

Snowshoe hares and the Canadian Lynx

David Hwang 10/18/2024

- Abstract

How do the populations of Snowshoe hares and Canadian Lynx grow in the same region? Given that they are prey and predator relative to each other, what aspects should we emphasize and reflect in our models to explain real-world patterns? While the original Lotka-Volterra model captures the basic cyclical interactions, models incorporating logistic prey growth and Holling's disk equation introduce a more realistic biological model by accounting for prey competition and predator saturation. Our final model shows a cyclic population pattern between the two species and it converges to a stationary point over time. Although this final model partially explains observed real-world data, the fact that hare cycles persist even in areas without lynxes and that cycles vary by location suggests that additional factors, such as environmental conditions and alternative predators, may influence population dynamics. Therefore, our results demonstrate that not only the prey-predator interactions but also other ecological influences are necessary to comprehensively understand these population dynamics.

- Introduction

"The Canada lynx (*Lynx canadensis*) a mid-sized wild cat is a specialist predator that preys upon the snowshoe hare (*Lepus americanus*) as a primary food source; reciprocally, the lynx is the foremost predator of the snowshoe hare. Both these species inhabit the boreal forest of northern North America and have nearly perfectly overlapping ranges of native presence. The populations of both species have been observed to oscillate with a cycle of about 10 years, making them literally a textbook example of cyclic predator-prey interactions and a natural test case of the Lotka-Volterra model." (Green 204p) Based on this information, we assume that under optimal conditions female hares bear an average of 18 offspring a year, only 33% of which survive the first month, the monthly survival rate of all hares more than a month old is 95%, and sexual maturity is reached at one year. Also, we assume that 30% of lynx die

per month in the absence of hares, and if each lynx consumes 1 hare per day when there are 1000 hares present per square kilometer, the mass of lynx and hares are 10 kg and 1.5 kg respectively, and 10% of consumed prey mass goes towards reproduction and rearing of kittens. A good approach to understanding the pre-predator growth pattern is creating mathematical models using the statistical information above and examining them by plotting their dynamics on the graph. So, returning to our goal, we want to see how difference between the original Lotka-Volterra model and a modified model that takes into account intraspecific competition and saturated predator responses. Finally how well does the modified model explain the actual pattern, if not we are going to think about what aspect we should consider.

The Lotka-Volterra model:

$$\begin{aligned} \frac{dU}{dt} &= \alpha U - \gamma UV & \frac{dU}{dt} = 0 &\rightarrow V = \frac{\alpha}{\gamma} \text{ or } U = 0 \\ \frac{dV}{dt} &= \epsilon \gamma UV - \beta V & \frac{dV}{dt} = 0 &\rightarrow U = \frac{\beta}{\epsilon \gamma} \text{ or } V = 0 \end{aligned}$$

More “correct” models that account for intraspecies competition between prey (using the Logistic equation) and a saturated predator-response function (for example, the Hollings disk model):

$$\begin{aligned} \frac{dU}{dt} &= A(U)U - \Gamma(U)V & A(U) &= \alpha \rightarrow A(U) = \alpha \left(1 - \frac{U}{K}\right) \\ \frac{dV}{dt} &= \epsilon \Gamma(U)V - \beta V & \Gamma(U) &= \gamma U \rightarrow \Gamma(U) = \left(\frac{\gamma U}{1 + \gamma \kappa U} \right) \end{aligned}$$

- Results and Discussion

To simulate both models, we need to find the values of coefficients in these differential equations by using statistical information. Single species exponential growth, $dN/dt = kN$, has an analytical solution of $N(t) = N(0)e^{(kt)}$. We know that $N(t+1) = R_a N(t) = N(0)e^{(k(t+1))}$ where ‘ R_a ’ is an annual per capita growth rate and ‘ t ’ is measured in years. Then if we set $t=0$ here, we can get $N(1) = R_a N(0) = N(0)e^{(k)}$. This implies that $e^{(k)} = R_a$ which means $k = \ln(R_a)$. Now we can use statistical information here.

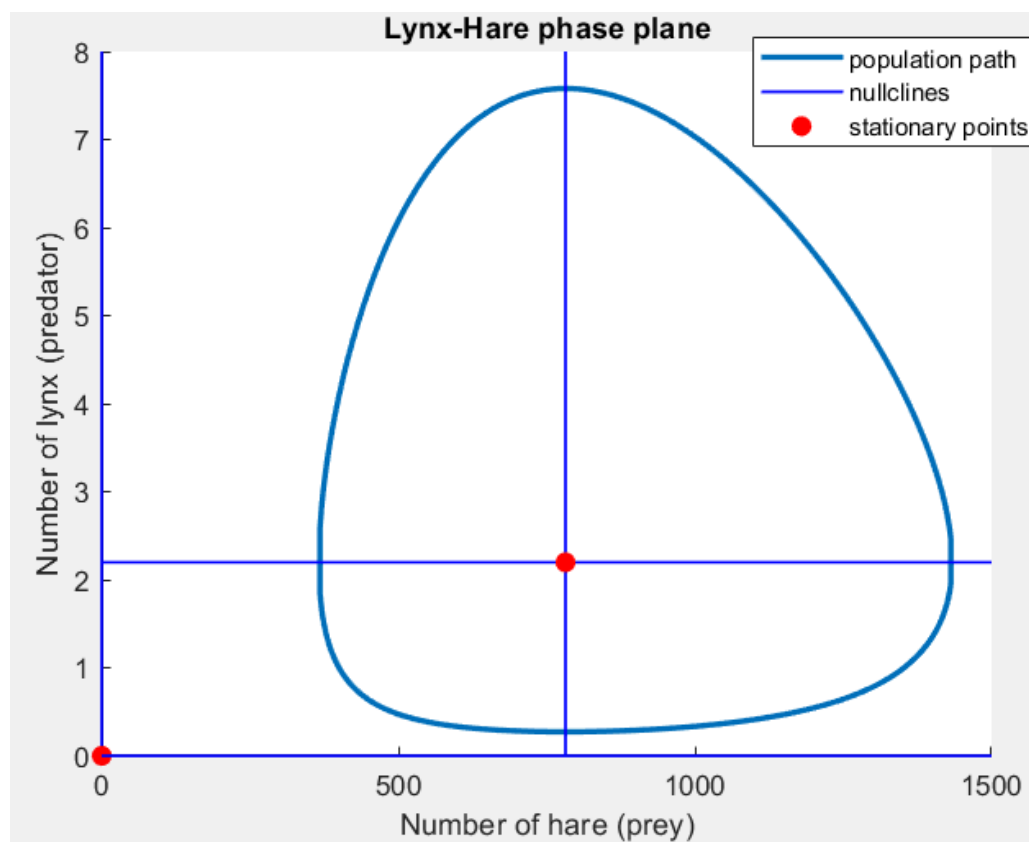
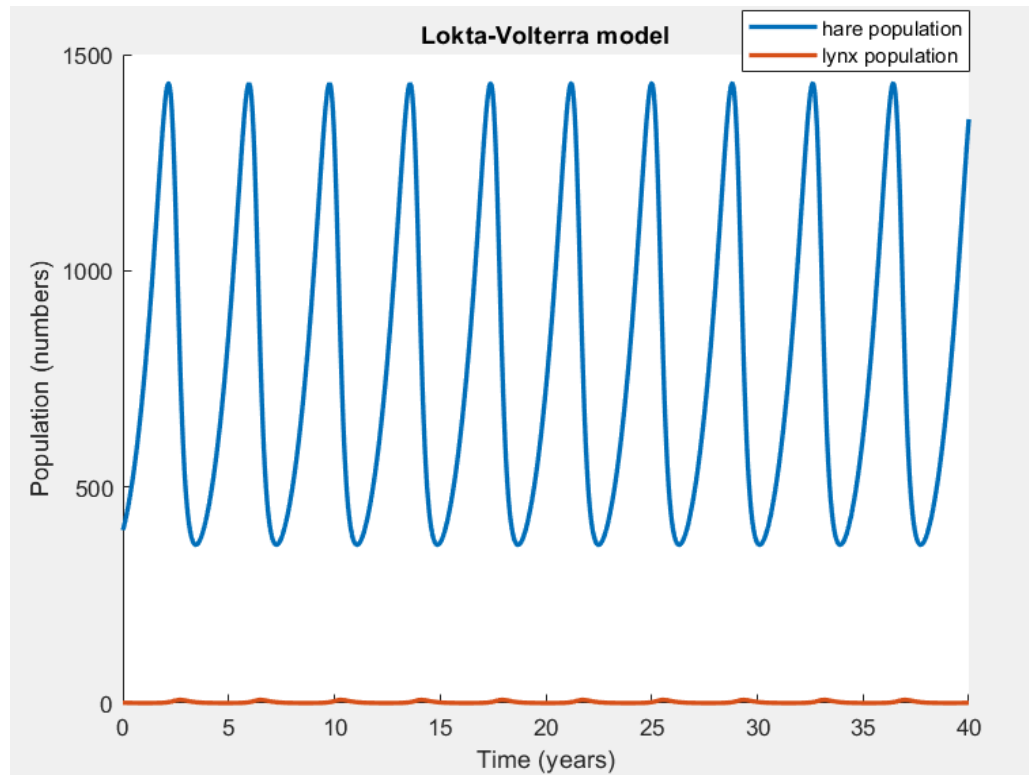
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%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
%% rate parameters of a hare(denoted as 'U')
%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
Birth_U=(18*0.33*0.95^11)/2; % annual per capita reproduction rate (the young
can survive to adult)
% Since males cannot produce offspring, we divide 2 here
Death_U=1-1*0.95^12; % annual death rate of an originally existed hare(a
parent)
Growth_U=1+Birth_U-Death_U; % a net annual per capita growth rate
alpha=log(Growth_U); % ln(R_a)
%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
%% rate parameters of Lynx(denoted as 'V')without hares
%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
Death_V=1-0.7^12; % annual death rate of an originally existing lynx
beta=-log(1-Death_V); % -ln(Ra_v)
% 1year=365days
gamma=1*365/1000;% annual per capita predation rate;
epsilon=1.5*0.1/10; % 10% of prey mass goes towards reproduction&rearing of
kittens

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The annual per capita reproduction rate of hare, as measured in terms of survival to reproductive age is **Birth_U = 1.6893**, the per capita annual death rate of adult hare is **Death_U = 0.4596**, and the overall optimal net annual per capita growth rate of hare, alpha, is **alpha = 0.8019**. We can also find the annual per capita death rate for the lynx, which is **Death_V = 0.9862**; through this, we can find **beta = 4.2801**. The annual per capita predation rate, **gamma = 0.3650**, and the conversion(efficiency) factor for predator growth, **epsilon = 0.0150**.

Now we simulate the original Lotka-Volterra model for 40 years from a starting density of 400 hares and 1 lynx per km².



From the graph above, we find that there is a certain cycle in the dynamics of each population. So, we can get some features of this dynamics.

The amplitude of hare: **amp_u = 533.7428**

The amplitude of lynx: **amp_v = 3.6538**

The period of observed cycles of hare and lynx are **c_u = 3.8080** and **c_v = 3.8080** respectively.

The minimum and maximum population density reached for each species:

Maximum of hare population: **max_u = 1.4336e+03**

Minimum of hare population: **min_u = 366.0832**

Maximum of lynx population: **max_v = 7.5796**

Minimum of lynx population: **min_v = 0.2720**

The maximum rate of change in population density observed for each species:

The maximum rate of change in the hare population: **mrates_u = 726.2290**

The maximum rate of change in the lynx population: **mrates_v = 13.5486**

The relative timing of the peak population for each species:

**relative_t = -0.5510 -0.5510 -0.5510 -0.5510 -0.5510 -0.5510 -0.5510
-0.5510 -0.5510 -0.5510**

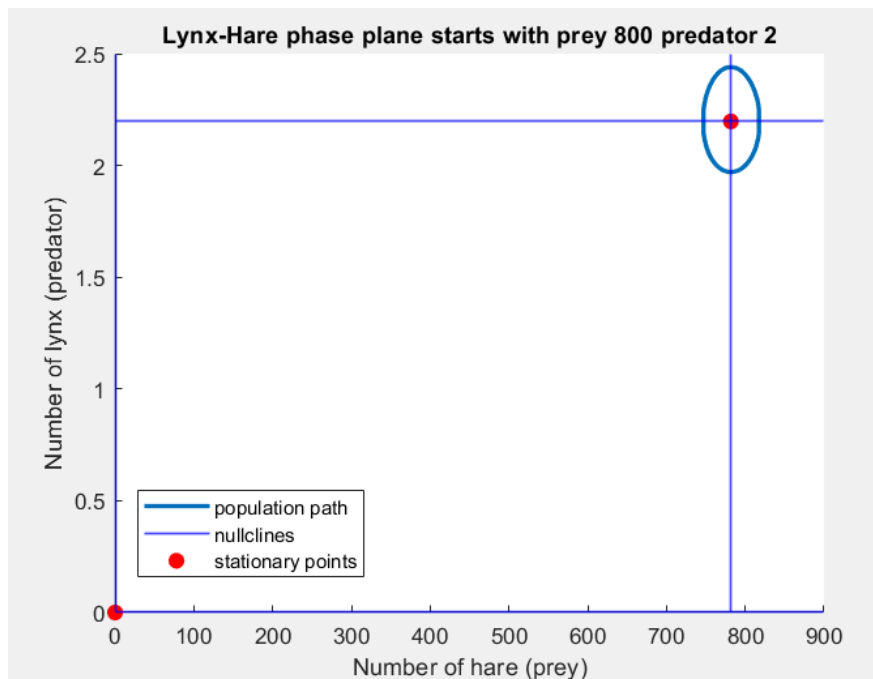
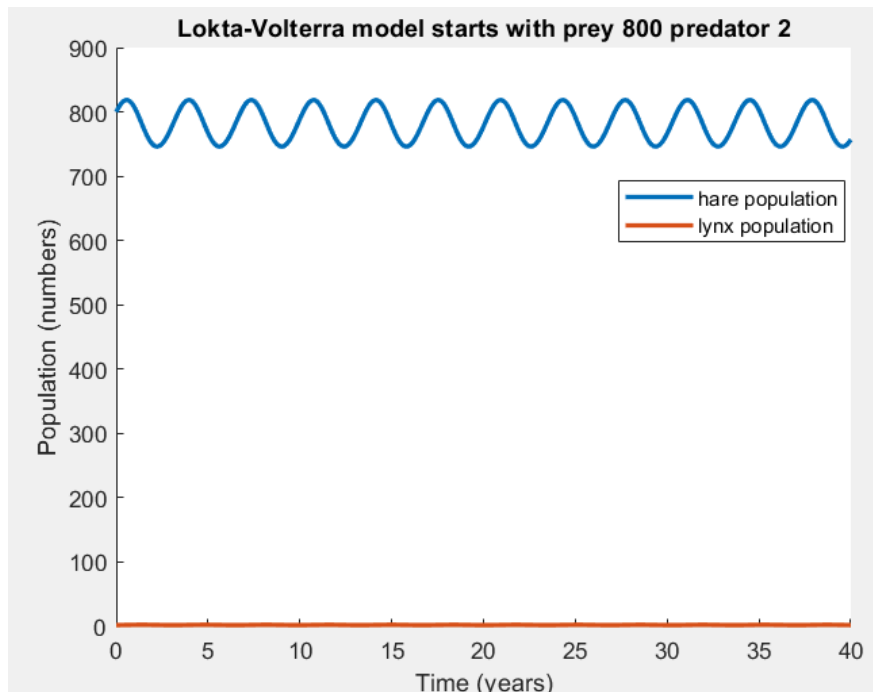
The length of time that any species spends at below 1 individual per 100km²:

Since $\min(\text{sim}_v) \cdot 100$ and $\min(\text{sim}_u) \cdot 100$ are bigger than 1. **So the hare and lynx population never go down under 1 individual per 100km².**

From the observed information about the amplitude and the maximum and minimum of each species, we find that compared to the predator population, the prey population fluctuates a lot because of the high value of the amplitude and the high difference value of the maximum and minimum population. The fact that both species have the same periods of the observed cycle and the relative timing of the peak population for each species is repeated with the same value supports the idea of coupled dynamics in predator-prey interaction with cyclic relationships. We can also verify this by the existence of a unique population path circle in the phase plane.

We simulate the same model with different initial population values to get more insights into the model.

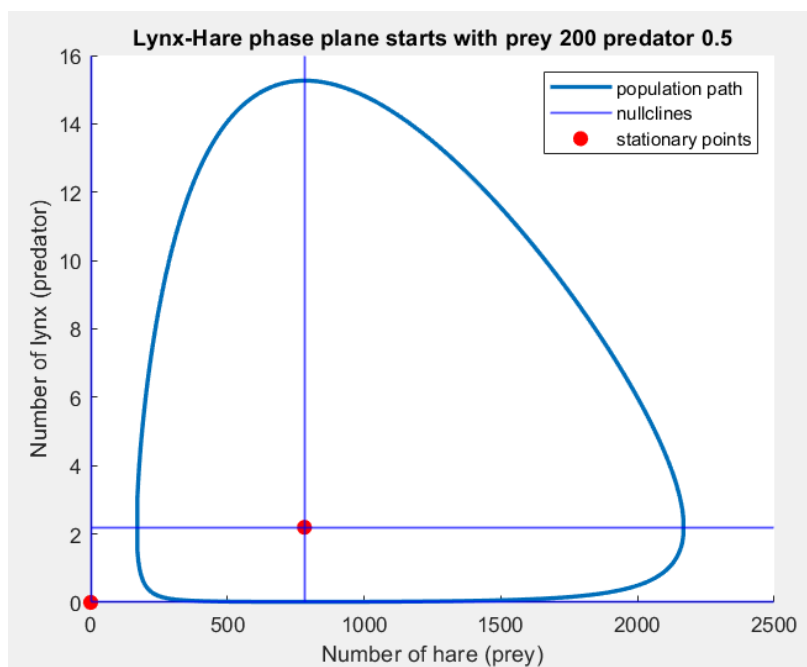
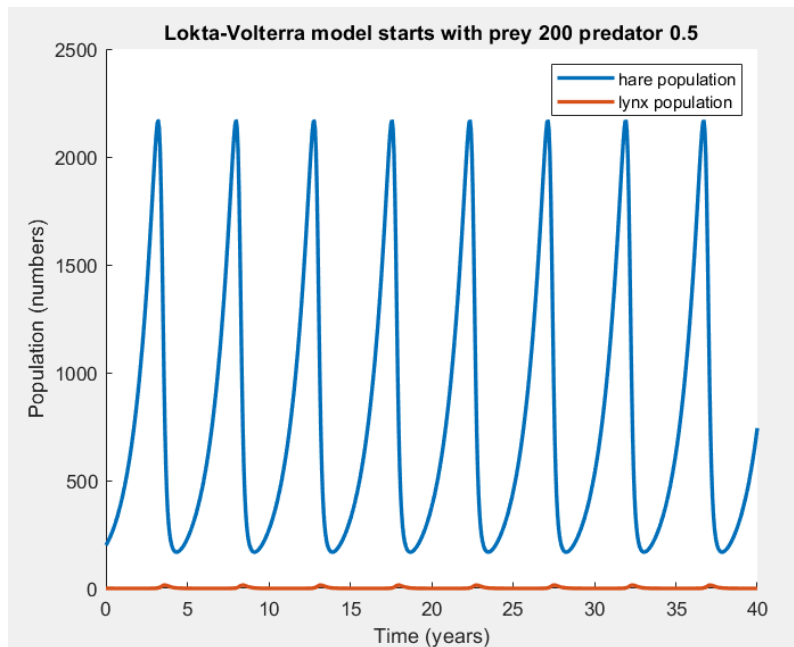
1) Simulation with 800 hares and 2 lynx



Since the population of lynx starts at a larger value, the hare population does not fluctuate much compared to the previous simulation run with 400 hares and 1 lynx. This is because starting with a larger population of lynx limits the hare population's

exponential growth. This is confirmed by the smaller circular size of the population path in the Lynx-Hare phase plane.

2) Simulation with 400 hares and 0.5 lynx

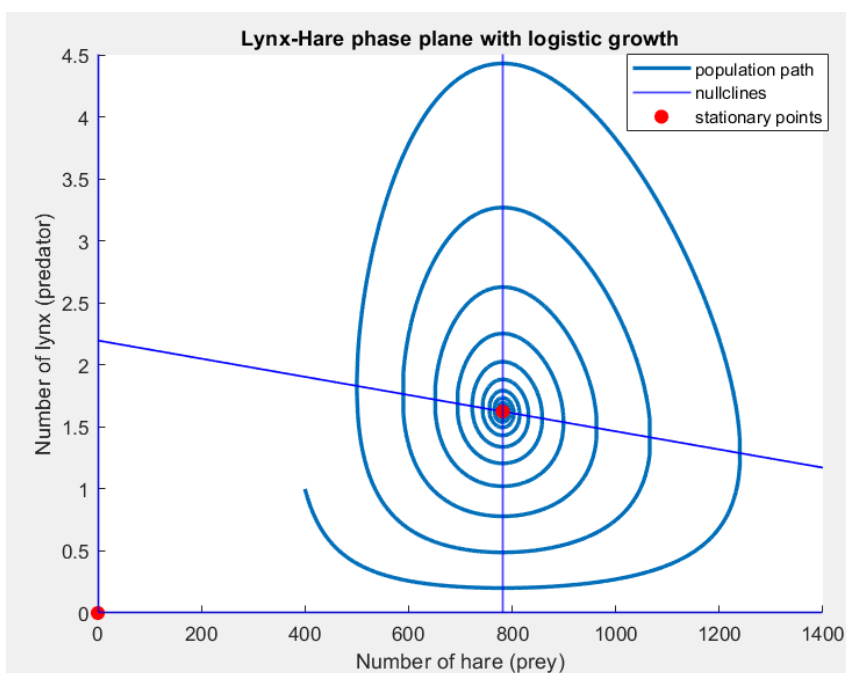
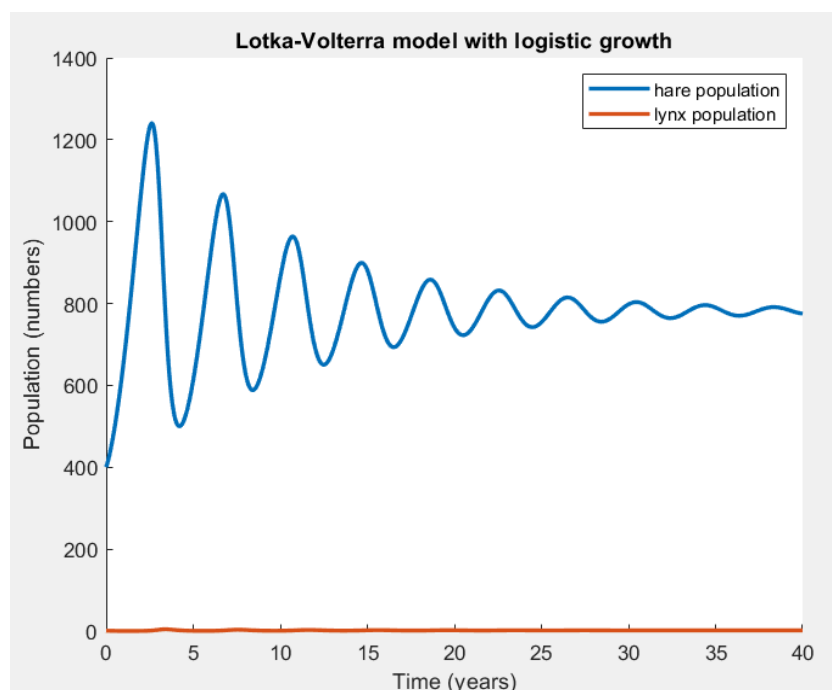


Since the population of lynx starts at a smaller value, the hare population does fluctuate much compared to the previous simulation run with 400 hares and 1 lynx. This is because starting with a smaller population of lynx does not significantly limit the

exponential growth of the hare population. This is confirmed by the larger circular size of the population path in the Lynx-Hare phase plane.

Now we implement a modified model where the constant per capita (Malthusian/exponential) prey growth model is replaced with logistic growth with a hare carrying capacity of 3000 per km². The differential equation that we use in the model is

$$\begin{aligned}\frac{dU}{dt} &= \alpha U \left(1 - \frac{U}{K}\right) - \gamma UV \\ \frac{dV}{dt} &= \epsilon \gamma UV - \beta V\end{aligned}$$

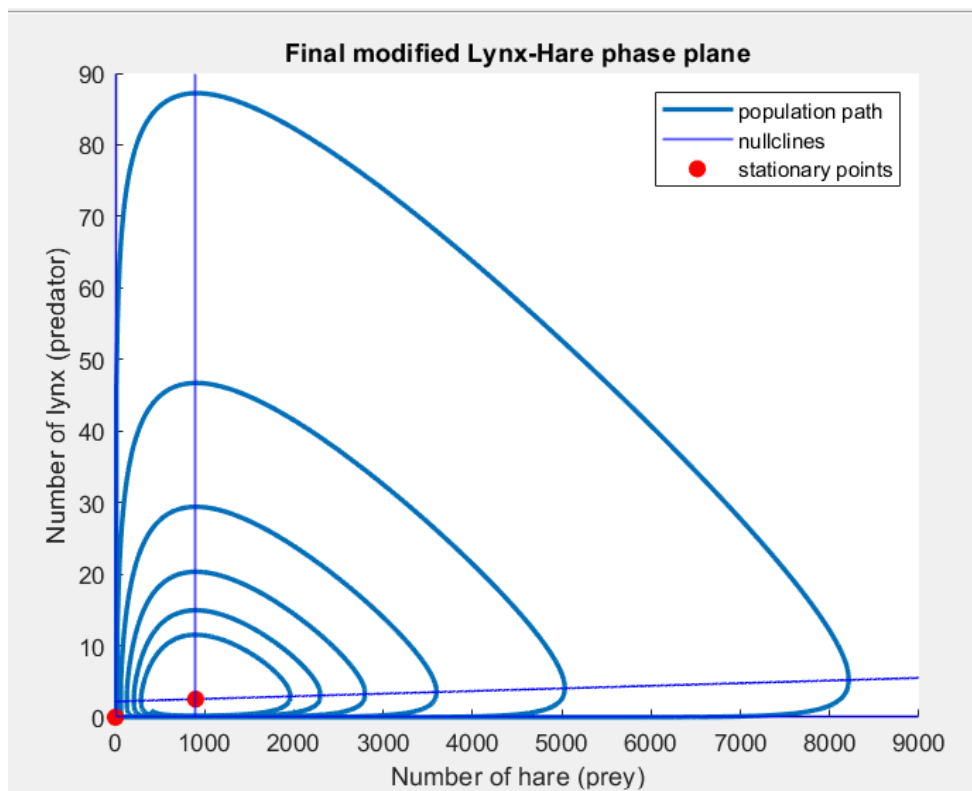
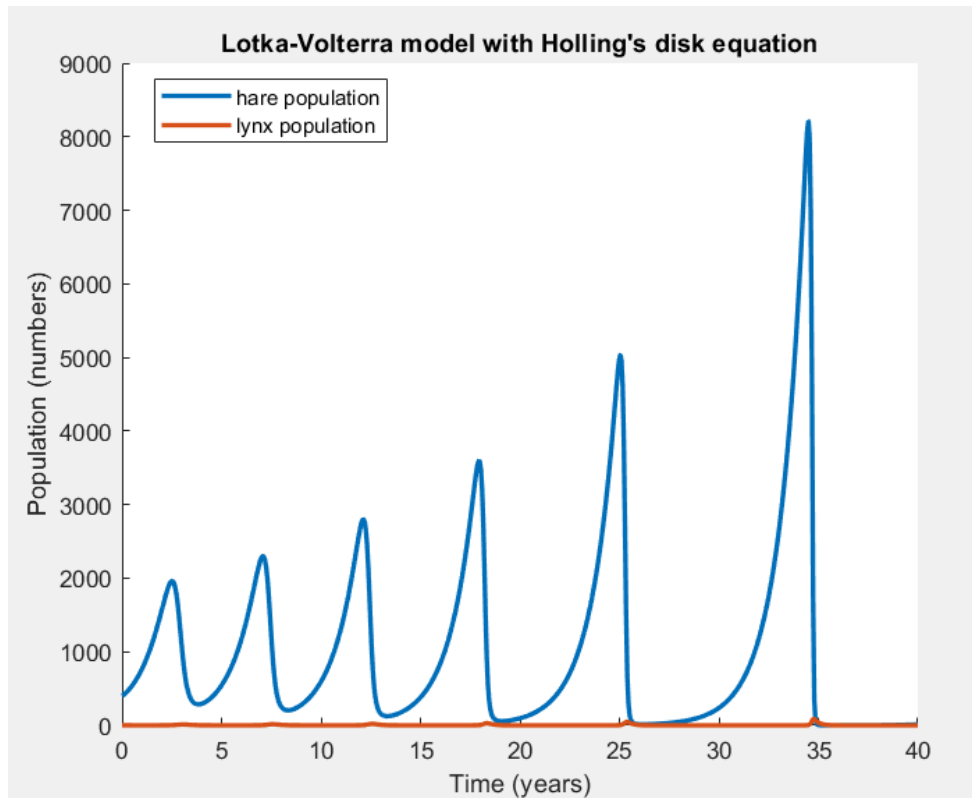


The similarity between the original Lotka-Volterra model and this model is that each population keeps fluctuating. However, when compared to the previous original Lotka-Volterra model, we can notice that the phase plane and the population VS. time graph show that in this model, each population converges toward a stationary point which is a stable stationary point over time. Thus the population versus time graph continues to fluctuate, but with smaller and smaller amplitudes over time. Also because of the modified differential equations, we can see a first-order equation null-cline line with a significant slope.

Next, we implement another modified model where prey has constant per capita growth, but the predator response follows the Hollings disk equation with prey handling time of 4 hours. The differential equation that we use in the model is

$$\begin{aligned}\frac{dU}{dt} &= \alpha U - \left(\frac{\gamma U}{1 + \gamma \kappa U} \right) V \\ \frac{dV}{dt} &= \epsilon \left(\frac{\gamma U}{1 + \gamma \kappa U} \right) V - \beta V\end{aligned}$$

The similarity between the original Lotka-Volterra model and this model is that each population keeps fluctuating. However, the difference is that if we modify the original model to consider the consuming limit of lynx, this will lead to lower pressure on the exponential growth of the hare population over time and the annual predation rate of lynx will be decreased. We can confirm this by seeing in the model below that the amplitude of the hare population increases over time. Also because of the modified differential equations, we can see a first-order equation null-cline line with a significant slope.



Finally, combining all the important factors above, implement a modified model where prey follow a logistic growth model and the predator response follows the Hollings disk equation; The differential equation that we use in our final model is

$$\begin{aligned}\frac{dU}{dt} &= \alpha U \left(1 - \frac{U}{K}\right) - \left(\frac{\gamma U}{1 + \gamma \kappa U}\right) V \\ \frac{dV}{dt} &= \epsilon \left(\frac{\gamma U}{1 + \gamma \kappa U}\right) V - \beta V\end{aligned}$$

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%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
% Final modified model with logistic and Holling's dist equation (Q10)
%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
% main parameters
U0=400; %initial value; 400 hares
V0=1; % initial value; 1 lynx
U=U0; % U is a number
V=V0; % V is a number
Birth_U=(18*0.33*0.95^11)/2; % annual per capita reproduction rate (the young
can survive to adult)
Death_U=1-1*0.95^12; % annual death rate of an originally existed hare(a
parent)
Growth_U=Birth_U+(1-Death_U); % a net annual per capita growth rate
alpha=log(Growth_U); % ln(Ra_u)
K=3000 ; % carrying capacity of 3000 per km^2
Death_V=1-0.7^12; % annual death rate of an originally existing lynx
beta=-log(1-Death_V); % -ln(Ra_v)
gamma=1*365/1000; % annual per capita predation rate;assume that there are 1000
hares per square km
epsilon=1.5*0.1/10; % 10% of prey mass goes towards reproduction&rearing of
kittens
kappa = 4/(24*365); % pre handling time of 4 hours
% simulation
dt=0.001; % time step; 0.001years
timev=0:dt:40; % time vector for 40 years which is 4 cycles
sim_u=zeros(length(timev),1); % vector to store the population of hares
sim_v=zeros(length(timev),1); % vector to store the population of lynx
k=0; %counter
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sim_u(1)=U;
sim_v(1)=V;
for t=timev
    k=k+1;
    % main equation
    if k~=1
        U = U + (alpha*U*(1-U/K)-((gamma*U)/(1+gamma*kappa*U))*V)*dt;
        V = V + (epsilon*((gamma*U)/(1+gamma*kappa*U))*V-beta*V)*dt;
    end
    if U<0 U=0; end;
    if V<0 V=0; end;

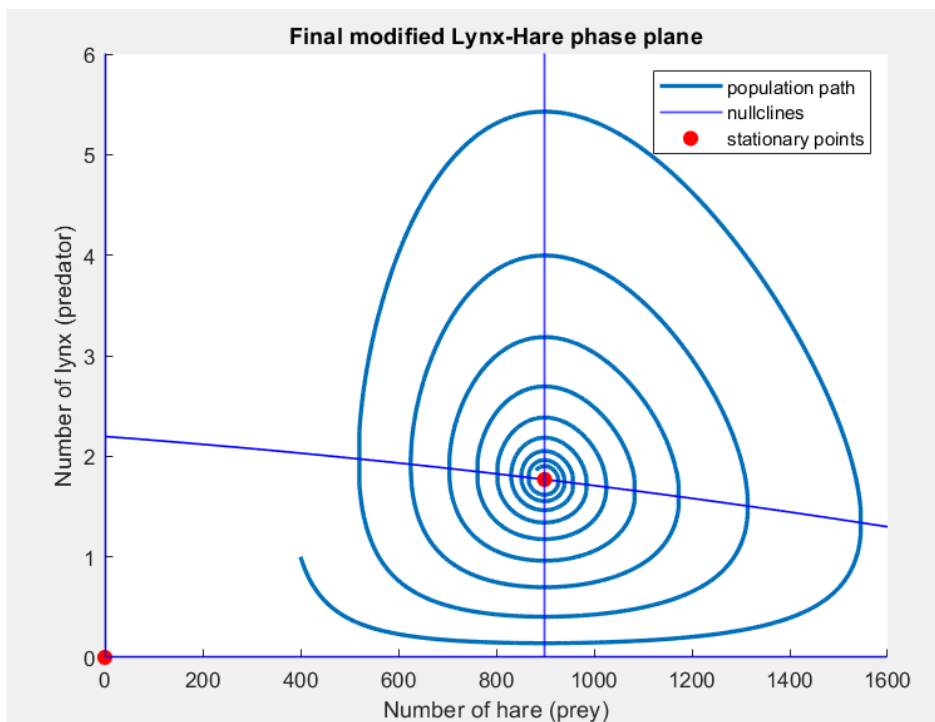
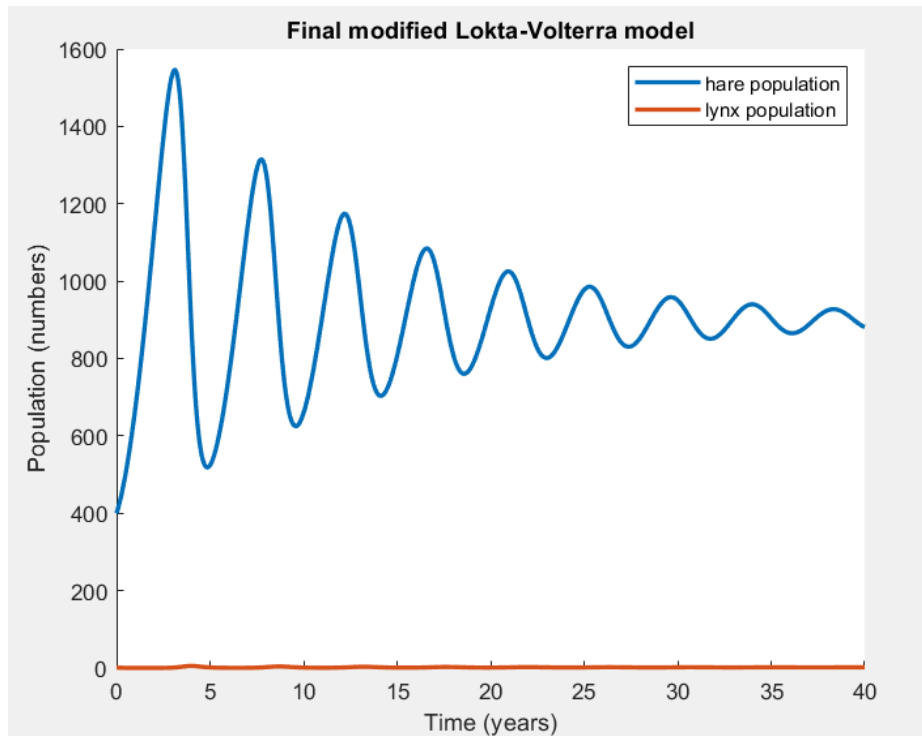
    % store value of U&V for plotting
    sim_u(k)=U;
    sim_v(k)=V;
end
x=0:1:1600; % x vector for plotting on the phase plane
% plot
figure(1); clf
hold on
plot(timev,sim_u,'LineWidth', 2)
plot(timev,sim_v,'LineWidth', 2)
hold off
legend('hare population','lynx population')
xlabel('Time (years)');ylabel('Population (numbers)')
title('Final modified Lokta-Volterra model')
figure(2); clf
hold on
plot(sim_u,sim_v,'LineWidth', 2)
xline(0,'-b','LineWidth', 1)
plot(0, 0, 'r.', 'LineWidth', 2, 'MarkerSize', 25);
plot(x,alpha/gamma*(1-((1-gamma*kappa*K)/K).*x-(gamma*kappa/K).*x.^2),'-b','Lin
ewidth', 1)
yline(0,'-b','LineWidth', 1)
xline(beta/((epsilon-beta*kappa)*gamma),'-b','LineWidth', 1)
plot(beta/((epsilon-beta*kappa)*gamma),
alpha/gamma*(1-(1-gamma*kappa*K)/K*(beta/((epsilon-beta*kappa)*gamma))-(gamma*k

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appa/K)*(beta/((epsilon-beta*kappa)*gamma))^2), 'r.', 'LineWidth', 2,
'MarkerSize', 25);
legend('population path','nullclines','stationary points')
xlabel('Number of hare (prey)');ylabel('Number of lynx (predator)')
hold off
title('Final modified Lynx-Hare phase plane')

```



The similarity between the original Lotka-Volterra model and this model is that each population keeps fluctuating. However, when compared to the previous original Lotka-Volterra model, we can notice that the phase plane and the population VS. time graph show that in this model, each population converges toward a stationary point which is a stable stationary point over time. Thus the population versus time graph continues to fluctuate, but with smaller and smaller amplitudes over time. Compared to the Lotka-Volterra containing the logistic equation model, we can see larger hare population amplitudes in this model because of the limit of the predation rate. Also because of the modified differential equations, we can see a second-order equation null-cline line with a significant slope.

Now we want to compare real-world information with the results of our model and consider other factors if there is information that our model cannot interpret. The real-world information states that the population of both species has been observed to oscillate with a cycle of about 10 years. However, our final model shows that the cycle starts at about 4.6 years and gets smaller over time. Since the populations have been consistently observed to follow a 10-year cycle throughout northern North America for more than 200 years, our model correctly predicts the existence of periodic oscillations, but it oversimplifies real-world ecosystems. This suggests that there are additional factors that contribute to the regulation and stability of the cycle. Additionally, we have real-world data showing that while circulation is synchronized over large areas of the continent, some subregions are out of phase with each other. This synchronization of the cycle across large swaths of the continent implies that continental-scale environmental factors such as broad climatic patterns may be the factors for the cycle. However, the existence of subregions out of phase suggests that there are stochastic environmental factors such as genetic drift may be the factors. The most interesting information is that the Islands from which lynx have been extinct preserve the 10-year cycle for hares. This implies that lynx predation is not the sole factor for the population cycle of hares. We can infer some additional factors such existence of other predators or diseases, but we need more information to explain the pattern exactly.

- Conclusion

In this study, we have made computational models for the population growth of hares and lynxes based on the Lotka-Volterra model considering the prey-predator relationship. Even though the original Lotka-Volterra model effectively captures the basic periodic predator-prey interactions, the modifications incorporating logistic prey growth and Holling's disk equation, which account for prey intraspecies competition and predator saturation, provide a more biologically realistic picture. Our final model shows that the two species follow the same cycle as they interact with each other, but at the same time, the populations of both species converge to a stationary point over time. Therefore, the real-world information that represents the 10-year cyclic variation in the lynx and hare population can be partially explained by our model. However, the fact that hare cycles persist in islands without lynxes and that some regions are out of phase while others are synchronized, indicates that not only the prey-predator relationship but also other additional factors such as environmental conditions or alternative predators might influence the population dynamics. Thus, even though prey-predator interactions can partially explain the dynamics of their population, because of the complexity of the ecosystem, including other factors that may affect the dynamics is necessary to fully understand the pattern.

- References

David Green (2024). *Snowshoe hares and the Canadian Lynx*

I have only used the information inside the homework paper