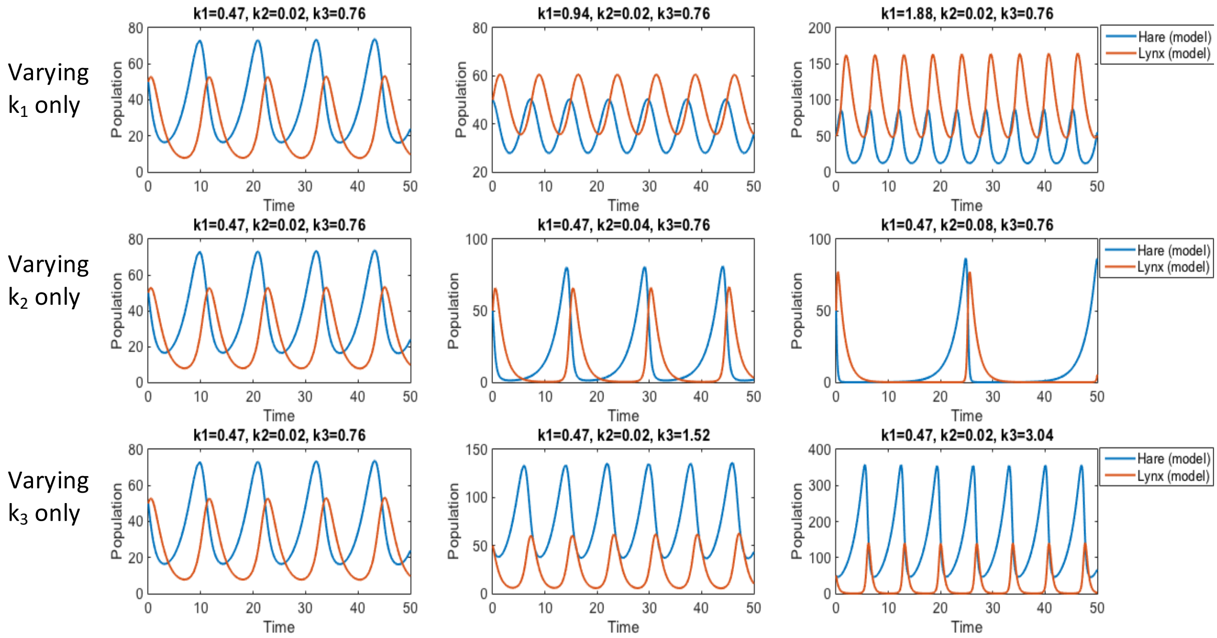

Figure 7. Effect of parameters on system behaviour.

From figure 7, we can see that increasing any parameter will result in an increase in oscillation amplitude and that the parameters play a critical role in determining the period. The simulation results show that increasing either k_1 or k_3 will reduce the period, whereas an opposite effect is achieved with k_2.

5 Outlook

Overall, the Lotka-Volterra model has managed to predict the general pattern exhibited by the dynamics between the Canadian lynx and snowshoe hare. Using the estimated parameters, the model generates stable oscillations (except at steady state or when initial populations are zero) that are similar in both amplitude and period to the given raw data. The model is able to predict the behaviour because the system is comparatively isolated and free from many external factors that could otherwise disrupt the cyclic pattern. Therefore, the model discussed in this report is useful mainly to relatively simple systems. Some of these systems can be found situated in the Artic regions where fewer species exist. Other examples such as the relationship between oceanic phytoplankton and zooplankton also very closely resemble Lotka-Volterra cyclic behaviour.(Ginzburg & Golenberg 1985)

The model may fail to reflect the real situation in more complex systems due to its unrealistic assumptions and oversimplification. The exponential responses are a good example of how unrealistic it can be. A logistic model can therefore be adopted to make the predictions more realistic and applicable to a wider variety of ecological systems. Here, the logistic approach may provide a more accurate picture because it introduces a term in the prey differential equation known as the carrying capacity, which considers the limitation of the prey population by other resources. By incorporating a carrying capacity for the system logistic equilibria will be reached rather than the indefinite increase observed earlier. This means the populations will eventually converge to a stable level and stop oscillating.

Another improvement that can be made is related to the evidence that the cyclic response of the hare population is a result of both lynx-hare interaction and plant-hare interaction(Krebs et al. 1995). This suggests that, for more complex systems, including an extra trophic level in the model will help generate a more realistic prediction.

Bibliography

Ginzburg, L.R. & Golenberg, E.M., 1985. *Lectures in theoretical population biology*, Englewood Cliffs, N.J: Prentice-Hall.

Jain, B. & Sheng, A.D., 2010. An Exploration of the Approximation of Derivative Functions via Finite Differences. *arXiv*. Available at: http://arxiv.org/pdf/1006.1620.pdf.

Krebs, C.J. et al., 1995. Impact of food and predation on the snowshoe hare cycle. *Science (New York)*, 269(5227), pp.1112–1115.

Krebs, C.J. et al., 2001. What Drives the 10-year Cycle of Snowshoe Hares? *Bioscience*, 51(1), p.25.