

Adapting a Predator-Prey System to Include Age Structuring

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Abstract This paper examines the process and final result of extending the basic

Lotka-Volterra predator-prey model to include different age groups within each population. Basic analysis of the results were performed to determine the relevance of the proposed extension. Calculations and graphing were handled with MatLab. The natural outcome of the model should be either a periodic cycle about an equilibrium, which is very similar to our original Lotka-Volterra model, all the populations should tend to a steady-state equilibrium, or at least one should go extinct.

Introduction In basic Differential Equations and Mathematical biology classes, simple models are used to examine natural systems. One common example in Differential Equations is the Lotka-Volterra model. This model was created to help explain the relationship between the decrease in fishing and the rise in predatory fish in the Mediterranean Sea during World War One. The model correctly indicated that, as the amount of fishing decreased, the predator population increased significantly more than the prey population. This model will be one of the starting equations for my adaptation.

The general Lotka-Volterra model is:

$$\frac{dH}{dt} = a(H) - b(H)(L) \quad (1)$$

$$\frac{dL}{dt} = -c(L) + d(H)(L) \quad (2)$$

These two equations show the rate of change per unit of time for the Hare (1) and Lynx (2) populations. H represents the entire Hare population, while L represents the entire Lynx population. The other four parameters are the growth factors (A and C) and the interaction factors between the species. The most basic way to model interaction between species is to say that the amount of interaction is proportional to how often they come into contact with each other. By multiplying both of the populations together, we find the greatest interaction when both populations are large, and the least interaction when both populations are small. The final results of these equations, given generic values for a, b, c, and d, produce cyclic populations for both the Lynx and Hare. These are graphed in figures 1 and 2. The periods for each population were the same, although the Lynx are slightly offset from the Hare. This will be true for every part of this model. For this to not be true, there would have to be another outside factor controlling the period. A more extensive background for this model can be found in my previous paper entitled "Predator-Prey Models" in which I examined the basic Lotka-Volterra model in more detail. [2]

A basic age-structured population model is the Leslie Matrix Model, also called a population projection matrix. This model was developed by P. H. Leslie to describe the growth of organisms through different age groups. An example of the general Leslie Matrix is [3]:

$$L = \begin{bmatrix} s_1 m_1 & s_1 m_2 & \dots & s_1 m_{w-1} & s_1 m_w \\ s_2 & 0 & \dots & 0 & 0 \\ 0 & s_3 & \dots & 0 & 0 \\ 0 & 0 & \dots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \dots & s_w & 0 \end{bmatrix}$$

This matrix would be multiplied by the current population vector to get each successive population. The factor s_n is the survival fraction and m_n represents the amount of breeding per individual, with each individual producing m_n offspring per year, n denoting the age group that the individual is in. Because only the female members of a species give birth, we will divide the total births by two to obtain the number of births per individual.

My final model needed to include features from both the Lotka-Volterra system of differential equations and the Leslie Matrix model. My model combined these models into a system of differential equations, rather than a matrix model. I chose the use of differential equations instead of a matrix model because adapting the matrix model to a set of differential equations is easier than turning the equations into a matrix.

For this model a few assumptions have to be made.

- The two populations interact only with each other.
- Each population contains three subpopulations (juvenile, mature, and post-mature).
- Each subpopulation can only mature into the next subpopulation, they cannot grow younger.
- The juvenile group:
 1. Is pre-pubescent and as such cannot produce offspring.
 2. Are sheltered by the mature group.
 3. Do not spend any time hunting/foraging for food alone.
- The mature group:
 1. Gives birth to juveniles.
 2. Spends the most time in the open.
 3. Is the most fit of all three groups.
 4. Is bounded by the average age for sexual maturity and the average death age.
- The post-mature group:
 1. Is the final group before death.
 2. Are defined from the average death age to the absolute death age.
 3. Gives birth to juveniles.
 4. Are less healthy than the other groups, so they are not as physically fit, which means they hunt or evade hunters less effectively.

The basic facts for the Snowshoe Hare came from [1] and [6]. From these sources I determined that the Hares are considered to be juvenile for about the first five months of life. The Hares are sexually mature by the next breeding period, which takes place an average of five months later. The average life expectancy for the Snowshoe Hare is marginally over two years, thus, following sexual maturity, the Snowshoe Hare spend about one year as a mature adult. The absolute life expectancy for the Snowshoe Hare is about two years, so the post-mature sub-population spans seven months, ranging from one year and five months to two years. Once they are sexually mature, the female Hares give birth to an average of three young per litter, with about two litters per year.

The Canadian Lynx facts came from [4] and [5]. The Lynx juvenile period is about 27 months long. Any hunting done during this period is under the supervision of a mature adult, and is therefore only reflected in the model as the mature group's interaction with the Hare population. They spend the subsequent 117 months as mature adults, before moving into the final 36 months of their life. The females give birth to one litter with about two to three young per year in the mature and post-mature periods.

First Attempt Putting these models together seems somewhat straightforward at first glance. It appears that you should be able to insert each Hare sub-population for H in the Lotka-Volterra model, replace L with each Lynx sub-population, and add in the breeding factors from the matrix model, to obtain a natural response. This initial attempt presents the following system of differential equations:

$$\begin{aligned}\frac{dH_j}{dt} &= a * s_1 * H_j + m_2 * H_m * s_1 + m_3 * H_p * s_1 \\ \frac{dH_m}{dt} &= b * s_2 * H_j + c * H_m * s_2 - M * H_m * L_m - N * H_m * L_p \\ \frac{dH_p}{dt} &= d * s_2 * H_m + e * s_2 * H_p - O * H_p * L_m - P * H_p * L_p \\ \frac{dL_j}{dt} &= E * s_4 * L_j + m_5 * s_4 * L_m + m_6 * s_4 * L_p \\ \frac{dL_m}{dt} &= R * H_m * L_m + S * H_p * L_m + g * s_5 * L_j * + h * s_5 * L_m \\ \frac{dL_p}{dt} &= U * H_m * L_p + V * H_p * L_p + i * s_6 * L_m + j * s_6 * L_p\end{aligned}$$

When these populations are graphed, it shows a fluctuating graph that displays almost everything expected. (Figures 3 and 4).

There are two seemingly unnatural characteristics in these graphs. The first one is that the mature and post-mature Lynx populations go through a growth phase at the same time. The post-mature population should be slightly off-set from the mature group in its peaks. When the mature population peaks, a lot of them are still moving into the post-mature group. So the post-mature group would peak just after it. This discrepancy from what we expect will be discussed in ore detail later. An additional problem is that the juvenile Lynx population dies out and does not come back from extinction, with no apparent effect on either the mature or post-mature populations. What should be seen is that once the juveniles go extinct, without any new births, then the mature and post-mature populations should go extinct as well, as they should not be able to grow at all without a previous population to mature into that group. This offset relationship is shown in the Hare populations where the peaks are offset between the juveniles, mature, and post-mature. The part of the equations that gives rise to the unnatural mature births is contained in the aspects of the mature and post-mature Lynx equations that increase the population from interaction with the Hares. Those sections are: $R * H_m * L_m + S * H_p * L_m$ and $U * H_m * L_p + V * H_p * L_p$. Any increase in population that does not come from a previous sub-group is not natural. It represents an individual who is born fully mature or post-mature.

A modification The Hare equations can be kept mostly unchanged. The decreasing interaction factor gives rise to the cyclic period that we expect from the original Lotka-Volterra solution. The equations for all of the populations have a growth factor in them

that will be changed to a death/maturation factor. Instead of using a growth rate such as $\frac{11}{12}$, we will change the factor to $-\frac{1}{12}$, so that the population decreases after a time unit given no other interactions. Using only a growth factor the populations would unnaturally grow without any previous sub-population needed. This means that if all of the populations were extinct, except for either the mature or post-mature Lynx, then the equation would reduce to $\frac{dP}{dt} = x * P$, which is increasing. This would be unnatural, given no food source this population should die off. Another change that needs to be made is that the factors comparable to $+d * L * H$ have to be modified or removed since they are the source of the spontaneous mature and post-mature births. The only positive factors that we can have in the mature and post-mature equations are the growth factors from the previous sub-population. However, having no interaction between the Hare and the Lynx populations represented in the equations pertaining to the growth of the Lynx population would be unnatural. We have to be able to account for both fluctuating Hare and Lynx populations in all equations. To fix this potential oversight we will add an inverse factor to the death rate of each Lynx population. When the Hare population is high, we expect the death rate of the Lynx to be lower then when there is a very limited prey population. This factor will be proportional to $\frac{L}{H_j + H_m + H_p}$ where the proportion is the death factor (in months) for the specific sub-population. When the Hare population is as large as possible, the death rate of the Lynx is almost totally from maturing into the next age group. When the Hares are in a low population, the death/maturation rate will be a lot higher. This is a natural response to population changes. While the prey population is much larger then the predators, the predators will not starve and will only move out of their sub-group by aging. When the prey is in short supply, the predators will starve and compete with each other for food, increasing their death rate. The equations now look like:

$$\begin{aligned} \frac{dH_j}{dt} &= m_2 * H_m * s_1 + m_3 * H_p * s_1 - b * H_j \\ \frac{dH_m}{dt} &= b * s_2 * H_j - d * H_m - M * H_m * L_m - N * H_m * L_p \\ \frac{dH_p}{dt} &= d * s_2 * H_m - k * H_p - O * H_p * L_m - P * H_p * L_p \\ \frac{dL_j}{dt} &= -g * L_j + m_5 * s_4 * L_m + m_6 * s_4 * L_p \\ \frac{dL_m}{dt} &= g * s_5 * L_j - \frac{i * L_m}{H_j + H_m + H_p} \\ \frac{dL_p}{dt} &= i * s_6 * L_m - \frac{l * L_p}{H_j + H_m + H_p} \end{aligned}$$

Graphing these equations requires putting in parameters for the many variables. The maturation/death factors (b, d, g, k, i, l) have already been figured out from the ages (in months) that a population will turn into the next sub-group, or die. One of my assumptions was that the only interaction is between these two species, therefore there shouldn't be any environmental effects in my model. The survivability factors (s_1 - s_6) would therefore be 1. The birth rates come from the number of litters and average litter size for each group. From my collected data, the birth rates are $m_2 = m_3 = 3$ and $m_5 = m_6 = 1.5$. Only the variables M, N, O, P need to be figured out. We assumed earlier that the all of the juveniles are sheltered, so they do not have any predation factors. We also assumed that the mature were the most fit and therefore could both hide and hunt most effectively. This leads us to

the conclusion that N is less than P and M is less than O , in addition to the fact that N is less than M and P is less than O . After some trial and error I came up with generic values for all four. My final result used:

- $M = .9$
- $N = .85$
- $O = 1$
- $P = .95$

I came up with these values by looking at the Hare population since the Lynx depend on them solely for food. If they seemed to be dying off too quickly, then I decreased these values, if they grew exponentially, I increased the values, to keep the population in check. When I graphed the six equations in MatLab I obtained figures 5 and 6. Figure 7 shows that if we extend our graph to a longer time frame, the populations are still going through the same cycles.

If we examine these graphs we see a few desirable properties.

- We have cyclic total populations that neither die out nor increase exponentially.
- Our Lynx population is offset from our Hare population.
- The total population makes one full cycle, and then repeats that same cycle over and over.
- As long as we don't have an outside factor enter our system, it will stay constant.

There is still one discrepancy between the model and what we expected to see. Ideally, the mature population should peak slightly after the juvenile group, and the post-mature group peak slightly after the mature group. In our model all the Hare groups peak at the same time and then all the Lynx groups peak at the same time. How would this happen in the wild? The Lynx population as a whole goes through a growth phase until the Hare population has almost bottomed out. By the time the juvenile Lynx start to decrease, the Hare population has almost dropped off completely. At this point the maturation/death factor for the mature Lynx group is also starting to grow significantly larger. So the mature Lynx population is decreasing as well despite an increased number of juveniles maturing.

A Further Modification While working on this project, Professor Shi proposed that I change my Hare dependence in the Lynx equations. The current model only shows a Hare dependence in the Lynx population in the death/maturation rate. There should be an inclusion of Hare dependence in the mature and post-mature equations which directly stifles or encourages the growth of each sub-population in the equations. There are two different places that this new factor could be included. It could go into the variables g , i , s_5 , or s_6 to signify that a larger Hare population would increase the hunting, and subsequently, would directly increase the number of Lynx that would survive into the next sub-population. The term could also factor into the variables m_5 , m_6 , or s_4 to signify that the increase in hunting would stimulate an increase in birth rates. The latter suggestion would break with previous data included in my model, so I will attempt to create a factor that would work with the

first case. The variables g and i appear in both positive and negative instances. If I make g or i increase with the Hare population, then a sub-population will actually decrease when the Hare population increases. Since this is not what we would expect to happen naturally, those variables are left unchanged. This leaves s_5 and s_6 to be modified.

We have to look at some fundamental elements of s_5 and s_6 to figure out a way to modify them. They are the survival factors for the mature and post-mature Lynx age groups, so they cannot be larger than 1. If they get larger than 1, our survival percentage is over 100, which is not physically possible. These two numbers should both go to 0 as the total Hare population ($H_t = H_j + H_m + H_p$) goes to 0. A function with an asymptote at 1 and passing through the origin would satisfy these two conditions. The function $s = -\frac{1}{H_t} + 1$ has an asymptote at 1, which is good but $s = 0$ when $H_t \neq 0$. The function $s = e^{H_t} - 1$ passes through the origin, but then increases exponentially. While the second function cannot be harnessed to satisfy both conditions, we were taught in basic algebra how to shift functions left and right. To get the function to pass through the origin we will re-write it as $s = 1 - \frac{1}{H_t + 1}$. This function has both properties that we want. The survivability of the Lynx now depends on the Hare population, so when the Hare are thriving, the Lynx will thrive, but when the Hare are in short supply, the Lynx will starve.

Another slight change is that to ensure a specific number of post-mature Lynx are dying off, I added in another term of $-l * L_p$. Now no matter what H_t they will lose a specific portion of their population. This is a very minor change, and the model would work without the change. This change is just to ensure that as many natural occurrences that can be modeled in this model are modeled. The post-mature Hare population does not need this additional term because their only death/maturation term for the post-mature is a non-varying one. They will always lose that number. These equations look like:

$$\begin{aligned} \frac{dH_j}{dt} &= m_2 * H_m * s_1 + m_3 * H_p * s_1 - b * H_j \\ \frac{dH_m}{dt} &= b * s_2 * H_j - d * H_m - M * H_m * L_m - N * H_m * L_p \\ \frac{dH_p}{dt} &= d * s_2 * H_m - k * H_p - O * H_p * L_m - P * H_p * L_p \\ \frac{dL_j}{dt} &= -g * L_j + m_5 * s_4 * L_m + m_6 * s_4 * L_p \\ \frac{dL_m}{dt} &= g * s_5 * L_j - \frac{i * L_m}{H_j + H_m + H_p} \\ \frac{dL_p}{dt} &= i * s_6 * L_m - l * L_p * \left(1 - \frac{1}{H_j + H_m + H_p}\right) \end{aligned}$$

Here s_5 and s_6 are $1 - \frac{1}{H_t + 1}$. The rest of the equations remained unchanged. The graphs of these equations show a new phenomena. (Figures 8 and 9). If you look at figure 8, you can see that we have the offset peaks that we were hoping for. However they are offset exactly opposite what we expected. The post-mature peak comes first, then the mature peak, and finally the juvenile peak. The juvenile peak coming after the mature peak can be explained by the fact that when the mature group is at its peak population, it will be giving birth to the most offspring, so the juvenile peak must come at or after the mature peak. The post-mature peak is a little bit before the mature peak and a bit more away from the juvenile peak. This can be explained by the fact that in the Hare population, the post-mature group is the first to get caught and eaten, so they will max out their population, then

start dying off from predation soon then the mature group, which can hide better. In the Lynx population, this can be seen as the post-mature group having too much competition for food, so it dies off once the Lynx population reaches a certain point, even though the Hare population is still increasing. So the peaks could be explained in both offset situations. This also explains why all the sub-populations can peak at the same time because if the hunting and competition factors even out, the peaks would not be offset.

The other phenomena is that both the total populations and the sub-populations tend toward a steady-state equilibrium. The cyclic period slowly decreases in amplitude until the populations are constant. This outcome is not as easy to find in the wild. Because the populations are constant, as soon as an individual is born, another juvenile dies/matures. As soon as an individual matures, another individual in that sub-population dies/matures. Technically this could happen, however it is not probable. A cyclic population is more likely to happen. The previous set of equations that had a constant survival percentage had a more realistic result.

Conclusion The attempted model is now complete. I have created a predator-prey model that incorporates age groups as well as two distinct populations. Either of the latter two sets of equations could be used. Further examination of both of them should be performed to figure out the better one for the populations that are being modeled. The models could be extended to include environmental effects as well by adding in another factor to the s_n amounts. This model could be used for research given a system of two species that only interact with each other. If they compete with each other for a resource a few of the factors would need to be changed, but it would not be too much more difficult than adapting the Lotka-Volterra model to a competition model. Anything that the Lotka-Volterra model can be adapted to handle, my model could be adapted to handle, provided there are distinct age groups.

Modifying the original one age group Lotka-Volterra model to the current model, required 4 additional equations. Incorporating an additional age group to each population in my model, I would need 8 equations. The amount of variables increases dramatically with each increase the number of in age groups included. Extending this model to encompass a full population complete set of age groups for both the predator and the prey would require numerous equations and a substantial investment of time. However, for the purposes of teaching the basics of predator-prey age-structured interactions, the obtained model works nicely.

Works Cited

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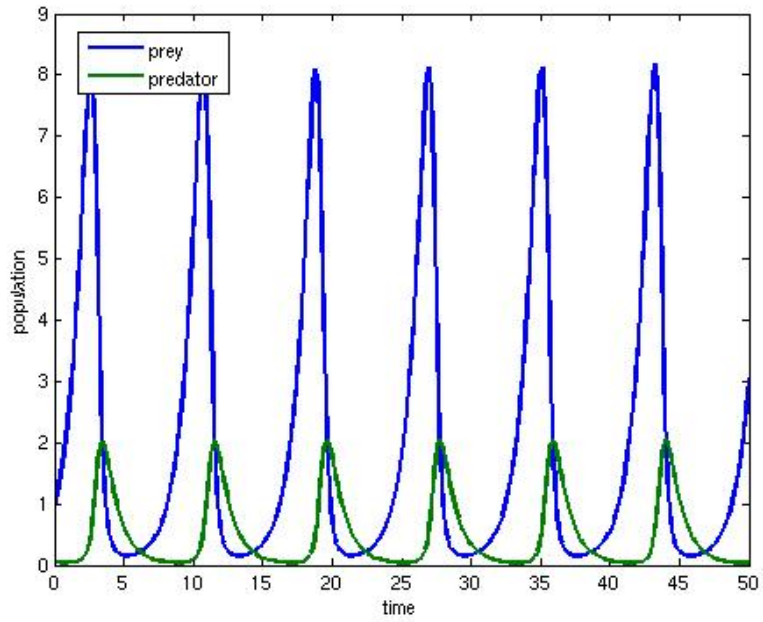


Figure 1: Cyclic populations in the Lotka-Volterra Model

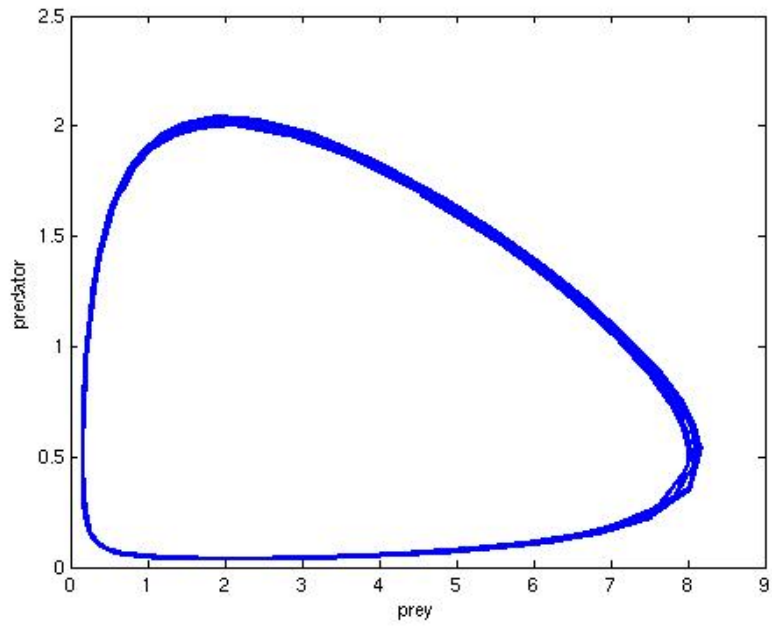


Figure 2: Two Stable populations in the Lotka-Volterra Model

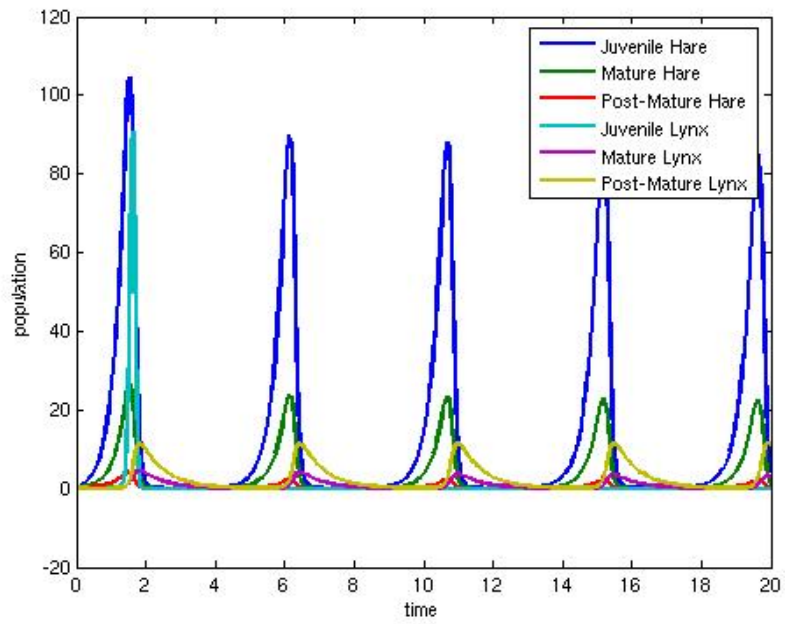


Figure 3: Cyclic populations in the first attempt

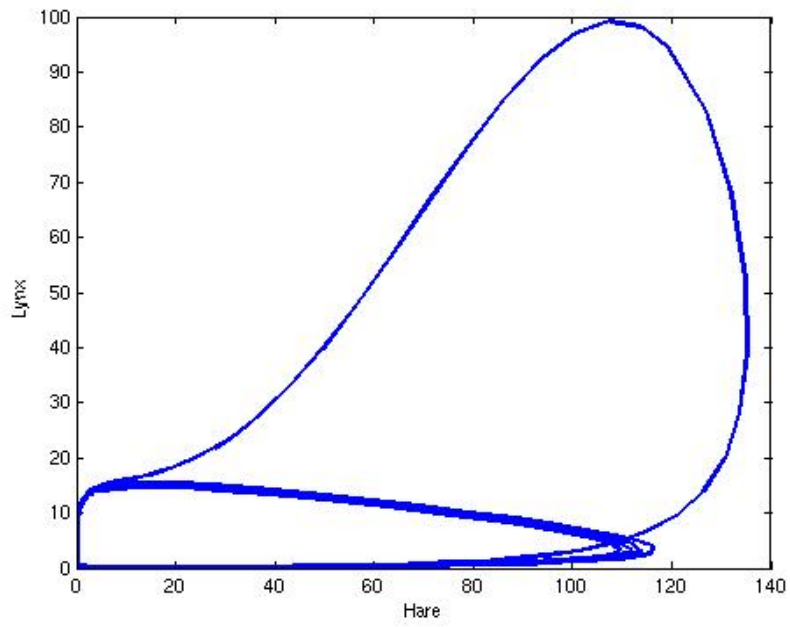


Figure 4: Total population in the first attempt

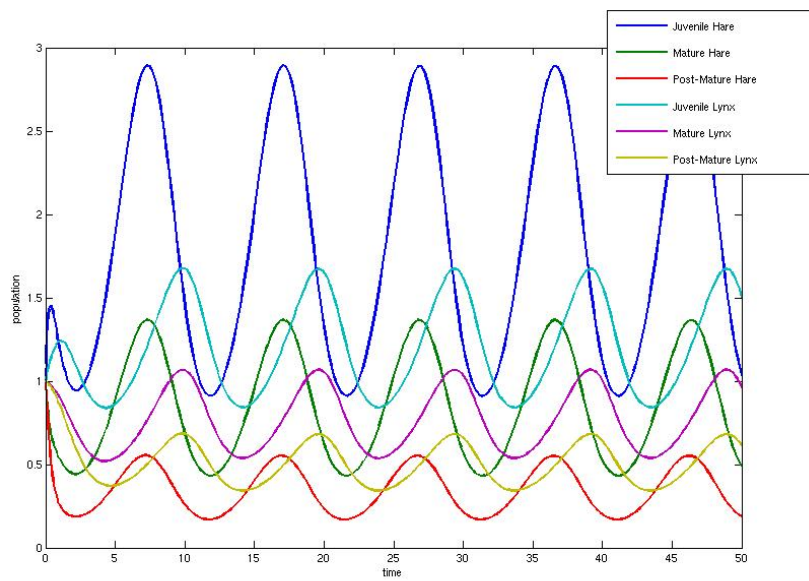


Figure 5: Cyclic populations in the Modification

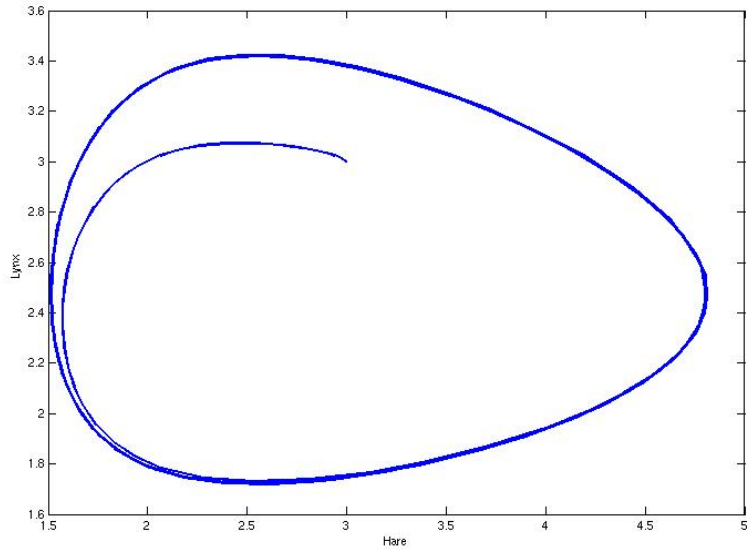


Figure 6: Total population in the Modification

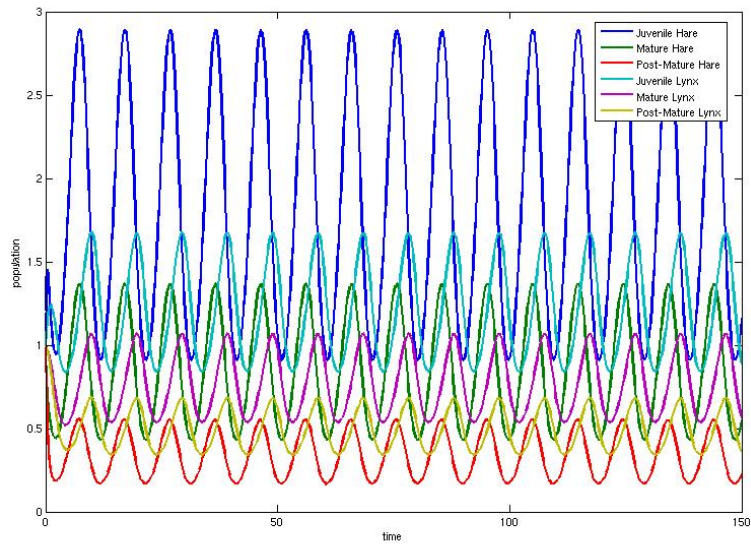


Figure 7: A Larger Time Scale for the Modification

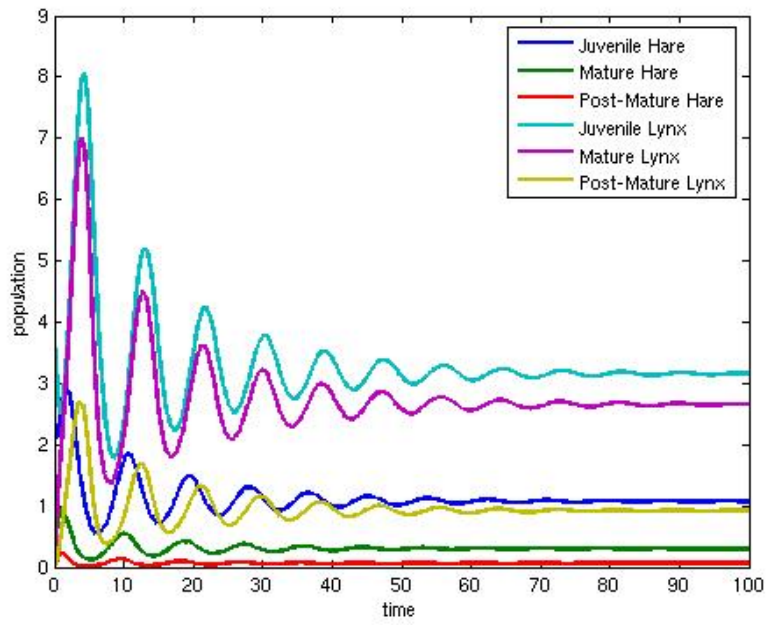


Figure 8: The Final Modifications Graphed

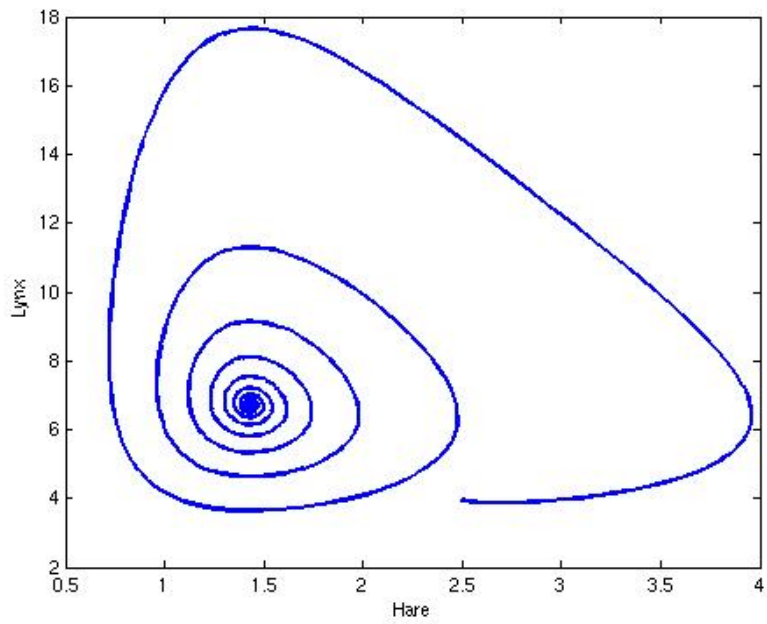


Figure 9: The Final Modifications Graphed