Modifying Lotka-Volterra equations to model wolf population in Yellowstone National Park

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Abstract

The population dynamics of a species is dependent on various factors such as resources, environmental conditions and interactions with other species. Predicting the population of a species is important as it can assess extinction risk and provide insight into the interconnectivity between different organisms. For example, the dependency that predators have on their prey to thrive and repopulate enables us to see how communities are sustained.

Our focus is on the predator-prey relationship between wolves and elk in Yellowstone National Park. We seek to determine how external factors such as weather and the introduction of another species influences their relationship using mathematical models. Exploring the long-term and short-term effects provides insight into the probabilities of both elk and wolf survival given different conditions.

We use the Lotka-Volterra differential equations to model the interaction between the wolves and the elk. The best scenario involves a lot of elk for the wolves to prey on. Our initial conditions are based on real data from the park. Our python program utilises Euler's method to solve the differential equations, using a time increment of a day.

The first model shows a fluctuation in both populations that repeats over the same time interval. This was as expected as it demonstrates the cyclical relationship observed between predators and prey in nature. Through this model we see how the population of wolves is positively related to the population of elk. However, this model is unrealistic as it was made under the assumption of a closed environment; therefore, the model does not consider external factors that could impact either population, such as disease outbreaks.

The second model introduces another species of prey - bison. This model shows how the bison's population fluctuates before becoming nearly extinct after hundreds of years. It also illustrates how the elk and wolves have similar changes in population as in the first model. When the population ratios are plotted, this model displays a damped oscillation that tends to a limit for each species after hundreds of years. This is unexpected as the predator-prey relationship should be cyclical in nature.

1 Introduction

In this project we are investigating the relationship between a predator species and a prey species, as it is commonly seen in nature that a carnivore's primary source of food is another organism, typically a herbivore. Modelling predator-prey relationships gives an insight into how a population of predators' survival is partially reliant on the population of prey. This allows us to assess extinction risk and the impact of external factors on their relationship. Specifically, we are exploring the relationship between wolves and elk within Yellowstone National Park.

One article investigated how populations of predators such as foxes and owls are affected by the amount of their preferred prey available (in this case the prey was voles for both predators). They found that as the population of voles increased, so did the population of predators. This increase in predators then caused a decline in the population of voles and then the cycle repeated itself[4]. From this study we should expect our model to show a similar cyclical nature.

2 Methods and Results

2.1 Lotka-Volterra

The typical model for predator-prey systems is the pair of Lotka-Volterra differential equations:

$$\begin{aligned}\dot{x}(t) &= \alpha x(t)y(t) - \gamma x(t) \\ \dot{y}(t) &= \delta y(t) - \beta x(t)y(t)\end{aligned} \tag{1}$$

They postulate that the predator, x, has a fixed death rate (proportional to their population), and that their growth is dependent on the amount of prey, y. The prey's population growth is a constant, and their death is related to the predator's population.

2.2 Euler's method

Since both the initial conditions and differential equations are known: we solved our equations using euler's method:

$$f(t + \Delta t) = f(t) + \Delta t f'(t)$$

Our python program Iterates over a given time, incrementing each population by it's current rate of change. We choose a time step of a day, therefore the constants are daily probabilities.

2.3 Initial model

To come up with our initial model we first had to understand how the populations of the wolves and the elk effect their respective growth and death rates. We made the following assumptions in out model:

- The wolves' only prey and source of food is the elk
- The elk's only predator is the wolves
- The elk have a constant supply of food
- There are no other variables affecting the birth and death rates of the animals (extreme weather, human impact etc.)
- Mating for both species is not seasonal and young are born throughout the year
- The model represents populations within the Yellowstone National Park area
- The wolves have an unlimited appetite

Our model has four main variables - the growth and death rates for both prey and predator. By considering the factors that affect these rates in addition with data about wolves from Yellowstone national park we are able to form suitable equations using these specific numbers. The growth rate of wolves is determined by the number of cubs born relative to the current population (which we found to be 80%), the survival rate of the cubs (which we found to be 50%) and lastly, the size of the elk population relative to its starting size. This means that the growth of wolves is affected by the number of elk. The death rate of the wolves is calculated solely from the average life expectancy of a wolf, which we found to be 5 years in the wild. The birth rate of the elk is calculated in a similar way to that of the wolves, but without the dependence on the wolf population. The number of elk that are born is usually 60% of the population and of that around 22% survive. Finally, we calculate the death rate of the elk by assuming a life expectancy of 13 years as well as the rate of predation (the product of the two populations and an arbitrary coefficient). However, these variables are not necessarily accurate representations of these rates as we have drawn the value from quite a limited pool of data. As a result, we add extra coefficients to the growth rates of both animals and the death rate of elk, allowing us to tweak both the model and the graphs produced by it. A time period of one day is used in our model, and the populations are plotted over a set period of time, letting us attain results such as those in Figure 1. The fluctuations in population can be adjusted by changing the coefficients for each variable.

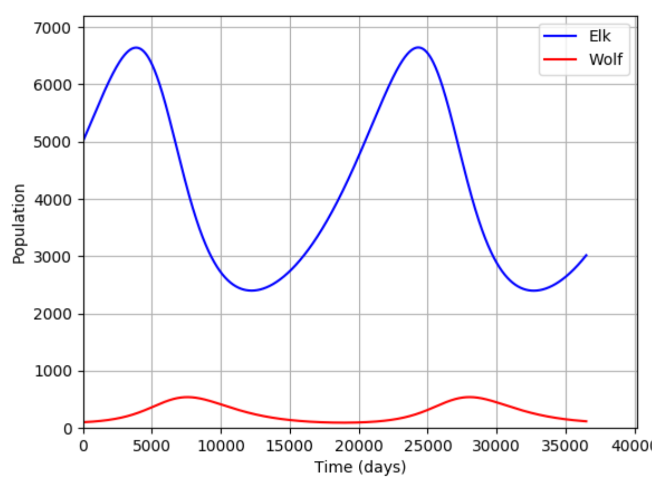

Figure 1: *A plot of our initial model over 100 years*

2.4 Modelling the seasonal elk population with trigonometry

The elk population experiences a very significant change throughout the year. Yellowstone reports as many as 20,000 elk in 6-7 herds during the summer months, and currently reports below 5000 elk in winter [1].

With a mating season from September through October, the birth of calves are expected May through to the end of June. Elk birth cycles coincide with the period of highest expected vegetation growth, this maximises calf health and survival - driving the increase of elk numbers in summer.

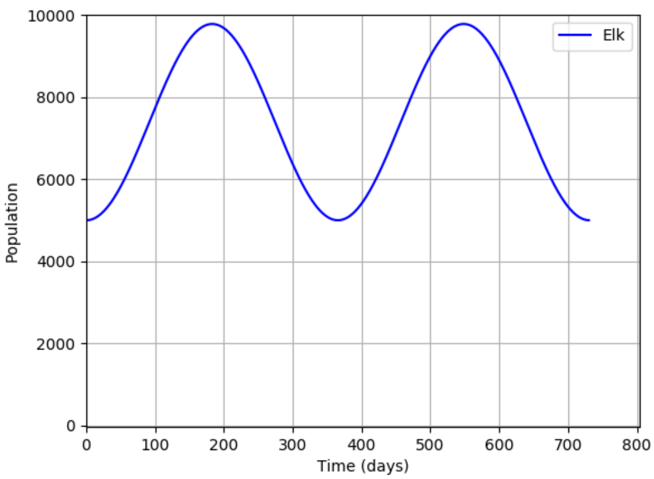

Figure 2: *Elk population over 2 years*

The equation used for this graph is

$$y(t) = 15000sin^2\left(\frac{\pi}{365}t\right) + 5000$$

We can use the graph in Figure 2 as a model for the elk population throughout the year. The limits were attained using data from[1]. The equation used is reducible to a cosine function, but a sine squared function was chosen since the coefficients are more useful to us at first glance. The 15000 represents the difference between the maximum and minimum number of elk, the $\frac{\pi}{365}$ represents the daily division and the 5000 represents the lowest number of elk in a period. This means that the model could be adjusted easily if needed, whereas the cosine equation's coefficients are not as translatable.

We start the year in early February, using the graph we can predict elk numbers at any time of the year. We notice that, by the start of April there are more than 6000 elk in Yellowstone, up from a low in February. We know these are migrating elk, since calves do not begin birthing until May.

The number of elk then reaches a maximum by the start of August. There are now no calves being born and all migrating elk have arrived in Yellowstone.

We can look further into this by observing the differential of the above equation, which gives us the rate of change of the elk population over the year.

$$\dot{y}(t) = \frac{3000}{73}sin\left(\frac{2\pi}{365}t\right) \tag{2}$$

And using the second order differential equation allows us access to even more information:

$$\ddot{y}(t) = \frac{1200\pi}{5329}sin\left(\frac{2\pi}{365}t\right) \tag{3}$$

We can find the maximum rate of change by setting (3) to zero. This returns a value of $t_1 = 91.25$ - the start of May when the birth of calves gets into full swing and the population is growing at the fastest rate.

Now setting (2) to zero we can find when the elk population begins to decline. This returns a result of $t_2 = 182.5$ - telling us that in early August elk mortality is no longer offset by births and migration. As such, the population declines after this point.

Furthermore, using $t_2 = 182.5$ in (3) gives us a value of -1, confirming our earlier observation on the graph of a maximum elk population in August.

Using (2) we can also find the minimum rate of change (the highest number of elk leaving the population). Again we set (2) to zero and find the next solution in the trigonometric period after the first value we found ($t_1 = 91.25$), doing this we find $t_3 = 273.75$, half a phase onward from the positive maximum t_1 and telling us the largest magnitude decline in the elk population occurs in early November, 273.75 days after the start of February.

Environmental information confirms this. As winter sets in, freezing temperatures and snow negatively impact the growth of forage, decreasing the amount of food available. In response, elk migrate out of Yellowstone in search of more abundant food, but are likely to return to Yellowstone in the spring.

Changes in climate particularly impact newborn elk. An early spring could mean vegetation reaching peak nutrition earlier than usual, leading to weaker calves that year. Implying that less calves may survive than expected in a standard season. This means that abnormal weather patterns would call for adjustments to the trigonometric model, since the current assumes regular patterns. Furthermore, outbreaks of disease such as Brucellosis or Chronic Wasting Disease may require changes to be made.

2.5 How much do seasonal wolf predation habits affect the elk population?

In Yellowstone, Elk comprise about 90 percent of winter wolf kills [1]. Being particularly vulnerable, as much as 67 percent of the calves born each may perish to predation [1]. Elk are an important food source to the Yellowstone ecosystem, providing partly for bears, mountain lions and many scavenger species.

It has been observed that wolves predation habits change throughout the season, with their heavy focus on elk in winter shifting to a more balanced collection of mammals in summer, including elk, deer and small mammals. This provides an interesting link between the wolf-elk populations, showing that the predator-prey relationship is not constant throughout the year. Winter elk numbers have been recorded as declining over the past couple of decades, raising public concern of over predation and over hunting.

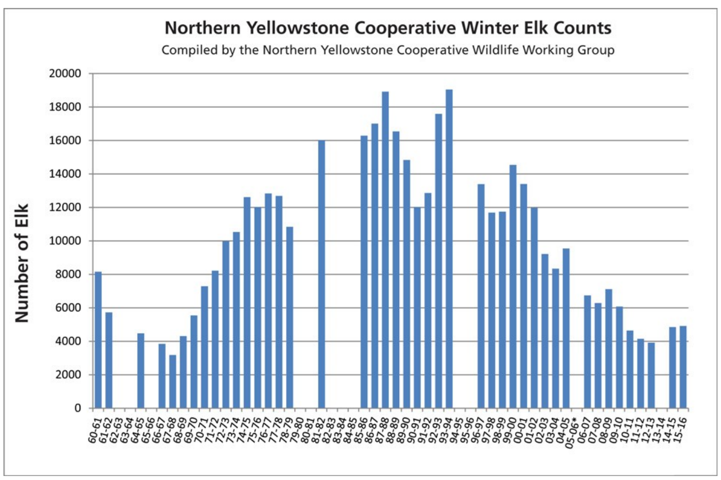

Figure 3: *A chart showing the elk population over the years*

After the reintroduction of wolves to Yellowstone in 1995, the winter elk count fell below 10,000 in 2003 down from 17000 in 1995. The elk population further declined to as low as 3,915 in 2013 [1]. The decline was partly attributed to predation (of which we know wolves contribute heavily, with other species such as humans also having an impact). This could provide a potential improvement for the model in Figure 2, by adding a decay coefficient in order to reflect the (anticipated) falling numbers in the years to come.

However, a survey performed by helicopter in March of 2016 reported a winter elk count of 6913, which could suggest a potential trend reversal [1].

2.6 Does the wolf population fluctuate seasonally?

It is reported that the number of wolves has been between 83 and 108 from 2009 to 2016 in Yellowstone, with 108 being recorded in December 2016 from 11 packs, and it's hard to identify a seasonal population pattern. However, a declining population has been noticed, down from 171 in 2007. Being extremely territorial animals, wolves are most likely to be killed by other wolves, accounting for 65 percent of deaths for wolves who have been collared[2].

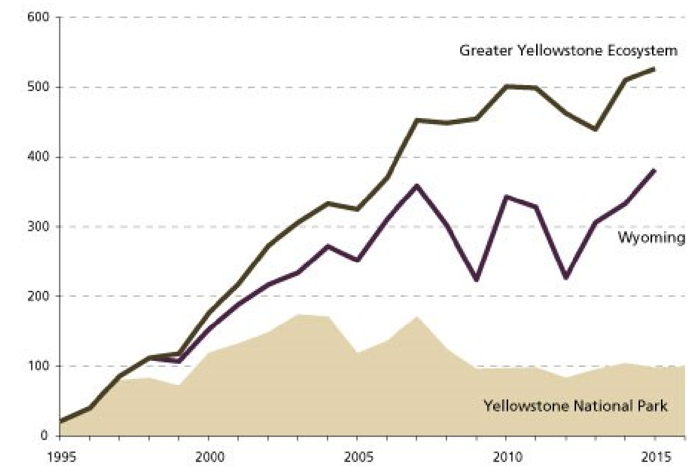

Figure 4: *A chart showing the wolf population over the years*

The decreasing wolf population in the park is connected with the also decreasing elk population, and thus fatal disputes occur between packs over territory, a clear example of how the two species are interconnected and depend upon each other.

Predicting and modelling the wolf population is difficult. Severe winters, dynamic behaviour, emigration and human interaction make for an unpredictable population [3].

In Yellowstone, collaring is used (wolves are briefly captured and electronic transmitters attached to them which then return data on the wolf and it's interactions) to gather data on individuals and monitor the population. Although, by the end of each winter it's estimated a mere 20 percent of the surviving population are actively collared and monitored, so conclusive results aren't available [2].

2.7 Investigating sudden changes

In the initial model, we assumed that there were no external effects to the death and birth rate. Many 'special events' are excluded in this assumption, for example dramatic changes in weather and human intervention. Realistically these would make sudden changes to both the elk and wolf population. Since wolves were reintroduced to the Yellowstone National Park in 1995, there have been 4 sudden substantial reductions in wolf population as a result of disease and weather. When the disease known as distemper spreads among pups, the survival rate of pups decreases to 30%. From equation 1, this leads to a lower food requirement and very low birth rate in another generation. In 2005, there was a 30% decline of wolves because of disease. Out-break disease can occur periodically, usually every 5 years. To model disease, we either set the death rate higher which could kill 30% of wolves, or set the survival rate lower to a third.[7] By manually lowering the population to two thirds, we can model a sudden periodical change in wolf population.

Disordered weather events have also made sudden changes in wolf population. Seasonal weather change only causes a population difference between summer and winter. We calculated the probabilities with data collected in the same month of each year, so this cancels the effect of normal weather variation. Wolves find it increasingly difficult to catch elk as a result of the atmosphere being either too warm or too cold in the national park. Thus, they would give birth to a smaller amount of pups (from 80% to 60%) due to a lower survival rate (45%).[8] To illustrate this in the model, we can change the eco-efficiency of wolf catching elk in a certain period.

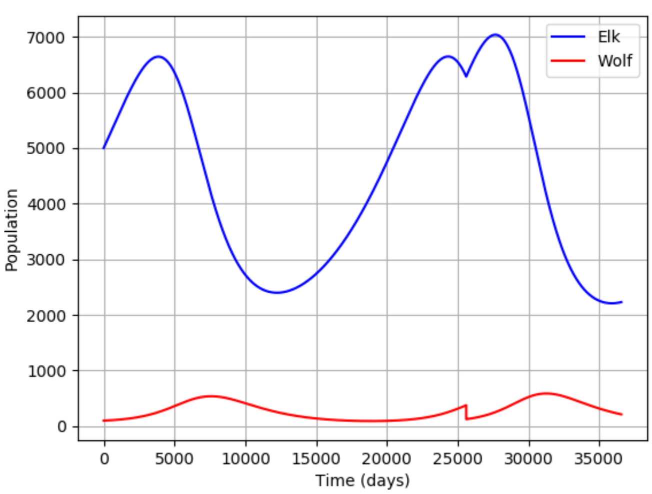

Figure 5: *A wolf cull*

The last special event includes human control which can directly decrease both the population, and intra-specific strife. When the population is beyond the tolerance of the park, fight between packs is the highest cause of death in wolves. This results in a 20% decline in wolf population after a generation or even more.[9] Back in the early 20 century, wolves were nearly wiped out by humans. Then the wolves completely vanished because they were out of numbers to hunt. This is simply a direct sudden decrease of the wolf population. Using this information, we make a graph to model human intervention reducing wolf population by two thirds.

Figure 6 is under the assumption that two thirds of wolves are killed by humans. The sudden decline in wolves causes a sudden increase in the elk population. As the amount of elk increases, the wolves gradually return to the ordinary fluctuation and once again become synchronized with the elk population. This represents the self-healing ability of this prey-predator relationship, as the wolves and elk will always return to their standard fluctuating pattern unless for example all of the wolves became suddenly extinct. Figure 6 illustrates that the greater the decline in wolves, the greater the increase in elk, and as soon as the elk reaches its peak population, the wolves begin to return to their standard oscillation.

2.8 Introducing a second prey

Elk only account for 83% of the wolves diet, as seen in [8]. If we add in bison as a prey we then account for 88% of the diet, this should then be sufficient.

Altering the assumptions for the pre-established Lotka-Volterra equations: The predator's growth is no longer solely proportional to the population of one prey, but now proportional to the sum of prey populations. Therefore we need to introduce a third variable, z, for the third prey. This prey's rate of population change is modelled essentially identically to the original preys.

We use constants such as alpha and then alpha prime as these values are closely related. Alpha relates to the effect of the product of wolf and elk population on the wolves, whereas alpha prime relates to their effect on the elk population.

$$\begin{aligned} \dot{x}(t) &= [\alpha y(t) + \beta z(t) - \gamma]x(t) \\ \dot{y}(t) &= [\delta - \alpha' x(t)]y(t) \\ \dot{z}(t) &= [\mu - \beta' x(t)]z(t) \end{aligned} \tag{4}$$

Since a new prey is being added, we needn't change the previous probabilities: Elks are still as likely to be eaten, and wolves' lifespan is constant. Hence we should only see a change in the wolf population as they suddenly have more food available.

Bison are larger animals than elk, have a slower birth rate than elk, and are targeted by wolves less. Therefore we have the effect of bison predation on wolves to have half the coefficient assigned to the elk's. This then has a lower toll on bison population as one bison feeds more wolves than a single elk.

2.8.1 Over 100 years

From plotting over 100 years we predict that both elk and bison populations will continuously oscillate, as expected. We start to see a trend that bison exhibit decreasing oscillations whereas elk show increasing oscillations.

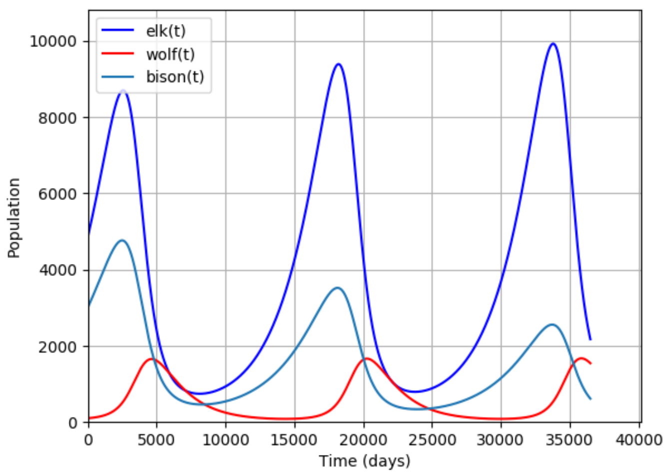

Figure 6: *A plot of our 2 prey model over 100 years*

2.8.2 Using total prey ratios

Previously we assumed that adding additional prey does not decrease the likelihood of a specific prey being targeted by predators. In retrospect this is as inappropriate model: for example if we added a new prey to a closed system our model predicts that the predator would eat exactly the same amount of the first prey in addition to a quantity of the new. This would then imply that the predator's were capable of catching more prey previously which would break the Lotka-Volterra Assumptions.

Thus we suggest that that prey are killed proportional to their ratio of the total prey, hence:

$$
\begin{aligned}
\dot{x}(t) &= \left[\frac{\alpha y^2(t) + \beta z^2(t)}{y(t)+z(t)} - \gamma\right] x(t) \\
\dot{y}(t) &= \left[\delta - \frac{\alpha' x(t) y(t)}{y(t)+z(t)}\right] y(t) \\
\dot{z}(t) &= \left[\mu - \frac{\beta' x(t) z(t)}{y(t)+z(t)}\right] z(t) \qquad (5)
\end{aligned}
$$

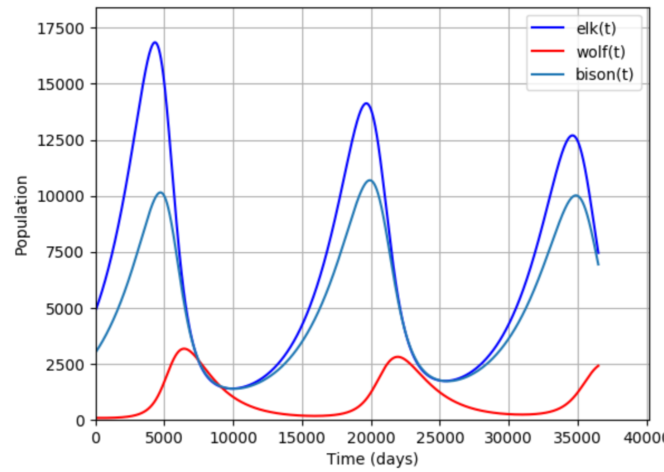

Figure 7: *A plot of our 2 prey model using ratios over 100 years*

2.8.3 Unexpected Equilibria

When the populations are plotted over several hundred years we get a sense of the general trend of the systems. From our first two prey implementation we see ongoing oscillations. However for our ratio based model we find that a limit does exist, all values tend towards an equilibrium point. Some might argue that this makes our model invalid, or the contrary, however since no modern day ecosystem will go undisturbed for thousands of years within human existence these results are irrelevant.

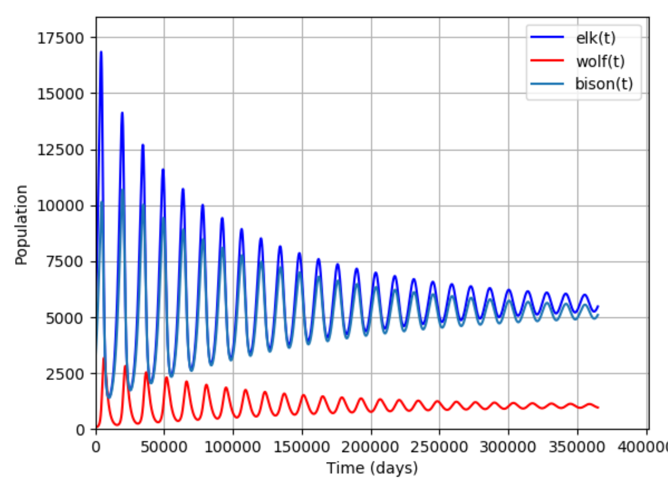

Figure 8: *A plot of our 2 prey model using ratios over 1000 years*

3 Discussion and Conclusion

The initial predator-prey model is a reliable model as there was lots of data provided by Yellowstone who many studies on the wolves and elk there. Through these real statistics we have accurate parameter values. The model is completely stable with a repeating oscillation for both the wolves and the elk (there is an equilibrium state), as seen in Figure 1. The density of predators is positively related to prey growth rate, which is as expected as it has been seen in previous studies [4]. The maximum values of the prey and predators are useful for national parks such as Yellowstone as it predicts the total maximum capacity that their given environment should be able to support if they want to introduce a certain number of these predator species and prey species. As seen in Figure 6, when the number of wolves is beyond the tolerance of the park, many wolves get killed through pack fights, so information on maximum capacity would be useful in reducing such occurrences. Overall, these fluctuations successfully demonstrate the relationship between the elk and the wolves, and the dependency the wolves have on the elk to thrive. However, this equilibrium state is an unrealistic representation of the predator-prey relationship as it assumes that there are no variables that could impact death or birth rates, when in nature many external factors can cause one or both populations to dramatically change. An example of this is a detrimental disease outbreak, and as seen in an article [5], disease outbreak in the predator species can cause its own extinction. Another article [6], observes how if the prey population goes extinct then the predator population should also go to extinction, highlighting the interconnectivity between both species as extinction of one can cause the extinction of the other. Another limitation of this model is that it is in a closed environment so there are no random increases or decreases in the populations of either species. An example of how there could be a random change in the population of elk is if their food resources were to become scarce, illustrating that the assumption of constant elk food resources is unrealistic.

Our second model consists of two prey (elk and bison) and a predator (wolves). From Figure 7 we see that similarly to the first model there are fluctuations of population size within all the species. However, as the time increases the maximum population size in the oscillations for elk increase as the ones for bison decrease, and wolves stays approximately the same. From this we can infer that the wolves are taking the bison as their primary food source because their oscillation maximum is decreasing over time, therefore allowing the elk population to gradually grow. Figure 7 does also illustrate that the population of predators is still positively related to the population of prey (even if there are two prey), reinforcing the same relationship as seen in the first model. It is interesting however to see that when the population ratios are plotted over a thousand years that each species' ratio tends to a unique limit. This shows that our model may be invalid as no environment would go unchanged for thousands of years, however the predator-prey relationships after 100 years are invalid and irrelevant to our model as we cannot confidently predict populations so far into the future as our assumptions are so limiting.

To improve our models, we could incorporate the seasonal affects into the parameters. For example, for every 180 days (approximately half a year) we could edit the parameters in accordance to the seasonal change between the summer and winter periods of the year. This would allow us to see more varying fluctuations in the models. This is due to elk population being at its lowest in the winter period and highest in the summer period as this where there is a high birth rate due to when their mating season occurs [1]. There would also be a higher death rate of elk in the winter period as they are hunted more by wolves during that time [1]. Adjusting the parameters in a similar way for the wolves, we would have a model with a more varying fluctuation pattern than the initial model. This improved initial model would still be repetitive over a specific time period, however would be more realistic as it incorporates the environmental factors that influence birth and death rates. Another improvement could be to introduce another predator of elk to the initial model and investigate the impact this would have on the wolf and elk population. In theory, we would expect the wolf and elk population to decrease as the wolves have less prey (assuming elk is their only food source) and the elk are being hunted by two species rather than one. With that model proposition we could also investigate which of the two predators would have a higher population as we could incorporate individual variability (which is ignored in our current models). This context specific information would produce different predator-prey population fluctuations between each predator and elk. This improved model allows us to see which behavioural and genetic traits makes for a better predator of elk, informing us on the impact that these traits have on predators hunting and survival. Including individual variability takes into consideration that populations are made up of complex individuals and provides insight into the effect that evolution plays in keeping communities sustained.

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