Modelling the Populations of the Canadian Lynx and Snowshoe Hare

Pehan Amarathunge[1], Kushani De Silva[2]

Research and Development Center for Mathematical Modeling, Department of Mathematics, University of Colombo, Sri Lanka

[1] pehanhansaja@gmail.com , [2] kdesilva@maths.cmb.ac.lk

Abstract: The 10 yr hare–lynx (Lepus americanus– Lynx canadensis) cycles in the Boreal forest of North America have been well known for over 100 years yet its underlying mechanism is still not fully understood. Their predator-prey cycles demonstrate certain peculiar features such as the prey and predator oscillations appearing approximately in phase and a relatively large cycle length compared to similar predator-prey systems. We argue these deviations from a classical predator-prey system stem from an imbalance in the power of the prey and predator with the large relative abundance of hare tipping the balance towards the prey. As a result, we address this imbalance by increasing the predatory pressure on the hare in the form of additional predators. We consider two different forms of predatory pressure, the first being a top predator, that hunts on both the hare and lynx (HLC model). Then, we add an additional general predator to further increase the predatory pressure on the hare (HLCG). Our findings testify our initial premise that the abundance of the hare is crucial to the dynamics of this system.

Key Words : Predator-Prey Systems , Canadian Lynx , Snowshoe Hare , Sigmoid Functional Response   © 2023 The Author(s)

1.   Introduction

The Canadian Lynx (Lynx canadensis) is an important predator for the snowshoe hare (Lepus americanus) in the Northern boreal forests of North America, as studies[1] have suggested that the snowshoe hare consists of over 75% of their diet. This relationship suggests that their populations could be closely intertwined and hence makes a strong case for an investigation of the Lynx and Snowshoe Hare population as a predator-prey system.

   Between 1845 and 1935, the Hudson Bay company kept good records on the numbers of lynx and snowshoe hare pelts traded in the Boreal Forests, Canada. Figure 1 shows a plot of their data [2], which we will refer to as the original data set.

   There are two key observations from the original data, that suggest that this is not a conventional predator - prey interaction. Firstly, the relative abundance of the hare is significantly higher than that of the lynx and secondly, the predator and prey oscillations are approximately in phase, as they rise and fall simultaneously. This effect is most pronounced during 1875 - 1900. In particular, we speculate that the first observation is critical to shifting the balance of power within this predator-prey system to the hare. As a result, when designing a model, we intend to suppress the power of the hare by amplifying the level of predation exerted on the hare in an attempt to restore the balance of power within this predator - prey system. Furthermore, the heightened levels of predation manifests itself in the form of a top-predator, that consumes the lynx in addition to the hare. This is motivated by the fact that the predator and prey oscillations are in phase and thus there must exist some form of a common external intervention that forces both the hare and lynx population cycles to rise and fall simultaneously.

   Upon reviewing past modelling efforts, we can classify their idiosyncrasies as either addressing one of the two mentioned observations. One class of models amplifies the predatory pressure on the hare in order to suppress their rapid growth due to their high relative abundance. This increased predation has often materialised as an additional predator of the hare in the model, such as Tyson (2010)[3], who considered 3 different predators: the lynx, coyote and great-horned owl. Likewise, Deng (2016)[4] incorporates human intervention (trappers) as a top intraguild predator, which consumes both the hare and the lynx. In general, it has emerged as a consensus among both theoretical studies[5][6] and experimental studies[7] that elevated levels of predation are critical to regulating the lynx-hare cycles. On the other hand, several models address the synchronisation (in phase nature)
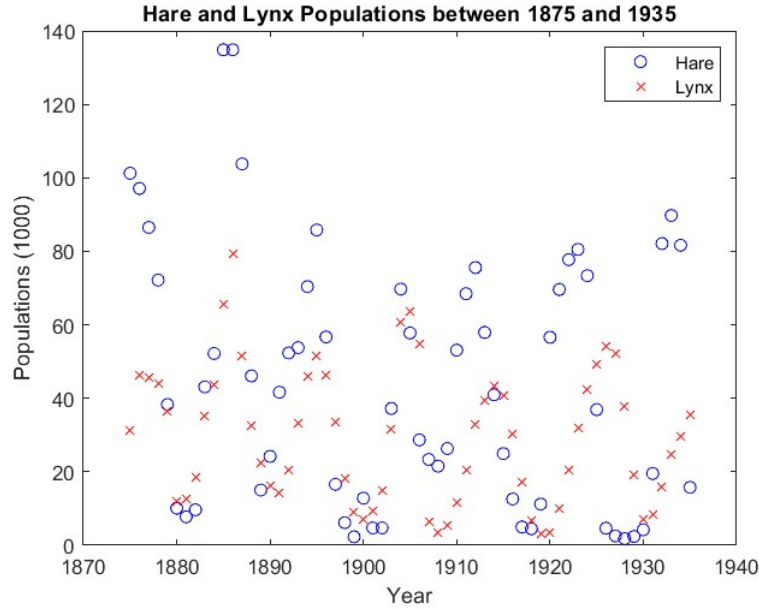
Fig. 1: Lynx and hare populations from 1845 to 1935 according to pelt trading records by the Hudson Bay Company

of the predator and prey oscillations by introducing an external force, which inhibits both the hare and lynx populations, thus causing both cycles to rise and fall simultaneously. The biological interpretation of this force may vary to a disease (Gilpin 1973[8]) to climate fluctuations[9]. Gilpin (1973) entails an epidemic, that passes through the hare once the hare population exceeds a certain threshold and the interaction between the hare and the lynx inflicts a particular percentage mortality in the lynx. Thus the disease forces the oscillations of both cycles to be in phase. Similarly, Yan (2013)[9] investigated the role of large scale climate fluctuations, such as the North Atlantic Oscillations and the El-Nino Southern Oscillations, which has been suggested to influence both the hare and lynx population[9][10]. The study reports that the external forcing of the cycles by the climate was crucial to the appearance of the 10 year cycles.

We consider the data in two separate sections: the first between 1875 and 1900; and the second between 1900 and 1930. We subsequently discover that a single top predator is insufficient to curtail the hare population during the first time period and hence we further accentuate the predation on the hare by including a distinct state variable (a general predator), that represents the combined effects of all predators on the hare, excluding the lynx and coyote. This general predator only consumes the hare and does not directly interact with any other of the species in this model.

In order to interpret our top predator in the biological context of the Boreal Forest in Yukon, we review other field studies and experimental research. According to a field study[11] in the North American Boreal forest, that used snow-tracking to record data about the snowshoe hare and its predator, the coyote and lynx are the two most important mammalian predators of the snowshoe hare. In addition, there is also evidence [7] that in Kluane Lake, Yukon, the coyote and lynx populations fluctuated with a similar frequency to that of the hare population, which suggests that both the coyotes and lynx showed clear functional responses to changing densities of snowshoe hares in Yukon.

It is important to note that the coyote is not considered as a specialist predator of the hare, which refers to the fact that the hare is not the only prey that it consumes, unlike the lynx, which is widely considered as a specialist. This is reflected by the findings in the same study, as among the 189 kills by coyotes, 47.1% were hares, 13.2% were red squirrels, and 37.6% were small mammals. In contrast, the lynx is often considered a specialist predator of the hare, as it forms a staple part of its diet. This is testified by several studies [12][13].

In addition, the same study states that the hare is victim to a myriad of predators, such as the Great Horned Owl, the Golden Eagle, the Red Fox, the Northern Harrier and Goshawks[7]. It is the combined effect of these

predators, that we represent as a generalist predator, which we subsequently introduce in a new model to further bolster the predatory pressure inflicted on the hare in the HLCT model.

2. The Hare Lynx Coyote (HLC) Model

We now formulate a model, that incorporates intraguild predation by the coyote. We have 3 state variables for the hare (H), lynx (L) and coyote (C). The ecological relationships between the hare, lynx and coyote are summarised in figure 2, where an arrow that points from species x to species y represents the consumption of x (prey) by y (predator). We refer to this model as the HLC model. As outlined in the introduction, the coyote's primary role is to regulate the abundance of the hare. In addition, it is modelled as intraguild top predator to comply with literature, [7][14][15] which has documented evidence that coyotes do in fact consume the lynx in this fashion. Therefore, the coyote acts as a form of external intervention, which could perhaps force the oscillations of predator and prey to be in phase.
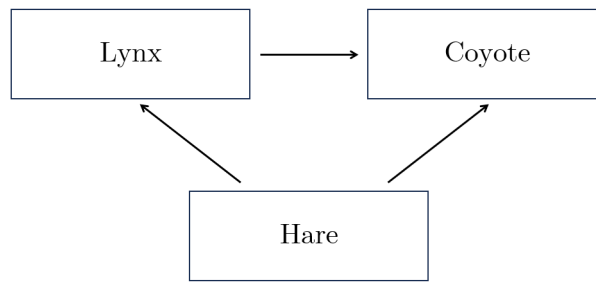

Fig. 2: Ecological relationships between the species in the model

2.1. Model Formulation

Below we introduce the governing equations behind our model. N, P_1 and P_2 represent the populations of the hare, lynx and coyote respectively. The biological interpretations of the parameters are given in table 1.

$$
\begin{cases}
\dot{H} = rH\left(1 - \dfrac{H}{K}\right) - aHL - \dfrac{bH^2C}{1+mH^2} \\[3mm]
\dot{P_1} = -cL + dHL - gLC \\[3mm]
\dot{C} = -eC + \dfrac{fH^2C}{1+mH^2} + hLC
\end{cases}
\tag{1}
$$

$$
H(0) > 0,\ L(0) > 0,\ C(0) > 0 \tag{2}
$$

2.2. Logistic Growth of the Hare

In the absence of predation, the governing equation for the hare population reduces to $\dot{H} = rH\left(1 - \frac{H}{K}\right)$. This equation describes logistic growth with the parameter k serving as a carrying capacity. Therefore, in the absence of predation, our hare population will not grow exponentially without bounds, which is biologically sensible, as intraspecific competition among the hare will eventually inhibit their growth.

2.3. Functional Response of the Coyote - Hare Interaction

The functional response is the way in which the number of prey eaten per predator (over a short period) changes with prey density. There is evidence[16] that the functional response of a generalist predator is different to that of a specialist predator. It is speculated that this difference is driven by "prey switching" : when a certain prey

Table 1: Biological Interpretation of the Parameters used in the HLC model

Parameter	Description
r	Hare Growth Rate
k	Hare carrying capacity
a	Hare predation rate by lynx
b	Hare predation rate by coyotes
c	Natural death rate of lynx
d	Rate of conversion of hare biomass to lynx biomass
e	Natural death rate of the coyotes
f	Rate of conversion of hare biomass to coyote biomass
g	Lynx predation rate by coyotes
h	Rate of conversion of lynx biomass to coyote biomass
m	Half-saturation constant of the coyote-lynx interaction

species occurs at low density, it is more economical for the predator to give up searching for it and instead concentrate on other prey.

Specialists predators are more suited to a Holling type 2 functional response, where the consumption rate of the prey by the predator initially increases (gradient at t=0 is positive) with prey population, but eventually plateaus as the prey population reaches very large numbers. On the other hand, the same study suggests that for a generalist predator, the sigmoidal Holling type III response, which has zero slope at zero, is much more appropriate, which is further testified by other studies [16][17]. In light of this new information, we amend the model, such that coyote's predation rate of the hare has a type 3 functional response.

2.4. Simulating the model and Parameter Estimation

To gauge the validity of the model, we will solve the governing equations for the system numerically using the Runge - Kutta method of order 4. The initial values of the populations of the lynx and hare have been obtained from the original data set. Due to the lack of data on the coyote population, we estimate the coyote population at relevant years based on other field studies[7] conducted during other time frames.

To numerically solve this system of differential equations, we will need to provide estimates for the parameters in the model. To estimate the parameters of the model, we attempt to choose our parameters such that the sum of the squares of the errors between the experimental (obtained from the data set) populations and theoretical or predicted populations are minimised by using an optimisation algorithm called the Nelder–Mead method (also known as the downhill simplex method). However, in order to implement this algorithm, we need an initial estimate for these parameters. To estimate these parameters, we consult the data obtained from several field studies and past modelling efforts of the snowshoe hare and Canadian Lynx at Kluane Lake, Yukon[7].

We will split the data into two different time periods. Time period 1 runs from 1900 to 1930, whereas time period 2 runs from 1875 - 1900. This split is motivated by the observation that the abundance of hare is much larger in period 2, than 1 and the phenomenon of the prey and predator oscillations being in phase is more pronounced in period 2. This implies that the 'strength' of the hare or rather the imbalance of power was more accentuated in period 2 than 1 and hence we fit our model to these two time periods separately.

2.5. Fitting the HLC Predation Model to Time Period 1

We now estimate parameters for the model, as explained in the former section. Our initial estimates for most parameters were derived from field studies[7] and other research papers[15] that were modelling the snowshoe hare and Canadian lynx populations and are listed in table 2 alongside their optimal values. The populations predicted by the model are illustrated in figure 3. This successful fit reflects on the fact that the level of predation induced on the hare by a single top predator is sufficient to curb the strength of the hare.

Table 2: Initial Estimates and Optimal Values of Parameters in the HLC Model for Time Period 1

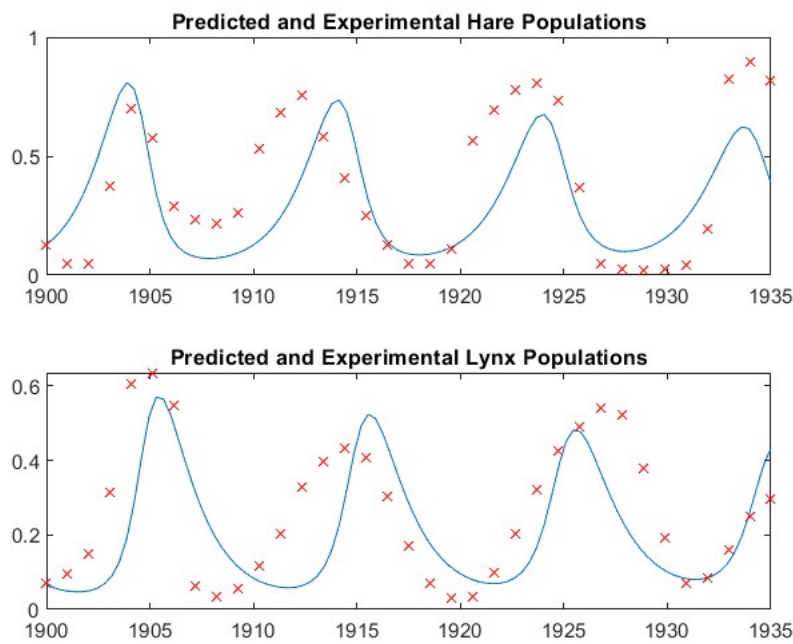| Parameter	Initial Estimate	Optimal Values
r	0.08	0.758342
k	0.0175	8.965561
m	2	12.251477
a	5.05	3.327033
b	8.58	7.457302
c	0.01	0.682326
d	0.01	2.321018
e	0.01	14.460451
f	0.01	2.488575
g	0.01	25.977797
h	0.01	12.690652

Fig. 3: Fitting the HLC Model to Time Period 1

2.6. Fitting the HLC Model to Time Period 2

We first attempt to fit the data to the HLC model using the same initial parameter estimates as for period 1, however this is unsuccessful and provides a poor fit. Nevertheless, the result of the optimisation is intriguing as it inflates the population of the lynx to a value considerably larger than the original data as shown in figure 4. The disparity between the predicted lynx population and the original lynx population represents the additional predation, that must be inflicted on the hare in order to obtain a satisfactory fit to the data. This consolidates the fact that further predation on the hare is necessary in order to provide us with an improved fit.

It is evident from the original data set that the hare population is considerably larger during period 2 than during 1900 - 1930 with the maximum hare population almost twice as large. Consequently, this suggests that the hare possesses substantially more power during time period 2 than 1, which could perhaps justify why one top predator was inadequate to restrain the power of the hare.
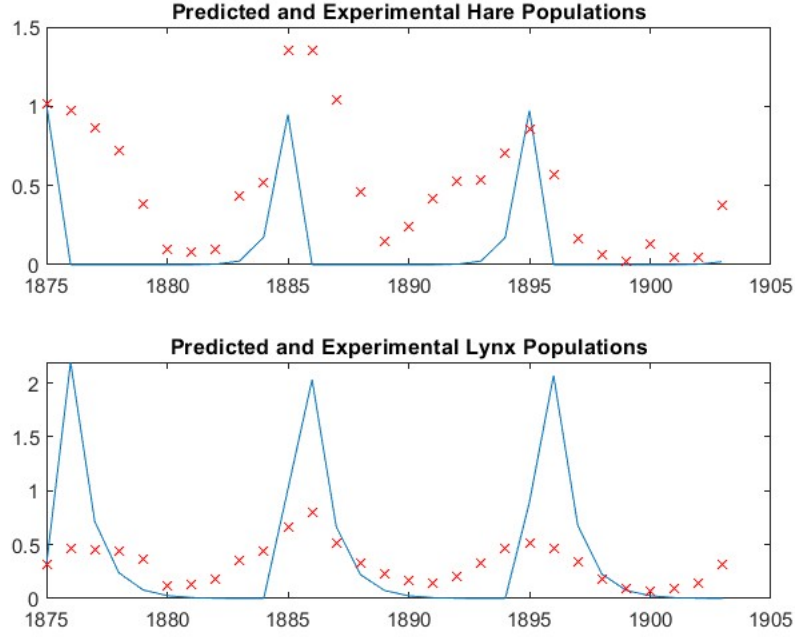
Fig. 4: Fitting the HLT model to data from 1875 to 1900

3. The Hare-Lynx-Coyote-General Predator (HLCG) Model

In light of the failures of the HLC model to obtain a reliable fit to the data from time period 2, we now refine the former HLC model to address some of its shortcomings, when explaining this data. Firstly, we need to implement an additional mechanism to restrain the hare population and this manifests in the form of an additional predator (G), that only consumes the hare. The model will be referred to as the HLCG model and the ecological relationships between these species are illustrated in figure 5. We follow the same convention for arrow direction as explained for figure 2.
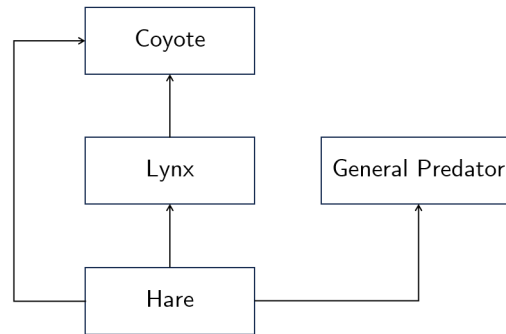

Fig. 5: The Ecological Relationships between species in the HLCG Model

3.1. The Governing Equations for the HLCG Model

It will be interpreted as a general predator, that combines the effects of all the other predators of the hare. The model includes 4 state variables the hare (H), the lynx (L), the coyote (C) and a general predator (G) and is adopted from another study[4]. The model is stated below in 3 and the biological interpretations of the parameters are stated in table 3.

The Governing System for Equations (3) for the HLCG Model

$$\begin{cases} \dot{H} = H\left(b - mH - \dfrac{a_1 L}{1 + h_1 a_1 H} - \dfrac{a_2 G}{1 + h_2 a_2 H} - \dfrac{u_1 C}{1 + u_1 v_1 H + u_2 v_2 L}\right) & \text{(3a)} \\[3ex] \dot{L} = L\left(\dfrac{b_1 a_1 H}{1 + h_1 a_1 H} - d_1 - m_1 L - \dfrac{u_2 C}{1 + u_1 v_1 H + u_2 v_2 L}\right) & \text{(3b)} \\[3ex] \dot{G} = G\left(\dfrac{b_2 a_2 H}{1 + h_2 a_2 H} - d_2 - m_2 G\right) & \text{(3c)} \\[3ex] \dot{C} = C\left(\dfrac{r_1 u_1 H + r_2 u_2 L}{1 + u_1 v_1 H + u_2 v_2 L} - d_3 - m_3 C\right) & \text{(3d)} \end{cases}$$

Table 3: Optimal Values of Parameters in the HLC Model for Time Period 2

Parameter	Description
b	Hare's per-capita growth rate
m	Hare's per-capita growth rate
a_1	Hare's encounter rate with Lynx
h_1	Lynx's handling time of Hare
a_2	Hare's encounter rate with the General Predator
h_2	Generalist Predators' handling time of Hare
u_1	Hare's encounter rate with the Coyote
v_1	Coyote's handling time of Hare
u_2	Lynx's encounter rate with the Coyote
v_2	Coyote's handling time of the Lynx
b_1	Lynx's consumption-to-birth ratio
d_1	Lynx's per-capita death rate
m_1	Lynx's intraspecifc competition rate
b_2	Generalist predators' consumption-to-birth ratio
d_2	Generalist predators' per-capita death rate
m_2	Generalist predators' intraspecifc competition rate
r_1	Coyote's Hare-to-recruitment ratio
r_2	Coyote's Lynx-to-recruitment ratio
d_3	Coyote's per-capita death rate
m_3	Coyote's intraspecific competition rate

3.2. Fitting the HLCG model to time period 2

We now attempt to fit the HLCG model to time period 2, using the same procedure as with the HLC model. We use the same initial estimates for these parameters as the original study from which the model was borrowed. The simulated model with these optimal parameters are compared to the original data in figures 6a and 6b. According to figure 6b, the coyote population goes extinct, which instantly invalidates our model.
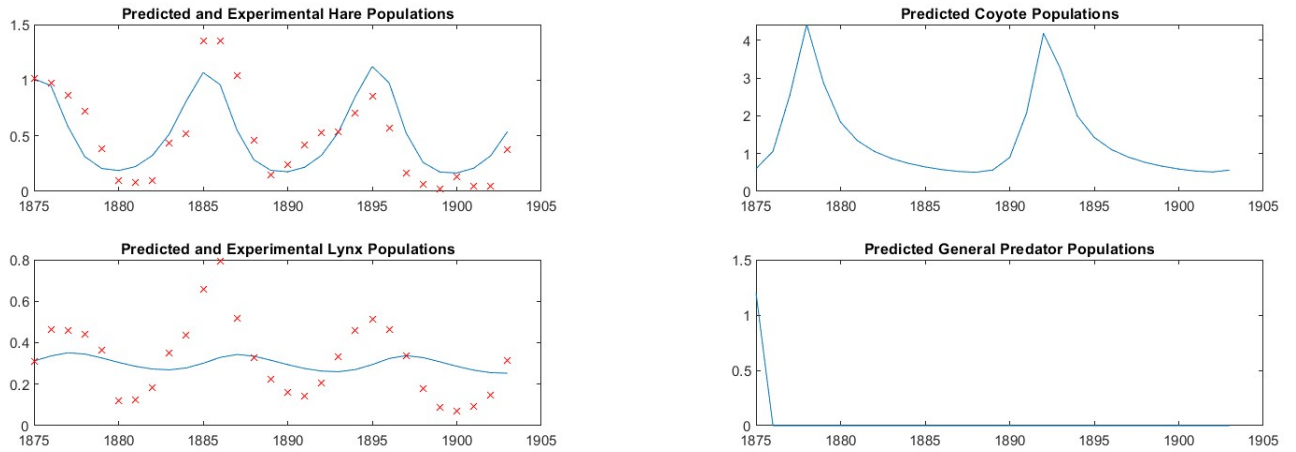
(a) Time Evolution of Hare and Lynx Populations Predicted by the HLGC Model

(b) Time Evolution of the general predator and coyote populations predicted by the HLGC model

There could be several possible reasons to explain the failure of the HLCG model and the discrepancy between the model and the original data. Firstly, our solution may be too simple. By including a single generalist predator that combines the effects of all the various predators of the hare, we have essentially overlooked the intricate interactions between these predators and their corresponding prey. The Boreal Forest in Yukon is home to a vast and diverse network of species[7] and it may be perhaps the case that these deeply interconnected interactions and ecological relationships play a key role in governing the hare and lynx population cycles in this complex system. However, incorporating such interconnected interactions would decrease the computational efficiency of the model, due to the sheer number of state variables and corresponding parameters involved. Therefore there is potential to further investigate the minimum level of sophistication that needs to be implemented into the model through the addition of more prey and predators along with the networks and ecological relationships that they encompass with the species that have already been included in the model.

On the other hand, there may be additional factors, that may be curtailing the strength of the hare population. As pointed out by Gilpin[8], there might be a certain disease developing in the hare population, which could possibly inhibit their reproduction. Another possibility could be additional seasonal factors. For example, many studies[18][19] have pointed to seasonal effects, such as the El Nino-Southern Oscillation (ENSO)[18], which occurs every 10 years. Such climate fluctuations could lead to food shortages by decreasing the quality of vegetation or could increase foraging time for the hare.

4. Conclusion

Both the HLGC and the HLC models were based on the premise that the relative abundance of the hare was critical to the dynamics of this predator-prey system. In particular, there was an imbalance of power between the predator and prey with the scale tipping towards the hare in this case, which motivated us to inflict greater predation on the hare. The success of the HLC model in describing the data from 1875-1900 and its subsequent failure in predicting the data from 1900 - 1930 is a testament to our original premise regarding an imbalance of the power between prey and predator.

References

[1] Ronald Hanson Kayla; Moen. "Diet of Canada Lynx in Minnesota Estimated from Scat Analysis". In: *University Minnesota Digital Conservancy* (2008).

[2] E. P. Odum. *Fundamentals of Ecology*. Philadelphia and London, 1953.

[3] Rebecca Tyson, Sheena Haines, and Karen Hodges. "Modelling the Canada lynx and snowshoe hare population cycle: The role of specialist predators". In: *Theoretical Ecology* 3 (May 2010), pp. 97–111. DOI: 10.1007/s12080-009-0057-1.

[4] Bo Deng. "An Inverse Problem: Trappers Drove Hares to Eat Lynx". In: *Acta Biotheor* (2018).

[5] Aaron A. King and William M. Schaffer. "The Geometry of a Population Cycle: A Mechanistic Model of Snowshoe Hare Demography". In: *Ecology* 82.3 (2001), pp. 814–830. ISSN: 00129658, 19399170.

[6] Stenseth NC and Krebs CJ. "Population regulation in snowshoe hare and Canadian lynx: asymmetric food web configurations between hare and lynx". In: *Proc Natl Acad Sci U S A* (1997).

[7] Boonstra R Krebs CJ Boutin S. "Ecosystem Dynamics of the Boreal Forest: The Kluane Project". In: *Oxford University Press, New York* (2001).

[8] Michael E. Gilpin. "Do Hares Eat Lynx?" In: *The American Naturalist* 107.957 (1973), pp. 727–730. ISSN: 00030147, 15375323. URL: http://www.jstor.org/stable/2459670 (visited on 07/14/2023).

[9] Chuan Yan et al. "Linking climate change to population cycles of hares and lynx". In: *Global Change Biology* 19.11 (2013), pp. 3263–3271. DOI: https://doi.org/10.1111/gcb.12321. URL: https://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.12321.

[10] Jim Hone, Charles Krebs, and Mark O'Donoghue. "Is the relationship between predator and prey abundances related to climate for lynx and snowshoe hares?" In: *Wildlife Research* 38 (Oct. 2011), pp. 419–425. DOI: 10.1071/WR11009.

[11] et al O'Donoghue Mark. "Behavioural Responses of Coyotes and Lynx to the Snowshoe Hare Cycle". In: *Oikos* (1998).

[12] "Lynx Demography during a Snowshoe Hare Decline in Alberta". In: *The Journal Wildlife Management* 43.4 (1979), pp. 827–849. ISSN: 0022541X, 19372817. (Visited on 07/25/2023).

[13] Richard S. Miller. In: *Oikos* 5.1 (1954), pp. 134–136. ISSN: 00301299, 16000706. URL: http://www.jstor.org/stable/3564656 (visited on 07/14/2023).

[14] Marissa A. Dyck, Eileen Wyza, and Viorel D. Popescu. "When carnivores collide: a review of studies exploring the competitive interactions between bobcats Lynx rufus and coyotes Canis latrans". In: *Mammal Review* 52.1 (2022), pp. 52–66. DOI: https://doi.org/10.1111/mam.12260.

[15] H. M. Safuan et al. "A two-species predator-prey model in an environment enriched by a biotic resource". In: *Proceedings of the 16th Biennial Computational Techniques and Applications Conference, CTAC-2012*. Ed. by Scott McCue et al. Vol. 54. ANZIAM J. 2014, pp. C768–C787.

[16] William W. Murdoch. "Switching in General Predators: Experiments on Predator Specificity and Stability of Prey Populations". In: *Ecological Monographs* 39.4 (1969), pp. 335–354. ISSN: 00129615. URL: http://www.jstor.org/stable/1942352 (visited on 08/09/2023).

[17] Heikki Hirvonen. "Shifts in Foraging Tactics of Larval Damselflies: Effects of Prey Density". In: *Oikos* 86.3 (1999), pp. 443–452. ISSN: 00301299, 16000706. URL: http://www.jstor.org/stable/3546649 (visited on 08/10/2023).

[18] Zhibin Zhang, yi Tao, and Zhenqing Li. "Factors affecting hare lynx dynamics in the classic time series of the Hudson Bay Company, Canada". In: *Climate Research* 34 (July 2007), pp. 83–89. DOI: 10.3354/cr034083.

[19] K. Kielland, K. Olson, and E. Euskirchen. "Demography of snowshoe hares in relation to regional climate variability during a 10-year population cycle in interior AlaskaThis article is one of a selection of papers from The Dynamics of Change in Alaska's Boreal Forests: Resilience and Vulnerability in Response to Climate Warming." In: *Canadian Journal Forest Research* 40.7 (2010), pp. 1265–1272. DOI: 10.1139/X10-053.