# Investigating Stability through Population Models

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**Abstract**

Throughout this paper, I will describe how one can use simple first order differential equations to model the relationship between a predator and its prey. Beginning with the simplest model, representing the growth of one species, I will add layers of complexity until we have a proper model representing the interaction of two species. The classical mechanical applications result from the oscillatory nature of interacting species. Also, because we can use first order differential equations to model the species, we can use the concepts taught in PHY 235W to analyze these equations without ever having to solve them, through phase diagrams and logistic maps. Finally, I will discuss the stability of each equation's equilibria, and different methods of determining each equilibrium's type of stability.

## 1 Introduction

In order to analyze any differential equation, one must solve it with an appropriate number of initial conditions. Yet, some equations, especially ones that are nonlinear, are very difficult to solve with traditional methods. The equations we will look at describe dynamic systems, meaning systems of elements that change over time. This class of equations gave rise to a class of theories, Dynamic Systems Theories, which provide "theoretical principles that aim to conceptualize, operationalize, and formalize these complex interrelations of time[1]."

The equations we will go through all model the rate of change of populations with respect to time. The common connection between all models is that each model has at least one equilibrium point, which we will call $N^*$, where the rate of change of that population is equal to zero. One of the principal goals of Dynamical Systems Theory is to gain insight into the stability of equilibrium points for various Ordinary Differential Equations, without directly solving them, through various graphical and numerical methods. This aspect of Dynamical Systems Theory is what will be discussed most when we go through all of my population models, as it is the strongest tie between population models and Classical Mechanics.

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[1] Smith, pg 258

First, I will qualitatively define what it means for an equilibrium point to be stable. Aleksandr Mikhailovich Lyapunov, a Russian mathematician, says that for a given dynamical system, "if the rate of change following a small displacement from equilibrium is always negative or zero, then the equilibrium is stable[2]." So that, by his definition, an equilibrium $N^*$ is stable if starting close enough to the equilibrium point guarantees you stay close to that point[3]. We will use this definition in our discussion of equilibrium. It allows for small deviations around the equilibrium point, yet some applications require all small deviations to eventually die out. When an equilibrium point models this behavior, we call it *asymptotically stable*[4]. In general, the behavior of first-order differential equations is dominated by their equilibria, with solutions either staying at the equilibria, moving monotonically towards or away from their equilibria, or going off monotonically to infinity[5]. For each model, I will discuss how we can determine the equilibrium points, and the stability of each point.

The definitions above will be sufficient for our first two, single-species models, yet for our third model, representing the interaction between two species, we will need a more quantitative way to determine stability. I will now describe how one can learn the stability of any coupled, two species model of the form:

$$f_1(x,y) = \frac{dx}{dt}, \qquad f_2(x,y) = \frac{dy}{dt} \tag{1}$$

Through a method called Linear Stability Analysis[6]. First, I will define equilibrium points $(x,y) = (x^*,y^*)$ to be any points that satisfy the relation:

$$f_1(x^*,y^*) = f_2(x^*,y^*) = 0 \tag{2}$$

Next, we determine the Jacobian Matrix, J, by calculating all relevant partial derivatives, which for this general example would look like:

$$J(x,y) = \begin{bmatrix} \frac{\partial f_1}{\partial x} & \frac{\partial f_1}{\partial y} \\ \frac{\partial f_2}{\partial x} & \frac{\partial f_2}{\partial y} \end{bmatrix}$$

Then, we calculate the Jacobian at the equilibrium points[7], which we will notate as $J^*$, and assume is now of the form:

$$J^*(x^*,y^*) = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix}$$

The final step in this analysis is to find the roots of the characteristic equation given by solving $\det(J^* - I_2\lambda)$=0, which results in a characteristic equation of

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[2] Stewart, pg 522

[3] Kot, pg 9

[4] Stewart, pg 526

[5] Kot, pg 13

[6] Roussel, pg 10

[7] Roussel, pg 2

the form:[8]

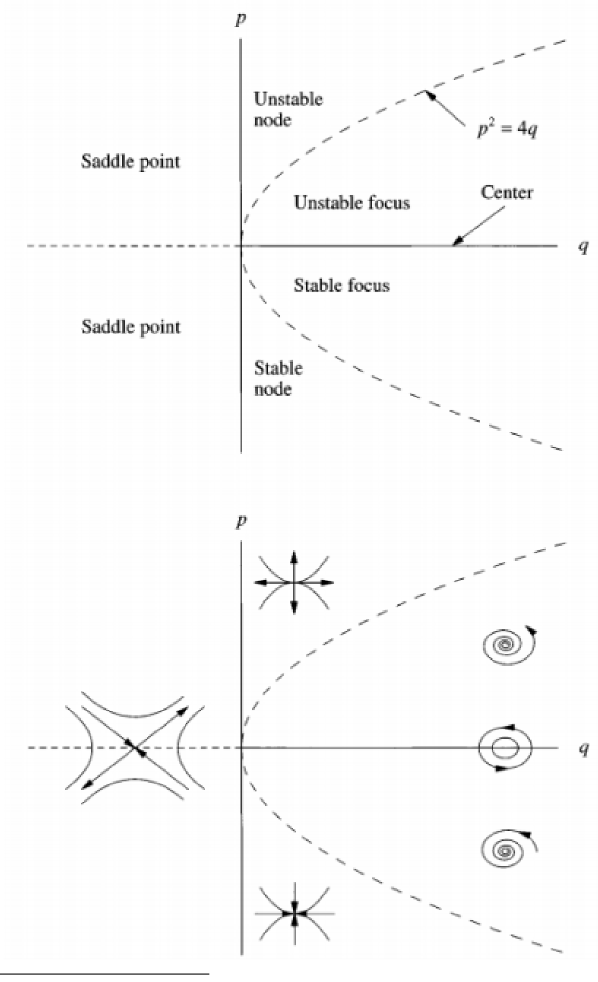
$$\lambda^2 - (a_{11} + a_{22})\lambda + (a_{11}a_{22} - a_{12}a_{21}) = 0 \tag{3}$$

which is easily rewritten as[9]:

$$\lambda^2 - p\lambda + q = 0 \tag{4}$$

The significance of p and q is twofold. First, it tells us information about $J^*$, namely p=Trace($J^*$) and q=Determinant($J^*$). Secondly, and most importantly, it gives us a relatively easy way to determine not only if an equilibrium is stable, but also what kind of stability it possesses. I will not explicitly go through how one can determine this, instead, I will refer to Fig. 1.[10]

**Fig. 1.** Classification of Equilibria



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[8] Kot, pg 118

[9] ibid.

[10] Fig. 1 from Kot, pg 119

# 2 Models for Single Species

## 2.1 Model 1: Exponential Model

The most basic way to model populations is a directly proportional relationship between the rate of change of the population, $\frac{dN}{dt}$, and the population's size, N(t). In this model, we will use r as the proportionality constant, where r=(rate of births)-(rate of deaths)=*intrinsic rate of growth*[11]. The assumption in this model is that each additional member of the population adds an undiminished contribution to the growth rate, so r=constant.

$$\frac{dN}{dt} = rN \tag{5}$$

This is a linear, first-order differential equation, so it can be easily integrated. Because our domain is only limited to time $t > 0$, we must know the population at time $t = 0$, which we will notate with $N(t = 0) = N_0$. Knowing this condition allows us to integrate to find how the population changes with time, yielding the exponential equation:

$$N(t) = N_0 e^{rt} \tag{6}$$

Now we can see explicitly that this model grows exponentially for positive intrinsic growth rates ($r > 0$), decreases exponentially for negative intrinsic growth rates ($r < 0$), and stays constant at the initial population if the amount of births (b) equals the amount of deaths (d), resulting in $r = 0$.[12]

The phase diagram of this ODE shown in Fig. 2 and Fig. 3 best demonstrates its exponential nature without the need to specify initial conditions or even solve the equation. For each time (t) and population (N), it plots an arrow representing $\frac{dN}{dt}$. So, by beginning at any initial population, one can follow the direction of the arrows to see how the population progresses.

Because we defined equilibria in equations (1) and (2) to be any value of N that when plugged in, results in $\frac{dN}{dt} = 0$, we see this model has only one equilibrium point, $N^* = 0$. For positive r, as shown in Fig. 2, this equilibrium is *unstable*. Beginning at the equilibrium, the arrows all point away, so any small displacement from zero population results in an exponentially increasing population away from the equilibrium $N^* = 0$. For negative r, as shown in Fig. 3, any small displacement

**Fig. 2.** $r > 0 = +0.6$

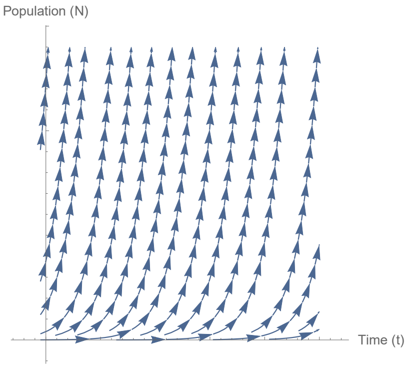
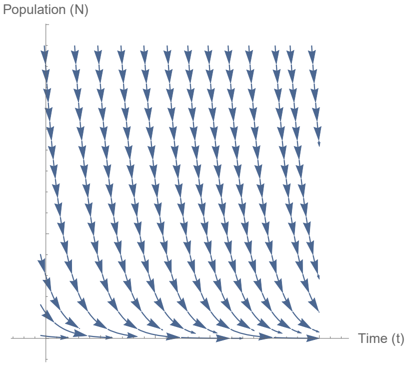


**Fig. 3.** $r < 0 = -0.6$



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[11] kot, pg 3

[12] Kot, pg 3

from zero population results in a negative rate of change, and an exponentially decreasing population back to its equilibrium point $N^* = 0$, thus for negative r, $N^* = 0$ is *asymptotically stable*[13].

## 2.2 Model 2: Logistic Model

There are two big problems with the exponential model which we will aim to alleviate in the Logistic Model.

1. The undiminished contribution that each additional member of the population adds results in limitless growth, and ignores overpopulation. Meaning the per capita growth rate, defined as $\frac{1}{N}\frac{dN}{dt}$, is constant.
2. Because of this constant growth rate, the model does not depend on the past. It instead responds instantaneously to any change in the population size[14].

In our study of nonlinear differential equations, we came across a technique called mapping, which describes the progression of a nonlinear system by looking at how the (n+1)th state depends on the nth state, by defining a relationship with the form $x_{n+1} = f(\alpha, x_n)$, where $f(\alpha, x_n)$ is called a *difference equation*, and $\alpha$ is a model-dependent parameter. This function acts recursively, by continually generating values of $x_{n+1}$ from $x_n$. This collection of points is called a map of the function itself. This technique can be very helpful in describing the evolution of a system in which the future depends on the immediate past[15]. The most used representation of this is called the **logistic equation**, which has the **iterative** form:

$$x_{n+1} = \alpha x_n(1 - x_n) \tag{7}$$

This equation was developed by Bessoir and Wolf in their study of population models on the ground that it depended on the immediate past[16], so it solves our second problem with Model 1. It also eliminates the possibility of limitless growth by including a variable K, which they defined as the maximum occupancy without overcrowding, so it also solves our first problem with Model 1. A way to analyze such an equation by graphical means is by using a logistic map. The **differential** form of the logistic equation that we will use in this section is:[17]

$$\frac{dN}{dt} = rN(1 - \frac{N}{K}) \tag{8}$$

For simplicity, K will be set constant in value. When the population N is equal to the carrying capacity K, the terms in the parenthesis sum to 0, resulting in a zero growth rate. Also, if the population is ever 0, the terms outside the parenthesis, rN, is equal to zero, which also results in a zero growth rate. Thus,

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[13] kot, pg 5
[14] Kot, pg 6
[15] Thornton, pg 169
[16] Thornton, pg 170
[17] Kot,pg 7

it is easily shown, just by observing the equation, that it has two equilibria, $N^* = 0$ and $N^* = K$. This is confirmed quantitatively by setting $\frac{dN}{dt} = 0$, resulting in a quadratic polynomial, which has the two solutions of 0 and K[18].

I will first discuss how we can learn more about this equation and its equilibria without solving it or graphing it. We see that when N is small, the terms in the parenthesis are negligible, so that with small N this model behaves exactly like the exponential model discussed in 2.1, so $N(t) \approx N_0 e^{rt}$. So that **assuming** $r > 0$, small deviations from N=0 result in exponential growth away from it, thus we can say that $N^* = 0$ is an unstable equilibrium[19].

**Fig. 4.** $r > 0 = +0.6$

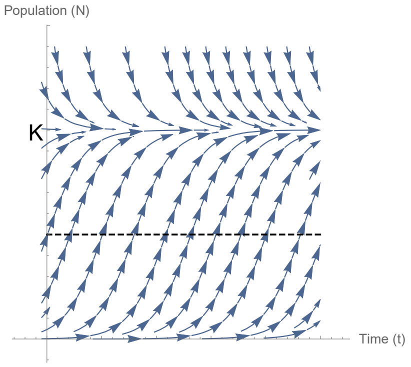
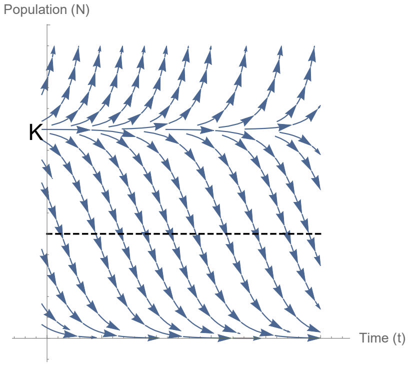


**Fig. 5.** $r < 0 = -0.6$



Now we turn our attention to the second equilibrium, $N^* = K$. To investigate its behavior, we first introduce a variable that will measure the deviation of N from K, which we will define as:[20]

$$x \equiv N - K. \tag{9}$$

The first thing to notice is that $\frac{dN}{dt} = \frac{dx}{dt}$, because as we said above, K=constant. We then use the relation $N = K + x$, to change the variables of equation (8) into the form:[21]

$$\frac{dx}{dt} = -rx - \frac{r}{K}x^2 \tag{10}$$

Because we know that for small values of x, $x >> x^2$, we see that for small x = deviation of population from its equilibrium, the equation reduces to:[22]

$$\frac{dx}{dt} \approx -rx \tag{11}$$

And because we have defined an equilibrium to be stable "if the rate of change following a small displacement from [that] equilibrium is always negative or zero", we have proved, without graphical methods and without even solving the equation, that if $r > 0$, $N^* = K$ is stable. Furthermore, because all small deviations will die out, if $r > 0$, $N^* = K$ is asymptotically stable[23]. **Vice-versa**, by the same logic, if $r < 0$, then $N^* = 0$ is asymptotically stable, and $N^* = K$ is

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[18] Kot, pg 7
[19] Kot, pg 7-8
[20] Kot,pg 8
[21] ibid.
[22] ibid.
[23] Kot, pg 8

unstable. The results of this analysis can be confirmed graphically by looking at the phase diagrams for the logistic model shown in Fig. 4 and Fig. 5.

What else can we find out about this equation? Well, we would need an initial condition if we wanted to integrate it to find the equation N(t), say $N(t = 0) = N_0$. This would result in the equation:[24]

$$N(t) = \frac{K}{1 + (\frac{K}{N_0} - 1)e^{-rt}} \tag{12}$$

Which is pretty useless because it only tells us information about one possible trajectory, beginning at $N_0$. So we lose information by integrating, so let's derive the ODE and see what we get:[25]

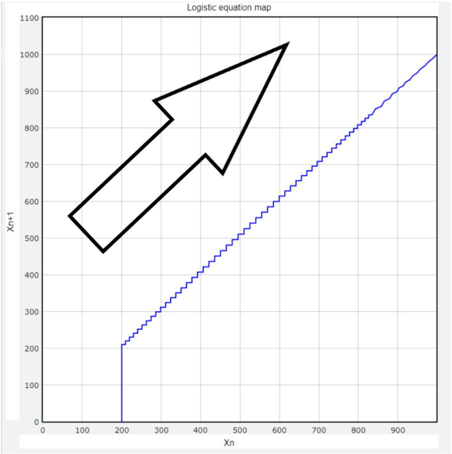
$$\frac{d^2N}{dt^2} = r(1 - \frac{2N}{K})\frac{dN}{dt} \tag{13}$$

By setting $\frac{d^2N}{dt^2} = 0$, we see that this is only possible if $N = \frac{K}{2}$. Thus, we know there must be an inflection point at $N = \frac{K}{2}$, where the curve flips its concavity, resulting in an "S" shaped curve. This observation is confirmed in the phase diagrams shown in Fig. 4, Fig. 5, and Fig. 6b, by the black dotted line placed at $N = \frac{K}{2}$. This "S" shaped curve is one of the defining traits of the Logistic Equation.

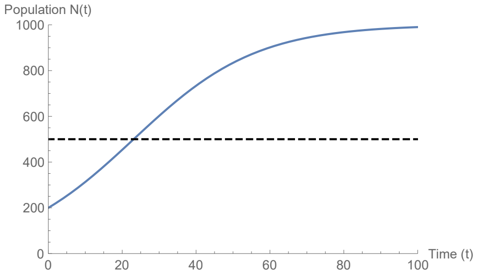
Now, to bring our discussion of the logistic equation back where we began it, we will need to find a way to convert the form of our logistic equation from a differential one to an iterative one. Doing so will give us another method to determine information about it and give us another relation of population models to classical mechanics by giving us the ability to produce a map of our logistic equation. We will use a method developed by the Swiss mathematician Leonhard Euler to do this.

This method lets us find out information about the solution of an ODE without solving it, but instead by beginning at an initial condition, and then "stepping" in the direction given by the arrow on that location in the phase diagram. The arrows at each point are representative of the slope

**Fig. 6.** $r > 0 = .6$, $N_0 = 200$, $K = 1000$



(a)Map of Logistic Equation (13)



(b) Plot Of N(t)

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[24] Kot, pg 8

[25] Kot, pg 9

$\frac{dN}{dt}$ at that specific point $(t, N(t))$. This method does not aim to find exact solutions, rather, it tries to approximate the solution, with increasing precision corresponding to decreasing step size. Formally, the general theorem for Euler's Method is:[26]

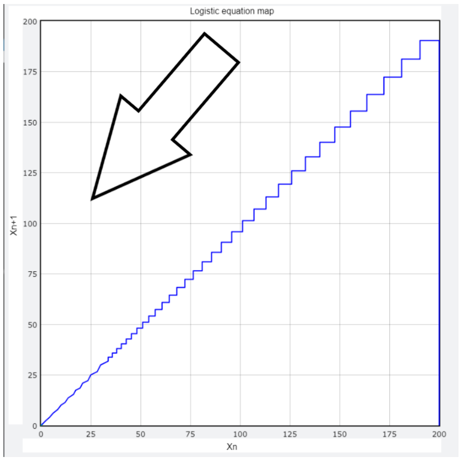
**Theorem 1 (Euler's Method)** *Approximate values for the solution of the initial value problem* $\frac{dy}{dx} = F(x, y)$, $y(x_0) = y_0$, *with step size* $h$, *at* $x_{n+1} = x_n + h$, *are*

$$y_{n+1} = y_n + hF(x_n, y_n) \qquad n = 1, 2, 3, ... \tag{14}$$

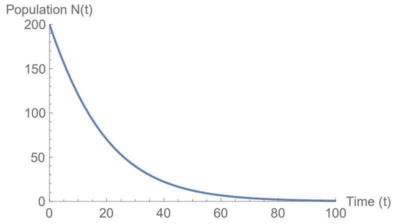
So, applying this theorem to our logistic equation (8) yields the iterative form of the equation:

$$N_{n+1} = N_n + h(rN_n(1 - \frac{N_n}{K})) = N_n(1 + hr - \frac{hrN_n}{K}) \qquad n = 1, 2, 3, ... \tag{15}$$

**Fig. 7.** $r < 0 = .6$, $N_0 = 200$, $K = 1000$



(a)Map of Logistic Equation (13)



(b) Plot Of N(t)

Now, to map this equation, I will choose my step size to be constant at h=1, for simplicity. Choosing an initial condition and carrying capacity is the only thing left to do if we want to map this equation. We choose $N_0 = 200$, and $K = 1000$. For a positive rate ($r > 0$), the resulting plots are in Fig. 6, and for negative rates ($r < 0$), the resulting plots are in Fig. 7. The behavior seen is exactly what we would expect from our previous analysis. In Fig. 6a, we see initially each step has an almost constant magnitude, corresponding to the almost constant intrinsic rate of growth for small N's. As the population (N) approaches the carrying capacity (K=1000), the magnitude of each step decreases exponentially, unil finally, $N = K = 1000$, and the rate of growth drops to zero. The same situation is mapped in Fig. 7a, yet the rate is $r < 0$, confirming our observation that a negative rate results in $N^* = 0$ being an asymptotically stable equilibrium.

In Fig. 6b, we see the characteristic "S" shaped curve. Additionally, we can see that our calculated inflection point is correct, shown by the dotted

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[26] James, pg 595

line at $N = \frac{K}{2} = 500$. The two plots in Fig. 6 and Fig. 7 show two different ways to model a differential equation that depends on the past, given an initial condition.

## 2.3 Model 3: Predator Prey Equation

Now that we have a satisfactory equation for the population growth of one species, the next step is formulate two equations that model the interaction of a species of predators interacting with a species of prey. For example, a population of wolves (predator) interacting with a population of rabbits (prey). We will build our equations around this example, and then change variables for the analysis. So, to begin, we will use W(t) to represent the amount of Wolves, and R(t) to represent the amount of Rabbits. Beginning with our method in Model 1, if there are no wolves, we expect the rabbit population to increase exponentially at a rate proportional to the current amount of rabbits, we will use $r$ as our proportionality constant, as we did in Model 1. Vice-versa, without any rabbits, the wolf population will decrease exponentially, at a rate proportional to the current amount of wolves., we will use $m$ as our proportionality constant[27].

$$\frac{dR}{dt} = rR, \quad \frac{dW}{dt} = -mW, \qquad r \,\&\, m \textit{ are positive constants} \tag{16}$$

Now, we add the aspects of interaction by making assumptions about each species. We assume that the interaction of the two species is directly proportional to the size of each population, so we will notate the size of the wolf/rabbit combined population as RW. Next, we assume that the main cause of death among rabbits is being eaten by wolves, so that interaction between species will deplete the number of rabbits. Thus we add the term $-aRW$ to the equation $\frac{dR}{dt}$ to show this, where a is a positive constant representing the amount of rabbits that are eaten during each interaction with the wolves. Vice-versa, we assume that the survival rates of the Wolves depend on their available food supply, which are rabbits, thus we add the term $+bRW$ to the equation $\frac{dW}{dt}$ to show this, where b is a positive constant representing the amount of lethal interactions with rabbits[28]. In terms of the logistic equation of Model 2, equations (16) become:

$$\frac{dR}{dt} = rR(1 - \frac{W}{(r/a)}) \tag{17}$$

$$\frac{dW}{dt} = -mW(1 - \frac{R}{(m/b)}) \tag{18}$$

Thus, we can use the same methods of analysis that we used on equation (8) from Model 2, with the important difference that the location of K in Model 2 is now occupied by an equilibrium point of the opposite species. This is realized by the fact that if you set $\frac{dR}{dt} = 0$, the R's will cancel, leaving only a W. Thus, the

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[27] James, pg 627

[28] James, pg 627

*nontrivial* equilibrium points for $\frac{dW}{dt}$ is $W^* = \frac{r}{a}$, and for $\frac{dR}{dt}$ it is $R^* = \frac{m}{b}$. The *trivial* equilibrium will be the same as in Model 2, so that $W^* = 0$ and $R^* = 0$. This is also a great demonstration of the coupled nature of the two equations. They are explicitly dependent on each other, so you physically cannot solve only one of the equations. I will now discuss how we can learn about these kinds of equations, without ever solving them.

Now, to generalize our equation to the interaction of any predator vs prey, we use a technique called *nondimensionalization.* The purpose of this technique is to simplify the equations (17) and (18) by applying a change of variables, it will also have the effect of rescaling our equilibrium to (1,1), assuming we pick an appropriate change of variables[29], and it will let us learn about the system using the techniques spoke about in the introduction. The change of variables we will use are:[30]

$$x \equiv \frac{b}{m}R = Prey, \quad y \equiv \frac{a}{r}W = Predators \tag{19}$$

So our equilibria now become:

$$x^* = \frac{b}{m}R^* = \frac{b}{m}\frac{m}{b} = 1, \quad y^* = \frac{a}{r}W^* = \frac{a}{r}\frac{r}{a} = 1 \tag{20}$$

From equation (19), we see that $R = (\frac{m}{b})x$, and that $W = (\frac{r}{a})y$. Also, because r, a, m, and b are constant, we see that $\frac{dR}{dt} = (\frac{m}{b})\frac{dx}{dt}$, and $\frac{dW}{dt} = (\frac{r}{a})\frac{dy}{dt}$. Plugging these relations into equations (17) and (18) yields the much simplified Predator-Prey equations:[31]

$$\frac{dx}{dt} = rx(1-y) \tag{21}$$

$$\frac{dy}{dt} = -my(1-x) \tag{22}$$

Where the only constants that have not been eliminated are r and m, which correspond to the intrinsic rate of growths of the prey and predators, respectively.

Now I can begin the analysis that I spoke about in the introduction. First, I specify again that:

$$f_1(x,y) = \frac{dx}{dt}, \qquad f_2(x,y) = \frac{dy}{dt}, \tag{23}$$

I have already found my equilibria, so I now I will determine the Jacobian for this system of equations, which is:

$$J(x,y) = \begin{bmatrix} \frac{\partial f_1}{\partial x} & \frac{\partial f_1}{\partial y} \\ \frac{\partial f_2}{\partial x} & \frac{\partial f_2}{\partial y} \end{bmatrix} = \begin{bmatrix} r - ry & -rx \\ my & m - mx \end{bmatrix}$$

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[29] Kot, pg 109

[30] Kot, pg 108

[31] Kot, pg 109

I must analyze each pair of equilibria separately, so I begin with the nontrivial equilibria $(x^*, y^*) = (1, 1)$. The Jacobian evaluated at that point becomes:

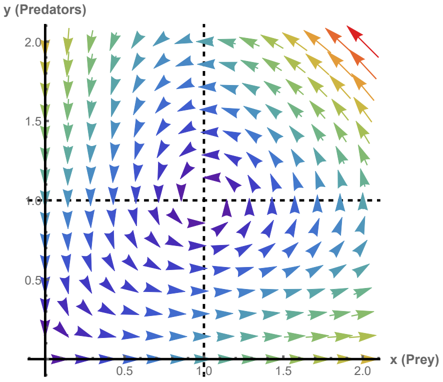
$$J^*(1,1) = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} = \begin{bmatrix} 0 & -r \\ m & 0 \end{bmatrix}$$

So, we see that at this equilibria:

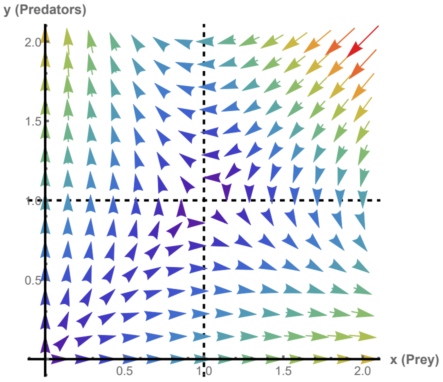
$$q = a_{11}a_{22} - a_{12}a_{21} = rm \tag{24}$$

$$p = a_{11} + a_{22} = 0 \tag{25}$$

**Fig. 8.** Phase Diagrams for Nontrivial Equilibrium $(x^*, y^*) = (1, 1)$



(a)$r = m = .6$



(b) $r = -m = .6$

From Fig. 1, assuming that r, m are positive constants, we see that the resulting phase diagram should have a center at $(x, y) = (1, 1)$, so that all trajectories form near-circular paths around that point. This is exactly what is shown in Fig. 8a. Where the dotted lines represent the values of $x = y = 1$, and the color corresponding to the magnitude of the slope at that point.

To further our trust in this diagram, we look at the hypothetical situation that arises when $r = .6$, and $m = -.6$. We see from equation (24) and (25) that p stays at zero, yet q becomes a *negative* value. So, by looking at Fig. 1, we would expect to see a saddle point where the center was prior. This is exactly what is shown in Fig. 8b.

Now, we turn our attention to the trivial equilibria $(x^*, y^*) = (0, 0)$. So the Jacobian evaluated at that point becomes:

$$J^*(0,0) = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} = \begin{bmatrix} r & 0 \\ 0 & -m \end{bmatrix}$$

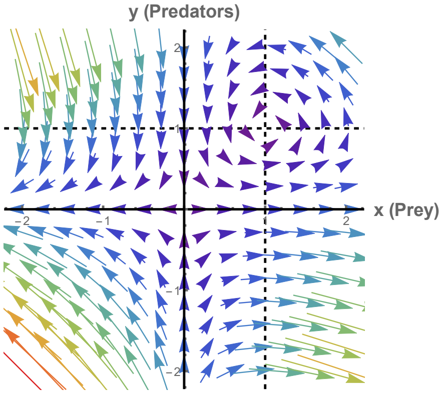
So, we see that at these equilibria:

$$q = a_{11}a_{22} - a_{12}a_{21} = -rm \tag{26}$$

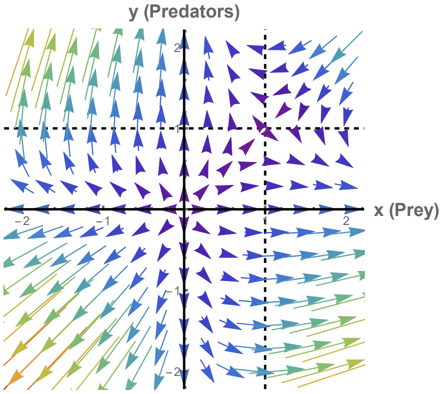
$$p = a_{11} + a_{22} = r - m \tag{27}$$

By looking at Fig. 1, we expect to see a saddle point at $(x, y) = (0, 0)$, just by the assumption that r, m are nonzero. I can graphically demonstrate this behavior by doubling the plots range used in Fig. 8 as to equally include negative values of x, y, even though realistically these areas of the graph are useless, you can't have negative rabbits. Regardless, this behavior is shown in Fig. 9.

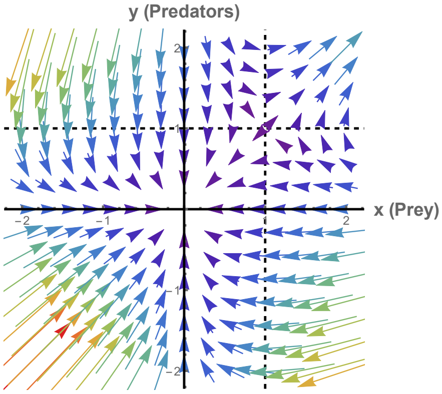
**Fig. 9.** Phase Diagrams for Trivial Equilibrium $(x^*, y^*) = (0, 0)$



(a)$r = m = .6$



(b) $r = -m = .6$



(c) $m = -r = .6$

Finally I will briefly show how I combined equations (21) and (22) into one equation that I used to graph the phase diagrams of Fig. 8 and Fig. 9:[32]

$$\frac{\frac{dy}{dt}}{\frac{dx}{dt}} = \frac{dy}{dx} = \frac{-my(1-x)}{rx(1-y)} \tag{28}$$

# 3 Conclusion

We have presented in this paper a derivation of the Predator-Prey Equations, beginning from the simplest single-species exponential model. We showed how the logistic model solves the problems in the exponential model, and how we can generalize the logistic model to model two interacting species.

Since the logistic model is a nonlinear differential equation, we used concepts taught in PHY 235W to analyze its properties through phase diagrams and logistic maps. There are many other methods that could have been employed to learn about these equations, from bifurcation diagrams to Poincare sections. The reasoning we neglected these methods was mainly due to lack of room.

The predator-prey equations are a great example of a how the concepts taught in PHY 235W can be applied not only to purely mechanical systems, but can be generalized to describe the relationship between a predator and it's prey. From here, we can further develop these equations to

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[32] Kot, pg 109

model almost any type of interaction between two species, from mutual cooperation, competition, and much more[33].

# 4 Referances

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[33] James, pg 631