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PROJECT 4 POPULATION MODELS

BEN HYATT

ABSTRACT. We present two mathematical models: one describing a population subject to harvesting and another representing the population dynamics of a predator-prey relationship. Before our derivation of these two models, we will discuss the models of Matlhus and Verhulst which serve as our inspiration. We will then examine phase portraits and conduct other investigations in order to draw conclusions about the qualitative behaviors of the harvesting model and predator-prey model.

1. Introduction

For a species to survive, it must consume resources for its sustenance and, on average, it must reproduce enough new individuals to replace those lives that are lost. But assuming that the species continues to have sufficient availability of resources and it continues to reproduce at an adequate rate, will it be able to grow without bound? This is the question that inspired the work of Thomas Robert Malthus, an English scholar who lived in the 18th and 19th centuries [3].

Malthus developed his views on population dynamics and their impact on the economics of resource production in his 1798 essay, An Essay on the Principles of Population [1]. In particular, on page 4, Malthus made the rough but simple assumptions that "food is necessary to the existence of man" and "the passion between the sexes is necessary and will remain nearly in its present state" [1]. In other words, Malthus assumed that, on average, we can take the rate of reproduction to be in roughly constant proportion to its current population size. As a result, this brought Malthus to claim that "population, when unchecked, increases in a geometrical ratio" [1]. Accordingly, the differential equation that assumes population will grow as if it were unchecked is often referred to as a Matlhusian model. But Malthus himself argued that such population growth would not be sustainable, given that "subsistence increases only in an arithmetical ratio" [1]. That being said, it was not until later that another scholar took this issue into account.

This assumption that a population can ever grow "unchecked" is, of course, highly questionable. If the resources available are unlimited and the rate of birth far outweighs any loss of life, then perhaps a population is able to grow without bound. But in the confines of reality, we know this generally isn't the case. As a population grows, the amount of resources available for each person will become less and less abundant, and it stands to reason that for a given amount of available resources there is a maximum population size that can be supported. This is

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the reasoning that led to the modification of the Malthusian model a few decades later by mathematician Pierre-François Verhulst [2]. As we will later see, Verhulst's model predicts that the rate of population growth would go to zero as the population size approaches a certain "carrying capacity", i.e., the largest amount of people that can be supported.

However, for any given animal, the situation is often more complicated than either of Malthus' or Verhulst's models would suggest. For example, if humans hunt an animal at some constant rate, this rate of "harvesting" will work against the usual population growth rate of the animal. Similarly, in a closely bound predatory-prey relationship, there is a certain ebb and flow in the interdependent population dynamics. After laying the foundations for the Malthus and Verhulst models, this paper will go on to explore these additional complexities.

2. Background

In this section, we will provide a background including brief derivations of Malthus' model and Verhulst's modified model of population dynamics. Specifically, we will first look at the differential equation describing Malthus' model and its solution, and then we will consider the Verhulst differential equation and its phase diagram.

2.1. Malthus' Model. Let p(t) denote the population size at time t. We assume that for a fixed population size, the rate of reproduction is given by some constant rate r, which we take to be strictly positive. In other words, as p(t) changes, the constant rate of reproduction r will yield proportionally more births as a result of there being more or less people able to reproduce. Then, without taking any other factors into account, we expect p(t) to be monotonically increasing for all t.

Suppose that the population at time t = 0 is given by some $p_0 > 0$. Then we can easily describe this population growth by the following initial value problem:

(1)
$$\begin{cases} \frac{dp}{dt} = rp, \\ p(0) = p_0. \end{cases}$$

The initial value problem (1) defines Malthus' model for population growth.

The differential equation in (1) is a separable first-order linear equation and so it can be solved using the separation of variables method. Separating variables, we have that:

$$\frac{dp}{p} = rdt.$$

Next, we integrate both sides:

$$\int \frac{1}{p} \, dp = \int r \, dt,$$

and we obtain that:

$$ln(p) = rt + C,$$

where C is an arbitrary constant. Next, we exponentiate both sides to rewrite this as:

$$e^{\ln(p)} = p = e^{rt+C} = C_1 e^{rt}$$
.

Finally, plugging in our initial condition of $p(0) = p_0$, we find that:

$$p(t) = p_0 e^{rt}.$$

It is easily seen in (2) that Malthus' model describes a population with unbounded, exponential growth. In the real world, such a system is highly unrealistic. We discuss an improvement for this model in Section 2.2.

2.2. Verhulst's Model. In order to improve the relevance of the mathematical model for population dynamics developed in Section 2.1, we must take into account how the growth of a population puts a strain on the availability of resources such as food, water, land, and so on. When a population grows to be quite large, these resources will become relatively scarce. In fact, if a population is so large that there are not enough resources to provide everyone with the minimum necessary for their survival, we expect for the population size to decrease until they reach a point where the size can be sustained.

To reflect this reasoning, Verhulst modified the per capita rate of change in the population. Let k>0 denote the carrying capacity of the population. Then we want the rate of population change to get smaller as p approaches k, whether from above or from below. As a result, we must subtract something from our constant per capita growth rate r, so that the effect of r is diminished, especially when p is close to k. Verhulst determined that the appropriate choice for this modification has the form:

(3)
$$\frac{dp/dt}{p} = r - \beta p,$$

where $\beta > 0$ is defined by $\beta = r/k$. Applying (3) and plugging in β , we find that:

$$\frac{dp}{dt} = \left(r - \frac{r}{k}p\right)p.$$

Then, pulling out a common factor of r, we can write our modified initial value problem as:

(4)
$$\begin{cases} \frac{dp}{dt} = r\left(1 - \frac{1}{k}p\right)p, \\ p(0) = p_0. \end{cases}$$

This modified initial value problem (4) defines Verhulst's model of population dynamics.

Notice that the differential equation in (4) is a first-order nonlinear equation, since it contains p^2 . As such, it will be more straightforward to analyze the behavior of (4) by performing a phase portrait analysis, and to examine its solutions by way of numerical computations performed in MAPLE.

Let $f(p) = r\left(1 - \frac{1}{k}p\right)p$ so that dp/dt = f(p), as per the differential equation in (4). Then by plotting f(p) versus p, we will be able to gain valuable insight into the behavior of the Verhulst population dynamics. Taking r=2 and k=8 as an example, we provide this plot, a phase portrait for the Verhulst model, in Figure 1. Observe that the plot of f(p) versus p in Figure 1 is quadratic, i.e., it has the form of a parabola, with two real roots. In particular, f(p) has roots at $r_1=0$ and $r_2=8$. We can easily see that $p=r_1$ and $p=r_2$ are equilibria of the system, since those are population sizes for which dp/dt becomes zero. This implies that populations with $p(0)=r_1$ and $p(0)=r_2$ will yield constant solutions, i.e. p(t) will remain at these values for all t if they happen to begin at one of them.

Furthermore, the sign of dp/dt is positive for all values of p on the interval $(r_1, r_2) = (0, 8)$, and it is negative for all values of p > 8. It follows that populations

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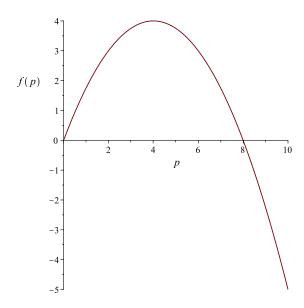


FIGURE 1. An example phase portrait for the Verhulst model, taking parameter values of r=2 and k=8.

with $p(0) = p_0 \in (0, 8)$ will always increase and approach p = 8 as $t \to \infty$, and populations with $p(0) = p_0 \in (8, \infty)$ will decrease and approach p = 8 from above as $t \to \infty$. In this respect, we see that $r_1 = 0$ can be characterized as an unstable equilibrium of (4), whereas $r_2 = 8$ is a stable equilibrium of the system. Of course, $r_2 = 8 = k$. Hence, we often refer to k as the carrying capacity of the Verhulst system: for any nonzero, positive initial condition $p_0 > 0$, p(t) tends towards k as $t \to \infty$ since this is the population that the available resources are able to support.

Having laid this foundation, we are still left desiring a more comprehensive description of population dynamics. Our first step will be to expand the Verhulst model developed here by accounting for harvesting.

3. The Verhulst Model With Harvesting

A more general population model will include some term that accounts for a regular loss in population. In practice, this term could represent many things, from a species that is hunted once a year during a prescribed hunting season, to a society of humans where a certain amount of people emigrate to another country each year. For our purposes, we will refer to this term as a harvesting term, where the rate of harvesting will be denoted by a parameter h.

3.1. Model Derivations. Of course, since the rate of harvesting causes a decrease in the population, the harvesting term $h \geq 0$ will be included on the right hand side of the equation in (4) with a negative sign. Making this modification gives us the following initial value problem:

(5)
$$\begin{cases} \frac{dp}{dt} = r\left(1 - \frac{1}{k}p\right)p - h, \\ p(0) = p_0. \end{cases}$$

This modification to the Verhulst model in (4) will serve as our model for population dynamics with harvesting.

3.2. Solutions and Phase Portraits for Dynamics with Harvesting. Returning to our phase analysis approach, we now let:

(6)
$$f(p) = r\left(1 - \frac{1}{k}p\right)p - h,$$

so that again dp/dt = f(p). Recalling that f(p) is quadratic in p, it is immediately clear that the -h term in (6) will serve to shift the parabola downwards. For various different values of h > 0, the roots of f(p) will change. Furthermore, for sufficiently large values of h, it is clear that the plot of f(p) will no longer intersect with the p axis, in which case there will be no real roots. We can compare several of these possibilities by keeping the parameter values of r = 2 and k = 8 held fixed, and varying our choices of the harvesting parameter h by allowing for $h = 0, 1, 2, \ldots, 5$ and plotting the corresponding f(p) for each case. Figure 2 displays these different cases side by side.

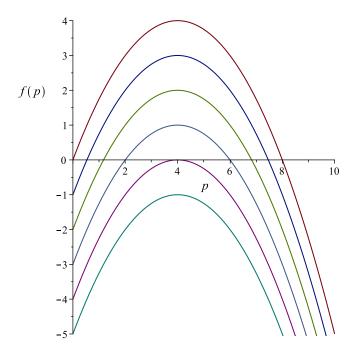


FIGURE 2. This plot shows, in descending order, the phase portraits for h = 0, h = 1, h = 2, h = 3, h = 4, and h = 5.

In Figure 2, we observe that as h increases from h = 0 to h = 3, there are two real roots of f(p), and the gap between them gets smaller and smaller. At h = 4, there is a single, repeated root of f(p) occurring at p = 4. Finally, at h = 5, we see that f(p) no longer has any real roots, as there is no intersection between f(p) and the p axis. The values of these roots, if any, are given in Table 1.

Looking back again at Figure 2, we note that for those values of h greater than 0 and up to 4, there is now a section to the left of the leftmost root where f(p) is

Choice of h	Roots (if any)
h = 0	$r_1 = 0, r_2 = 8$
h=1	$r_1 = 0.5359, r_2 = 7.4641$
h=2	$r_1 = 1.1716, r_2 = 6.8284$
h=3	$r_1 = 2, r_2 = 6$
h=4	r = 4 (root of multiplicity 2)
h=5	no real roots

TABLE 1. The first column displays the value of the harvesting rate parameter h. The second column displays the corresponding real root(s) if any. These values were computed in MAPLE. Of course, just as in discussed in Section 2.2, wherever there are roots, we have equilibria of the system.

negative. This implies that the population will be decreasing if the population is smaller than some minimum threshold. This indicates that if the population is too small, then it will not be able to survive and instead of growing it will die out. Of course, in our mathematical model, this will only happen if p_0 starts out too small. But in reality, this might occur if a natural disaster or a disease spontaneously causes a drop in the population into this range below the minimum threshold, in which case the population may be too small to recover.

We also still need to address the new cases exemplified by h=4 and h=5. When h=4, we see that f(p) has only a single, repeated root at p=4. More importantly, f(p) is either zero or strictly negative for all p, i.e., there is no potential for population growth. Hence, h=4 represents a unique case where: (a) if $p_0 > 4$ then p will decrease and approach p=4 from above as $t \to \infty$, (b) if $p_0=4$, then p will be constant and remain at this value for all t, and (c) if $p_0 < 4$, then p will decrease until the population dies out (mathematically, it will actually keep decreasing past p=0, but we ignore this for our purposes). The case where h=5 is also interesting in that f(p) has no real roots, and f(p) is now strictly negative everywhere. Hence, unlike the h=4 case's saddle point equilibrium of p=4, there are now no equilibria anywhere. Such a population will always die out for any IC.

Notice that we have observed stable behaviors for example values of $0 \le h < 4$, an interesting edge case when h = 4, and a case without any kind of population stability for a value of h > 4. From this perspective, we see that the *critical harvesting value* for this choice of parameters (r = 2 and k = 8) is given by $h_c = 4$. This is demonstrated by the fact that (i) for any value of $h < h_c = 4$ there are two real roots of f(p), (ii) when $h = h_c = 4$ there is one repeated real root, and (iii) if $h > h_c = 4$ there are no real roots. Hence, harvesting rates less than this critical value represent an amount of harvesting that is, to some extent, healthy for the population (barring spontaneous natural disasters), and any harvesting rate exceeding this critical value is never sustainable. Harvesting precisely at the critical rate h_c therefore represents a very delicate situation where any slight deviation into the over-harvesting range could result in an irreversible loss of the population.

In general, we can derive an equation for the value of this critical harvesting rate h_c in terms of the other model parameters r and k. In all cases, f(p) is a quadratic, concave down function, so the critical case will correspond to when the maximum of the f(p) parabola just intersects the x axis. That is, h_c occurs when the maximum

of f(p) is equal to zero. Of course, the maximum of f(p) occurs when f'(p) = 0, indicating a critical point of f. Taking the first derivate of f with respect to p, we have that:

$$\frac{df}{dp} = r - \frac{2r}{k}p.$$

Then setting this equal to zero, we find that the location of the maximum of f occurs at a value of $p_{max} = k/2$. Now we plug this value of p_{max} into f and set that expression equal to zero:

$$f(p_{max}) = 0 = r(1 - \frac{1}{k}\frac{k}{2})\frac{k}{2} - h_c,$$

where we have rewritten h as h_c , as setting $f(p_{max}) = 0$ precisely corresponds to the case where $h = h_c$. Hence, solving for h_c , we obtain that:

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

We can confirm our conclusions drawn from the phase diagrams by plotting some example solution trajectories. In particular, we consider a range of initial conditions of the form:

$$(8) p_0 = 0, 0.4, 0.8, \cdots, 9.2, 9.6, 10,$$

i.e., starting values ranging from 0 to 10 in step sizes of 0.4. For consistency, we retain our parameter values of r=2 and k=8, and we vary h again from 0 to 5 in step sizes of 1. Figure 3 displays the six plots of the resulting solution trajectories, generated in Maple, for each of the six values of the harvesting rate h.

As seen in Figure 3, our suspicions were confirmed. To begin with, the p(t) trajectories approach the stable equilibrium (when available) from above and below, though only if their initial conditions start within a certain range. Usually, it is the lower, unstable equilibrium (when available) that sets the lower bound for this "stable range". Of course, when $h = h_c = 4$, we have the critical case where if the p(t) trajectories begin above the single equilibrium value of p = 4, then that is where p will tend to, but if the trajectories begin below this value, then the population will collapse. Finally, the trajectories in the h = 5 case all result in death, as the harvesting rate is simply too high for the population to be able to sustain itself.

4. The Predator-Prey Model

We now move on to develop a model for a predator-prey system. Qualitatively, there will be some similarities to the Verhulst model with harvesting, which is why we explored it first. However, as we will soon see, there will also be new behaviors arising from the interdependent relationship of the predatory and prey populations.

4.1. **Model Derivations.** Let x(t) and y(t) denote the populations of the prey and the predator at time t, respectively. Much like the Verhulst model, for the prey population x(t), we assume there is some positive growth rate per capita $a_1 > 0$ that is offset by a term $-b_{11}x$ that accounts for the population's tendency to level off as it approaches its carrying capacity, where $b_{11} > 0$. However, we must also account for the death in the prey population due to being hunted by the predator. For this, we will assume that the rate of deaths per capita due to being hunted by the predator will be proportional to the current population size of the predator.

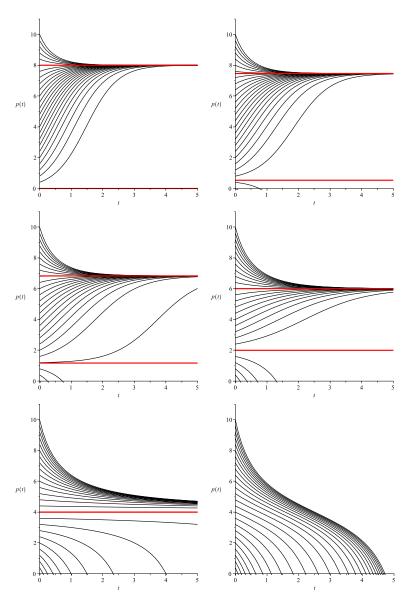


FIGURE 3. The solution trajectories for initial conditions of the form described in (8) and parameters r=2 and k=8 for six different values of the harvesting rate: h=0 (top-left), h=1 (top-right), h=2 (middle-left), h=3 (middle-right), h=4 (bottom-left), and h=5 (bottom-right). In red, we plot the equilibria values, if any.

Hence, we will include another term of the form $-b_{12}y$, where $b_{12} > 0$. Then the rates per capita can be expressed as:

(9)
$$\frac{dx/dt}{x} = a_1 - b_{11}x - b_{12}y.$$

On the other hand, we expect that since the predator's only source of sustenance (in this simplified model) is this one prey, its natural tendency in isolation is to die out at some rate per capita $a_2 > 0$ (and we expect this to show up as $-a_2$ in our differential equation). We can also expect the predator to suffer some of the same consequences of having a carrying capacity, so there will also be a term of the form $-b_{22}y$, where $b_{22} > 0$. All that remains then is to account for its sustenance gained from hunting the prey. Following a similar pattern, we assume that the predator's population growth per capita due to eating the prey will be proportional to the current prey population size. Hence, we will include another term of the form $b_{21}x$, where $b_{21} > 0$. Then the rates per capita can be expressed as:

(10)
$$\frac{dy/dt}{y} = -a_2 + b_{21}x - b_{22}y.$$

Finally, putting Equations (9) and (10) together, we arrive at the initial value problem:

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

This initial value problem in (11) serves as our predator-prey model. Notice that (11) consists of a set of coupled first-order nonlinear equations. Evidently, it would not be possible to first solve one equation and then substitute this result into the other, as both equations contain both unknowns in x and y. As such, we will have to resort to numerical methods in MAPLE in order to examine the solution trajectories of the system.

4.2. Phase Portraits and Solution Trajectories for the Predator-Prey **Model.** We will proceed in our analysis by discussing the phase portraits of this system. Of course, for the predator-prey model, we now have two unknowns, x and y, and as such, the entire (x,y) plane represents the region of possible solution values for a given time t (though we will restrict our focus to the first quadrant where x, y > 0). In light of this, we could try to plot some f(x, y) and g(x, y) in a 3D plot where f and g represent the right hand sides of the two differential equations in (11). But there is an easier way to convey the same meaning while staying in two dimensions. In particular, we can interpret the slope field (dx/dt, dy/dt) as having a certain magnitude and direction for a given point in the (x,y) plane. That is, for any point (x_0, y_0) , we will be able to consider both the signs and magnitudes of $dx/dt(x_0,y_0)$ and $dy/dt(x_0,y_0)$ to interpret how the solution trajectory would evolve from that point.

To begin, let us first determine the set of points in the (x, y) plane where either dx/dt or dy/dt are zero. Examining the right hand sides of the equations in (11), we find the following four conditions:

(12a)
$$\frac{dx}{dt} = 0 \text{ if } x = 0, \text{ or } a_1 - b_{11}x - b_{12}y = 0,$$

(12a)
$$\frac{dx}{dt} = 0 \text{ if } x = 0, \text{ or } a_1 - b_{11}x - b_{12}y = 0,$$
(12b)
$$\frac{dy}{dt} = 0 \text{ if } y = 0, \text{ or } -a_2 + b_{21}x - b_{22}y = 0.$$

Notice that these 4 conditions each describe a line in the (x,y) plane. It stands to reason that along the lines in (12a) where dx/dt=0, there will be no changes in the prey population x, only changes in the predator population y. In other words, the trajectory of (x(t),y(t)) along these lines will be perpendicular to the x axis. Similarly, along the lines in (12b) where dy/dt=0, there will be no changes in the predator population y, only changes in the prey population x. As such, the trajectory of (x(t),y(t)) will be perpendicular to the y axis. These lines indicated in (12a) and (12b) are referred to as the "nullclines" of the system.

We might also notice that we can predict the directions of the solution trajectories when they are somewhere between the nullclines. Note that we are restricting ourselves to the first quadrant where x and y are non-negative, and so the signs of dx/dt and dy/dt will depend on the other two nullclines in (12a) and (12b) aside from x=0 and y=0. As we will later confirm, it stands to reason that on one side of the remaining nullcline for x, dx/dt will be strictly positive on one side and strictly negative on the other. Likewise, on either side of the remaining nullcline for y, dy/dt will take on one of two possible signs.

Furthermore, we expect that these four lines will have a certain number of points of intersection with each other. At these points, since we will have that both dx/dt=0 and dy/dt=0, we will have the equilibria of the predator-prey system. For different parameter values, we expect the number of these points that occur in the first quadrant will vary, as will the relative positions of the nullclines. That being said, we can determine the coordinates of the points of intersection algebraically, for arbitrary parameter values. Using MAPLE, we obtain the following four points of intersection:

(13)
$$\begin{cases} (x_1, y_1) = (0, 0), \\ (x_2, y_2) = \left(0, \frac{-a_2}{b_{22}}\right), \\ (x_3, y_3) = \left(\frac{a_1}{b_{11}}, 0\right), \\ (x_4, y_4) = \left(\frac{b_{12}a_2 + b_{22}a_1}{b_{11}b_{22} + b_{12}b_{21}}, -\frac{b_{11}a_2 - b_{21}a_1}{b_{11}b_{22} + b_{12}b_{21}}\right). \end{cases}$$

Hence, (13) lists the four equilibria of the system.

By inspection, there are qualitatively two distinct cases which arise depending on whether $a_1/b_{11} < a_2/b_{21}$ or $a_1/b_{11} > a_2/b_{21}$. As we will see, this condition relates to where the nullclines given by $a_1-b_{11}x-b_{12}y=0$ from (12a) and $-a_2+b_{21}x-b_{22}y=0$ from (12b) intersect the x axis. Put another way, the direction of this inequality determines the sign of the y-component in the point of intersection/equilibrium (x_4, y_4) : if $a_1/b_{11} < a_2/b_{21}$, then $y_4 < 0$, and if $a_1/b_{11} > a_2/b_{21}$, then $y_4 > 0$. Why is this so significant? If (x_4, y_4) is below the line y = 0, then the nullcline given by $a_1 - b_{11}x - b_{12}y = 0$ from (12a) will intersect the y = 0 nullcline from (12b) before intersecting the nullcline given by $-a_2 + b_{21}x - b_{22}y = 0$ from (12b). Hence, instead of (x_4, y_4) being the main stable equilibrium in the first quadrant, we will instead see (x_3, y_3) play this role.

With all of this introduction out of the way, this is a good time to inspect the phase portraits produced in MAPLE to confirm our analysis. Figure 4 displays the phase portrait for the case where $a_1/b_{11} > a_2/b_{21}$, while Figure 5 displays the phase portrait for the case where $a_1/b_{11} < a_2/b_{21}$. For simplicity, we take

parameter values of the form $a_1 = 4$, $a_2 = 1$, and $b_{11} = b_{12} = b_{21} = b_{22} = 1$ to achieve the scenario where $a_1/b_{11} > a_2/b_{21}$, and similarly, we take $a_1 = 2$, $a_2 = 3$, and $b_{11} = b_{12} = b_{21} = b_{22} = 1$ to achieve the scenario where $a_1/b_{11} < a_2/b_{21}$. In addition, we plot example solution trajectories for a wide range of inputs with step sizes of 0.3 beginning along (or otherwise near) the x and y axes and the lines x = 5 and y = 4.

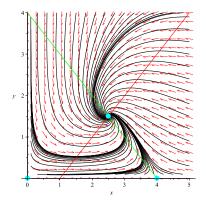


FIGURE 4. The phase portrait and solution trajectories for the predator-prey dynamics when $a_1/b_{11} > a_2/b_{21}$.

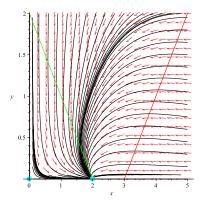


FIGURE 5. The phase portrait and solution trajectories for the predator-prey dynamics when $a_1/b_{11} < a_2/b_{21}$.

In both Figures 4 and 5, the x-nullcline given by $a_1 - b_{11}x - b_{12}y = 0$ is depicted in green, whereas the y-nullcline given by $-a_2 + b_{21}x - b_{22}y = 0$ is depicted in red. This is clear since all solution trajectories moving across the green x-nullcline are vertical (i.e., there is no change in x) and all solution trajectories moving across the red y-nullcline are horizontal (i.e., there is no change in y).

Furthermore, in both of the figures, the points where the nullclines in (12a) and in (12b) intersect have been marked by cyan dots. As previously stated, these are (a priori) equilibria of the predator-prey system, and their general coordinates are listed in (13). Notice that in each of Figures 4 and 5, there is apparently only one

stable point of equilibrium. In Figure 4, this point occurs at a point that isn't on either of the coordinate axes, so it must correspond to (x_4, y_4) in (13), as we predicted. On the other hand, in Figure 5, the stable equilibrium occurs along the line y = 0, but not along x = 0, so it corresponds to (x_3, y_3) in (13), again as predicted. As a result, we arrive at the following important conclusion. When, as in Figure 4, we have that $a_1/b_{11} > a_2/b_{21}$, the system tends to approach a stable equilibrium where both the predator and prey are alive. However, when we have that $a_1/b_{11} < a_2/b_{21}$ as in Figure 5, the stable equilibrium of the system occurs along y = 0, which implies that the predator population will always die out.

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DEPARTMENT OF MATHEMATICS AND STATISTICS, UMBC $Email\ address$: benhyal@umbc.edu