

Predator-Prey Dynamics

Josh Baxter Alicia Sit

Final Project MAT3395

Department of Mathematics University of Ottawa April 28, 2017

Contents

1	Intr	oduction	2		
2	The model: Lotka-Volterra				
	2.1	Equilibria	3		
	2.2	Stability	3		
	2.3	Time evolution	4		
3	Mod	lifying the model	5		
	3.1	Logistic growth	5		
	3.2	Fuctional responses	8		
	3.3	Competition	9		
4	Ecos	system	10		
	4.1	Food Web	10		
	4.2	Creating the Model	10		
	4.3	The Model	12		
	4.4	Numerical Values	14		
	4.5	Results	15		
5	Spat	tial Dependence	18		
	5.1	Solving this Model	19		
	5.2	Initial Conditions	21		
	5.3	Starting at the Same Position	22		
	5.4	Starting at Different Positions	25		
	5.5	Ideas For Improvement	28		
6	Con	clusion	28		

1 Introduction

The endeavor of this project is to investigate the evolution and dynamics of interacting animal populations. Starting with a basic model with one predator and one prey population (Lotka-Volterra model), we will analyze in the usual way its equilibria points, stability and time evolution of the populations. In an effort to bring this model closer to a realistic system, we will introduce various modifications that can be applied to the basic model. For example, limiting the growth rates of the prey, including the effects of interspecies competition, and adding a functional response for the predation mechanism.

Of course, in a realistic ecosystem, there are multiple predator and prey populations that interact. Combining the above mentionned modifications to the basic Lotka-Volterra equations, we numerically model the dynamics of a simple food web which include beetle, rabbit, fox and owl populations. As a bonus, we also present preliminary results if the animals are allowed to move around in a 2dimensional space.

2 The model: Lotka-Volterra

Given two populations in which share a predator-prey relationship, we can describe their population dynamics using the basic Lotka-Volterra equations. This model was simultaneously and independently developed by Alfred Lotka and Vito Volterra in the 1920's [1, 2].

$$\frac{dP}{dt} = \alpha P - \beta P V \tag{1}$$

$$\frac{dV}{dt} = c\beta PV - \delta V \tag{2}$$

where *P* and *V* are the prey and predator populations, respectively; α is the prey birth rate; β is the predation rate, i.e. the rate at which predators kill prey; *c* is the conversion rate from eaten prey to new predators; and δ is the predator death rate. All parameters are assumed to be positive.

There are several assumptions built into this model. The first is that there is an unlimited food supply for the prey (e.g. plants and vegetation for herbivores); in such a way, the prey maintain a constant birth rate, independent of population density. On the converse, the growth of the predator population relies solely on the presence of prey, and predators have limitless appetite. Another assumption is that prey do not live out their full life, but are inevitably eaten at some point for the duration of this model. Predators, on the otherhand, can die of natural causes at a constant rate. Additionally, these assumptions mean that there are no seasonal variations that might negatively or postively affect either population.

2.1 Equilibria

Let us investigate the potential equilibria of the Lotka-Volterrra equations. We begin setting Eq. 1 and Eq. 2 to zero:

$$0 = \frac{dP}{dt} = P(\alpha - \beta V) \implies \bar{P} = 0 \text{ or } \bar{V} = \frac{\alpha}{\beta},$$
(3)

$$0 = \frac{dV}{dt} = V(c\beta P - \delta) \implies \bar{P} = \frac{\delta}{c\beta} \text{ or } \bar{V} = 0.$$
(4)

We thus have two potential equilibria that give us both differential equations zero simultaneously: $(\bar{P} = 0, \bar{V} = 0)$ and $(\bar{P} = \frac{\delta}{c\beta}, \bar{V} = \frac{\alpha}{\beta})$. The first equilibrium is the morbid point where both populations are extinct; the second is a positive, real point.

2.2 Stability

To determine the stability of our two equilibria, we need to first calculate the Jacobian of the system. Recall that the Jacobian of our system is defined as,

$$J(P,V) = \begin{bmatrix} \partial_P \dot{P} & \partial_V \dot{P} \\ \partial_P \dot{V} & \partial_V \dot{V} \end{bmatrix},$$
(5)

where ∂ is shorthand for the partial derivative with respect to the subscripted symbol, and the dotted variables are shorthand for the time derivatives. The Jacobian is thus calculated to be,

$$J(P,V) = \begin{bmatrix} \alpha - \beta V & -\beta V \\ c\beta V & c\beta P - \delta \end{bmatrix}.$$
 (6)

Evaluating this at our extinction equilirium point,

$$J(0,0) = \begin{bmatrix} \alpha & 0\\ 0 & -\delta \end{bmatrix}.$$
 (7)

Since this is a diagonal matrix, the eigenvalues are simply $\lambda_1 = \alpha$ and $\lambda_2 = -\delta$. Both α and δ are positive by assumption, so we have a positive and negative equilibrium. Knowledge from our ordinary differential equations (ODEs) classes tells us that (0,0) is a saddle point, which is stable along one arm and unstable along the other in a P-V phase plane diagram. Thankfully (0,0) is not completely stable! Otherwise no matter what our predator and prey would be doomed to extinction. We see that solutions with P = 0 will move towards (0,0) along the stable arm; this can be interpreted as the predator population starving to death. On the other hand, solutions with V = 0 will move away from (0,0) along the unstable arm, which occurs since the nothing is eating the prey and thus the population explodes.

For non-zero populations, we need to analyze the second equilibrium point; the Jacobian evaluated at it is:

$$J\left(\frac{\delta}{c\beta},\frac{\alpha}{\beta}\right) = \begin{bmatrix} 0 & -\frac{\delta}{c} \\ c\alpha & 0 \end{bmatrix}.$$
 (8)

Since this matrix is neither diagonal, nor upper triangle, we will calculate the characteristic equation to find the eigenvalues. To do so, we take the determinant,

$$0 = \begin{vmatrix} -\lambda & -\frac{\delta}{c} \\ c\alpha & -\lambda \end{vmatrix} = \lambda^2 + \alpha\delta.$$
(9)

Therefore, the eigenvalues are $\lambda_{\pm} = \pm i \sqrt{\alpha \delta}$, which are purely complex. This corresponds to $(\frac{\delta}{c\beta}, \frac{\alpha}{\beta})$ being a stable, i.e. a point that solutions orbit. This suggests cyclical behaviour.

2.3 Time evolution

To better visualize the behaviour of the solutions of the Lotka-Volterra equations, we will use MAT-LAB to numerically solve them. Figure 1 is numerical simulations of the Lotka-Volterra equations over a 20 month period with initially 500 prey and 150 predators, and the following parameters: $\alpha = 0.5 \text{ month}^{-1}$, $\beta = 0.002 \text{ predator}^{-1} \text{ month}^{-1}$, c = 0.02 predator/prey, and $\delta = 0.4 \text{ month}^{-1}$.

In the time series plot, we see a oscillatory behaviour between the predator and prey populations. Initially, the prey population increases. However, after a short time, the predator population also begins to increase caused by the increase in prey. Then there comes to be a tipping point in which the number of predators overwhelm the prey and the prey population begins to decrease. Of course,



Figure 1: Numerical simulation of the Lotka-Volterra equations: time series (left) and phase plane plot (right).

this then means there comes a point when there is not enough prey for all the predators, and thus the predator population decreases. But now that there are less predators, the prey population can recover and the cycle starts all over again.

Since there are no other factors that might tip the favour to either one population, this oscillatory behaviour continues forever. This periodic behaviour is precisely cyclic orbits about the non-zero equilibrium in the phase plane. Trajectories cycle in the counter-clockwise direction, consistent with the saddle having its stable arm along the vertical axis and unstable arm along the horizontal axis.

3 Modifying the model

The Lotka-Volterra model provides a simple set of equations and useful starting point for understanding the interactions of a predator and prey population. Of course, despite its beautiful constant oscillatory behaviour and periodic orbits, some assumptions of this model are a little less than realistic. As is such, we will explore different options to make the model more realistic.

3.1 Logistic growth

The first assumption that we made with the Lotka-Volterra model is that the prey population have an unlimited food supply and grow exponentially. Perhaps over short enough periods of time this might be true, but over longer periods the prey will exhaust their food supply. More precisely, the ecosystem

that the prey live in has the ability, or carrying capacity K, to support only a certain population size. We say that the population grows logistically, and can be written mathematically as,

$$\frac{dP}{dt} = \alpha P \left(1 - \frac{P}{K} \right). \tag{10}$$

Again, the population has birth rate α ; however, now, it is limited by the carrying capacity. As we have seen, if the population is smaller than the carrying capacity, it will grow until it saturates to *K*. If the population begins larger than the carrying capacity, it will decrease to *K*.

Suppose we now modify the growth of the prey in Eq. 1 to be logistic, but leave Eq. 2 untouched,

$$\frac{dP}{dt} = \alpha P \left(1 - \frac{P}{K} \right) - \beta P V, \tag{11}$$

$$\frac{dV}{dt} = c\beta PV - \delta V. \tag{12}$$

To determine the equilibria and stability for this new system, we follow the same procedure as in Sec. 2. Setting the derivatives to zero,

$$0 = \frac{dP}{dt} = P\left(\alpha\left(1 - \frac{P}{K}\right)\right) \implies \bar{P} = 0 \text{ or } \bar{V} = \frac{\alpha}{\beta}\left(1 - \frac{\bar{P}}{K}\right), \tag{13}$$

$$0 = \frac{dV}{dt} = V(c\beta P - \delta) \implies \bar{P} = \frac{\delta}{c\beta} \text{ or } \bar{V} = 0.$$
(14)

Again, we have two equilibria, the extinction one at (0, 0) and the positive one. For the stability of each, the Jacobian is calculated to be,

$$J(P,V) = \begin{bmatrix} \alpha \left(1 - \frac{2P}{K}\right) - \beta V & -\beta V \\ c\beta V & c\beta P - \delta \end{bmatrix}.$$
 (15)

Evaluating the Jacobian at (0, 0) yields the same stability conditions as before: it is a saddle. As for the second equilibrium, we have,

$$J(\bar{P}, \bar{V}) = \begin{bmatrix} -\frac{\delta}{c\beta K} & -\frac{\delta}{c} \\ c\alpha \left(1 - \frac{\delta}{c\beta K}\right) & 0 \end{bmatrix}.$$
 (16)

As opposed to going through the messy algebra of solving for the eigenvalues, we shall instead call upon our knowledge from ODEs once again. We will determine the stability by analyzing the signs of

the Jacobian's trace and determinant using the Fig. 2.



Figure 2: Stability and Equilibrium analysis using a Jacobian's trace and determinant. [3]

Right off the bat, we see that our Jacobian as a negative trace; this land us on the left side of the trace vs. determinant plot. The determinant, on the other hand, is,

$$\det(J) = \alpha \delta \left(1 - \frac{\delta}{c\beta K} \right). \tag{17}$$

Since all the parameters are assumed positive, the determinant could be positive or negative depending on the sign of the quantity in the brackets. If $K > \delta/(c\beta)$, then according to the figure, we have a stable equilibrium that solutions spiral in towards. However, if $K < \delta/(c\beta)$, then we would have an unstable saddle-like equilibrium. We will note however that usually this is an unphysical scenario given that the typical parameters are on the order of $\delta \approx 10^{-4} \ days^{-1}$ and $c\beta \approx 10^{-5} \ prey^{-1} \ days^{-1}$, which gives $\delta/(c\beta) \approx 10 \ prey$. In contrast, the carrying capacity is on the order of 1000s of prey. Thus, *K* tends to be much larger than $\delta/(c\beta)$, meaning that we have a stable spiral.

Figure 3 shows the numerical simulation of the Lotka-Volterra equations with the addition of logistic prey growth; the same parameter values as before are used, and now with K = 10000. Compared to the time series of the basic Lotka-Volterra equations, we still see an offset oscillatory behaviour between the predator and prey populations. However now with the logistic growth, this dampens the oscillations of the prey — and in turn the predator — population. In particular, this means that the two



Figure 3: Numerical simulation of the Lotka-Volterra equations with logistic prey growth: time series (left) and phase plane plot (right).

populations do reach the positive equilibrium, as can be seen in the phase plot: the solutions spiral into the equilibrium.

3.2 Fuctional responses

Another modification that we can add to our base model is to impose a saturation limit on the predation rate. We do this in hopes to massage the assumption that predators have a limitless appetite into something more realistic. We can classify how the predator and prey interact by their type of functional response [4, 5]. The linear interaction, βPV , found in the basic Lotka-Volterra equations is classified as Type 1: the number of prey consumed is independent of the prey population.

Instead, we could introduce a hunting mechanism for the predators that is dependent on the density of the prey population. The predation rate could take, for example, the following functional form in the prey equation:

$$\frac{dP}{dt} = \alpha P - \frac{aPV}{1 + aT_H V},\tag{18}$$

where *a* is the attack rate, and T_H is the handling time. This form is known as a Type 2 functional response, and corresponds to a plateau in hunting. This term can be interpreted as predators having less of a need to hunt as often since they can find food more quickly as the prey population increases. This functional response separates the time it takes a predator to hunt (with the attack rate *a*) from the time it takes for it to eat by introducing a handling time T_H . For fixed attack rates and handling times,

for small prey populations, a larger proportion of prey are killed per predator; however, as the prey population increases, a smaller and smaller proportion of prey is killed per predator. Thus a plateau in hunting. This functional response has been observed in some bug species in an attempt to overwhelm their predators by sheer numbers.



Figure 4: Numerical simulation of the Lotka-Volterra equations with Type 2 function response: time series (left) and phase plane plot (right).

Figure 4 shows the numerical simulation of the Lotka-Volterra equations with the addition of a Type 2 functional response. In contrast to the logistic growth plots that displayed dampened oscillations, we see here that the oscillations are now increasing in the time series. This corresponds to the positive equilibrium point being unstable now, and can be interpreted as the fact that the predators can no longer control the prey population.

3.3 Competition

In the wild, there is more than just predation as an interation between species. Indeed some species might compete for resources and have a negative effect on each other (interspecies competition), or they might benefit each other (mutualism). Given two species, X and Y, that are not necessarily predator and prey populations, a simple set of differential equations to describe interspecies competition is,

$$\frac{dX}{dt} = \alpha_X X - \gamma_{XY} X Y, \tag{19}$$

$$\frac{dY}{dt} = \alpha_Y Y - \gamma_{YX} Y X, \tag{20}$$

where α_i is the growth rate of the *i*^{*i*} *h* population, and γ_{ij} is the effect that the *j* species has on *i* (assumed to be positive constants). It is not necessary that $\gamma_{XY} = \gamma_{YX}$ as one species might be more affected by the other species rather than vice versa. If we were to model mutualism instead, we would just need to flip the negative signs to positive signs.

4 Ecosystem

In the previous sections, we discussed different modifications that can be applied to the Lotka-Volterra model to account for different effects such as logistic growth, competition, functional response, etc. In this section, we will use these tools to model a mini-ecosystem.

4.1 Food Web

The first step in creating a model is to map it out. This is generally done using a block diagram — a diagram which shows how a given population affects other populations. When it comes to a biological system, like an ecosystem, such block diagrams should be nothing new, assuming you had an adequate fifth grade teacher. In such a system, we call the block diagram a food web.

Figure 5 shows the bare-bones food web of the ecosystem that we wish to model. Here, we have two primary predators and two primary prey. The prey are the beetle and the rabbit, and the predators are the fox and the owl. The catch here is that despite being a predator, the owl is also a prey to the fox. Of course this diagram does not cover everything. If we want to create a realistic model, we need to add some complexity. Animals are born and animals die by both natural causes and by being eaten. The prey need to compete for resources, and the Predators can only consume so many prey in a given amount of time. All of these things need to be reflected in the model.

4.2 Creating the Model

Beginning with the prey, we need to start with growth rates. We are assuming a realistic environment with limited resources. This environment can only supports so many prey. However, for the rabbits and the beetles, despite sharing some resources (eating similar plants), it can be assumed that they both have individual interests. Some beetle species for example eat fungus and dung; whereas rabbits have the tendency to eat twigs and bark when resources are low. With this in mind, we can assume logistic growth for each of the prey where the carrying capacity is independent of the other animals.



Figure 5: Basic Food Web of the ecosystem we wish to model

To account for any competition between the Beetle and the Rabbit, a competition term will be included in the model.

Next, we need a background mortality rate. The simplest technique for this is to assume the background mortality be proportional to the population of the given animal itself. It should be mentioned that in the classic Lotka-Volterra, background mortality of the prey is ignored. This is not exactly physical since in the wild some prey have been known to live out their days naturally. For example, when considering the beetle, some species like the *Callosobruchus maculatus* are only expected to live for half a month [6]. Our model will thus include background death for all animals in the system.

The most important part of this model is predation. That's why you are reading this, right? There are two types of predation models discussed; the type 1 and type 2 functional responses. Recall that where type 1 assumes a predator can eat continuously, type 2 includes a handling time, a time length in which the predator will be satisfied with what they have just ate. Keeping this in mind, for the Beetle,



Figure 6: Summary of our ecosystem model

both the Fox and the Owl will have a type 1 (linear) interaction since it's such a small and abundant creature. As for the Rabbit, since it is a relatively large prey, it will require a handling time for both the Fox and the Owl and will be given type 2 interaction with both. Similarly, the Fox-Owl interaction will be given a type 2 functional response. Figure 6 summarizes the key points discussed above that make up the model. The next step is to form the system of Ordinary Differential Equations that will be the basis of the model.

4.3 The Model

In previous sections, mathematical formulations of the functional responses, logistic growth, and competition were discussed. Applying these to the previous discussion, we can form our system of ODEs that describe the population dynamics of our system.

$$\frac{dB}{dt} = e_B B \left(1 - \frac{B}{K_B} \right) - g_{BF} B F - g_{BO} B O - \delta_{BR} B R - m_B B$$
(21a)

$$\frac{dR}{dt} = e_R R \left(1 - \frac{R}{K_R} \right) - \frac{g_{RF}}{1 + g_{RF} T_{RF} R} RF - \frac{g_{RO}}{1 + g_{RO} T_{RO} R} RO - \delta_{RB} RB - m_R R$$
(21b)

$$\frac{dF}{dt} = c_{BF}g_{BF}FB + \frac{c_{RF}g_{RF}}{1 + g_{RF}T_{RF}R}RF + \frac{c_{OF}g_{OF}}{1 + g_{OF}T_{OF}O}OF - m_FF$$
(21c)

$$\frac{dO}{dt} = c_{BO}g_{BO}OB + \frac{c_{RO}g_{RO}}{1 + g_{RO}T_{RO}R}RO - \frac{g_{OF}}{1 + g_{OF}T_{OF}O}OF - m_OO$$
(21d)

To make the equations easier to understand, Figure 7 shows our food web only this time with more details and parameters.



Figure 7: Labeled Food Web of our ecosystem

In Equation 21, there many parameters which may cause confusion. However, these parameters were denoted in such a way to reduce any uncertainty. First, the beetle, rabbit, fox, and owl populations themselves are denoted B, R, F, and O, respectively. Prey birth rates are denoted e where the subscript indicates the animal. K is the carrying capacity and m is the mortality rate of the sub-scripted animal. Parameters describing interaction (predation and competition) have two subscripts. The predation terms are g, T, and c which represent the predation rate, handling time, and predation-predator birth rate conversion factor, respectively. In these parameters, the first subscript represents the prey in the

interaction and the second represents the predator. The last term is δ which represents competition between the prey species. The first subscript represents the victim of the interaction whereas the second represents the competitor.

4.4 Numerical Values

As you can see, creating a model of a small ecosystem using some basic assumptions is not very difficult. The challenging part of modeling this system is finding the appropriate numerical values for the parameters. In order to solve these equations however, numerical values are required. The first step is to determine units. Almost all of the parameters have some aspect of time, so we need to find an appropriate unit of time. In the case of an ecosystem, a month seems to be a good start.

Now for some simple parameters. Prey birth rates are simple as they are quite clearly reported and can be found on numerous web pages. Rabbits seem to have a rather varying birth rate. We focus on the Eastern Cottontail Rabbit or *Sylvilagus floridanus*, which can have five litters of up to eight babies per year [7]. This averages out to about three babies per month and hence we have $e_R = 3 month^{-1}$. In a similar fashion, the *Callosobruchus maculatus* can lay up to 100 eggs in a year — most of which will hatch. This can be averaged out to 8 beetles hatched per month by a single beetle or $e_B = 8 month^{-1}$.

Background mortality rates are rather simple as well. These can be approximated as being the inverse life span of the given animals. The lifespan of a fox is expected to be two years, so $m_F = 1/(2 * 12) \approx 0.04 \text{ month}^{-1}$ [8]. Similarly the cottontail rabbit is expected to live about three years $(m_R \approx 0.028 \text{ month}^{-1})$, and an owl about four years $(m_O \approx 0.02 \text{ month}^{-1})$ [9]. Of course, the beetle is expected to live about half a month, so $m_B = 2 \text{ month}^{-1}$.

As for the actual predation parameters g, c, and T, numerical values are not readily available, and those that are available work for their individual ecosystem. So for this particular system, such values are approximated or guessed, and tested by using them to solve the equations. One example of such an approximation is the handling time for the Fox-Rabbit interaction. It is assumed that a Fox can eat two Rabbits every day. So $T_{RF} = 2/30 = 0.0667$ month. Similarly, the Owl can eat one Rabbit every day $T_{RO} = 0.033$ month. As for g and c, these values were found via trial and error (in the hopes of finding a stable system).

The parameters used in solving this system are all found in Table 1.

Parameter	Value	Parameter	Value
e _B	8	8 _{RF}	0.0005
e_R	3	T_{RF}	0.0667
K _B	75000	8ro	0.0002
K_R	10000	T_{RO}	0.0333
m_B	2	C_{RF}	0.01
m_R	0.028	c_{RO}	0.03
m_F	0.04	<i>gof</i>	0.0003
m_O	0.02	T_{OF}	0.0167
g_{BF}	0.001	c_{OF}	0.03
8в0	0.0005	δ_{RB}	0.00002
c_{BF}	0.0001	δ_{BR}	0.0002
CBO	0.05		

Table 1: Numerical Values used to solve Equation 21

4.5 Results

To solve the above system of ODEs with the numerical values listed, MATLAB's ODE45 function was utilized. The time series plots for this system of ODEs is show in Figure 8. Note that the Beetle population is two times the displayed value; it is plotted this way to make the other populations more visible.



Figure 8: Time series plot of our food over a 200 month period.

These results are not particularly interesting. The populations quickly evolve into an equilibrium

state. However, the qualitative equilibrium points are what one may expect. The prey populations are higher than the predator populations with the population sizes ranging from the smallest prey (highest population) to the largest prey (lowest population). The troubling issue with these results is the lack of oscillations that are expected from a Lotka-Volterra Model. One would expect fluctuations in the predator and prey populations, since not only is this a consequence of the Lotka-Volterra Equations, but it is also a physical phenomenon in nature.

The problem here is the complexity of the ecosystem. The Lotka-Volterra equations provide a simple qualitative model to show the effects a single predator has on a single prey. The addition of more than one of each adds a level of complexity for which this model is not well-suited. Though it can provide an approximate equilibrium point for the ecosystem, which may even account for the average population over a year, it cannot be used to model the week-by-week or even month-by-month dynamics. This model also ignores climate and weather fluctuations that may occur throughout the year. For example, the plant life available to the beetles and the rabbits in the summer may not be around in the winter. Food becomes more scarce, and we can expect to see the populations decrease in those months.

To reiterate, this model does provides us with an approximation for the equilibrium populations for this system. One use for such a model is to determine how each population affects the others. If the fox population gets a disease and suddenly there are much less, or perhaps they eat less, how does this affect the population? What if the winter was particularly harsh and the Owl population is killed off? These are some things that this model could help us predict.

Suppose for example, Billy Bob, a lone hermit, lives by himself in the vicinity of this ecosystem. He's not really a hunter (he prefers vegetables from his garden) so he does not affect the animal population in the ecosystem. However, one thing about Billy Bob is that he HATES Beetles. They are small, ugly, and frankly they eat his veg. He decides that he wants to spray around his home and kill off the Beetle population. Now, Billy loves animals like foxes and rabbits. He is also an avid owl photographer. He could never live with himself if he ended up harming these populations.

Like any rational human being, Billy decides to create a model of the ecosystem, and *gasps!*, his math gives him Equation 21. He decides to numerically solve his model by guessing some initial populations and gets similar results to those in Figure 8. As it is currently summer, he assumes that the equilibrium values are a better approximation for the current populations than his initial guesses. He now simulates the system after spraying, using the equilibrium values as initial conditions and

setting the initial Beetle Population to be zero (assuming instantaneous death). The results he gets are those shown in Figure 9 and Figure 10, which show how the populations of the other animals respond to a sudden lack in Beetles in the short term and long term, respectively.



Figure 9: Food Web Time Series Plot with no Beetles (short term)



Figure 10: Food Web Time Series Plot with no Beetles (long term)

Needless to say, Billy Bob was shocked at the fact that simply eliminating a pest could totally

kill off the predator population and cause an overthrow of the Rabbit population. With all the rabbits, maybe food will become scarce and they will attack his garden. What about the Owls? They die almost right away from a lack of Beetles. And sure, it's long term, but the foxes will eventually die off as well. Because of Billy's proactive thinking and his Mathematical Modeling skills, he was able to stop himself from ruining an entire ecosystem.

To conclude, we have developed a system of ODEs that model a small ecosystem. This model was used to find the equilibrium populations of this hypothetical system. The model was then used to show the effect of eliminating a single organism from the system showing that it would result in the long term destruction of the system.

5 Spatial Dependence

A feature of predator prey dynamics that is ignored by the Lotka-Volterra model and its modifications is spatial variation. Very rarely is a predator-prey pair restricted to a single location, so a variation that ensures spatial dependence in the Lotka-Volterra model should be considered.

When modeling the spatial dynamics of a biological system, it is common practice to use random walk models. In such models, an object (a particle, bacteria, protein, etc) is placed in a grid at the origin. At each increment in time, the particle can take a single step forward, backwards, left or right (assuming a 2-D model). The direction of choice is generally chosen at random (using random number generators). When many particles are modeled in a random walk, the behavior becomes diffusive. The random walk of a large number of particles can be described using the diffusion equation.

$$\frac{\partial f}{\partial t} = D\nabla^2 f \tag{22}$$

where *D* is the constant diffusion coefficient that characterizes the system, and ∇^2 is the Laplacian operator. The solution of the diffusion equation is one which shows the "downhill travel" of some sort of substance through a medium. In other words, the substance will travel from an area of high density to an area of low density (Fick's law) in such a way that mass is conserved (Continuity Equation). This makes it ideal for modeling population dynamics. As an animal (or human for that matter) population grows in a certain area, it seems to spread outwards. This is why it seems natural to apply the diffusion equation to population dynamics. To include a spatial dependence in the Lotka-Volterra model, we will be assuming that the predator and prey systems both start at a given point and that the motion of a given animal of either species can be described using a random walk. So to model the spatial dynamics of the entire system, a diffusion coefficient will be added to the original Lotka Volterra model.

$$\frac{\partial P}{\partial t} = D_P \nabla^2 P + \alpha P - \beta P V \tag{23a}$$

$$\frac{\partial V}{\partial t} = D_V \nabla^2 V - \delta V + c\beta P V \tag{23b}$$

As with the original Lotka-Volterra Model, α represents the prey birth rate, β is the predation rate, c is the conversion rate (proportionality constant describing how many prey are killed for a predator to be born), and δ is the Predator mortality rate. Now we have added a D_V and D_P which are the diffusion coefficients for the Predator (*P*) and Prey (*V*) systems, respectively. These coefficients describe the rate of spread of both system and their units are Area/Time. It is worth noting that we are assuming that the diffusion coefficients are constant; however, much more complicated systems can be modeled using spatially-dependent or even population-dependent diffusion coefficients.

5.1 Solving this Model

This, like most other systems of PDEs needs to be solved numerically. Here, we will make use of a simple Forward Euler solution scheme. First, we need to make our solution space discrete. This means we choose a Δx and Δy that represent the spatial step sizes in the x and y directions. This means that every point in our solutions space can be described by a coordinate (x_i, y_j) where $x_i = i\Delta x$ and $y_j = j\Delta y$, where *i* and *j* are integers that represent the x and y coordinates of each grid space. Coordinates can take on values ranging from 1 to N_x or N_y where N is the number of cells in the x or y direction of the system. At the same time, we need to also make time discrete so that any time can be described by $t_n = n\Delta t$ where Δt is our time step size. This discrete scheme is represented in Figure 11 with $\Delta y = \Delta x$.

Now we need to turn our derivatives into finite differences. So for the first order time derivative:

$$\frac{\partial P}{\partial t}(x_i, y_j, t_n) \approx \frac{P_{i,j}^{n+1} - P_{i,j}^n}{\Delta t}$$
(24)



Figure 11: Discrete Solution Space Scheme

For our second order spatial derivative, the finite difference approximation is given by:

$$\frac{\partial^2 P}{\partial x^2}(x_i, y_j, t_n) \approx \frac{P_{i+1,j}^n - 2P_{i,j}^n + P_{i-1,j}^n}{\Delta x^2}$$
(25)

Using these finite difference approximations, we can rewrite our model (Equation 29) into finite differences.

$$\frac{P_{i,j}^{n+1} - P_{i,j}^n}{\Delta t} = D_P \left(\frac{P_{i+1,j}^n - 2P_{i,j}^n + P_{i-1,j}^n}{\Delta x^2} + \frac{P_{i,j+1}^n - 2P_{i,j}^n + P_{i,j-1}^n}{\Delta y^2} \right) + \alpha P_{i,j}^n - \beta P_{i,j}^n V_{i,j}^n$$
(26a)

$$\frac{V_{i,j}^{n+1} - V_{i,j}^n}{\Delta t} = D_V \left(\frac{V_{i+1,j}^n - 2V_{i,j}^n + V_{i-1,j}^n}{\Delta x^2} + \frac{V_{i,j+1}^n - 2V_{i,j}^n + V_{i,j-1}^n}{\Delta y^2} \right) - \delta V_{i,j}^n + c\beta P_{i,j}^n V_{i,j}^n$$
(26b)

Both parts of Equation 26 can be rearranged and solved for $P_{i,j}^{n+1}$ and $V_{i,j}^{n+1}$. Then, using a simple computer code these equations can be solved. The algorithm involves creating four matrices, two for each animal. One will represent the *n* time step, and the other will represent *n* + 1. The solution will start with initial conditions which will be stored in the *n* matrix (for *n* = 0). By looping through the

spatial indexes *i* and *j*, we get $P_{i,j}^{n+1}$ and $V_{i,j}^{n+1}$ using the rearranged versions of Equation 26 and stored in the n + 1 matrices (for n + 1 = 1). Once the n + 1 matrices are solved, the *n* matrices are reset and used to store the n + 1 matrices that were just calculated. And then we repeat this for the rest of the *n*. Solve for n + 1 using *n*, replace old *n* with n + 1, and repeat.

Of course a couple small details arise when trying to solve this. Initial conditions (n = 0) were already mentioned and will be further discussed later. However when it comes to solving any point with the index i = 1 or N_x (where N_x is the number of discrete cells that our solution space has in the *x* direction), we need data for points i = 0 or $N_x + 1$. Because of this we require boundary conditions. For our solution, we will keep things simple and use Dirichlet Boundary Conditions (DBC) where we set all boundary values to be zero. This can be implemented by only solving for i = 2 to $N_x - 1$ and j = 2 to $N_y - 1$ and keeping all outer cells in the simulation domain (i = 0 and N_x or j = 0 and N_y) equal to zero for all time. Physically this represents the fact that there are no animals outside of our 2D system.

5.2 Initial Conditions

The algorithm and boundary conditions are now set up. All that is missing is a set of initial condition and numerical values needed to actually numerically solve our model. Let's start with algorithm parameters. We are going to assume that our system is rather large: $10 \, km$ by $10 \, km$. In order for our code to solve the solution in a reasonable amount of time, we need to pick a broad spatial resolution, so we choose $\Delta x = \Delta y = 100 \, m$ so that $N_x = N_y = 100$. So our solution matrices (for *n* and *n* + 1) are going to be 100×100 in size (meaning 10000 calculations per time step). Our time step is chosen $\Delta t = 0.0025 \, months$. This time step was chosen because it is relatively large but stable (the solutions don't explode to infinity).

Now we need to think about actual model parameters. The prey birth rate is set to be $\alpha = 0.5 \text{ month}^{-1}$. We set the predation rate to be $\beta = 0.05 \text{ month}^{-1} \text{ predator}^{-1}$. We set the predationpredator birth rate conversion parameter to be $c = 0.5 \frac{\text{predator}}{\text{prey}}$. The predator death rate is $\delta = 0.04 \text{ month}^{-1}$. As for the diffusion coefficients, it was assumed that both the predator and prey could cover as much area in the same amount of time, thus having the same diffusion coefficient. A reasonable assumption for the diffusion coefficient was chosen to be $D_V = D_P = D = 10000 \frac{m^2}{\text{month}}$.

As for actual initial populations, it was decided that the Predators would start with $V_0 = 1500$

and the Prey would start with $P_0 = 10000$. The original idea was to have the populations start in one discrete step (almost like a delta function) and have them spread out over time. This however is problematic as it leads to instabilities. So, it was decided to use 2-D normalized Gaussian Distributions for the initial conditions. This is because the natural solution to the diffusion equation with an Delta function initial condition is a spreading Gaussian Function. So the Initial Conditions are given by Equation 27. The coefficient in front ensures that if integrated over 2-D space the total populations will be V_0 and P_0 . And x_0 and y_0 denote the position of the center of the Predator and Prey distributions.

$$V(x, y, t = 0) = \frac{V_0}{4\pi D} e^{\frac{(x-x_0)^2 + (y-y_0)^2}{4D}}$$
(27a)

$$P(x, y, t = 0) = \frac{P_0}{4\pi D} e^{\frac{(x-x_0)^2 + (y-y_0)^2}{4D}}$$
(27b)

This model is now ready to be solved. This will be done twice. The first solution will assume that the initial (x_0, y_0) of both populations are the same. The second will assume that the two populations start at different locations.

5.3 Starting at the Same Position

The first solution will be done by assuming the Predator and Prey populations start at the same spot. This point is conveniently chosen to be at the center of the domain $(i_0, j_0) = (50, 50)$. This initial distribution is shown in Figure 12 which qualitatively shows the initial population spread of both the Predators and the Prey.



Figure 12: Initial population distribution of the Predator and Prey.

Using the previously discussed algorithm, a MATLAB code is used to solve our model. The results are plotted in Figure 13, 14, and 15. These figures show the time series and phase plots of the Predator Prey systems at positions R=0km, R=2km, and R=4km from the center (starting) point. What we see at each of these locations are population oscillations that we expect to see from the basic Lotka-Volterra model. An increase in prey population will shortly lead to an increase in predator population through predation. This in turn leads to further increased predation followed by a decrease in the prey population. With a lack of prey, the predation decreases, and the predator population also decreases, allowing for the prey population to reproduce and increase. This repeated cycle is the natural solution of the L-V model.



Figure 13: Population Dynamics of the spatial dependent Predator-Prey Model at R=0km from the center position

What we see in the spatial dependent results is the amplitude of the oscillations decreasing. This of course is caused by the diffusive spread of the population. Initially, outside of the initial population spread, the populations are zero. As the simulation runs, the populations quickly spread (diffuse). This is why we see a fast decrease in population at R=0km at the beginning of the simulation and a fast increase at the same time at positions R=2km and R=4km. As time wears on, the populations continue to spread outwards thus leading to a decrease in "population amplitudes" over time.

Analyzing the phase plots, we see a surprising result. This system is cycling into a non-zero equilibrium. This is very interesting as with the Dirichlet Boundary Conditions, we would expect that the system would tend to zero. This expectation is from the fact that the steady state solution of the basic diffusion equation is simply the Laplace equation (Equation 28).



Figure 14: Population Dynamics of the spatial dependent Predator-Prey Model at R=2km from the center position



Figure 15: Population Dynamics of the spatial dependent Predator-Prey Model at R=4km from the center position

$$\nabla^2 V = 0 \tag{28}$$

The Laplace equation with Dirichlet Boundary conditions is simply V = 0 (this is simple to see in one dimension where the solution is a linear function which must be zero at x=0 and x=L). The reason we don't see our system evolving to this point is simply that we have a birth rate that outweighs the death rate and the rate of diffusion. This also explains why the minima in the oscillating Predator and Prey population cycles are increasing over time.

It would be interesting to see the system completely evolve into equilibrium, however, the simula-

tion takes too long to run.

5.4 Starting at Different Positions

The second solution will be done by assuming the Predator and Prey populations start at different locations. These points will be at positions $(i_0, j_0) = (60, 60)$ for the Prey and $(i_0, j_0) = (40, 40)$ for the Predators. This is shown in Figure 16.



Figure 16: Initial Population Spread of Predator and Prey Populations



Figure 17: Population Dynamics of the spatial dependent Predator-Prey Model at the Prey Starting Point

The results are plotted in Figure 17, 18, and 19. These figures show the time series and phase plots of the Predator Prey systems at the Prey starting point, the Predator starting point, and a point directly



Figure 18: Population Dynamics of the spatial dependent Predator-Prey Model the Predator Starting Point



Figure 19: Population Dynamics of the spatial dependent Predator-Prey Model directly between the Predator and Prey Starting Points

in between (i = j = 50).

At the Prey Starting Point (Figure 17), the time series shows that right at the beginning we have zero Predator population and a quickly diffusing Prey Population. Because of the birth rate of prey, and the lack of predator in this area, the prey population quickly starts to recover from the diffusive deterioration. Due to the scaling, it's difficult to see in the figure, however, slowly the Predator population is growing in the area due to diffusion (t=100 and on). However, the growth of the Predator population seems to accelerate due to the increase in prey population (at around t=1000). After this sudden growth, both populations seem to reduce to 0. A video showing the population dynamics of this system shows that the highest predator population at t=1100 is in the vicinity of the Prey starting

point. This means that the center of the predator population density moved from its starting point to that of the Prey's population density center (from (40, 40) to (60, 60)). After that sudden growth at the Prey starting point, the predator population diffuses outwards.

At the Predator Starting Point (Figure 18), we see similar dynamics. The predator population quickly diffuses away and the prey population diffuses in and grows due to an imbalance between the predation rate and birth rate. And again with the growth of the prey population, we see a growth of the predator population, though not as great as that seen at the Prey Starting Point. Near the end as both populations seem to decrease due to mortality and diffusive spread, we seen what seems to be the beginning of another cycle. The prey population seems to start to grow slightly near the end. However due to simulation time, the idea of a second cycle, though likely, has yet to be explored. It is likely that as time goes to infinity, this system would evolve similarly to that of the previous section (same starting point).

The point directly between (Figure 19) has particularly interesting dynamics. We see a sudden growth of the prey population with a high growth rate (slope). With the increase in predator population due to diffusion and predation, the rate of the Prey growth is slowed almost to zero (around t=50) in an interesting balance between growth, diffusion and predation. This balance is unstable and the prey population begin to climb again, thus leading to a large increase in the predator population. As a result the prey population decreases, however, near the end of the simulation a slight increase is a tell-tale sign that a second cycle would have happened if the simulation were run longer.

The dynamics of this system was particularly interesting. The traveling of the predator area of highest density from (40, 40) to (60, 60) is what would be expected due to the fact that in nature, animals tend to follow the food. They chose to live in areas where food is in abundance. Since there were more prey at the prey starting point, then it would make sense that a large portion of the predator population would want to move there. Near the end of the simulation both populations seem to tend towards the middle of the solution space (their points of highest density end at around (50, 50)). It is hard to determine if that is the natural resting place for the highest population density, or if it is a result of the limited solution space and the boundary conditions. This could be investigated further with a more powerful computer simulating a much larger domain size (for longer time periods), but this is beyond the scope of this project.

5.5 Ideas For Improvement

This model added extra layers of complexity to the Lotka-Volterra model. Further complexities could be implemented using the manipulations mentioned in previous sections (Logistic Growth, Functional Response, Competition, etc). These have already been discussed. A further improvement would be to investigate the effects of different Diffusion Coefficients. It is beyond the scope of this project, however, an interesting study would be to investigate the collective movements of different predatorprey systems, and determine diffusion coefficients based off the amount of area covered over time.

Further, more interesting locations could be investigated using spatially varying diffusion coefficients. For example, one could model a system where half of the simulation domain is a grass meadow, and the other half is forest. If the animal has an easier time traveling through the meadow, the diffusion coefficient for that area of the domain would be higher than that of the forest. For this a slight manipulation would have to be made to the model:

$$\frac{\partial P}{\partial t} = \nabla \cdot (D_P(x, y) \nabla P) + \alpha P - \beta P V$$
(29a)

$$\frac{\partial V}{\partial t} = \nabla \cdot (D_V(x, y)\nabla V) - \delta V + c\beta P V$$
(29b)

Similarly, population dependent diffusion is another area worth investigating ($D_V(V)$ as opposed to $D_V(x, y)$) where one may want to take into account the fact that an area with an already highly dense population may be less favorable (lower diffusion constant for higher populations).

On top of that the other improvements would involve using high performance methods and more powerful computers in order to simulate larger systems where the boundary condition will have less effect on the long term results (as is likely the case in the above results). All that said, the spatially dependent model investigated in this section was a huge success, and shows realistic spatially-varying predator-prey population dynamics.

6 Conclusion

Needless to say, a real world ecosystem has many more complex interactions. This report has covered some preliminary dynamics of predator-prey systems, starting from the basic Lotka-Volterra equations, then building up to a simple food web that incorporated various modifications. Modifications

included limiting the growth rate of the prey, limiting the predation rate of the predators, and introducing a different kind of interaction in the form of competition. We found that if a foodweb is broken, it can have detrimental effects on the rest of the populations. Building off of this, a 2-dimensional model was constructed in which predator and prey populations had the freedom to move around and interact. The results show the movement of predator populations in order to be closer to the prey population. It showed how the growth and depletion of each population affected the other and how that can be affected by the diffusive motion of animal populations. With a more powerful computer, it would be interesting to explore larger systems with multiple different populations and perhaps different boundary conditions.

References

- [1] A.J. Lotka. Elements of Physical Biology. Williams and Wilkins, (1925).
- [2] V. Volterra. Variazioni e fluttuazioni del numero d'individui in specie animali conviventi. *Mem. Acad. Lincei Roma*, 2, 31-113 (1926).
- [3] "Journal Activity: Systems of Linear ODE Summary". http://www.amshonors.com/journal-activity-systems-of-linear-ode-summary/>, April 27, 2017.
- [4] C.S. Holling. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *The Canadian Entomologist*, **91**(5), 293-320 (1959).
- [5] C.S. Holling. Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist*, 91(7), 385-98 (1959).
- [6] C.W. Beck, and L.S. Blumer. Life Cycle of Bean Beetles, Callosobruchus maculatus (Coleoptera Chyrsomelidae). http://www.carolina.com/teacher-resources/Interactive/life-cycleof-bean-beetles/tr25103.tr>, April 27, 2017.
- [7] Sylvilagus floridanus (eastern cottontail). Animal Diversity Web. http://animaldiversity.org/accounts/Sylvilagus_floridanus/, April 27, 2017.
- [8] Red Fox. National Geographic. http://www.nationalgeographic.com/animals/mammals/r/red-fox/, April 27, 2017.

[9] Great Horned OW1. National Geographic. http://www.nationalgeographic.com/animals/birds/g/great-horned-owl/, April 27, 2017.