



Modeling Prey and Predator Populations

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December 15, 2006

Abstract

In this document, we will explore the modeling of two populations based on their relation to one another. Specifically we will focus on the relation between prey and predator populations. We will explain ourselves as we go along, so buckle your seat belts because we are about to take off.

1. Introduction

In the biological world there are many species interacting with each other in a myriad of ways. Some help each other out; take for example the clownfish and the sea anemone. The clownfish defends his or her anemone and receives a safe shelter in return. These interactions are beneficial, and help increase the populations of the respective species. The interactions between prey and predators are quite different. These interactions are detrimental to the population of the prey, and beneficial to the population of the predators.

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Let's imagine we're studying the populations of ants and anteaters. These populations are stranded on an island and have no contact with other sources of food or predation. The anteaters feed solely on the ants and the ants are eaten solely by the anteaters. This is the type of population that will be referenced throughout this document. Keep in mind that the equations representing discussed scenarios are not exact and are expressed loosely for the purpose of understanding how real world situations work.

2. Population Model

We want to produce a model representative of the changes in the populations of the prey and predator species over time. Let ΔP represent the change in population of the prey, and ΔQ represent the change in population of the predator. We can look at each population individually before trying to add the influence of each on the other.

We might want to start with $\Delta P = rP$, with $r > 1$. This would represent some sort of growth of the prey population over time. However, this by itself is very unrealistic. As time goes by the prey population would grow to infinity, and the environment can only support a finite number. Let K equal the carrying capacity of the environment. The population can only get as large as K in their current living conditions before Mother Nature puts a stop to their growth.

We want the rate of growth, r to start out high and then slowly decrease until P is equal to K , or $r = 0$. So r is no longer a constant, it is a function of P . We can call it $r(P)$, and $\Delta P = r(P)P$. Figure 1 is an image of what $r(P)$ should look like. With this image we can construct a simple form of the

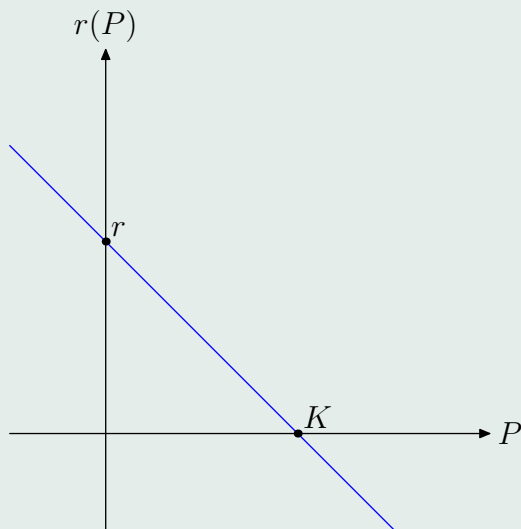


Figure 1: The rate of growth of P as a function of P .

function $r(P)$ using $f(x) = mx + b$. It should intersect the $r(P)$ axis at some point r , and have slope of rise over run, or $-r/K$. So we have something like Equation (1).

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$$\begin{aligned}r(P) &= -\frac{r}{K}P + r \\ &= r\left(1 - \frac{P}{K}\right)\end{aligned}\quad (1)$$

Since $\Delta P = r(P)P$, we can plug Equation (1) in and get a more complete model in Equation (2).

$$\begin{aligned}\Delta P &= r\left(1 - \frac{P}{K}\right)P \\ &= rP\left(1 - \frac{P}{K}\right)\end{aligned}\quad (2)$$

However, we are not yet finished with ΔP , because we don't have the influence of the predator population. We want to subtract off the detrimental impact of prey and predator interactions. We'll represent this impact with sPQ , where s is some percentage of PQ , the interactions between prey and predators. The final form of ΔP is shown as Equation (3).

$$\Delta P = rP\left(1 - \frac{P}{K}\right) - sPQ\quad (3)$$

ΔQ is a little simpler to compute. Without the prey population present, the population of predators would simply die of starvation. So we start with $\Delta Q = -uQ$, with $u < 1$ as some positive constant representing the death rate



of the predators. We now want to add on the benefit of the interactions between the two populations. Using a method similar to what we did with ΔP , we come up with Equation (4).

$$\Delta Q = -uQ + vPQ \quad (4)$$

We now model our equations differently, so that Q becomes Q_t , P becomes P_t , ΔQ becomes $Q_{t+1} - Q_t$ and ΔP becomes $P_{t+1} - P_t$. Remember that ΔP and ΔQ represent the change in the population with each step in time. Our ΔP will change to look like Equation (5).

$$\begin{aligned} \Delta P &= rP \left(1 - \frac{P}{K}\right) - sPQ \\ P_{t+1} - P_t &= rP_t \left(1 - \frac{P_t}{K}\right) - sP_tQ_t \\ P_{t+1} &= rP_t \left(1 - \frac{P_t}{K}\right) + P_t - sP_tQ_t \\ P_{t+1} &= P_t \left(1 + r \left(1 - \frac{P_t}{K}\right)\right) - sP_tQ_t \end{aligned} \quad (5)$$

Similar work for ΔQ will give us the result in Equation (6).

$$Q_{t+1} = (1 - u)Q_t + vP_tQ_t \quad (6)$$

Now, if given an initial point, and values for r, s, u, v , and K , we can plot the populations of Q and P using time t as a parameter. We will discuss more of what this looks like in later sections.

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3. Eigenvalues and Model Behavior

Let's take a step back from the idea of population modeling, and take a look at eigenvalues. In this section we will explore the meaning of eigenvalues in linear systems of two equations and two unknowns and how they effect the behavior of their graphs.

If our linear system is represented in terms of the vector \mathbf{x}_n , which when multiplied by the matrix A gives us the vector \mathbf{x}_{n+1} with our next values, then we can show the system as:

$$\mathbf{x}_{n+1} = A\mathbf{x}_n$$

There are five ways for the convergence of our system to behave depending on the eigenvectors. Or, more precisely, five ways that we are going to discuss. There are sinks, sources, spiral sinks, spiral sources, and saddle points. We assume that our matrix A containing the coefficients from the linear system has two eigenvalue-eigenvector pairs. In other words,

$$A\mathbf{v}_1 = \lambda_1\mathbf{v}_1 \quad \text{and} \quad A\mathbf{v}_2 = \lambda_2\mathbf{v}_2$$

where $\lambda_1 \neq \lambda_2$ implies that \mathbf{v}_1 and \mathbf{v}_2 are independent.

This means that \mathbf{v}_1 and \mathbf{v}_2 span \mathbb{R}^2 , and our initial values in \mathbf{x}_0 can be written as:

$$\mathbf{x}_0 = \alpha_1\mathbf{v}_1 + \alpha_2\mathbf{v}_2$$



We know that:

$$\begin{aligned}\mathbf{x}_1 &= A\mathbf{x}_0 \\ &= A(\alpha_1\mathbf{v}_1 + \alpha_2\mathbf{v}_2) \\ &= \alpha_1(A\mathbf{v}_1) + \alpha_2(A\mathbf{v}_2) \\ &= \alpha_1\lambda_1\mathbf{v}_1 + \alpha_2\lambda_2\mathbf{v}_2\end{aligned}$$

We move on to \mathbf{x}_2 , which will show the beginnings of a pattern:

$$\begin{aligned}\mathbf{x}_2 &= A\mathbf{x}_1 \\ &= A(\alpha_1\lambda_1\mathbf{v}_1 + \alpha_2\lambda_2\mathbf{v}_2) \\ &= \alpha_1\lambda_1A\mathbf{v}_1 + \alpha_2\lambda_2A\mathbf{v}_2 \\ &= \alpha_1\lambda_1(A\mathbf{v}_1) + \alpha_2\lambda_2(A\mathbf{v}_2) \\ &= \alpha_1\lambda_1^2\mathbf{v}_1 + \alpha_2\lambda_2^2\mathbf{v}_2\end{aligned}$$

With repetition we will eventually discover that \mathbf{x}_n is, in fact following the λ^n pattern that we can see emerging.

$$\mathbf{x}_n = \alpha_1\lambda_1^n\mathbf{v}_1 + \alpha_2\lambda_2^n\mathbf{v}_2$$

This tells us something very important about the behavior of the graph of our variables. If the eigenvalues of A are $\lambda > 1$, then values of \mathbf{x}_n will blow up to infinity. If the eigenvalues of A are $\lambda < 1$, then values of \mathbf{x}_n will converge to zero. If one eigenvalue is less than one and the other greater than one, the values of \mathbf{x}_n will display as a saddle point. One of the variables out of \mathbf{x}_n will go to infinity while the other goes to zero.

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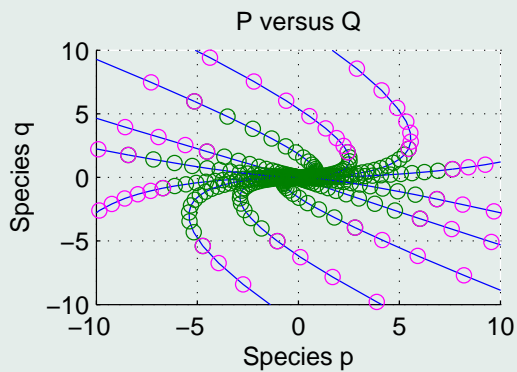
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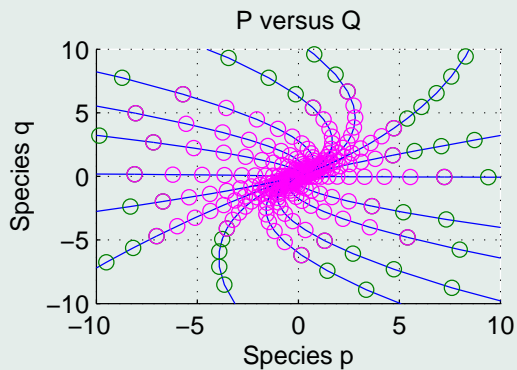
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(a) Sink, $\lambda_1, \lambda_2 < 1$



(b) Source, $\lambda_1, \lambda_2 > 1$

Figure 2: Real Eigenvalues



Figure 2 shows two of these three cases, the case where λ_1 and λ_2 are less than one and where they are greater than one. The MatLab code that generated the images started at some point and used green markers for ever step forward in time, and magenta markers for every step backward in time. As you can see, the sink on the left goes forward to the origin. The source on the right goes forward out to infinity.

If the eigenvalues are imaginary, we will get models that spiral in and out. If one eigenvalue is imaginary, there must be another eigenvalue that is the complex conjugate of the first. That is, if $\lambda_i = a + bi$, then $\lambda_j = a - bi$. With our two by two matrices, one imaginary eigenvalue is indicative of the second. If the magnitude of these eigenvalues is less than one, we will get a spiral sink. The model will spiral into the origin, in a similar way to a sink. If the magnitude is greater than one, we will get a spiral source. The model will spiral out to infinity, in a similar way to a source.

Figure 3 shows these two cases. The first image shows a spiral sink. It spirals forward into the origin as shown by the green markers. The second image shows a spiral source. It spirals away from the origin.

These last two cases are especially important for our topic. We will get to how they apply in the next section.

4. Equilibria and Eigenvalues

Now we can return to our population modeling. When one thinks about the fluctuations of the two populations, one might wonder whether the populations fluctuate forever, or if they reach a stable point and stay there. This stable point

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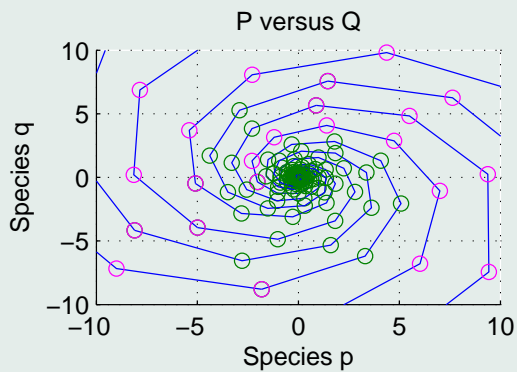
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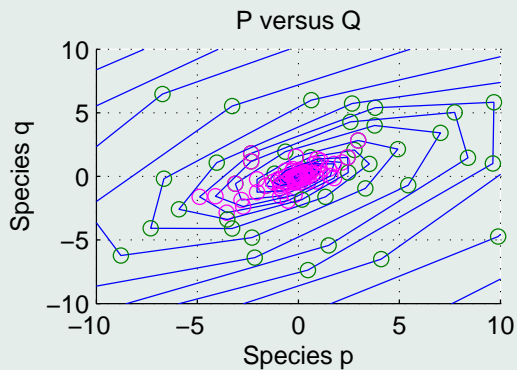
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(a) Spiral Sink, imaginary $\lambda < 1$



(b) Spiral Source, imaginary $\lambda > 1$

Figure 3: Imaginary Eigenvalues



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is what we call an equilibrium point. This is where $P_{t+1} = P_t$, and $Q_{t+1} = Q_t$; each iteration will produce the same number thereafter. We will use these two equations derived in the section Population Growth,

$$P_{t+1} = P_t \left(1 + r \left(1 - \frac{P_t}{K} \right) \right) - sP_tQ_t$$
$$Q_{t+1} = (1 - u)Q_t + vP_tQ_t$$

If we let $P_{t+1} = P_t$, and replace all P_{t+1} s and P_t s with P^* s, and similar for Q_{t+1} and the Q_t s, we can solve this equation by factoring:

$$P^* = P^* \left(1 + r \left(1 - \frac{P^*}{K} \right) \right) - sP^*Q^*$$
$$Q^* = (1 - u)Q^* + vP^*Q^*$$

We let the carrying capacity $K = 1$ after this point for the sake of simplifying our model, and it will no longer appear in our equations. Without going into all the trivial math work, if we set the left side equal to zero and factor we will get:

$$0 = P^* (r(1 - P^*) - sQ^*)$$
$$0 = Q^* (-u + vP^*)$$

This means that for ΔQ to equal zero, $Q^* = 0$, or $P^* = u/v$, and for ΔP to equal zero, $P^* = 0$, or $Q^* = (r/s)(1 - P)$. With these conditions we can create what are called nullclines, shown in Figure 4. These nullclines represent



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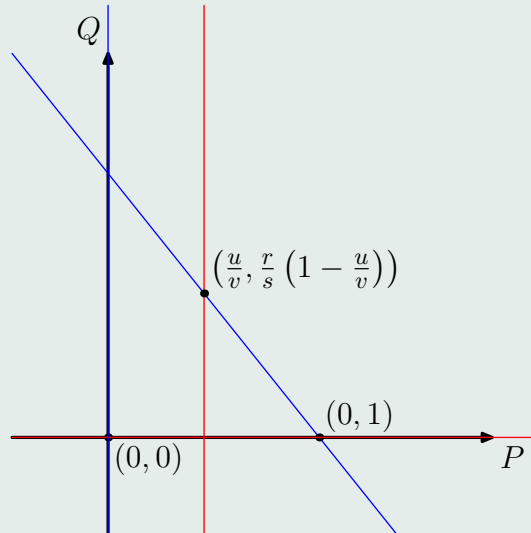


Figure 4: Nullclines



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the equations of each possible zero. The red nullclines are derived from ΔQ , and the blue nullclines are derived from ΔP .

The intersections of the red and blue nullclines are the loci of the equilibrium points. Notice that there are three possible equilibria, at $(0,0)$, $(1,0)$, and at $(u/v, (r/s)(1 - u/v))$. You can do some basic algebra to find these equilibria with the equations already given above.

The first two equilibria, $(0,0)$ and $(1,0)$ are points that we do not care about. In both cases at least one population becomes extinct, leaving the whole premise of prey-predator interactions. Instead we focus on the third point: $(u/v, (r/s)(1 - u/v))$. This point will change depending on our values of u, v, r , and s . If we have these values, we can find where this third equilibrium point is.

If we let $u = .7$, $v = 1.6$, $r = 1.3$, and $s = .5$, then

$$\begin{aligned} P^* &= \frac{u}{v} \\ &= \frac{.7}{1.6} \\ &= .4375 \end{aligned}$$

and:



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$$\begin{aligned}Q^* &= \frac{r}{s} \left(1 - \frac{u}{v}\right) \\&= \frac{1.3}{.5} \left(1 - \frac{.7}{1.6}\right) \\&= 2.6(1 - .4375) \\&= 1.4625\end{aligned}$$

Once we have the equilibrium point, we can linearize the equations for prey and predator populations. The first thing we do in our step to linearizing the equations is to consider how the model behaves very close to the equilibrium point. As the model gets closer to the equilibrium point, P and Q get very close, but not necessarily together or at the same time. In other words, our P may be getting closer, then further away, then even closer then a little further away. At the same time Q could be getting further away and then closer, etc..

To picture what I'm saying, think of a spiral sink. This spiral sink specifically has the shape of an ellipse. As it approaches the center of the sink, the Q will get closer then drift a little farther before coming back around, and P does the same. We will represent this small distance from the equilibrium by $P_t = P^* + p_t$ and $Q_t = Q^* + q_t$. Similarly, $P_{t+1} = P^* + p_{t+1}$ and $Q_{t+1} = Q^* + q_{t+1}$. We now have:

$$\begin{aligned}P^* + p_{t+1} &= (P^* + p_t) (1 + r (1 - (P^* + p_t))) - s (P^* + p_t) (Q^* + q_t) \\Q^* + q_{t+1} &= (1 - u) (Q^* + q_t) + v (P^* + p_t) (Q^* + q_t)\end{aligned}$$



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Now let us plug in our values for P^* , Q^* , u , v , r , and s .

$$\begin{aligned} .4375 + p_{t+1} &= (.4375 + p_t) (1 + 1.3 (1 - (.4375 + p_t))) - .5 (.4375 + p_t) (1.4625 + q_t) \\ p_{t+1} &= (.4375 + p_t) (1 + 1.3 - .56875 - 1.3p_t) - (.21875 + .5p_t) (1.4625 + q_t) - .4375 \\ &= .4375 + .56875 - .248828125 - .56875p_t + p_t + 1.3p_t - .56875p_t \\ &\quad - 1.3p_t^2 - .319921875 - .21875q_t - .73125p_t - .5p_tq_t - .4375 \\ &= .4375 - .4375 + .43125p_t - .21875q_t - 1.3p_t^2 - .5p_tq_t \\ &= .43125p_t - .21875q_t - 1.3p_t^2 - .5p_tq_t \end{aligned}$$

Finding q_{t+1} is a little less ugly.

$$\begin{aligned} 1.4625 + q_{t+1} &= (1 - .7) (1.4625 + q_t) + 1.6 (.4375 + p_t) (1.4625 + q_t) \\ q_{t+1} &= .3 (1.4625 + q_t) + 1.6 (.63984375 + .4375q_t + 1.4625p_t + p_tq_t) - 1.4625 \\ &= 1.4625 - 1.4625 + q_t + 2.34p_t + 1.6p_tq_t \\ &= 2.34p_t + q_t + 1.6p_tq_t \end{aligned}$$

If you actually read through all that, you are superhuman or mental. Normally I would have left you to assume the calculations were correct, instead of slogging through all the number crunching. However, in this case I was motivated by a desire to show just how ugly and tedious computing these equations can be. This will make an easier method of computation seem extra desirable. An easier method exists in the form of Jacobian Matrices, a concept we will get to in the last section of this paper.



Now we have two new equations for the behavior of the model very near the equilibrium point:

$$\begin{aligned}p_{t+1} &= .43125p_t - .21875q_t - 1.3p_t^2 - .5p_tq_t \\q_{t+1} &= 2.34p_t + q_t + 1.6p_tq_t\end{aligned}$$

So we've gone from one nonlinear system to another nonlinear system. Doesn't seem as though much has been accomplished, but it has! The difference is that these p_t and q_t values are very small. If p_t is very small, then p_t^2 is even smaller. If q_t is also very small, then p_tq_t is even smaller than p_t and q_t . Since we want to have a linear system, we can declare these extremely small values negligible, and throw them out when no one is looking. So our system really (almost) looks like this:

$$\begin{aligned}p_{t+1} &= .43125p_t - .21875q_t \\q_{t+1} &= 2.34p_t + q_t\end{aligned}$$

Finally, we have a linear system. We can use a new set of axes with the equilibrium point at the origin to see exactly how this system behaves around that point. The eigenvalues of the matrix containing the coefficient will tell us whether or not the equilibrium point is stable. Will the populations approach the point, or will they go away as they would in a source. Obviously the populations cannot go to infinity, the carrying capacity prevents that, but as related to that tiny area around the equilibrium point, they can look like they are going to infinity.

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Let us call our coefficient matrix A , so that A equals:

$$\begin{bmatrix} .43125 & -.21875 \\ 2.34 & 1 \end{bmatrix}$$

The eigenvalues of A are determined by this characteristic polynomial:

$$0 = \lambda^2 - T(A)\lambda + D(A)$$

$T(A)$ is the trace of A , which is equal to the sum of the diagonal elements. $D(A)$ is the determinant of A , which is equal to the difference of the product of the diagonal elements and the product of the reverse diagonal elements. In other words,

$$\begin{aligned} T(A) &= .43125 + 1 \\ &= 1.43125 \\ D(A) &= 1(.43125) - (-.21875)(2.34) \\ &= .943125 \end{aligned}$$

With the trace and the determinant of the characteristic polynomial, we have a simple quadratic in terms of λ .

$$0 = \lambda^2 - 1.43125\lambda + .943125$$

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From here we can use the quadratic equation to solve for λ .

$$\begin{aligned}\lambda &= \frac{1.43125 \pm \sqrt{2.0484765625 - 4(.943125)}}{2} \\ &\approx .715625 \pm \frac{\sqrt{-1.7240234375}}{2} \\ &\approx .71563 \pm .65651i\end{aligned}$$

The magnitude of these two eigenvalues is $\sqrt{.71563^2 + .65651^2}$. This is approximately .97115. Because the magnitude of the two eigenvalues is less than one, and they are imaginary, the model behaves like a spiral sink and the populations are stable around that equilibrium point. Figure 5 is a representation of how the populations behave very near the equilibrium point. Because our eigenvalues have a magnitude less than one, over time this model is spiraling inward toward the origin. The origin in this figure is the equilibrium point (.4375, 1.4625).

If we had found a complex eigenvalue pair with magnitudes greater than one, the population would have been unstable. The image produced would have resembled a spiral source. If the eigenvalue pair had been real, with one less than and one greater than one, the image would have resembled a saddle point. The population would have traveled in toward the equilibrium point and then veered away just before reaching it. Both of these would indicate unstable equilibrium points.

That is how we find the stability of two populations around an equilibrium point.

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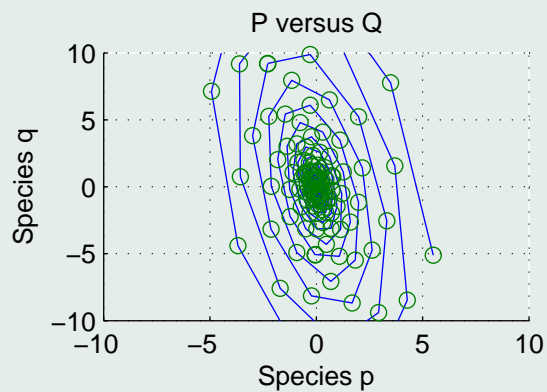


Figure 5: A representation of the linear model of equations.



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5. Jacobian Matrices

I know that you're eager to learn an easier method of linearizing the original model. The Jacobian method creates the coefficient matrix without having to do all the number crunching. What we do is take our original equations shown below.

$$P_{t+1} = P_t \left(1 + r \left(1 - \frac{P_t}{K} \right) \right) - sP_tQ_t$$
$$Q_{t+1} = (1 - u)Q_t + vP_tQ_t$$

Now, the Jacobian Matrix of this system is a two by two matrix with the first partial derivatives of each equation occupying an entry.

$$J = \begin{bmatrix} \frac{\partial P_{t+1}}{\partial P_t} & \frac{\partial P_{t+1}}{\partial Q_t} \\ \frac{\partial Q_{t+1}}{\partial P_t} & \frac{\partial Q_{t+1}}{\partial Q_t} \end{bmatrix}$$

So we simply need to find the first partials of P_{t+1} and Q_{t+1} . The previous values of $u, v, r, s,$ and K are used in this example. We now need to take the partial of the right hand side of

$$P_{t+1} = P_t (1 + 1.3(1 - P_t)) - .5P_tQ_t$$

with respect to P_t . First, expand the right-hand side of the last result.

$$P_{t+1} = P_t + 1.3P_t - 1.3P_t^2 - .5P_tQ_t$$



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Now, take the partial of the right-hand side of the last result with respect to P_t .

$$\frac{\partial P_{t+1}}{\partial P_t} = 1 + 1.3 - 2.6P_t - .5Q_t$$

Then we take the partial of the same thing with respect to Q_t .

$$\frac{\partial P_{t+1}}{\partial Q_t} = -.5P_t$$

Next we need to take the partial of

$$Q_{t+1} = (1 - .7)Q_t + 1.6P_tQ_t$$

with respect to P_t .

$$\frac{\partial Q_{t+1}}{\partial P_t} = 1.6Q_t$$

Lastly, we take the partial of Q_{t+1} with respect to Q_t .

$$\frac{\partial Q_{t+1}}{\partial Q_t} = .3 + 1.6P_t$$

So with these four results we can construct the Jacobian matrix.

$$J = \begin{bmatrix} 2.3 - 2.6P_t - .5Q_t & -.5P_t \\ 1.6Q_t & .3 + 1.6P_t \end{bmatrix}$$

To find how the graph behaves around the equilibrium point, we can plug in the equilibrium values P^* and Q^* to produce the coefficient matrix A .



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$$A = \begin{bmatrix} 2.3 - 2.6P^* - .5Q^* & -.5P^* \\ 1.6Q^* & .3 + 1.6P^* \end{bmatrix}$$
$$= \begin{bmatrix} .43125 & -.21875 \\ 2.34 & 1 \end{bmatrix}$$

Note that this is the same matrix that was found using the drawn out number crunching. Constructing a Jacobian matrix is a much cleaner method of finding the linear behavior of two populations around an equilibrium point.

6. Conclusion

Thank you for reading this article on prey and predator population modeling. I would recommend reading further materials on eigenvalues and model behavior, and taking a more in depth look at the whys and wherefores of the Jacobian Matrix.

References

- [1] Allman, Elizabeth S., and Rhodes, John A. *Mathematical Model in Biology* 2004. Cambridge University Press
- [2] David Arnold of College of the Redwoods for spending uncountable hours helping us to understand.