# Analysing The Trophic Cascade of Yellowstone National Park Using Predator-Prey Models

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**Abstract**

A trophic cascade is defined as a powerful, indirect interaction that can control an entire ecosystem. The ecosystem in question being the Greater Yellowstone Ecosystem, which experienced an extinction and subsequent reintroduction of the gray wolf after many decades of absence. The reintroduction of the top predator (gray wolf) into the ecosystem resumes control over the primary consumer population (elk) returning to a natural equilibrium. In turn, the primary producer population (vegetation) begins to thrive. Using variations of predator-prey models, the effect on elk populations caused by the reintroduction of the gray wolf is analysed and the subsequent effects on the greater ecosystem is considered.

# 1 Introduction

Established in 1872, Yellowstone National Park is the first national park in the U.S. and is widely believed to be the first in the world. Located in the western U.S., stretching into parts of Wyoming, Montana and Idaho, Yellowstone National Park is host to a myriad of flora and fauna and forms the centrepiece of the Greater Yellowstone Ecosystem.

The subject of this study revolves around the predator-prey relationship between the gray Wolf (predator) and the Rocky Mountain elk (Prey). Historically, both species thrived in the national park, however, due to human hunting, the gray wolf population declined during the late 1800s and early 1900s, culminating in the extinction of the species in the area in 1926.

The elk saw predators in the local coyotes, black bear, grizzly bears, mountain lions and man, however, their apex predator was the gray wolf. Without their primary natural predator, the elk population experienced an explosion in numbers as other predators and government culling efforts were inadequate to suppress elk numbers. The elk population peaked close to 20,000 during the late 1980s [1]. The ecology of the park suffered greatly as a result, vast quantities of vegetation, such as aspen tree saplings, were being consumed at a drastically increased rate due to the inflated elk population. This left for very little new growth of flora to develop in the park, leading to a cascading breakdown of the ecosystem as many of species which depended on the flora saw a decline in numbers [1].

In an effort to restore the natural balance of the park's ecosystem, a reintroduction of gray wolves was conducted in 1995 by Canadian wildlife officials. In this report I aim to use predator-prey models to study this reintroduction and the resulting ecological effects this had on the environment of Yellowstone.

## 2 Initial Model

To construct the initial predator-prey model of the elk and wolf populations some assumptions must first be considered. The scope of the model will be limited to the direct interactions of the predators and the prey, that is to say outside effects such as disease, harsh winters, migration of populations etc. will not be considered in the preliminary model.

The rate of change of both predator ($\dot{y}$) and prey ($\dot{x}$) will be considered to be proportional to the current population of the respective species, that is to say $\dot{x} \propto x$ and $\dot{y} \propto y$, and hence

$$\dot{x} = xf(x,y) \tag{1}$$

$$\dot{y} = yg(x,y) \tag{2}$$

The elk population ($x$) will be considered to have a constant growth rate ($a$) which is unaffected by the wolf population. The wolves will hunt the elk, decreasing the elk population, the number of elk hunted is given by the number of wolves present ($y$) and a predation rate ($b$) which represents the overall likelihood of a wolf or pack of wolves to hunt and successfully kill an elk.

For the wolf population, it is considered that there is no natural predators for the wolf, and thusly, wolves will die naturally at a constant rate ($c$). Unlike the elk, the wolf population will grow at a rate which is proportional to the number of elk present ($\mathrm{d}x$). The reason for this is that in a situation where food is abundant, the wolves are more likely to breed and increase their population. In a situation where food is scarce, the wolves are expected to breed less.

Substituting these parameters in for $f(x,y)$ and $g(x,y)$ the following equations (3) and (4) are obtained. This pair of coupled equations are known as the Lotka-Volterra equations [2][3]. With these equations, the population dynamics of the elk and wolves can be modelled as functions of time.

$$\dot{x} = x(a - by) \tag{3}$$

$$\dot{y} = y(dx - c) \tag{4}$$

In the absence of a wolf population, the elk was seen to fluctuate yearly due to external effects such as disease, harsh winters and migration. The general trend of elk population generally increases over multiple years [4]. In years where there is a population growth of elk, this growth typically ranges between 5% to 20%, excluding years where a harsh winter or disease caused a large decrease in population. By taking a conservative estimation of the average growth rate per year of elk to be 11.3%, a value for ($a$) in equation (3) can be acquired.

After the reintroduction of wolves in 1995, the population of elk begin to decrease by the wolves hunting the elk. In 2011 it was reported that a population of 98 wolves hunted 268 elk out of a total population of 4,300 elk. If the predation rate remains constant throughout the years, an estimate for ($b$) in equation (3) can be obtained with $b = (268)/(98 \times 4300) = 0.00064$

Calculating the average death rate of the wolves ($c$) using the data in [1] [4] [5] is difficult, given the relatively small population of wolves, the wolf deaths due to natural causes is somewhat sporadic and unique to each individual wolf. Alternatively, the average lifespan of a typical gray wolf in the wild is about 8 years. With this lifespan one can expect that after an eight year period the first generation of a wolf pack would have all died and been replaced by the newer generation. With this information, if all the ages of the wolfs are equally spaced out, one can expect the average death rate of wolves ($c$) to be 12.5% per year.

To calculate the growth rate of wolves per year per elk, the case when the rate of change of wolf population is zero (i.e. $\dot{y} = 0$ ) will be considered. This point occurs when the number of elk is low enough that the number of wolves reproducing is equivalent to the number of wolves dying naturally each year

$$\dot{y} = 0 \rightarrow dxy - cy = 0 \rightarrow d = c/x \tag{5}$$

This equilibrium has reportedly occurred when the elk population reached roughly 5,000, during which the number of wolves fluctuated between 83 and 108 wolves but maintained within this population since 2009 [6] [7]. If, considering that $\dot{y} \sim 0$ when $x = 5000$, using equation (5) a wolf growth rate per elk of 2x$10^{-5}$ per year is obtained.

Over the winter of 1995, 25 wolves were released into Yellowstone National Park [5], the reported population of elk at the time was roughly 19,000. This provides suitable initial conditions for the model

$$x(0) = 19000 \quad and \quad y(0) = 25 \tag{6}$$

Accompanying this with the previously determined values for $a$,$b$,$c$, and $d$

| Symbol | Description | Value | Unit |
|---|---|---|---|
| $a$ | Elk growth rate | 0.113 | year$^{-1}$ |
| $b$ | Predation rate | $6.4 \times 10^{-4}$ | year$^{-1}$ predator$^{-1}$ |
| $c$ | Wolf death rate | 0.125 | year$^{-1}$ |
| $d$ | Wolf growth rate | $2.5 \times 10^{-5}$ | year$^{-1}$ prey$^{-1}$ |
| $x(t)$ | Prey (Elk) population | N/A | prey |
| $y(t)$ | Predator (Wolf) population | N/A | predator |

Table 1: Values of constants and variables used in predator-prey model

Using Maple and the accompanying code from Appendix 1, the model of equations (3) and (4) is run as a function of time ($t$), where each integer of $t$ is the equivalent of 1 year. In figures 1 and 2, the elk and wolf populations are calculated for $(x(t = 0), y(t = 0))$ to $(x(t = 120), y(t = 120))$, the equivalent of 120 years.

To compare the population dynamics of elk and wolf using different initial conditions, $x(t)$ is plotted against $y(t)$ in figure 3, where the number of wolves initially reintroduced to the park is varied. The initial conditions used are

$$x(0) = 19000 \quad and \quad y(0) = 25 \tag{7}$$

$$x(0) = 19000 \quad and \quad y(0) = 100 \tag{8}$$

$$x(0) = 19000 \quad and \quad y(0) = 500 \tag{9}$$

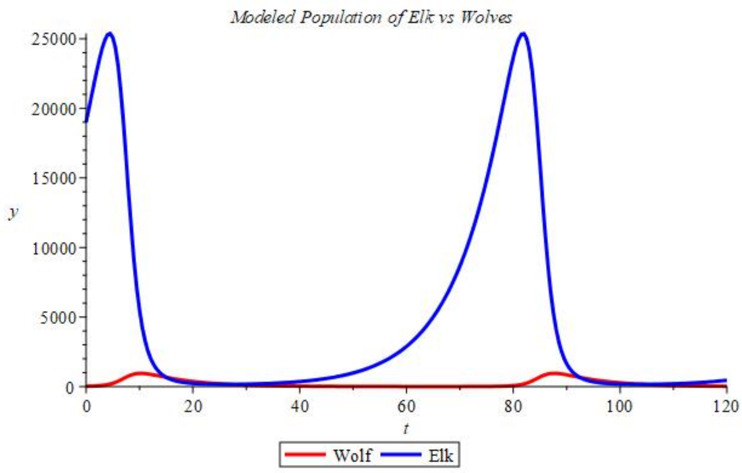



Figure 1: Equations (3) and (4) plotted as a function of time, showing the population dynamics of elk (blue) and wolves (red).

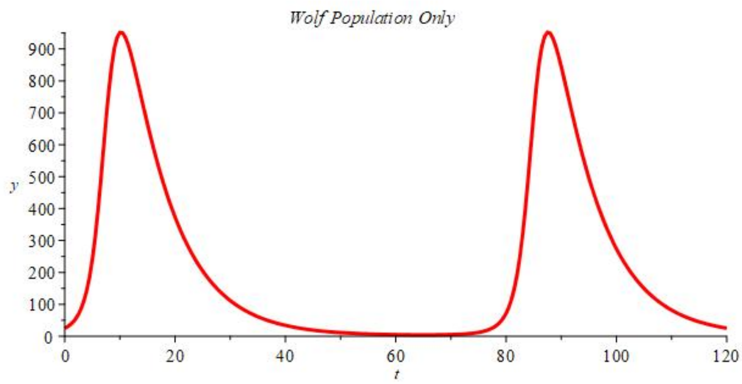



Figure 2: Zoom in of the wolf population as seen in figure 1.

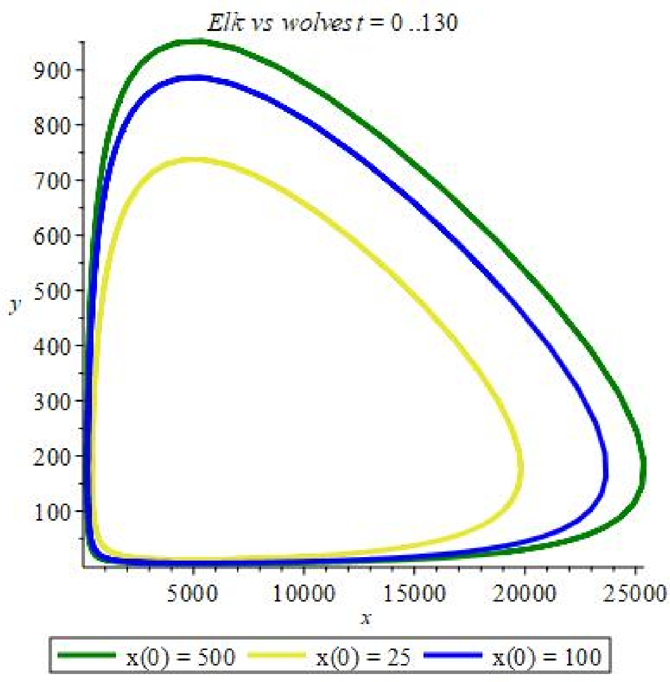



Figure 3: Phase-space plot of the predator-prey model from equations (3) and (4) using varying initial conditions from equations (7 - 9).

## 2.1 Nondimensionalization

In order to nondimensionalize equations (3) and (4), let the variables $x$, $y$ and $t$ be equal to their dimensional constants $(x_0, y_0, t_0)$ and nondimensional variables ($\tilde{x}$, $\tilde{y}$,$\tilde{t}$) such that

$$x = x_0\tilde{x} \quad y = y_0\tilde{y} \quad t = t_0\tilde{t} \tag{10}$$

Substituting equation (10) into equation (3)

$$\frac{x_0}{t_0}\dot{\tilde{x}} = x_0 a\tilde{x} - x_0 y_0 b\tilde{x}\tilde{y} \tag{11}$$

Dividing across by $x_0$ and multiplying by $t_0$

$$\dot{\tilde{x}} = at_0\tilde{x} - bt_0 y_0\tilde{x}\tilde{y} \tag{12}$$

Choosing the appropriate scalings as

$$t_0 \sim \frac{1}{a} \quad and \quad y_0 \sim \frac{a}{b} \tag{13}$$

Substituting equation (10) into equation (4)

$$\frac{y_0}{t_0}\dot{\tilde{y}} = x_0 y_0 d\tilde{x}\tilde{y} - y_0 c\tilde{y} \tag{14}$$

Dividing across by $y_0$ and $c$, and replacing $t_0$ with $1/a$

$$\frac{a}{c}\dot{\tilde{y}} = \frac{dx_0}{c}\tilde{x}\tilde{y} - \tilde{y} \tag{15}$$

Choosing the scaling for $x_0$ as

$$x_0 \sim \frac{c}{d} \tag{16}$$

Leaving one dimensionless constant $\mu = a/c$, in summary

$$\dot{\tilde{x}} = \tilde{x} - \tilde{x}\tilde{y} \tag{17}$$

$$\mu\dot{\tilde{y}} = \tilde{x}\tilde{y} - \tilde{y} \tag{18}$$

And the initial conditions

$$\tilde{x}(\tilde{t} = 0) = 19000\frac{d}{c} \quad and \quad \tilde{y}(\tilde{t} = 0) = 25\frac{a}{b} \tag{19}$$

## 2.2 Comments on the Initial model

The predator-prey relationship depicted in figure 1 exhibits a periodic effect where a large population of elk is expected to develop, which will cause a large population of wolves to develop, leading to a large decrease in the number of elk as the increased population of wolves hunts the elk more often. As the wolves hunt the elk to a very low population, their own numbers see a large decrease due to the lack of available food, leading to a large increase of elk and hence the cycle continues with a period of roughly 80 years.

However, several issues are present in this situation. By observation, the populations of both species experience periods where their populations are extremely low which would likely lead to an extinction of the species at this point in nature, a case which this model cannot account for. As a result, this model depicts repeating cases where both species undergo an extinction and seemingly recover after a number of years, which in reality is somewhat unrealistic.

Another issue is that in the absence of any predators, the elk's population will exponentially grow unbounded. This is not realistic as, even without natural predators, the elk would be limited by the abundance of food and by other herds of elk in the area competing for grazing land or by diseases etc. This has been observed prior to the reintroduction of wolves in 1995, where the elk population was seen to peak in the late 1980s where the elk numbers almost reached 20,000 multiple times before starting to decline [4]. This leads to some limiting factor where the park itself has come carrying capacity, preventing the elk from numbering >20,000. It will be seen later that the implementation of a carrying capacity produces a more lifelike predator-prey model.

# 3 Amended Model

To prevent the elk population from growing unbounded in the absence of predators, a carrying capacity ($r$) will be introduced into equation (3) such that

$$\dot{x} = ax\left(1 - \frac{x}{r}\right) - bxy \tag{20}$$

If $r$ is taken to be 20,000, then as the population of elk approaches $r$ the effect of the growth rate on $\dot{x}$ is decreasing and the predation effect will become dominant and $\dot{x}$ will become negative.

Applying equation (20) in the Maple code from earlier (see Appendix 2) produces the following

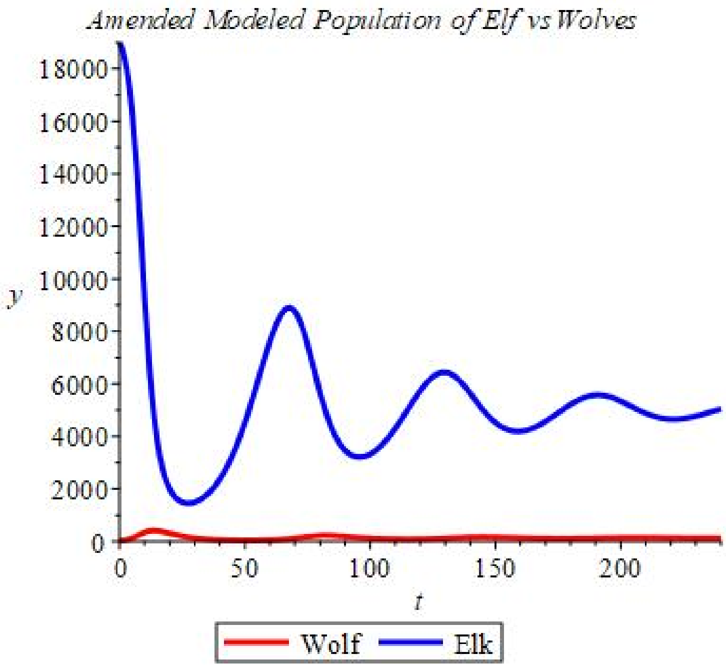



Figure 4: Equations (20) and (4) plotted as a function of time, showing the population dynamics of elk (blue) and wolves (red).

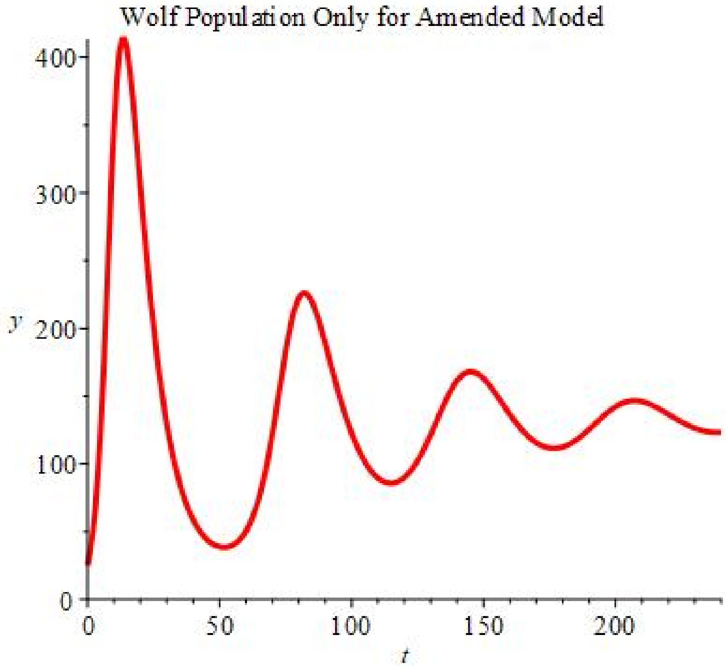



Figure 5: Zoom in of the wolf population as seen in figure 4.

Plotting the phase plane for the initial values (7 - 9)

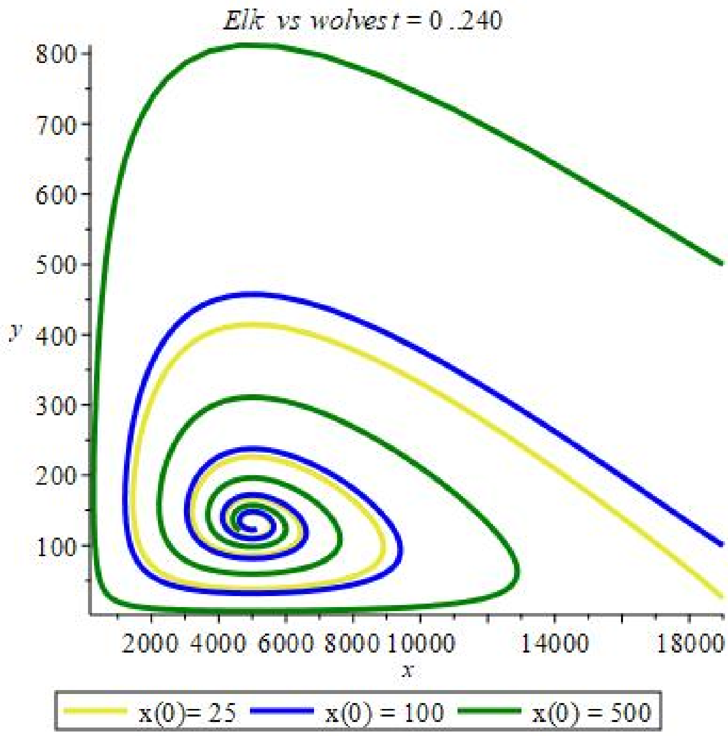



Figure 6: Phase-space plot of the amended predator-prey model from equations (20) and (4) using varying initial conditions from equations (7 - 9).

### 3.1 Nondimensionalization of the Amended Model

By considering the same splitting of variables into dimensional constants and dimensionless variables as was previously done in equation (10), the equations of (20) and (4) are

$$\dot{\tilde{x}} = at_0\tilde{x}\left(1 - \frac{x_0}{r}\tilde{x}\right) - by_0\tilde{x}\tilde{y} \tag{21}$$

$$\frac{y_0}{t_0}\dot{\tilde{y}} = x_0y_0d\tilde{x}\tilde{y} - y_0c\tilde{y} \tag{22}$$

As before, the scaling of $y_0$ and $t_0$ are unchanged

$$t_0 \sim \frac{1}{a} \quad and \quad y_0 \sim \frac{a}{b} \tag{23}$$

However, there is now a choice to be made in the scaling of $x_0$ and an additional dimensionless variable, $\kappa = \frac{c}{dr}$, will appear in either (21) or (22), depending on the choice of scaling for $x_0$. If $x_0$ is chosen to be scaled as $x_0 \sim r$, then the amended model becomes

$$\dot{\tilde{x}} = \tilde{x}\left(1 - \tilde{x}\right) - \tilde{x}\tilde{y} \tag{24}$$

$$\mu\dot{\tilde{y}} = \frac{\tilde{x}\tilde{y}}{\kappa} - \tilde{y} \tag{25}$$

Having the initial conditions

$$\tilde{x}(\tilde{t} = 0) = \frac{19000}{r} \quad and \quad \tilde{y}(\tilde{t} = 0) = 25\frac{a}{b} \tag{26}$$

If $x_0$ is chosen to be scaled as $x_0 \sim \frac{c}{d}$, the amended model is

$$\dot{\tilde{x}} = \tilde{x}\left(1 - \kappa\tilde{x}\right) - \tilde{x}\tilde{y} \tag{27}$$

$$\mu\dot{\tilde{y}} = \tilde{y}\left(\tilde{x} - 1\right) \tag{28}$$

With initial conditions

$$\tilde{x}(\tilde{t} = 0) = 19000\frac{d}{c} \quad and \quad \tilde{y}(\tilde{t} = 0) = 25\frac{a}{b} \tag{29}$$

# 4 Discussion

Implementing the carrying capacity into the amended model of (20, 4) produced a very different result than the initial model (3, 4). The amended model resolved the issue where extreme populations of elk and wolves were causing possible extinction scenarios, instead the populations tend toward a steady equilibrium point. This is a characteristic which has been observed currently in the park where the wolf population has fluctuated between 83 and 108 and the elk population has maintained around 5000 since 2009 [4][6][7]. This is reflected in the amended model where the populations will tend toward a similar equilibrium.

The amended model does not account for outside events causing a disturbance in populations such as diseases or harsh winters which may decline the populations significantly. Therefore the amended model is somewhat of an overestimate of the projected species population.

Two nondimensionalised forms of the amended model are possible (24, 25) and (26, 27), both with a difference scaling for $x_0$. As the population of elk approaches the carrying capacity ($r$), it is more suitable to use the scaling $x_0 \sim r$ for (24, 25). As the elk population decreases, it is more suitable to use the scaling $x_0 \sim c/d$ for (26, 27).

By plotting $x(t)$ against $y(t)$ in the phase plane, as done in figures 3 and 6, it is possible to compare the behaviour of the models for different initial values. In the initial model, periodic orbits about a fixed point were observed for all initial values, for which each phase of the model would return to its original populations and repeat indefinitely. In the amended model, all phases of the model eventually terminated at a fixed point. The time taken for the model to reach this fixed point was determined by the initial conditions, where it was observed that a higher initial wolf population would take increasing time to reach equilibrium. It was also observed that for an initial population of 500 wolves, the elk and wolf population would decrease drastically at separate points before reaching equilibrium. This is likely to lead to an extinction event for one if not both of the species before reaching equilibrium due to low populations not being able to recover. This suggests the existence of a maximum number of wolves which can be reintroduced into the ecosystem at once.

A large discrepancy between the amended model's populations and the actual reports of Yellowstone National Park's populations of elk and wolves, is the time taken to reach equilibrium. In actuality, it took between 15 to 20 years for the elk and wolf populations to reach a stable equilibrium [4], whereas the same equilibrium was achieved in 150+ years in the amended model. This is likely due to many factors, such as the assumption that the growth rates of both prey ($a$) and predator ($d$), the predation rate ($b$) and the predator death rate ($c$) all remained constant throughout the calculations. This is most certainly not the case and these 'constants' are more likely to change in response to the prey or predator's condition. The large spike in wolf population in the first few years of the model is an example of this, as the wolf population reaching $\sim$400 quickly and then rapidly declining to $\sim$50 over a short period is not realistic unless in extreme situations. A remedy for this would be to apply a limiting function to the wolf populations just as was done for the elk population. In addition, there exist many other predators for elk in the ecosystem which this model does not account for, which may increase the time taken for the elk population to reach equilibrium. It was also observed that the behaviour of the elk changed significantly due to the reintroduction of the gray wolf which could have lead to large elk numbers migrating elsewhere [4].

The effect the reintroduction of the gray wolf had on the ecosystem of Yellowstone National Park is not limited to just the elk population. Due to the decreased elk population, much more vegetation was allowed to develop and flourish in the area. An example of this being the young aspen trees whose mean height pre reintroduction was less than 50cm. As of 2010, the mean height of young aspen trees now measures at roughly 230cm [5], (see figures 7a and 7b)

Due to the healthier abundance of flora, many more species began to return and thrive in the area such as the beaver. With a larger abundance of fresh timber, the number of beaver colonies increased from 1 in the northern range in 1996 to 12 colonies in 2009. Damming of the rivers and streams in the park increased massively as a result, having a huge impact on the landscape of the area.

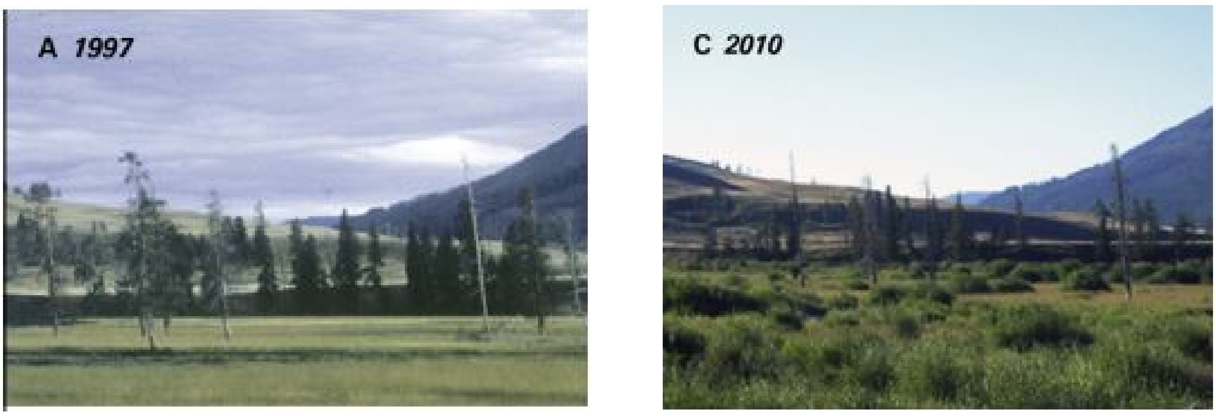
# 5 Conclusion

Modification of the initial predator-prey model leading to the amended model has shown realistic equilibrium populations for both elk and wolf. The amended model provides significant evidence for the decrease in population of elk to a number which is more sustainable for the national park. When the wolves were first reintroduced, their populations numbered 25 while the elk numbered around 19,000 heads. As what was reported and what the model predicted, these populations tended toward an equilibrium with wolf numbers fluctuating between 80-110 wolves and population of elk numbering around 5,000. The expected populations of elk and wolves in the amended model is somewhat higher than the actual reports as it does not take into account other effects such as diseases, unusual weather such as harsh winters, migration etc. which may have an effect on the both populations.

There is significant evidence that suggest a top-down trophic cascade on the local ecosystem due to the reintroduction of the apex predator of the primary consumer species into the area. Reports [1] [4] [5] indicate that due the reduced number of elk present in the area, vegetation is allowed to grow and develop in a much higher abundance now that the number of elk consuming the new vegetation has decreased. A revitalisation of other consumer species, such as the beaver, began as the competition for food was reduced. The increased number of species similar to the beaver, which can affect its surrounding landscape by constructing dams, coupled with the increased vegetation causing the soil to be less erosive leads to a gradual change in the landscape as rivers were less likely to meander and more likely to evolve into more fast flowing rivers.


(a) (b)

Figure 7: (7a) August 2006, showing a lack of recent aspen recruitment (aspen <1 m tall). (7b) September 2010, showing the same site with significant aspen recruitment (some aspen >2 m tall).




(a) (b)

Figure 8: Comparison photographs taken in 1997 and 2010 showing the recovery of vegetation due to the decreased number of elk.

# References

[1] R. L. Beschta and W. J. Ripple, "Riparian vegetation recovery in yellowstone: the first two decades after wolf reintroduction," *Biological Conservation*, vol. 198, pp. 93–103, 2016.

[2] A. J. Lotka, “Contribution to the theory of periodic reactions,” *The Journal of Physical Chemistry*, vol. 14, no. 3, pp. 271–274, 2002.

[3] N. S. Goel, S. C. Maitra, and E. W. Montroll, “On the volterra and other nonlinear models of interacting populations,” *Reviews of modern physics*, vol. 43, no. 2, p. 231, 1971.

[4] N. Varley and M. S. Boyce, “Adaptive management for reintroductions: updating a wolf recovery model for yellowstone national park,” *Ecological Modelling*, vol. 193, no. 3-4, pp. 315–339, 2006.

[5] W. J. Ripple and R. L. Beschta, “Trophic cascades in yellowstone: the first 15 years after wolf reintroduction,” *Biological Conservation*, vol. 145, no. 1, pp. 205–213, 2012.

[6] “Gray wolf,” https://www.nps.gov/yell/learn/nature/wolves.htm.

[7] “Elk,” https://www.nps.gov/yell/learn/nature/elk.htm.

# 6 Appendix 1

restart; with(plots); with(DEtools);

*# ‘Set Constants’*

*# ‘prey growth rate (a)’*

a := 0.1128:

*# ’predation rate (b)’*

b := 0.00064:

*# ‘Preadtor death rate (c)’*

c := 0.125:

*# ‘predator growth rate (d)‘*

d := 0.000025:

eqn1 := diff(x(t), t) = -b*x*y + a*x;

eqn2 := diff(y(t), t) = d*x*y - c*y;

vars := [x(t), y(t)];

*# ‘set initial conditions‘*

init1 := [x(0) = 19000, y(0) = 25]; init2 := [x(0) = 19000, y(0) = 100]; init3 := [x(0) = 19000, y(0) = 500];

*#‘set time ‘*

domain := 0 .. 120;

W := DEplot([eqn1, eqn2], vars, domain, init1, stepsize = 0.5, scene = [t, y], arrows = NONE, linecolor = red);

E := DEplot([eqn1, eqn2], vars, domain, init1, stepsize = 0.5, scene = [t, x], arrows = NONE, linecolor = blue);

display(E, W, title = ’Modeled*Population*of*Elk*vs*Wolves’);

display(W, title = ’Wolf*Population*Only’);

DEplot(eqn1, eqn2, vars, t = 0 .. 130, init1, init2, init3, stepsize = 0.5, scene = [x, y], title = ’Elk*vs*wolves*t = 0 .. 30’, arrows = NONE)

# 7 Appendix 2

restart; with(plots); with(DEtools);

*# ‘Set Constants’*

*# ‘prey growth rate (a)’*

a := 0.1128:

*# ’predation rate (b)’*

b := 0.00064:

*# ’prey carrying capacity (r)’*

r := 20000

*# ’predation rate (b)’*

b := 0.00064:

*# ‘Preadtor death rate (c)’*

c := 0.125:

*# ‘predator growth rate (d)‘*

d := 0.000025:

eqn1 := diff(x(t), t) = a*x*(1 - x/r) - b*y*x

eqn2 := diff(y(t), t) = d*x*y - c*y

vars := [x(t), y(t)]

*# ‘set initial conditions‘*

init1 := [x(0) = 19000, y(0) = 25]; init2 := [x(0) = 19000, y(0) = 100]; init3 := [x(0) = 19000, y(0) = 500];

*#‘set time ‘*

domain := 0 .. 120;

W := DEplot([eqn1, eqn2], vars, domain, init1, stepsize = 0.5, scene = [t, y], arrows = NONE, linecolor = red);

E := DEplot([eqn1, eqn2], vars, domain, init1, stepsize = 0.5, scene = [t, x], arrows = NONE, linecolor = blue);

display(E, W, title = ’Modeled*Population*of*Elk*vs*Wolves’);

display(W, title = ’Wolf*Population*Only’);

DEplot(eqn1, eqn2, vars, t = 0 .. 130, init1, init2, init3, stepsize = 0.5, scene = [x, y], title = ’Elk*vs*wolves*t = 0 .. 30’, arrows = NONE)