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Lotka-Volterra Modeling: The Predator-Prey Dynamics of *Lynx canadensis* and *Lepus americanus*

Introduction:

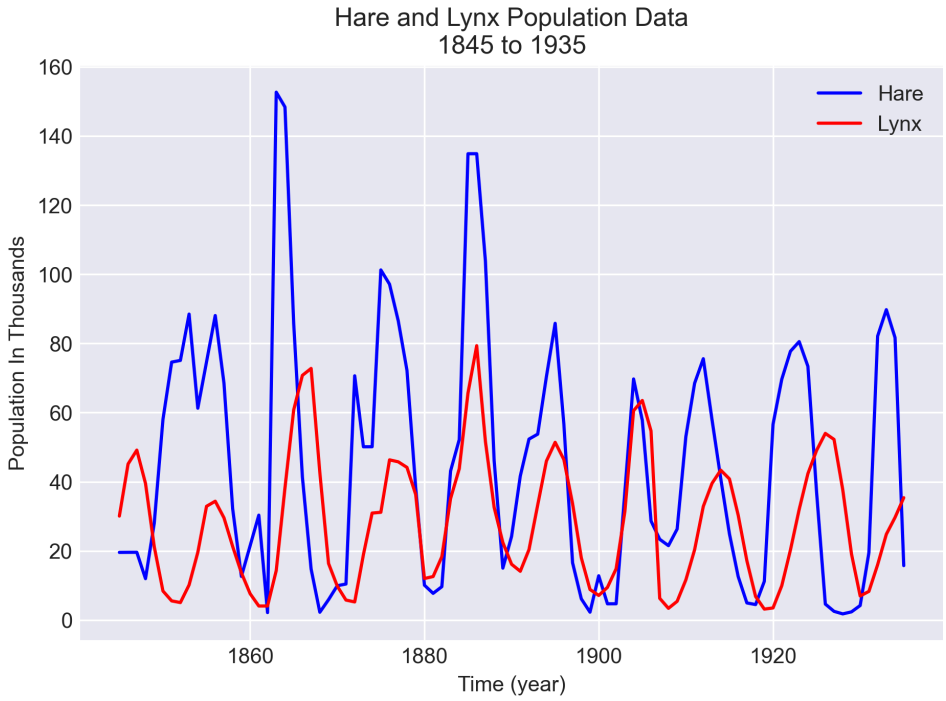
The fascinating cycles of snowshoe hares and Canadian lynx have captured the attention of ecologists for decades. Before predator-prey and ten-year cycles were well established in ecology, these cycles violated one of the implicit assumptions in the field: that within nature there is balance. Population cycles driven by predation have been largely understood mathematically by using the Lotka-Volterra predator-prey model. The differential equation was independently derived by Vito Volterra and Alfred Lotka, and is the simplest model of predator-prey interactions. Predator-prey relationships are seen as the building blocks of ecosystems, and therefore understanding them allows for a better understanding of ecosystems as a whole.

The data used in this study were first published in the *Journal of Animal Ecology* in 1942 by Charles Elton and Mary Nicholson (Elton and Nicholson 1942). Elton and Nicholson created this dataset by extrapolating from fur trading records that were made by the Hudson's Bay Company. This meticulous record has data on the number of furs traded at different posts spread across Canada. The population cycles drawn from these data have become extremely famous, and are often cited as a textbook example of predator-prey oscillations (Zhang et al 2003, 2015, Stenseth et al. 1997, Krebs et al. 2001).

In 1831, the manager of a Hudson's Bay Company post wrote to the head office in London to report that the local Ojibway people were starving due to a shortage in "rabbits" (Krebs et al. 2001). These shortages occurred in the company's record approximately every 10 years. Ten-year cycles of animal populations were first analyzed quantitatively when biologists, such as Elton and Nicholson, began to plot these fur trading records.

The purpose of this study is to attempt to create an accurate predator-prey model that could predict hare-lynx population oscillations using the Lotka-Volterra equation and historic population data. An accurate and validated model of hare-lynx population cycles would shed light on the inner workings of the North American boreal forest ecosystem.

Methods:



Data

Fur harvest data, taken from Elton and Nicholson (1942).

Fig.1 - *Lepus americanus* and *Lynx canadensis*. Hare populations in blue and lynx populations in red, redrawn.

Assumptions

Being that there are so many environmental and trophic pressures on both the Canadian lynx and especially the snowshoe hare, there are several assumptions that must be made to simplify the population cycle. For the Lotka-Volterra model, we assume the following:

1. Hare always have ample food
2. Lynx only eat hare, hare are only eaten by lynx
3. The rate of change of a population is proportional to its size
4. Lynx will always eat hare
5. The environment does not favor any population over another

Equation

There are many versions of the Lotka-Volterra predator-prey equation. This study uses the following, taken from Bowman & Hacker's *Ecology* (2020)*:*

$$\frac{dN}{dt} = rN - aNP$$

$$\frac{dP}{dt} = baNP - mP$$

In these equations, N represents the number of hare individuals and P represents the number of lynx individuals. The equation for change in the prey population over time (dN/dt) assumes that when lynx are absent ($P = 0$), the hare population grows exponentially, which is covered by assumptions 1 and 2 above. When lynx are present ($P \neq 0$), the rate at which they kill hare depends in part on how frequently predators and prey encounter one another. This frequency is expected to increase with the number of hare (N) and with the number of lynx (P), so a multiplicative term (NP) is used in the equation for dN/dt. The rate at which lynx kill prey also depends on the efficiency with which lynx can capture prey, which is represented by the constant a. The overall rate at which lynx kill hare is therefore aNP.

Assumption 2 means that lynx will starve when there are no hare. Following this, the equation for change in the predator population over time (dP/dt) assumes that in the absence of hare ($N = 0$), the number of lynx decreases exponentially with a mortality rate of m. When hare are present ($N \neq 0$), individuals are added to the lynx population according to the number of hare that are killed (aNP) and the efficiency with which hare are converted into lynx offspring (represented by the constant b). Thus, the rate at which individuals are added to the predator population is $baNP$.

Software and calculations

First, iterative calibration will be done using three different samples: the first 20 years, the first 55 years, and the first 79 years of the dataset. The calibration data that provides the most accurate model will be found by comparing reduced chi-square values. The remaining years will be used to validate the model. Validation will consist of plotting the model on top of the empirical data.

All figures, models, and calculations were made in Python version 3.9.1 using the pandas, matplotlib, numpy, seaborn, scipy and lmfit libraries. Lmfit is a python package inspired by (and named after) the Levenberg-Marquardt algorithm, and is used as an interface for non-linear optimization and curve-fitting problems. The lmfit package builds on the optimization methods of scipy, and is used in this study for curve-fitting.

All libraries and packages used are shown below:

```
import numpy as np
import pandas as pd
import matplotlib
import matplotlib.pyplot as plt
import seaborn
from scipy.integrate import odeint
from lmfit import Model, Parameters, report_fit, minimize
```

Parameters are stored in a dictionary with their initial guesses. The function 'lvmodel' below is used to fit the model, and explicitly unpacks each Parameter value:

```
#create function for lotka volterra model
def lvmodel(params, x, y, data):
    """Lotka Voltera model with data subtracted"""
    r = params['r'] # r = prey pop. growth rate
    a = params['a'] # a = capture efficiency
    b = params['b'] # b = efficiency with which prey are converted into predators
    m = params['m'] # m = mortality rate of predators

    #L-V EQUATIONS
    modelx = r*x - a*x*y
    modely = b*a*x*y - m*y

    #subtracting data
    modelx = modelx - data[:,0]
    modely = modely - data[:,1]

    model = modelx, modely
    return model

#inital guesses for parameters
params = Parameters()
params.add('r', value = 4.5, min = 0, max = 100)
params.add('a', value = 0.2, min = 0, max = 100)
params.add('b', value = 0.2, min = 0, max = 100)
params.add('m', value = 0.4, min = 0, max = 100)
```

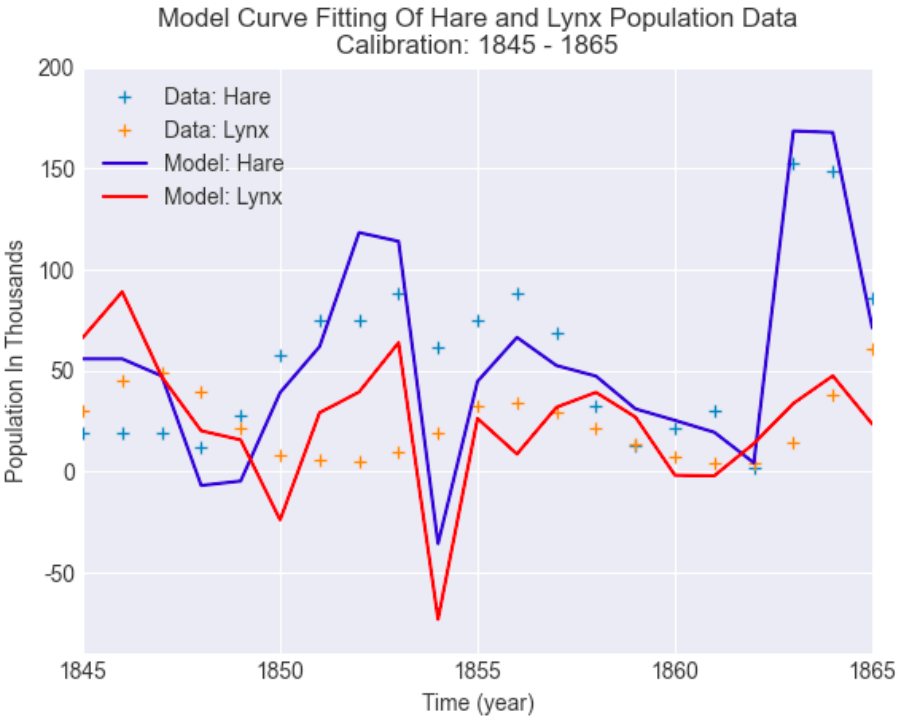
The minimize function is used to find the curve of best fit. The function takes an objective function to be minimized ("lvmodel"), a dictionary containing the model's parameters ("params"), and several arguments ("x"," y", and "data") including the fitting method, which for this problem is the least squares method ("leastsq"). It returns an array, which is stored ("result"). An error report is generated by the report_fit function, as seen below:

```
#fit with least squares method
result = minimize(lvmodel, params, args=(x, y, data), method = 'leastsq')

#final is an array with the model values
final = data + result.residual.reshape(data.shape)

#error report
report_fit(result)
```

Results: *Calibration*

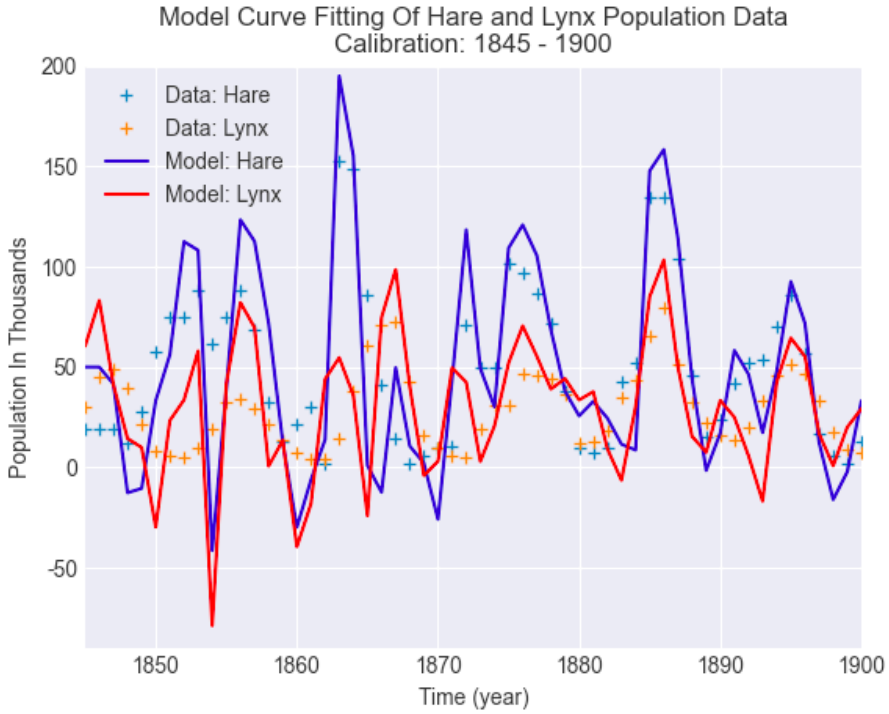


Key values from first calibration set:

Reduced chi-square = 1092.912

r = 7.932
a = 0.169
b = 0.541
m = 1.008

Fig.2 - Empirical data from 1845-1865 redrawn with calibration curve. Hare data is marked with a blue '+', lynx with orange. Hare model is drawn in blue, lynx in red.

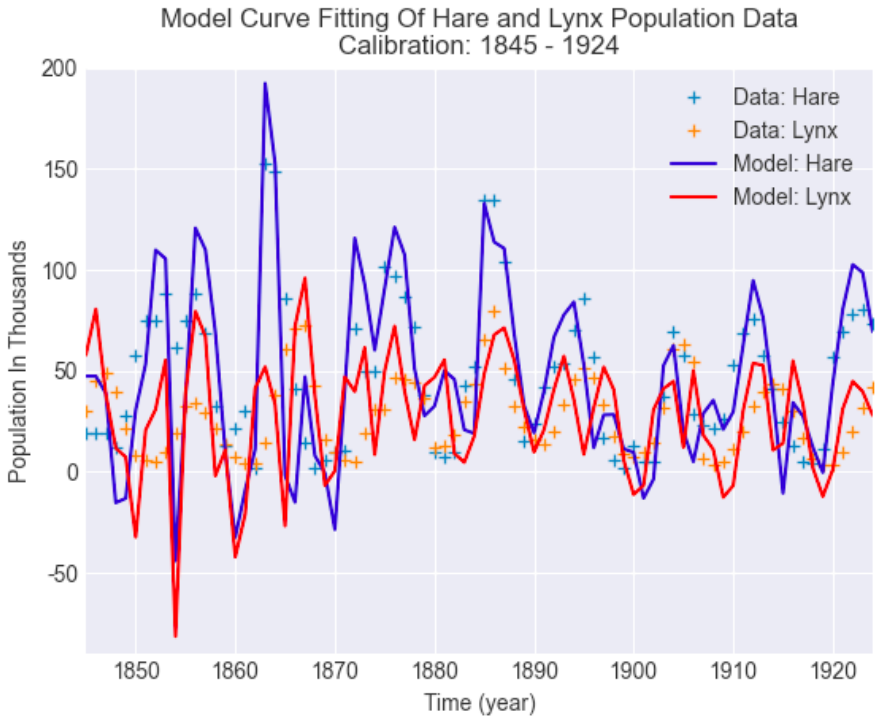


Key values from second calibration set:

Reduced chi-square = 981.649

r = 10.098
a = 0.250
b = 0.470
m = 1.335

Fig.3 - Empirical data from 1845-1900 redrawn with calibration curve. Hare data is marked with a blue '+', lynx with orange. Hare model is drawn in blue, lynx in red.



Key values from third calibration set:

Reduced chi-square = 850.595

r = 6.930
a = 0.149
b = 0.318
m = 4.342e-04

Fig.4 - Empirical data from 1845-1924 redrawn with calibration curve. Hare data is marked with a blue '+', lynx with orange. Hare model is drawn in blue, lynx in red.

Validation

The reduced chi-square value decreased as the amount of calibration data increased. The confidence interval in the calculated variables increased as calibration data increased. Because of these two issues, the second calibration set was selected as an (un)happy-medium for validation.

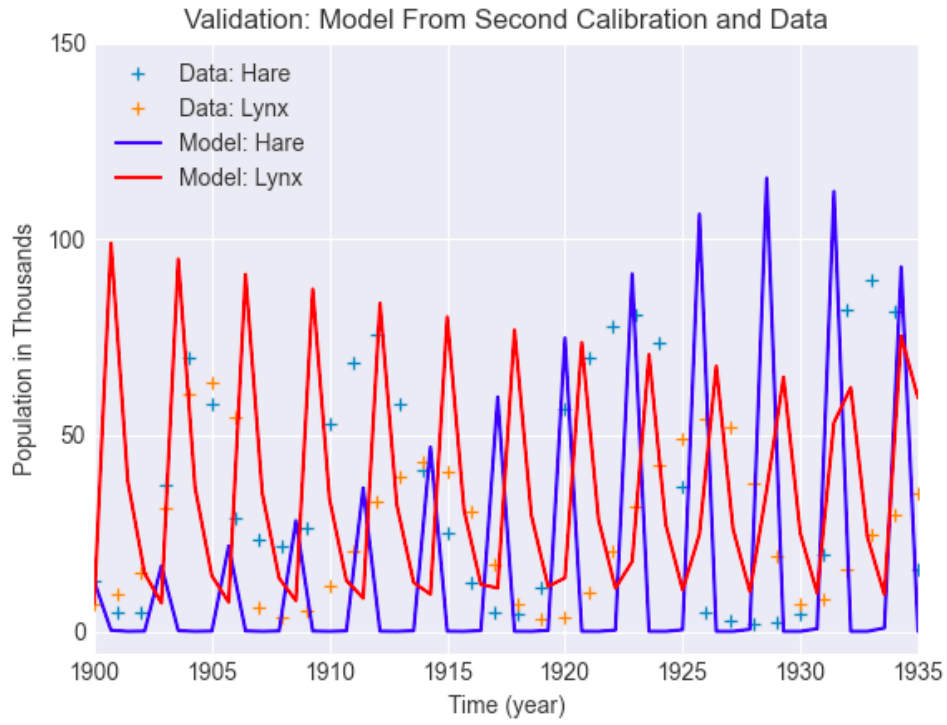


Fig.5 - Empirical data from 1900-1935 redrawn with model curve. Hare data is marked with a blue '+', lynx with orange. Hare model is drawn in blue, lynx in red.

Code used for validation:

```
#import data
df = pd.read_csv('total_hare_lynx_data.csv')
df = df[df['Year'] >= 1900] #grab only validation data
#separate columns
year_data = df['Year']
hare_data = df['Hare']
lynx_data = df['Lynx']

#set timeseries to span last 35 years of data
t = np.linspace(0, 35)

#parameters from second calibration
r = 10.098
a = 0.250
b = 0.470
m = 1.335

start_year = 1900 #year that the validation starts
prey = 12.82 #real hare pop. from 1900
predator = 7.13 #real lynx pop. from 1900
pops = [prey, predator] #starting values

pars = [r, a, b, m] #initalize parameters
```

```
def lvmodel(pops, t, pars):
    '''Lotka-Volterra model'''
    n = pops[0] # n = hare population level
    p = pops[1] # p = lynx population level

    r = pars[0] # r = prey pop. growth rate
    a = pars[1] # a = capture efficiency
    b = pars[2] # b = efficiency with which prey are converted into predators
    m = pars[3] # m = mortality rate of predators

    dndt = r*n - a*n*p
    dpdt = b*a*n*p - m*p

    return([dndt, dpdt])

y = odeint(lvmodel, pops, t, args = (pars,)) #solve ODE to y

t = t+start_year #modify t to start at start_year

#plotting
plt.style.use('seaborn-darkgrid') #import style of plot from seaborn library
plt.plot(year_data, hare_data, '+', label = 'Data: Hare')
plt.plot(year_data, lynx_data, '+', label = 'Data: Lynx')
plt.plot(t, y[:,0], 'b', label = 'Model: Hare')
plt.plot(t, y[:,1], 'r', label = 'Model: Lynx')
plt.xlim([1900,1935])
plt.yticks([0, 50, 100, 150], labels=['0', '50', '100', '150'])
plt.legend()
plt.show()
```

<u>Discussion:</u>

Neither the calibration nor the validation of the model showed accuracy. All calibration sets had a massive reduced chi-square value, and were therefore not good fits. The variables were

inaccurately backed out of the calibration data, as they had large confidence intervals and resulted in a model that immediately broke down. Based on this information, my model cannot be validated.

Alternative hypotheses

Despite the hare-lynx population cycles being cited as a textbook example of predator-prey oscillations, multiple other studies have shown that a regression fit to the Lotka-Volterra model was poor (Zhang 2007). An alternative to the hare-lynx interaction hypothesis is the plant-hare interaction hypothesis, which states that the cycle results from the interaction between hares and their winter food supply (Zhang 2007 (Fox & Bryant 1984). Under the plant-hare hypothesis, population crashes are triggered by a shortage of palatable winter forage, and the duration of cycles is determined by the grow-back time of the browse. Following this, the oscillations of lynx populations are not causal, but consequential.

Another hypothesis, the plant-hare-lynx interaction hypothesis, views the cycle as affected by the relationship between three trophic levels. Analysis done by Stenseth et al. (1997) found that the classic view of a symmetric predator-prey interaction is too simplistic for these data, and that "the dominant dimensional structure of the hare series is hypothesized to be due to a three-trophic level model in which the hare may be seen as simultaneously regulated from below and above." Stenseth et al. created a food web of the boreal forest ecosystem with the links directly influencing the snowshoe hare highlighted (Fig.6).

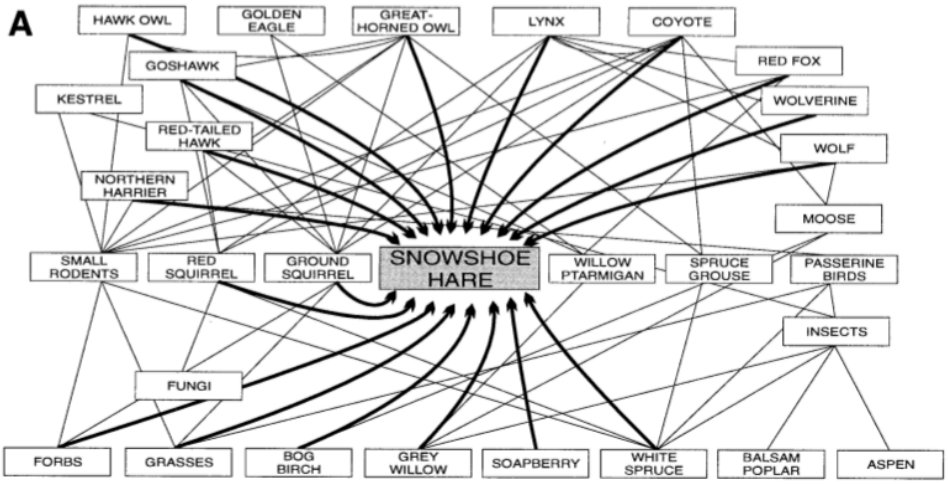


Fig.6 - Food web of *Lepus americanus,* taken from Stenseth et al. 1997.

As shown, hares feed on a variety of plants and are eaten by a wide array of predators. Lynx, although considered specialists, will also utilize other prey species. The analysis of Stenseth et al. (1997) suggests that the dual-trophic hare-lynx interaction is too simplistic. Zhang et al. (2007) found no significant predation effect for both hare and lynx populations, and concluded that "self-regulation or density dependence may be the major forces driving population cycles of hare and lynx for this time series." However, previous studies have

demonstrated a predation effect in hare-lynx cycling (Stenseth et al. 1997, 2004). To explain these inconsistencies, there are many factors that could be affecting the data's accuracy and the cycles of the species.

Data quality and accuracy

Because this historic time series is used in so many studies and is derived from fur records, it may have been edited in different ways. A number of disturbances (such as scale and fur price fluctuation in the market) could have affected the data quality. Predation effects would be more obvious at local scales but could be reduced at larger scales if the data are not appropriately combined (Zhang 2007). Hare and lynx population outbreaks also had a time lag among neighboring sites which was probably caused by surplus killing from lynx or other predators in the decline phase of a hare cycle (Krebs at al. 2001).

There is debate about the methods used to model the historic data set as well. Nedorezov (2016) rejected the use of the least-squares method:

> "The least-squares method is rejected due to a number of factors. These are the absence of criteria for selecting the type of minimized functional (which, as a rule, has nothing to do with the biological problem, or the available data, or the model) and the final result, i.e., the decision on the applicability or inapplicability of the model to data approximation is rendered on the basis of properties of the single point of the space of parameters (the global minimum of the functional). Consequently, there is an abundance of incorrect results from nonlinear models." (Nedorezov 2016)

Climatic influence

The exact role of climate in hare-lynx population cycles remains uncertain. Since the oscillations of hare and lynx populations are so strongly synchronized across Canada, it has been suggested, and since rejected, that large-scale meteorological factors (like sunspots) and climate forcing could be responsible (Zhang et al. 2007, Elton & Nicholson 1942). The models with predation but without climate forcing can produce only damped oscillations, but models that include climate forcing as well as sunspot signals can produce stable cycles (Yan et al. 2013).

The North Atlantic Oscillation (NAO), El Niño-Southern Oscillation, and other large climate phenomena can strongly impact local weather patterns and influence population dynamics of small mammals (Yan et al. 2013, Stenseth et al. 2004, Zhang et al. 2003). Yan et al. (2013) studied local and global climate to identify major pathways that influence the hare and lynx system:

> "Our results clearly indicate that the observed 10-year cycle is the result of joint forces of both intrinsic and external factors. Asymmetric predation, density dependence, and time lag play key roles in producing the damped oscillations, while the external climatic factors are essential in the appearances and intervals of sustained cycles of the hare and lynx system in Canada. Our results revealed the pathways from global climate to lynx populations through local climate, and highlighted the significance of delayed effects of climate factors on hare and lynx populations. Future studies should focus on investigating the underlying mechanism of the observed pathways and the population declines of lynx caused by climate warming." (Yan et al. 2013)

Biotic factors

There are major reproductive differences between hare and lynx that the Lotka-Volterra model doesn't account for. One of which being that hare breed like rabbits: Snowshoe hare can have three or four litters over a summer, with five leverets on average in each litter. Sexual maturity is reached at 1 year of age (Krebs et al. 2001). Lynx have much longer life spans than hare, and young lynx need approximately 10 months' parental care and 2 years to attain adult size. (Yan et al. 2013).

In Yan et al. 's study (2013), direct density dependence was found in hare population and a 2-3 year delayed density dependence was found in lynx populations. They speculated that this delayed density dependence in the lynx population could be caused by the necessary time for lynx's rearing, reproduction and maturity. Density dependence is mainly caused by intraspecific competitions for resources, which is a factor not included in the Lotka-Volterra model. Delayed density dependence produces damped oscillations in a Lotka-Volterra model, which is a problem for accuracy (Yan et al. 2013, Weisberg and Reisman 2008).

There is also the impact of hunting as a factor on the lynx population. One study analyzed the lynx population series to look for evidence of ecosystem bifurcation, which is defined as an abrupt or persistent regime shift that affects several trophic levels and results from environmental changes. Javier et al. (2000) studied the sudden shifts in the amplitude of oscillations from the Hudson Bay Company lynx time series, and found evidence that an increased trapping pressure aligned with amplitude fluctuations in lynx population. Being that this data came from fur trading records and our model assumes lynx have no predators, this contradiction will obviously result in at least some inaccuracy.

Conclusion

Applying a Lotka-Volterra predator-prey equation to this historic lynx and hare population data will result in a model that is only partially correct, because it excludes many

factors that influence the oscillation of both populations: climatic pressures, reproductive differences, human impact (hunting), and the inclusion of a third trophic level. The biological impacts of these three trophic levels ripple across many other species of predators and prey in the boreal forests of North America (Krebs et al. 2001). Creating a more accurate model with these missing factors included is an important next step, as the limits of lynx and hare resilience are still unknown. Until this is better understood, anthropogenic impacts will continue to threaten this complex and fascinating system.

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