MATH 481, SPRING 2021

PROJECT 4
POPULATION MODELS

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Abstract. We present two different population models, one is a differential equation that is a slight modification of a model developed by Verhulst in the 19-th century to include harvesting/hunting, and the other is a version of the predator prey model, initially developed by Lotka and Volterra in the early 20-th century, which accounts for competition within of the two species. We will take a qualitative approach to understanding the overall behaviour of each system.

1. Introduction

The study of population growth has been of great interest since at least the end of the 1700's, at which point the anonymously written, *An Essay on the Principle of Population* was published. This essay focused on addressing the issues of population growth affecting food availability and ultimately leading to increased poverty rates. The idea was to compare the geometric progression associated with population growth to the arithmetic progression associated with food production, and then observing how the differing growth rates between the two leads to potential problems of increased demand and lower supply. A very important part of the book, which as been dubbed the *Malthusian growth model*, named after the real author Thomas Robert Malthus, discussed increased population size leading to increased labor supply and thus lowering wages, leading to poverty. This model is mathematically characterized as an exponential growth model. The assumption is simply that the population will increase exponentially indefinitely with no competition or carrying capacity accounted for [1, 4].

Malthus eventually discussed in his essay that this initial model would not suffice to explain the population accurately, as he knew that competition would certainly play a factor with increased population size. Nevertheless, the aforementioned model is named after him. About 30 years later, in 1838 a mathematician named Pierre François Verhulst introduced what is called the *logistic growth model*. This model assumes that as the carrying capacity, which is assumed to be a constant value, is reached the population growth rate will reach a turning point from exponentially increasing to logarithmically decreasing, asymptotically [3].

In the early 20-th century, polymath Alfred J. Lotka had developed a preliminary predator - prey model based on Verhulst's work in the context of discussing autocatalytic chemical reactions. In 1920 the model was refined to study an herbivorous

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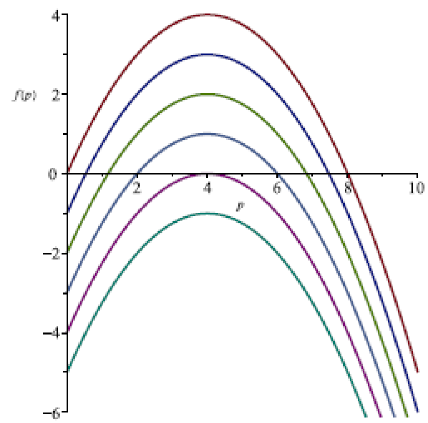

FIGURE 1. This plot represents the parabolic behavior of f(p), given our choice of parameters, for $h = 0 \dots 5$. It becomes immediately apparent that as h becomes larger, the parabola not only shift downwards as expected, but the equilibrium values approach each other, leading to increasingly more narrow windows of species survival

system, and in 1925 the model was published to analyze predator - prey relationships in his book on biomathematics. The Italian mathematician and physicist Vito Volterra had independently developed the same model within a different context. Volterra was aiming to explain the observation of the increased fishing of predatory fish in the Adriatic sea during World War I, which was considered peculiar at the time as fishing had decreased during that time. These equations are now know as the *Lotka - Volterra equations* [2].

In section 2 we will look at a modification of Verhulst's model by including a harvesting term. We will be taking a qualitative approach to analyzing the associated differential equation to understand how different harvesting quotas affect the equilibrium values associated with the population growth rate. In section 3, we will then look at a competitive predator - prey model, a set of coupled differential equations that cannot be solved analytically. Hence, we will also have to look at the dynamics of this system and analyze the equilibrium positions for various parameters.

2. Verhulst Population Model

We begin by defining a few terms. Let $p(t)$ be the population at time t and $\frac{dp}{dt}$ be the rate of population change. Although a perfectly reasonable measure of growth, the population growth rate alone does not allow us to make comparisons between different populations. We thus want to us the *per capita rate of change*, which can be expressed as $\frac{dp/dt}{p}$. This represents the population growth rate normalized with respect to a specific population.

Malthus' model assumes that $\frac{dp/dt}{p} = r =$ constant. With simple rearrangement we see that $\frac{dp}{dt} = rp$, with initial condition, $p(0) = p_0$. This equation has the

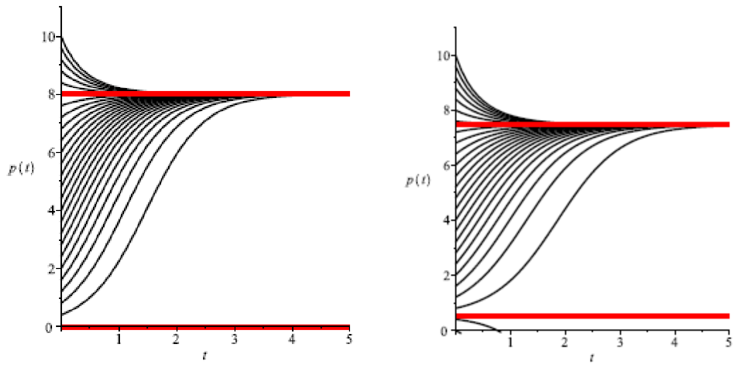

FIGURE 2. These plots aim to represent the overall behavior of the differential equation given in (2) given two different choices for the harvesting quota, h. We can see that as h increases for a reasonably large population, the survival region or the region between the two equilibrium values shrinks.

solution $p(t) = p_0 e^{rt}$, which assumes continuous, exponential growth. We have to modify this equation because as the population grows competition between members of the same species increases as resources are not infinite. We will adjust the previous equation by accounting for carrying capacity. Let $\frac{dp/dt}{p} = r - \beta p$ represent the adjusted per capita rate. This assumes that the population growth rate will eventually slow down with some constant β. Now with rearrangement we end up with a version of Verhulst's model: $\frac{dp}{dt} = (r - \beta p)p$. This equation is typically written much differently, first by factoring out the the growth rate constant, r: $\frac{dp}{dt} = r(1 - \frac{\beta}{r}p)p$. Finally, let $\frac{\beta}{r} = \frac{1}{k}$, where k is the carrying capacity. Thus, we achieve the equation in its most common form:

$$\frac{dp}{dt} = rp\Big(1 - \frac{p}{k}\Big), \qquad p(0) = p_0. \tag{1}$$

This is indeed a separable differential equation that can be solved analytically with roots at $p = 0$ and $p = k$. These represent the equilibrium values for this equation.

We will include an additional term, h, which represents a harvesting quota. This can also represent a harvesting quota, i.e. hunting a certain number of bears within a given time frame. This simple addition of a term creates the model of interest to us:

$$\frac{dp}{dt} = rp\Big(1 - \frac{p}{k}\Big) - h = f(p), \qquad p(0) = p_0. \tag{2}$$

We can begin analyzing equation 2 by first analyzing equation 1 without the vertical shift. we will choose the parameters to be $r = 2$ and $k = 8$. If we look in Figure 1, we can see that this corresponds to the top parabola whose x-intercepts lie at $x = 0$ and $x = 8$. We can begin the phase analysis by observing that as we move along any point between the two x-intercepts, the function outputs positive values and thus the solution in this region should output continuously increasing values. However, if we move along the peripheral regions of each of the equilibrium values, i.e. when $x < 0$ or $x > 8$, the values are negative and thus the solution in these regions will represent a decreasing function. We are only interested in the positive solutions or solutions relevant to analyses in the first and fourth quadrant. The first graph in Figure 2 demonstrates the solution curves for various initial conditions. We can see that the survival region is relatively large for population sizes between 0 and 8. However, as the population size reaches beyond $p(t) = 8$ we see that the population will decrease asymptotically back to the equilibrium point.

Now we can study equation 2, essentially the same equation with a vertical shift. In Figure 1 we can see that as we let $h = 0 \ldots 5$, the parabola shifts downwards, but also the equilibrium values get closer and closer together. This directly corresponds to a decreasing survival region, as seen in Figure 2 on the right. With the addition of the harvesting quote we also see a rise in a new region below the survival region, or an extinction region. This is because as we shift the parabola down vertical we see a region below the smaller equilibrium value that is in the fourth quadrant. This corresponds to a region were the values of the $f(p)$ are negative and hence the growth rate is negative.

This now allows us to generalize the observations for Verhulst's model with harvesting. If there is a small population, harvesting causes the population to decrease. If the population is relatively large, then we see stabilization to the upper equilibrium value even with the harvesting condition. Finally, if the population is too large or above the largest equilibrium value, competition between members of the same species increases, causing the population growth rate to decrease until eventually stabilizing again. It should be noted that any unanticipated changes to a population, such as a natural disaster, can shift the population into an extinction region even with harvesting not being at the critical value.

We want to ask what is the critical harvesting value h_c so that the population has no chance of survival when $h > h_c$? We can observe that for equation (1), the maximum value, which can be found by differentiation, occurs at $x = \frac{k}{2}$. Thus, solving $f(\frac{k}{2})$ yields the value for the critical harvesting value:

$$h_c = \frac{rk}{4}.$$

This value represents the maximum possible growth rate for the population, above which the population faces extinction.

3. Predator - Prey Model

We now shift our focus to a much more complicated model, namely, the predator - prey model with interspecific competition. In this model we will observe members of different species, x and y, competing for limited resources. We let $\frac{dx}{dt}$ represent the rate of growth of the prey and $\frac{dy}{dt}$ represent the rate of growth of the predator. The Lotka-Volterra equations for this model are as follows:

$$\frac{dx}{dt} = (a_1 - b_{11}x - b_{12}y)x = f(x,y), \qquad x(0) = x_0,$$
$$\frac{dy}{dt} = (-a_2 + b_{21}x - b_{22}y)y = g(x,y), \qquad y(0) = y_0.$$

The model is set up such that a_1 represents the constant growth rate of the prey, as competition increases with increasing growth rate, we again adjust the growth rate by subtracting $b_{11}x$ from the initial growth rate. Because we also have a predator,

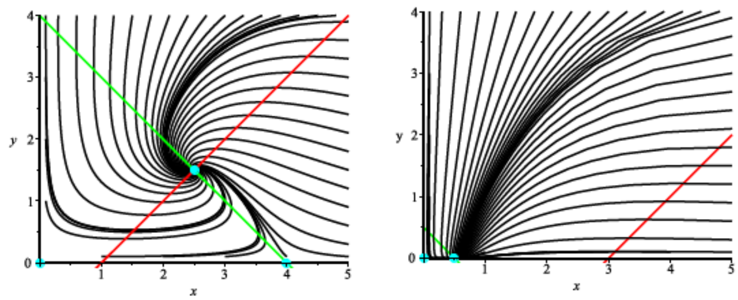

FIGURE 3. The plot on the left represents an example for the case $a_1/b_{11} > a_2/b_{21}$, whereas the graph on the right represents an example for the case $a_1/b_{11} < a_2/b_{21}$

the predator will also reduce the population periodically, and so we subtract a $b_{12}y$ term, where y represents the predator population. The b_{12} constant represents population 2 acting on population 1 or y acting on x. Similarly, for the predator, let a_2 represent the natural growth rate. It is negative because the predator population actually decreases without the presence of prey. Hence, we now add a $b_{21}x$ term, which represent the increased growth rate with an increased supply of prey. Finally, we need to account for overcrowding of the predator species, which is given by the term $b_{22}y$. The growth rate declines as the predator species grows too large due to increased competition.

The first thing about the system that we observe is that it is a set of coupled, *non-linear*, differential equations, and so none of the usual methods of solving ODE's are of use in solving this system. We this take a qualitative approach by observing the dynamics of the system. Namely, we will look at what happens when $a_1/b_{11} < a_2/b_{21}$ or $a_1/b_{11} > a_2/b_{21}$?

We look for the equilibrium values, by setting $f(x,y)$ and $g(x,y) = 0$. We observe that the equilibrium values are $x = 0$ and $a_1 - b_{11}x - b_{12}y = 0$ for the first equation, and $y = 0$ and $-a_2 + b_{21}x - b_{22}y = 0$ for the second. We can solve the linear equations by studying the x - and y - intercepts. For $a_1 - b_{11}x - b_{12}y = 0$, $x = \frac{a_1}{b_{11}} > 0$ and $y = \frac{a_1}{b_{12}} > 0$. For $-a_2 + b_{21}x - b_{22}y = 0$, $x = \frac{a_2}{b_{21}} > 0$ and $y = \frac{-a_2}{b_{22}} < 0$. These x - and y - intercepts allow us to create the nullclines that we will use to create a vector diagram that represents the solutions to the differential equations. The equilibrium values are $x_{e1} = 0, x_{e2} = \frac{a_1}{c_{11}}$, as well as the point of intersection between the two lines, $x_{e3} = \frac{b_{12}a_2 + b_{22}a_1}{b_{11}b_{22} + b_{12}b_{21}}$. There is a fourth equilibrium point, $x_{e4} = \frac{-a_2}{b_{22}}$, however, this point is negative and is of no practical use in this analysis.

We can now observe the phase diagram for two cases, $a_1/b_{11} < a_2/b_{21}$ or $a_1/b_{11} > a_2/b_{21}$. We can best illustrate the scenario when $a_1/b_{11} > a_2/b_{21}$ by choosing parameters for all values of r and b appropriately. Let

$$a = \begin{pmatrix} 4 \\ 1 \end{pmatrix}, \; b = \begin{pmatrix} 1 & 1 \\ 1 & 1 \end{pmatrix}$$

be the matrices that contain the parameters for this case. We can see that when $a_1/b_{11} > a_2/b_{21}$ for these parameters, the natural growth rate for the prey is larger than that for the predator. Using these parameters we see that the nullclines are given by $y = -x + 4$ and $x - 1$, along which $g(x, y)$ and $f(x, y) = 0$. The point of intersection is $(\frac{5}{2}, \frac{3}{2})$. We can now use Maple to analyze the dynamics of our differential equations:

$$\frac{dx}{dt} = (4 - x - y)x,$$
$$\frac{dy}{dt} = (-1 + x - y)y,$$

and we subsequently arrive at the first graph in Figure 3. One of the primary features of this graph is that at the point $(\frac{5}{2}, \frac{3}{2})$ we have a stable equilibrium, the point at which the populations of both predator and prey remain steady. All the other equilibrium points are unstable.

To analyze the situation when $a_1/b_{11} < a_2/b_{21}$, we choose a new set of parameters. Let

$$a = \begin{pmatrix} 1 \\ 6 \end{pmatrix}, \; b = \begin{pmatrix} 2 & 2 \\ 2 & 2 \end{pmatrix}$$

be completely arbitrary values. In this case the growth rate of the predator is significantly larger than that of the prey. We can again use Maple to analyze the dynamics of this system for the new set of equations:

$$\frac{dx}{dt} = (1 - 2x - 2y)x,$$
$$\frac{dy}{dt} = (-6 + 2x - 2y)y.$$

The nullclines are now given by $y = -x + \frac{1}{2}$ and $y = x - 3$. The point of intersection of these lines lies in the fourth quadrant, at the point $(\frac{7}{4}, -\frac{5}{4})$ The solution curves for this new system is given in the second graph of Figure 3. We can see that with the natural growth rate of the predator being so much greater than that of the prey, the resources are quite limited, and the equilibrium point is much lower on the graph, at which point the predator population has effectively been reduced to zero and the prey population is only slightly higher.

References

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