Extending the Lotka-Volterra Equations

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1 Introduction

The Lotka-Volterra model is a pair of differential equations representing the populations of a predator and prey species which interact with each other. The model was independently proposed in 1925 by American statistician Alfred J. Lotka and Italian mathematician Vito Volterra. In this paper, we will review the paper *A Lotka-Volterra Three-Species Food Chain* by E. Chauvet, J. Paullet, J. Previte, and Z. Walls, where the authors present the three-species extension to the traditional Lotka-Volterra equations and we will propose a more generalized form of the equations - extending the system to allow for more diverse interactions between the three species.

2 The Classic Model

Lotka and Volterra's proposed model was the pair of differential equations given by

$$\frac{dx}{dt} = \alpha x - \beta xy$$

$$\frac{dy}{dt} = \delta xy - \gamma y$$

where $x(t)$ represents the population of the prey species and $y(t)$ represents the population of the predator species. The other values, α, β, δ, and γ are positive constants. The αx represents the growth factor of the prey species and $-\gamma y$ represents the natural death factor of the predator species. Each of these are proportional to the population of the species. The expression $-\beta xy$ represents the number of the x population that are killed by the y population and the expression δxy represents the growth of the y population as a result of consuming the x species. These two expressions are proportional to the population of both species.

3 Definitions

When using this model, the goal is to find equilibrium states - that is, to find constant population values x and y so that for some t_0 all $t > t_0$ have $x(t) \approx x$ and $y(t) \approx y$. When two species are in such a state, we say that the system is in **equilibrium**. The values $x(t)$ and $y(t)$ will remain approximately constant. We aim to find equilibria positions since these positions tend to show us the behavior of the species over time. We can use them to determine whether the populations will stabilize and remain constant (and the values to which they will stabilize), if the populations will constantly fluctuate, or if one or both species will die out.

To this end, we further classify equilibrium states. We call an equilibrium position (x_{eq}, y_{eq}) an **unstable equilibrium** if the initial conditions (x_0, y_0) close to (x_{eq}, y_{eq}) tend to move away from (x_{eq}, y_{eq}) rather than towards it. Otherwise, if (x_0, y_0) tends toward (x_{eq}, y_{eq}) for sufficiently close (x_0, y_0), we call this equilibrium position an **asymptotically stable equilibrium position**.

To find equilibrium positions, we want to solve the system for x_{eq} and y_{eq} such that $\frac{dx}{dt} = 0$ and $\frac{dy}{dt} = 0$ at (x_{eq}, y_{eq}). This ensures that once the two populations both reach x_{eq} and y_{eq} at the same time, then they will remain constant at that value. We find the equilibrium positions for the classic Lotka-Volterra model as follows:

$$\frac{dx}{dt} = 0$$

$$\alpha x - \beta xy = 0$$

$$x(\alpha - \beta y) = 0$$

This equation has solutions $x = 0$ and $y = \frac{\alpha}{\beta}$.

$$\frac{dy}{dt} = 0$$

$$\delta xy - \gamma y = 0$$

$$y(\delta x - \gamma) = 0$$

This equation has solutions $x = \frac{\gamma}{\delta}$ and $y = 0$. Together, we find that the equilibrium positions are $(0, 0)$ and $(\frac{\gamma}{\delta}, \frac{\alpha}{\beta})$.

In this paper, we will also consider the Jacobian (the matrix of first-order partial derivatives) when solving for equilibrium positions of the three-species case. For the three dimensional case, it takes the form

$$J = \begin{bmatrix} \frac{df_1}{dx} & \frac{df_1}{dy} & \frac{df_1}{dz} \\ \frac{df_2}{dx} & \frac{df_2}{dy} & \frac{df_2}{dz} \\ \frac{df_3}{dx} & \frac{df_3}{dy} & \frac{df_3}{dz} \end{bmatrix} \tag{1}$$

where each of $f_1(x, y, z)$, $f_2(x, y, z)$, and $f_3(x, y, z)$ represent the differential equations given in the three-species system.

4 A Simplified Three-Species Model

Now suppose we extended the two-species model and consider the authors' proposed three-species model with one species at the bottom of the food chain, one in the middle, and one at the top. Let these species be x, y, and z and denote the differential equations modeling their behavior by

$$\frac{dx}{dt} = ax - bxy$$

$$\frac{dy}{dt} = -cy + dxy - eyz$$

$$\frac{dz}{dt} = -fz + gyz$$

This model has similar parameters as the classic model: x has a growth rate denoted by ax while y and z have a natural death rate denoted by $-cy$ and $-fz$, respectively. dxy and gyz denote the growth rate of y and z from hunting their prey and $-bxy$ and $-eyz$ denote the death rate of the prey as a result of being hunted. It is interesting to note that the authors chose to give species y a death rate (the negative sign in front of $-cy$) instead of a growth rate in the absence of a predator z. This is to avoid inaccuracy in the case that species x goes extinct at some point. If it had a positive growth rate (instead of death rate), then y's population would still increase, despite having no food source.

This model is a very slight generalization of the two-species model: it adds a third species, but it only allows for a chain of predation (i.e. this model does not allow us to consider the case where both y and z prey on x or where x and y are at the bottom of the food chain and z preys on both).

5 Analysis of Simplified Three-Species Model

To find the equilibria of this model, we consider the values (x_{eq}, y_{eq}, z_{eq}) for which $\frac{dx}{dt} = \frac{dy}{dt} = \frac{dz}{dt} = 0$. We have:

$$\frac{dx}{dt} = x(a - by)$$

$$\frac{dy}{dt} = y(dx - c - ez)$$

$$\frac{dz}{dt} = z(gy - f)$$

Besides the trivial equilibrium position $(0,0,0)$, we also consider the case where $(a - by) = (gy - f) = (dx - c - ez) = 0$. We then find that we need $y_{eq} = \frac{a}{b} = \frac{f}{g}$. Therefore, a second equilibrium position exists only when the constant parameters $ga = fb$.

We now consider the Jacobian of the system we have proposed. Taking appropriate partial derivatives, we find that

$$J = \begin{bmatrix} a - by & -bx & 0 \\ dy & -c + dx - ez & -ey \\ 0 & gz & gy - f \end{bmatrix} \tag{2}$$

We note that the system will have an asymptotically stable solution if and only if all the real parts of the eigenvalues of the Jacobian are negative. We consider the roots of the characteristic equation of the above Jacobian, given by

$$det(J(x, y, z) - \lambda I) = \begin{bmatrix} a - by - \lambda & -bx & 0 \\ dy & -c + dx - ez - \lambda & -ey \\ 0 & gz & gy - f - \lambda \end{bmatrix} \tag{3}$$

We can test for the stability of an equilibrium position (x, y, z) of a system with constants a, b, etc. by plugging in these values into the Jacobian and finding the eigenvalues. The equilibrium will be stable if and only if the real parts of each of the eigenvalues is negative.

6 Generalized Three-Species Model

We have mentioned that the model proposed by the authors in their three-species model is very simplified as it is restricted to the case of a linear food chain model (z preys on y and y preys on x). We will now propose a generalized three-species model that allows for any number of species to be the prey or predators (or both!). We will also allow the existence of mutual symbiosis: the phenomenon where two species benefit from coexisting in the same environment. Examples of this include cleaner fish - small fish that help clean off dead skin and parasites from larger predatory fish.

Let the three species be p_1, p_2, and p_3. We may use the column vector $P(t)$

to represent the populations of each of the three species at time t:

$$P(t) = \begin{bmatrix} p_1(t) \\ p_2(t) \\ p_3(t) \end{bmatrix} \quad (4)$$

and we let $P(0)$ contain the initial populations of each of the species.

Let D be the matrix differential operator containing the interactions between any two species. It will have the form

$$D = \begin{bmatrix} 0 & d_{1,2} & d_{1,3} \\ d_{2,1} & 0 & d_{2,3} \\ d_{3,1} & d_{3,2} & 0 \end{bmatrix} \quad (5)$$

Where $d_{i,j}$ for $1 \leq i, j \leq n$ and $i \neq j$ represents the constant coefficient of interaction (the effect the j-th species has on the i-th species). In our model, we will treat these values as constants which will be given as parameters. This coefficient will be multiplied by the population of the i-th and j-th species to represent the interaction (since the effect should be proportional to each of the populations). We will avoid making many assumptions about the coefficients, but we see that in a practical example, we will usually expect to find $d_{i,j}$ and $d_{j,i}$ to have opposite signs (since the idea is that if the i-th species preys on the j-th species, then $d_{i,j}$ should be negative and $d_{j,i}$ should be positive. There may be some instances when we will see that $d_{i,j}$ and $d_{j,i}$ have the same sign (either both positive or both negative). When they are both positive, for example, we say that the two species have a mutual symbiosis: they both benefit from each others presence. When they are both negative, they may have a negative impact on each other, without necessarily preying on each other. For example, goats and sheep do not prey on each other, but the presence of each species would reduce available resources such as food and so they would have a harmful effect on the other species' population.

Returning to our matrix, we notice that we the diagonals of D are 0. We will not consider $d_{i,i}$ in this matrix (hence they are set to 0) since we want a growth rate or natural death rate to be proportional to the i-th population and we choose not to consider this growth/death rate to be an interaction between a species and itself. Instead, we define the constant column vector G to contain each of the growth or natural death rate constants for each species. We have

$$G = \begin{bmatrix} g_1 \\ g_2 \\ g_3 \end{bmatrix} \quad (6)$$

where g_i represents the natural growth (or death) rate of of the i-th species. For example, a species at the bottom of the food chain (e.g. grass) would grow from

the nutrients in the ground and from sunlight. The constant g_i represents this factor and we claim that in the absence of predators, grass would grow at a rate of $g_i p_i(t)$ at time t, which is proportional to its present population. Similarly, if a species were at the top of the food chain (e.g. a lion in the savannah, which has no natural predators), g_i would represent its natural death rate. Again, its death rate would be $g_i p_i(t)$. We see that in these two cases, the difference is in the sign of g_i if $g_i > 0$, we can consider the i-th species to be at the bottom of the food chain and grow independently of the other species in our system. For all other species (those not at the bottom), we can choose $g_i < 0$ and assume that in the absence of prey, these species will die off. This assumes that all of a species' food sources are in the system (with the exception of those at the bottom of the food chain, which are presumed to always have a surplus of sustenance - such as sunlight).

We define the three-species system to be:

$$\frac{dp_1}{dt} = g_1 p_1(t) + d_{1,2} p_1(t) p_2(t) + d_{1,3} p_1(t) p_3(t)$$

$$\frac{dp_2}{dt} = d_{2,1} p_2(t) p_1(t) + g_2 p_2(t) + d_{2,3} p_2(t) p_3(t)$$

$$\frac{dp_3}{dt} = d_{3,1} p_3(t) p_1(t) + d_{3,2} p_3(t) p_2(t) + g_3 p_3(t)$$

In our differential equations, we notice that the j-th species contributes an effect of $d_{i,j} p_i(t) p_j(t)$ to the differential $\frac{dp_i}{dt}$, which represents the rate of change of the i-th population at time t. We see that this is desired since we follow the standard model's assumption that the interaction should be directly proportional to each of the predator's population and the preys population at the current time. We also see that $g_i p_i(t)$ represents either the growth or natural death rate of the i-th species and it is proportional to the species' population. Finally, we will define the column vector of differentials $V(t)$ as:

$$V(t) = \begin{bmatrix} \frac{dp_1(t)}{dt} \\ \frac{dp_2(t)}{dt} \\ \frac{dp_3(t)}{dt} \end{bmatrix} \tag{7}$$

We return to the differential equations that we want to solve, of the form:

$$\frac{dp_i}{dt} = g_i \cdot p_i(t) + \sum_{1 \leq i,j \leq n, i \neq j} d_{i,j} \cdot p_i(t) \cdot p_j(t)$$

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For $1 \leq i \leq n$. We would now like to express this in terms of our vectors and matrices that we have defined. We first notice that

$$\frac{dp_i}{dt} = (g_i + \sum_{1 \leq i,j \leq n, i \neq j} d_{i,j} \cdot p_j(t)) \cdot p_i(t)$$

And we see that when we consider all the equations at once, we find

$$V(t) = (G + D \cdot P(t)) \cdot P(t)$$

.

7   Numerical Solution

We can now consider a numerical solution to the problem. We may use a simple Forward Euler approximation for this system. We start from the definition of the derivative

$$\frac{dp_i}{dt} = \lim_{h \to 0} (\frac{p_i(t+h) - p_i(t)}{h})$$

and see that our column vector of differentials becomes

$$V(t) = \lim_{h \to 0} (\frac{P(t+h) - P(t)}{h})$$

We would like to approximate $P(t + \Delta t)$ given the column vector $V(t)$, the previous iteration $P(t)$, and a small time step Δt. If we choose some small $\Delta t > 0$ for our time step, we find

$$P(t + \Delta t) = \Delta t \cdot V(t) + P(t)$$

Now we substitute the expression we found for $V(t)$ earlier and see that

$$P(t + \Delta t) \approx \Delta t \cdot (G + D \times P(t)) + P(t)$$

We have now found our recursive relation for $P(t + \Delta t)$ and we can use it to approximate $P(t)$ for $t > 0$, using a suitably small time step. Over our iterations, we would like to keep Δt fixed. To implement this in Matlab, we can first improve the efficiency of the code by using

$$P(t + \Delta t) \approx (\Delta t \cdot G + \Delta t \cdot D \times P(t) + I) \cdot P(t)$$

where I is the 3×3 identity matrix. We see that this arrangement is correct since we have $I \times P(t) = P(t)$ and since addition is distributive over the dot product. We then define a column vector $F = \Delta t \cdot G + \mathbf{1}$ (where $\mathbf{1}$ is a column vector of 1's) and 3×3 matrix $H = \Delta t \cdot D$ and find that

$$P(t + \Delta t) \approx (H \times P(t) + F) \cdot P(t)$$

We have simplified the operations performed for each iteration of the forward Euler algorithm since now we only have to compute a matrix product, a column vector addition, and a dot product. We only need to calculate F and H once at the beginning of the algorithm, since our values for F and H are determined by constants.

The code implementing this algorithm is below. The code is generalized to model an n-species model and can accept an $n \times n$ matrix of inputs and for simplicity, we have chosen to use $n = 3$ in the code.

```
clear all; close all; clc;
n = 3; % number of species/equations we are dealing with
D = [
    0 −0.04 −0.04;
    0.04 0 −0.02;
    0.02 0.04 0;
]; % this is the nxn matrix storing interactions between
species (parameter)
G = [0.25; −0.5; −0.5]; % this is the natural growth
or death rate (n−length vector as a parameter)
P_0 = [50; 10; 5]; % these are initial conditions
(n−length vector as a parameter)
dt = 0.002; % this is the time step (parameter).
Smaller the time step, the more accurate our end results
P = P_0; % initial conditions to matrix storing results
num_steps = 50000; % number of iterations
H = dt*D;
F = dt*G+ones(n,1);
for i=1:num_steps−1 % forward Euler method
    P_last = P(:,i); % this takes P_(n−1)
    % this computes our forward Euler equation for P_n
    P_n = max(0,(H*P_last + F) .* P_last);
    % we needed the max function to ensure that no
    population will go below 0 at any time
    P = [P P_n]; % append the result to matrix storing
    our results
end

% plot results against time
% prey in green
plot((0:num_steps−1)/dt,P(1,:),'Color','g');
hold on;
% middle species in blue
```

```
plot((0:num_steps−1)/dt,P(2,:),'Color','b');
% top predator in red
plot((0:num_steps−1)/dt,P(3,:),'Color','r');
```

Running this code gives the following graph, which indicates how the populations of the species fluctuate for the constants we have provided.
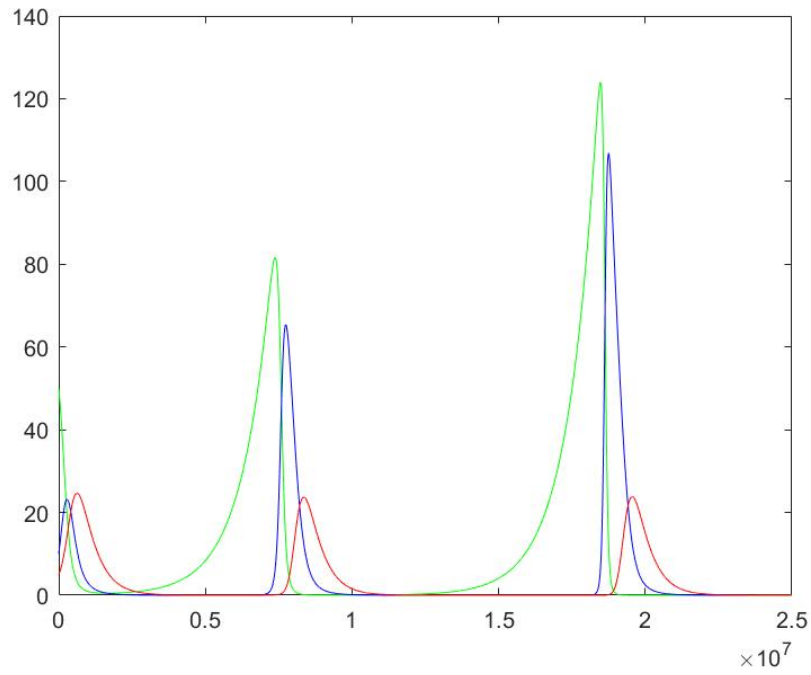

Figure 1: Populations over time

8   References

[1] Chauvet, Erica, Joseph E. Paullet, Joseph P. Previte, and Zac Walls. "A Lotka-Volterra Three-Species Food Chain." *Mathematics Magazine* 75.4 (2002): 243-55. *Departamento De Ingeniera De Sistemas E Industrial.* Universidad Nacional De Columbia. Web. 14 Feb. 2016.