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Some Extensions to Classic Lotka-Volterra Modeling For Predator Prey Applications

Migdat I. Hodzic

FENS, International University of Sarajevo, Sarajevo, Bosnia and Herzegovina
School Of Engineering, Santa Clara University, Santa Clara, USA
mhdzic@ius.edu.ba, mhdzic@scu.edu

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Abstract

In this paper we present some specific cases of the classic Nonlinear Lotka-Volterra (NLV) approach to modeling predator-prey dynamic systems [1,5], and propose to implement them using "mathematical" (Matlab) approach as well as "ad-hoc" approach using Agent Based Modeling (implemented using NetLogo modeling environment), [6]. Examples of various scenarios are introduced in a gradual way, from simpler to more complex ones. The emphasis is given to gaining insight into predator-prey relationship, as well as some structural results [2,3] as applied to classic complex systems modeling and control, as well as understanding stability in multispecies communities. The paper sets the scene for further research using NLV (mathematical) and ABM (ad-hoc) models. With this "parallel" approach we hope to address some classic problems such as Gause's Law and Paradox of the Plankton, Paradox of Enrichment (system level instability), Oksanen's description and trophic level numbers, and other current Complex Systems paradigms such as adaptivity, emergence, etc..

1. LINEARIZED NONLINEAR MODEL

As it is typically done, NLV as any other well-behaved nonlinear system can be linearized around equilibrium points X^* , and this approach works well close to equilibrium points. Also, there are well known stability results for linear complex systems [1,4]. Unfortunately, linearization may be very restrictive and limited in its usefulness, hence analysis of nonlinear predator-prey systems will produce more realistic results. We propose here a step-by-step build-up of nonlinear models which will allow us to better understand effects of nonlinearities and interconnections in multi species environments.

2. HUMAN CHROMOSOME KARYOTYPING

General nonlinear model in the context of our problem of interest is described by [1]:

$$S: \frac{dX}{dt} = A(t,X) X$$

where X is vector of (for example aquatic) species. X may be as simple as a two dimensional vector (one prey, one predator). $A(t,X)$ is "community" matrix with its elements as nonlinear time-dependent functions $a_{ij}=a_{ij}(t,X)$, where "ij" indicates position in the matrix, i for the rows, j for the columns. In the case of X of dimension 2, matrix A is 2 by 2, and its elements are a_{11} , a_{12} , a_{21} , and a_{22} , and they describe self and cross interactions among the two species.

3. NONLINEAR LOTKA-VOLTERRA MODEL

Nonlinear Lotka-Volterra Model (NLV) is a special case of the above more general nonlinear model [1]. In our further examples we will go beyond simple one prey-one predator model, with NLV and also use Agent Based Modeling (ABM) as well, as a validation tool. The key is that we will be able to use existing rigorous stability results using NLV [1] and compare with ABM (ad-hoc) results, as we gradually increase the complexity of the models. As a starting point we can consider one prey and one predator model which is typically described by simple Lotka-Volterra equations [1]:

Model #1

$$dX_i/dt = X_i (A_i + \sum A_{ij} X_j)$$

where $i=1,2$ and j is different than i , with $j=1,2$.

The above equation captures two equations:

$$\begin{aligned} dX_1/dt &= X_1 (A_1 + A_{12} X_2) \\ dX_2/dt &= X_2 (A_2 + A_{21} X_1) \end{aligned}$$

or in terms of the general nonlinear model:

$$dX/dt = A(t,X) X$$

where there is no time dependency and the (community) matrix A is

$$A(t,X) = A = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix}$$

with $a_{11} = A_1$, $a_{12} = A_{12} X_1$, $a_{21} = A_{21} X_2$, and $a_{22} = A_2$, with A_{12} and A_{21} being negative coefficients indicating reduction in the prey as result of predator presence [1]. The species vector is $X = [X_1, X_2]$.

Model #2

The next example is to include an additional term in NLV which corresponds to "crowding" species dynamic when disconnected from the other specie(s). The extended NLV is as follows:

$$dX_i/dt = X_i (A_i + \sum A_{ij} X_j),$$

where $i = 1,2$ and sum \sum is over $j = 1,2$.

This would be equivalent to adding another "crowding" term (self multiplication without predator) in dX_i/dt . In this case community matrix elements are:

$$A = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix}$$

with $a_{11} = A_1 + A_{11}X_1$, $a_{12} = A_{12} X_1$, $a_{21} = A_{21} X_2$, and $a_{22} = A_2 + A_{22}X_2$, and $X = [X_1, X_2]$.

As before, A_{12} and A_{21} are negative and newly introduced A_{11} and A_{22} are positive coefficients.

For example, when using ABM approach, there will be a (programming) facility to implement for the "crowding" effect in prey.

Model #3

Next step is to make community matrix elements time varying as well as dependent on the species population, i.e.

$$dX_i/dt = X_i (A_i(t,X) + \sum A_{ij}(t,X) X_j)$$

where $i=1,2$ and sum \sum is over $j=1,2$, or in compact form

$$\begin{aligned} dX/dt &= A(t,X) X, \text{ with} \\ A = A(t,X) &= \begin{bmatrix} a_{11}(t,X) & a_{12}(t,X) \\ a_{21}(t,X) & a_{22}(t,X) \end{bmatrix} \end{aligned}$$

with $a_{11}(t,X) = A_1(t,X) + A_{11}(t,X) X_1$, $a_{12}(t,X) = A_{12}(t,X) X_1$, $a_{21}(t,X) = A_{21}(t,X) X_2$, and $a_{22}(t,X) = A_2(t,X) + A_{22}(t,X) X_2$, and $X = [X_1, X_2]$. Note that community matrix elements are functions of the overall vector X , i.e. both X_1 and X_2 . This will give us lots of freedom in modeling dynamic of two interconnected species. The modeling should be done in individual steps so we can have full understanding of the consequences of making even the simplest change. For example, here are several examples for both ABM and NLV approaches to compare:

Example 1: Coefficients only functions of time and not of X

$$\begin{aligned} a_{11}(t) &= A_1(t) + A_{11}(t) X_1 \\ a_{12}(t) &= A_{12}(t) X_1 \\ a_{21}(t) &= A_{21}(t) X_2 \\ a_{22}(t) &= A_2(t) + A_{22}(t) X_2 \end{aligned}$$

Example 2: Coefficients only functions of X and not of time

$$\begin{aligned} a_{11}(X) &= A_1(X) + A_{11}(X) X_1 \\ a_{12}(X) &= A_{12}(X) X_1 \\ a_{21}(X) &= A_{21}(X) X_2 \\ a_{22}(X) &= A_2(X) + A_{22}(X) X_2 \end{aligned}$$

Example 3: Coefficients only functions of X_1 and/or X_2 and not of time

$$\begin{aligned} a_{11}(X_1) &= A_1(X_1) + A_{11}(X_1) X_1 \\ a_{12}(X_2) &= A_{12}(X_2) X_1 \\ a_{21}(X_1) &= A_{21}(X_1) X_2 \\ a_{22}(X_2) &= A_2(X_2) + A_{22}(X_2) X_2 \end{aligned}$$

where we assumed local dependencies only (for example $a_{11}(X_1)$ is function of X_1 and not of X_2 , etc. Obviously we can have more complicated case such as:

Example 4: Coefficients only functions of X_1 and/or X_2 and not of time

$$\begin{aligned} a_{11}(X_1) &= A_1(X_1, X_2) + A_{11}(X_1) X_1 \\ a_{12}(X_2) &= A_{12}(X_2) X_1 \\ a_{21}(X_1) &= A_{21}(X_1) X_2 \\ a_{22}(X_2) &= A_2(X_1, X_2) + A_{22}(X_2) X_2 \end{aligned}$$

where we left "crowding" coefficients functions of only of their corresponding species.

Finally, we introduce time and have the following time varying version of Example 4:

Example 5: Coefficients functions time as well as of X_1 and/or X_2 :

$$\begin{aligned} a_{11}(t, X_1) &= A_1(t, X_1, X_2) + A_{11}(t, X_1) X_1 \\ a_{12}(t, X_2) &= A_{12}(t, X_2) X_1 \\ a_{21}(t, X_1) &= A_{21}(t, X_1) X_2 \\ a_{22}(t, X_2) &= A_2(t, X_1, X_2) + A_{22}(t, X_2) X_2 \end{aligned}$$

Comment: As we develop more complicated NLV and ABM, our approach here is to follow the above formulas in implementing NLV (Matlab) and ABM (NetLogo) to implement corresponding features into both models. This way we will be able to carefully and precisely interpret every step of the ever increasing complexity of the two models. For example, if we take Example 5 from the above, we would agree on what does "A12(t,X2)" mean in terms of dependency on X_2 , and so on, similarly for other coefficients.

Model #4

Next, we extend the NLV towards general nonlinear model to include multiple species, such as:

$$dX_i/dt = X_i [A_i(t, X) + \sum A_{ij}(t, X) X_j]$$

where $i = 1, 2, \dots, n$, and sum \sum is over all $j = 1, 2, \dots, n$.

We can start our investigation by going from one prey and one predator (as in simpler examples earlier), to two preys and one predator, 4 preys and 2 predators (2 predators per each 2 preys), etc., hence building up the complexity of the models (both NLV and ABM). Here are some specific examples, where we simply continued from Example 5 above and increased the number of species. This method may be influenced by a specific multispecies situation, such as an aquatic fish environment with a variety of preys and predators involved.

The following Example 6 models two preys and one predator.

Example 6: Two preys and one predator, coefficients functions time as well as of X_1 and/or X_2 and/or X_3 or the total vector X :

$$\begin{aligned} a_{11}(t, X) &= A_1(t, X) + A_{11}(t, X_1) X_1 \\ a_{12}(t, X_2) &= A_{12}(t, X_2) X_1 \\ a_{13}(t, X_3) &= A_{13}(t, X_3) X_1 \end{aligned}$$

$$\begin{aligned} a_{21}(t, X_1) &= A_{21}(t, X_1) X_2 \\ a_{22}(t, X) &= A_2(t, X) + A_{22}(t, X_2) X_2 \\ a_{23}(t, X_3) &= A_{23}(t, X_3) X_2 \end{aligned}$$

$$\begin{aligned} a_{31}(t, X_1) &= A_{31}(t, X_1) X_3 \\ a_{32}(t, X_2) &= A_{32}(t, X_2) X_3 \\ a_{33}(t, X) &= A_3(t, X) + A_{33}(t, X_3) X_3 \end{aligned}$$

where 3rd species is predator. In compact form, community matrix can now be represented as:

$$A(t, X) = \begin{bmatrix} a_{11}(t, X) & a_{12}(t, X_2) & a_{13}(t, X_3) \\ a_{21}(t, X_1) & a_{22}(t, X) & a_{23}(t, X_3) \\ a_{31}(t, X_1) & a_{32}(t, X_2) & a_{33}(t, X) \end{bmatrix}$$

Example 7: Four preys (species 1, 2, 4, 5) and two predators (species 3,6), one predator per two preys, for simplicity, and coefficients functions of time as well as of X_i or the total vector X :

$$\begin{aligned} a_{11}(t, X) &= A_1(t, X) + A_{11}(t, X_1) X_1 \\ a_{12}(t, X_2) &= A_{12}(t, X_2) X_1 \\ a_{13}(t, X_3) &= A_{13}(t, X_3) X_1 \\ a_{14}(t, X_4) &= A_{14}(t, X_4) X_1 = 0 \\ a_{15}(t, X_5) &= A_{15}(t, X_5) X_1 = 0 \\ a_{16}(t, X_6) &= A_{16}(t, X_6) X_1 = 0 \end{aligned}$$

$$\begin{aligned} a_{21}(t, X_1) &= A_{21}(t, X_1) X_2 \\ a_{22}(t, X) &= A_2(t, X) + A_{22}(t, X_2) X_2 \\ a_{23}(t, X_3) &= A_{23}(t, X_3) X_2 \\ a_{24}(t, X_4) &= A_{24}(t, X_4) X_2 = 0 \\ a_{25}(t, X_5) &= A_{25}(t, X_5) X_2 = 0 \\ a_{26}(t, X_6) &= A_{26}(t, X_6) X_2 = 0 \end{aligned}$$

$$\begin{aligned} a_{31}(t, X_1) &= A_{31}(t, X_1) X_3 \\ a_{32}(t, X_2) &= A_{32}(t, X_2) X_3 \\ a_{33}(t, X) &= A_3(t, X) + A_{33}(t, X_3) X_3 \\ a_{34}(t, X_4) &= A_{34}(t, X_4) X_3 = 0 \\ a_{35}(t, X_5) &= A_{35}(t, X_5) X_3 = 0 \\ a_{36}(t, X_6) &= A_{36}(t, X_6) X_3 = 0 \end{aligned}$$

$$\begin{aligned} a_{41}(t, X_1) &= A_{41}(t, X_1) X_4 = 0 \\ a_{42}(t, X_2) &= A_{42}(t, X_2) X_4 = 0 \\ a_{43}(t, X_3) &= A_{43}(t, X_3) X_4 = 0 \\ a_{44}(t, X) &= A_4(t, X) + A_{44}(t, X_4) X_4 \\ a_{45}(t, X_5) &= A_{45}(t, X_5) X_4 \\ a_{46}(t, X_6) &= A_{46}(t, X_6) X_4 \end{aligned}$$

$$\begin{aligned} a_{51}(t, X_1) &= A_{51}(t, X_1) X_5 = 0 \\ a_{52}(t, X_2) &= A_{52}(t, X_2) X_5 = 0 \\ a_{53}(t, X_3) &= A_{53}(t, X_3) X_5 = 0 \\ a_{54}(t, X_4) &= A_{54}(t, X_4) \\ a_{55}(t, X_5) &= A_5(t, X) + A_{55}(t, X_5) X_5 \\ a_{56}(t, X_6) &= A_{56}(t, X_6) X_5 \end{aligned}$$

$$\begin{aligned} a_{61}(t, X_1) &= A_{61}(t, X_1) X_6 = 0 \\ a_{62}(t, X_2) &= A_{62}(t, X_2) X_6 = 0 \\ a_{63}(t, X_3) &= A_{63}(t, X_3) X_6 = 0 \end{aligned}$$

$$\begin{aligned} a_{64}(t, X_4) &= A_{64}(t, X_4) X_6 \\ a_{65}(t, X_5) &= A_{65}(t, X_5) X_6 \\ a_{66}(t, X) &= A_6(t, X) + A_{66}(t, X_6) X_6 \end{aligned}$$

and community matrix $A(t, X)$ is now 6x6:

$$\begin{matrix} a_{11} & a_{12} & a_{13} & 0 & 0 & 0 \\ a_{21} & a_{22} & a_{23} & 0 & 0 & 0 \\ a_{31} & a_{32} & a_{33} & 0 & 0 & 0 \\ 0 & 0 & 0 & a_{44} & a_{45} & a_{46} \\ 0 & 0 & 0 & a_{54} & a_{55} & a_{56} \\ 0 & 0 & 0 & a_{64} & a_{65} & a_{66} \end{matrix}$$

where we dropped various parameters in the coefficients for simplicity. Any of the zero coefficients a_{ij} indicates lack of influence of j -th specie to i -th specie, or that a predator j does not prey on i -th specie. This example illustrates how we can build various species communities, by combining number of preys and predators. A slight variation can be done in the Example 7 by assuming that predators can prey on all of the species, but not on each other, hence producing Example 8 which follows.

Example 8. Community matrix $A(t, X)$ is still 6x6, with less 0 elements:

$$\begin{matrix} a_{11} & a_{12} & a_{13} & 0 & 0 & a_{16} \\ a_{21} & a_{22} & a_{23} & 0 & 0 & a_{26} \\ a_{31} & a_{32} & a_{33} & 0 & 0 & 0 \\ 0 & 0 & a_{43} & a_{44} & a_{45} & a_{46} \\ 0 & 0 & a_{53} & a_{54} & a_{55} & a_{56} \\ 0 & 0 & 0 & a_{64} & a_{65} & a_{66} \end{matrix}$$

If predators can prey on each other, then we have Example 9:

Example 9. Community matrix $A(t, X)$ is still 6x6, with even less 0 elements:

$$\begin{matrix} a_{11} & a_{12} & a_{13} & 0 & 0 & a_{16} \\ a_{21} & a_{22} & a_{23} & 0 & 0 & a_{26} \\ a_{31} & a_{32} & a_{33} & 0 & 0 & a_{36} \\ 0 & 0 & a_{43} & a_{44} & a_{45} & a_{46} \\ 0 & 0 & a_{53} & a_{54} & a_{55} & a_{56} \\ 0 & 0 & a_{63} & a_{64} & a_{65} & a_{66} \end{matrix}$$

Model #5

Finally we add environmental effects [1] into NLM by:

$$S: \quad dX/dt = A(t, X) X + B(t, X)$$

where $B(t, X)$ models external effects of the environment (food, space, temperature, etc.). Following previous examples, we can introduce environment into each of them. For example, let us look at Example 6, and add environmental vector $B(t, X)$.

Example 10. Based on Example 6, we obtain community matrix as:

$$A(t, X) = \begin{bmatrix} a_{11}(t, X) & a_{12}(t, X_2) & a_{13}(t, X_3) \\ a_{21}(t, X_1) & a_{22}(t, X) & a_{23}(t, X_3) \\ a_{31}(t, X_1) & a_{32}(t, X_2) & a_{33}(t, X) \end{bmatrix}$$

with species vector

$$X = [X_1, X_2, X_3]^T$$

and corresponding environmental vector

$$B(t, X) = [B_1(t, X), B_2(t, X), B_3(t, X)]^T$$

or even simpler case, where each environmental component depends only on individual specie, i.e.

$$B(t, X) = [B_1(t, X_1), B_2(t, X_2), B_3(t, X_3)]^T$$

Comment: As the community matrices become larger and more complex, we note that there are certain structural properties in the way "0" elements are distributed. This is calling for certain approaches described in [2,3,4] which take advantage of these special structures to simplify calculations and expose key structural properties of the underlying models. For example, there are elements of "overlapping" components in community matrices, which can be "expanded and contracted" [3,4] in building effective and simpler control schemes for multispecies communities. Similarly, as the number of species grow and community matrices become very large, simple shuffling of the position of species in the vector X may produce hierarchical structure of community matrix A [2] hence lending itself to much simpler (computationally) control schemes, as well as simpler stability analysis whereas the overall community matrix can be split into subsystems (agents) interconnected in a hierarchical manner. These are all topics for further research.

4. EXPECTED RESULTS

Our proposed approach in this paper, a step by step approach, using NLV (implemented in Matlab using the above equations), and in parallel, using an ad-hoc ABM (implemented in NetLogo) can accomplish several things:

(i) Two models will be built step-by-step, and that will make it easier to understand various species interconnection effects. For example as we build ABM using NetLogo, we will be able to separate very specific effects (per above examples) to very specific agent's characteristics, interactions, etc., as we would do the same in terms of NLV. This seems to be an exceptionally strong proposition and robust method to gain insight into real multispecies communities where a number of prey and predator species exist and compete for the resources, and try to survive and multiply.

(ii) This (parallel) approach adds to the overall rigorousness of the obtained results and their validation and interpretations, by meticulously checking and comparing results of ABM and NLV as more and more complex models are built.

(iii) Somewhere along the way, as we make the models more and more complex, we expect an emergence of some indications which would help understand such properties as Gause's Law and Paradox of the Plankton, Paradox of Enrichment (system level instability), Oksanen's description and trophic level numbers, and maybe more than that. This "emergence" would be via our ability to rigorously address stability of these multi-species models and their interactions in the context of our understanding of concepts of "complexity" and "stability", and their relation in multispecies environments.

5. STABILITY CONSIDERATIONS

There are some key existing mathematical results related to NLV which can be used and which can accommodate multi-species modeling and stability in particular [1]. They give regions of stability estimates and point to specific reasons for instability and balance between stability and complexity. These regions can be tested using both NLV and ABM approaches which will add a measure of confidence and practicality to the stability results. As several ecology researchers (not mathematicians) pointed out in literature, there seems to be a balance in competing multi-species environments between number of interconnections among the species versus interconnection strengths. Our (obvious) mathematical conjecture is as follows:

If we denote by N number of interconnections for a given species (in a multi species environment) and by S their intensity, then:

$$N \text{ times } S = \text{Constant}$$

where equality sign is just an approximation and measure of closeness of two sides of the expression. Or we could rephrase this intuitive notion and add stochastic measure by using Expected Value $E(\)$ as:

$$N \text{ times } E(S) = E(\text{Unknown Constant})$$

where averaging may be over time, space, or some combination of the two.

Our expectation is that we will come to this conclusion mathematically and using simulations via NLV and via ABM in parallel (as they reinforce and validate each other).

6. CONCLUSION

In this paper we aim to set the scene for a robust and effective, model based (NLV plus AMB) approach to build simple-to-complex predator-prey examples, which will lead us to explain and better understand various classic notions in multi-species models, such as Paradox of the Plankton. Other classic Complex Systems notions of emergence, adaptivity, and so on, may also be tackled and explained using proposed methodology of step-by-step model build-up and reinforcement using two very different

approaches, i.e. mathematical NLV and ad-hoc ABM. In the research which follows, we will explore specific examples from this paper using Matlab and NetLogo modeling and tools and report the results in subsequent papers.

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