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Complex Ecological System Modeling

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Abstract

In this paper we extend our previous results in dual approach to analysis and simulation of a complex ecological system of preys and predators. We first define nonlinear dynamic equations Lotka-Volterra Model (LVM) with three preys and three predators and then simulate the equivalent situation with an Agent Based Model (ABM) which models a variety of species attributes and behaviors using NetLogo simulation environment for ABM model. The idea is that the LVM and ABM methods reinforce each other as the predator-prey models become more complex and their dimensionality rises. In particular LVM's parameters, components of community matrix, can be fine tuned using ABM simulations. Dual approach may be able to answer and qualify some of the long standing ecological paradoxes.

1. INTRODUCTION

In analysis and simulation of complex ecological systems, we often start with a nonlinear Lotka Volterra Model (LVM) of predator-prey dynamic system [1, 2]. The problem with this approach is that the LVM is very simplified model and apart from a detailed stability analysis [2], there are no real life complex ecological dynamic system models which are flexible and useful enough. Some of the reasons are (i) Lack of any general model build up methodology, (ii) Lack of any structural analysis of complex dynamical ecological models, and (iii) Very few results explaining some well know ecological paradoxes. In our earlier paper [1] very simple single prey and single predator system was modeled and analyzed by using both LVM and ABM. In this paper we extend the results in [1] and define two main paper goals:

(i) Define mathematical details of a dynamic system with three aquatic predators and three prays (3+3 model) using a notion of community matrix and classic Lotka-Volterra predator-prey nonlinear model. This serves as a mathematical background which will be used in later research to reconcile two models, LVM and ABM, with the idea that two models reinforce each other. In particular we plan to use ABM to fine tune LVM and community matrix parameters which is at its heart.

(ii) Next we simulate ABM 3+3 model using NetLogo simulation tool where we can define ABM parameters, in particular related to various properties of preys and predators. These properties include their total numbers, consumption rates, how they are "born" and how they "die" in simulation cases, and several other tuning "knobs" allowed by NetLogo environment.

The results of this paper can be extended to higher number of species as well. Our goal is also to gain further insight into predator-prey population dynamics, structural properties of the models, understanding of stability in multispecies communities, and improve rigor, usability, robustness and adaptivity of both LVM and ABM models. We believe that the dual approach can bring about very usable but complex predator-prey ecological models which are also mathematically tractable.

2. SINGLE PREY SINGLE PREDATOR MODELS

General ecological nonlinear model is described by [2]:

$$S:\ dX/dt = A(t,X)\,X \qquad (1)$$

where X is a species vector. The model has an appearance of a linear system. The vector X may be a 2-dimensional vector, i.e. one pray, one predator [1], or it could consist of many more species arranged in tropical levels of preys and predators. Matrix A(t,X) is a "community" matrix with nonlinear elements, time-dependent functions $a_{ij}=a_{ij}(t,X)$, where "ij" indicates position in the matrix. In 2-dimesional X, matrix A is 2 by 2, with the elements a_{11}, a_{12}, a_{21}, and a_{22}, which describe self and cross interactions among the two species. A special case of (1) is well known nonlinear Lotka-Volterra Model (LVM). For purposes of this paper, we review briefly what was covered in [1] for Single Prey Single Predator (SPSP) model.

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2.1 LVM Basic Mathematics

Let us assume $X = [X_1, X_2]^T$, X_1 is prey species, X_2 is predator species. The classic LVM [2] is:

$$dX_1/dt = X_1 (A_1 + A_{12} X_2) = A_1X_1 + A_{12}X_2X_1$$
$$dX_2/dt = X_2 (A_2 + A_{21} X_1) = A_2X_2 + A_{21}X_1X_2 \quad (2)$$

which can also be written in a compact form as:

$$dX_i/dt = X_i (A_i + A_{ij} X_j) \quad (3)$$

where i,j=1,2 and i≠j, A_1 is the growth rate of the prey. With $A_{12} = 0$ (no predator X_2) the prey population X_1 increases exponentially,. With $A_{12} < 0$, predator X_2 controls prey population from growing exponentially. For the predator population, growth is dependent on $A_2 < 0$, the rate of predator removal from the system (death or migration), and A_{21}, the positive growth rate for predators. The solution to Equations 2 and 3 is periodic, with the predator population always following the prey. Figure 1 gives an example with constant values of positive coefficients A_1 and A_{21}, and negative growth rates A_{12} and A_2. The other SPSP models can be defined, such as positive A_2 and negative A_{21} for the predator, depending on the model. The interest is to keep the basic model stable. General LVM stability results are given in [2].

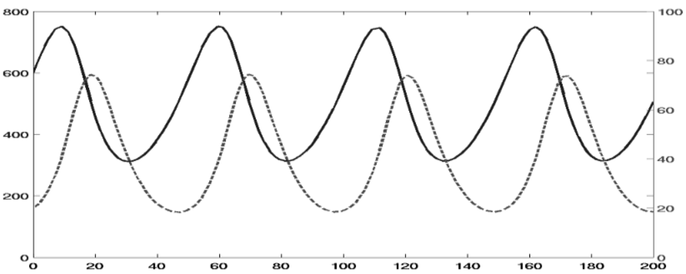


Figure 1. SPSP LVM Population Levels (Prey Solid, Predator Dashed)

In terms of (1) and, the community matrix A is:

A(X) = (4)

$a_{11}(X)$	$a_{12}(X)$
$a_{21}(X)$	$a_{22}(X)$

with:

$$a_{11} = A_1, a_{12} = A_{12} X_1, a_{21} = A_{21} X_2, a_{22} = A_2 \quad (5)$$

The LVM can be extended to incorporate crowding effect:

$$dX_i/dt = X_i (A_i + \sum A_{ij} X_j) \quad (6)$$

where i = 1,2 and sum is over j = 1,2. This would be equivalent to prey self multiplication without predator. In this case community matrix elements are:

$$a_{11}=A_1+A_{11}X_1,\ a_{12}=A_{12} X_1,\ a_{21}=A_{21} X_2,\ a_{22}=A_2+A_{22}X_2 \quad (7)$$

In this model, A_{12} and A_{21} are negative, with positive A_{11} and A_{22}. Next LVM feature could be time varying community matrix:

$$dX_i/dt = X_i [A_i(t,X) + \sum A_{ij}(t,X) X_j] \quad (8)$$

or in compact form:

$$dX/dt = A(t,X) X \quad (9)$$

with:

A(t,X) = (10)

$a_{11}(t,X)$	$a_{12}(t,X)$
$a_{21}(t,X)$	$a_{22}(t,X)$

For example:

$$a_{11}(t,X) = A_1(t,X) + A_{11}(t,X) X_1 \quad (11)$$

and similarly for the rest of the coefficients in (10). We can also add environmental effects [2] into LVM by:

$$S: \quad dX/dt = A(t,X) X + B(t,X) \quad (12)$$

where B(t,X) models external environmental effects (food, space, temperature), and it can be considered as a model control vector. More details can be found in [1],[2].

2.2 ABM and LVM Combined

The Equations 2 and 3 present a very simple ecological model, where unlimited food available to the prey is assumed, and so the prey (and predator) growth rates are limited by corresponding "growth" coefficients. The prey growth coefficient is A_1 and A_{21} for the predator. On the other hand, in ABM, the growth rate for both populations can be determined by how successful they are at finding food. This can be modeled as a stochastic process which averages out to a stable rate across populations, hence corresponding practically to LVM model, in the limit. Various effects/ model attributes can be incorporated in ABM. As an example, the predators disappear from the simulation at a constant rate by reaching the end of their programmed lifetime. This parallels negative A_2 in LVM. The predator population increases linearly based on the prey consumption. This is proportional to the number of both populations, and thus represented by $A_{21}X_1X_2$ in LVM. Within the ABM various LVM features can be accommodated by simply adding new features into the ABM. Hence LVM coefficients can be estimated using ABM simulations. Figure 2 gives a typical agent based snapshot of NetLogo simulation control window. Let us also note that the initial ABM is not intended to include all the properties of an existent ecosystem, but rather to indicate the most fundamental properties of the predator–prey relationship as a general model. For example, the environment is assumed homogeneous with no variations in sea temperature, depth, or ocean currents. This can be changed as more complex models are developed. One of the ABM parameters is the amount of food available to prey and predator. This corresponds to B(t,X) in LVM given by (12). When the food is increased initially, both A_1 and A_{21}, increase initially. In the steady state, the prey growth rate A_1 remains constant with their population growth offset by increased predator population.

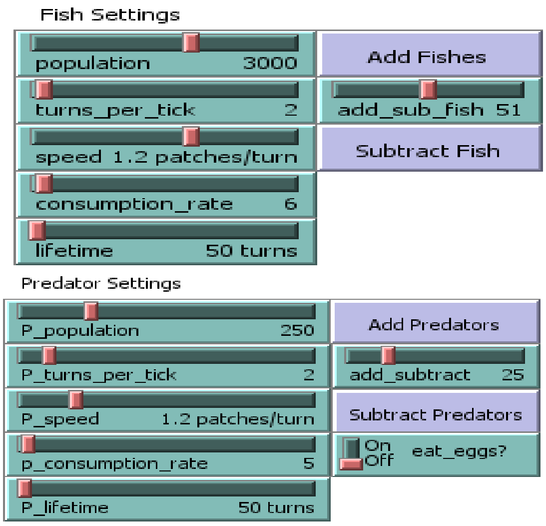


Figure 2. Typical NetLogo ABM simulation control

The rate of predator removal A_2, by death or migration, is determined by the predator ABM attribute age and a limited lifetime for each individual. The prey also has an attribute for age, but in practice, very few fish die of old age. This is particularly true at higher levels of resources, because their average age drops as a consequence of fish being born faster while their population remains stable. It is this last fact that may cause the system instability, at very high levels of resources. Analytical LVM stability results are discussed in details in [2]. In [1] we described one specific ABM SPSP in details.

Per Figure 2, ABM gives lots of flexibility to model the system, but essentially gives no analytical insight and the solution such as the case with LVM. That is the essence of our dual approach here, i.e.

(i) Use ABM for its flexibility and intuitiveness, and

(ii) LVM for its mathematical elegance and rigor.

This way we can use ABM to improve LVM, and vice versa as complexity of the model increases. As we develop more complex predator-prey models, the approach is to rely on the LVM formulas and feature based ABM to reiterate each other findings. This will require a very disciplined research work, so we will be able to precisely interpret every step of the two models.

3. MULTIPLE PREY-PREDATOR MODEL

As described in details in [1], Multiple Prey Multiple Predator (MPMP) model is described in LVM by:

$$dX_i/dt = X_i \, [\, A_i(t,X) + \sum A_{ij}(t,X) \, X_j \,] \qquad (13)$$

where $i = 1,2, \ldots, n$, and sum $\sum$ is over $j = 1,2, \ldots, n$. We can model 2 preys 1 predator, 4 preys 2 predators, 10 preys 3 predators, etc., hence building up complexity of the LVM's. Some examples of (6x6) community matrix are repeated here from [1] as references. More details are given in a specific example of Section 4 where we model 3+3 scenario, i.e. three preys and three predators.

(i) Four preys (species 1,2,4,5) and two predators (3,6) produce the following (6x6) community matrix:

A(t,X) = (14)

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}

which consists of two decoupled predator-prey systems. Any of the zero coefficients a_{ij} indicates lack of influence of j-th specie to i-th specie. This type of model is advantageous due to decoupling which simplifies any species estimation and control algorithms [2].

(ii) Assuming that predators can prey on all of the species, but not on each other, we have:

A(t,X) = (15)

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}

(iii) If predators prey on each other, then we have:

A(t,X) = (16)

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}

(iv) Two almost decoupled specie communities share a common four (**boldfaced**) elements:

A(t,X) = (17)

a_{11}	a_{12}	a_{13}	0	0	0
a_{21}	a_{22}	a_{23}	0	0	0
a_{31}	a_{32}	$\mathbf{a_{33}}$	$\mathbf{a_{34}}$	0	0
0	0	$\mathbf{a_{43}}$	$\mathbf{a_{44}}$	a_{45}	a_{46}
0	0	0	a_{54}	a_{55}	a_{56}
0	0	0	a_{64}	a_{65}	a_{66}

Any estimation and control for this model can be handled by an approach in [6], where the model is "expanded" into a larger species vector space to decouple it effectively. Note that the shape of the community matrix will also depend on how the prey and predators are ordered in the species vector X. As the community matrices become larger, we note that there are certain structural properties in the way "0" elements are placed. This is calling for "structural" approaches described in [3,5,6] which take advantage of special structure of system matrices to (i) simplify calculations and (ii) expose key structural properties of the models. As the number of species grow, smart shuffling of the position of species in the vector X may produce hierarchical (or almost hierarchical) structure of community matrix A(t,X) [5], producing much simpler controls and stability analysis, as the overall community matrix is split into subsystems hierarchically interconnected. We will address estimation and control aspect of ecological system models in future research.

4. THREE PREYS THREE PREDATORS MODEL

Before we illustrate one specific 3+3 example, few comments are in order related to general model assumptions.

4.1 General Assumptions

The ABM is not intended to include all the properties of an existent ecosystem, but rather to expose the most fundamental properties of the predator–prey-resource relationship as a general model. As such, the environment is largely homogeneous: that is, there are no variations in sea temperature, depth, or ocean currents. Furthermore, each tropic level is represented by a single species. Important refinements such as species growth over time, variable predation strategies, environmental heterogeneities and dynamics, more complex food web networks, and different functional responses can be selectively added to future models in an iterative process to ensure that one understands the basic dynamics at each level before proceeding to the next level of complexity.

Other simplifying assumptions include: all species are of the same size, produce the same amount of resources when consumed, and share the same set of simple strategic rules. For the fish these rules are: if there is one or more predators on the current patch, pick one and move in the opposite direction; if no predators are present and there is food on the current patch, eat one unit; otherwise, move randomly. For the predators the rules are: if there is one or more fish on the current patch, eat one. After eating (or not, if no fish are present), move randomly.

The fishes and predators all have a limited lifetime. Also, the patches grow food (resources for the fish) stochastically, based on an operator controlled setting that defines the percentage chance of growth for each individual patch. Food is simulated as units per patch, from zero (no food) to a maximum, such that if food is present a fish can eat one unit per turn. Specifically, a 0.20 food growth rate translates into a 20% chance for each patch to add one unit of food, during each simulation time step. Aggregated across the 22,801 patches in the simulation, this rate becomes a linear, but still stochastic, rate of growth for food. In all experiments reported here the maximum number of food units per patch is set to ten.

The population of fish eggs is included to provide another step towards a more realistic simulation; however, all major results listed here exhibit LV like oscillations. The majority of experiments are run with a baseline model from which any experimental deviations are made. As with classic LV oscillations of Figure 1, ABM models are inherently volatile where certain parameter settings can be adjusted to emphasize or de-emphasize certain system behavior and produce a desirable system from which to experiment. This allows us to compare results under the following settings to produce desired scenarios, such as:

(i) Stable model
(ii) Oscillating-but stable model
(iii) Unstable model

as well as expose which settings produce each.

4.2 LVM (3+3) Model Details

In this paper we focus on a specific 3+3 model with:

$$X = [X_1, X_2, X_3, X_4, X_5, X_6]^T \qquad (18)$$

where the first three vector components are preys and the last three are predators. We assume that each predator preys on each prey but not on each other. The preys are not affecting each other. The community matrix is then:

$A(t,X) =$ (19)

a_{11}	0	0	0	0	0
0	a_{22}	0	0	0	0
0	0	a_{33}	0	0	0
a_{41}	a_{42}	a_{43}	a_{44}	0	0
a_{51}	a_{51}	a_{53}	0	a_{55}	0
a_{61}	a_{62}	a_{63}	0	0	a_{66}

where the community matrix main diagonal coefficients are:

$$a_{ii}(t,X) = A_i(t,X_i) + A_{ii}(t,X_i)\, X_i\ , \ i=1,2,3,4,5,6 \qquad (20)$$

and off diagonal (lower left corner) coefficients are:

$$a_{ik}(t,X) = A_{ik}X_i \quad i=4,5,6 \ \text{and}\ k=1,2,3 \qquad (21)$$

Typically A_{ii} are positive (crowding effect), or it could be 0 for the predators X_4,X_5, and X_6. The A_{ik} are negative, and A_i could be positive or negative, depending on what we want to simulate. To illustrate the ABM model behavior, some initial values for various prey/predator parameters were chosen. In this example prey species are represented by three fish populations, i.e. X_1, X_2, and X_3. The predators are fish eating species (dolphins, sharks).

4.3 NetLogo ABM (3+3) Stable Model Simulation

To set the scene, we use NetLogo modeling and have Figure 3 which shows initial (left) and final (right) prey/predator distribution in a certain area after a number of simulation turns. The following Figures show more details for this generic oscillatory model between preys and predators. Figure 4 shows cumulative count of predators and prays (fish in this simulation) which exhibits general LVM type of equations oscillatory behavior (such as Figure 1) confirming LVM validity in general. Figure 5 shows more details on three types of predators, and similarly Figure 6 has the counts for three types of prays. They all indicate typical oscillatory behavior between number of preys and predators. This corresponds to community matrix in (19) which indicates how species interact in general. In Figure 7 we have an indication of number of fish eggs which "produce" fish in simulation, as well as number of fish and predators. Figure 8 summarizes predators elimination rate set by the ABM model. Finally, Figure 9 indicates preys consumption rate by predators. All of these parameters can be set in NetLogo ABM control window (Figure 2).

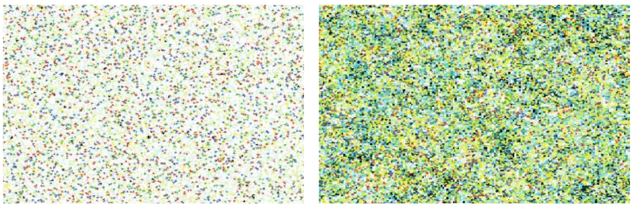


Figure 3. Initial and Final Prey/Predator Distribution

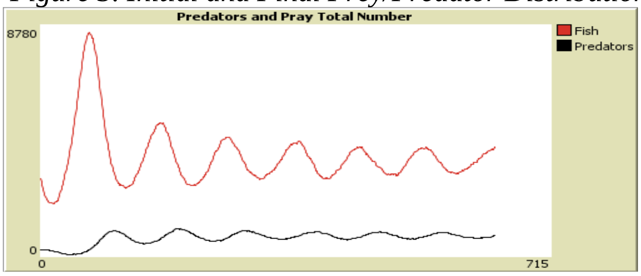


Figure 4. Total 3 predators and 3 preys count

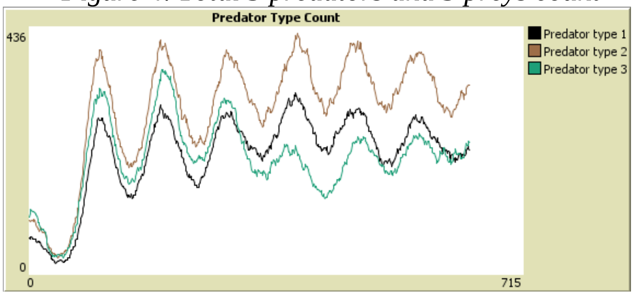


Figure 5. Detailed three predators count

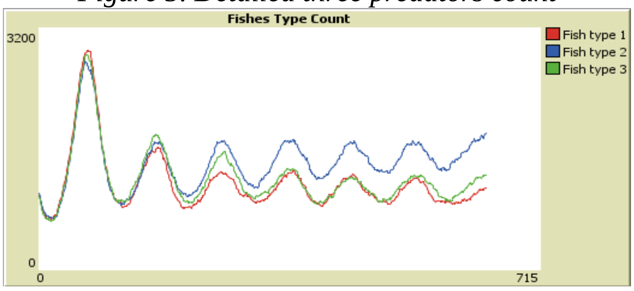


Figure 6. Detailed three preys count

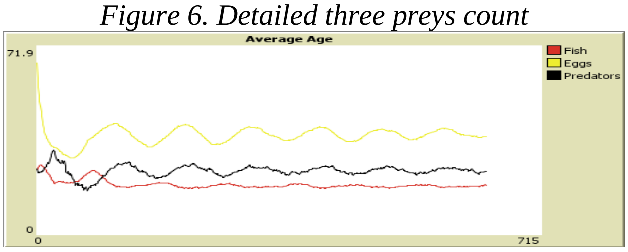


Figure 7. Eggs, fish and predator numbers

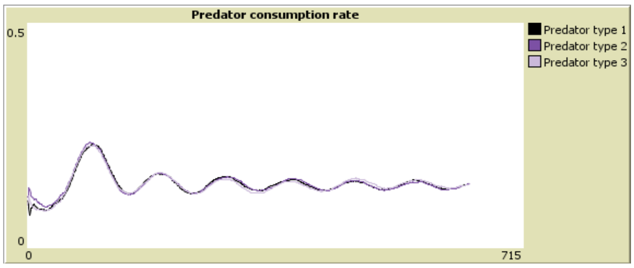


Figure 8. Predators eliminating rate

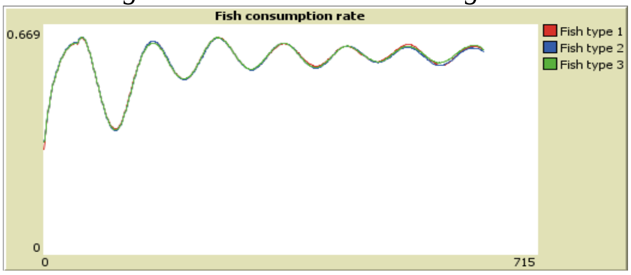


Figure 9. Preys consumption rate by predators

Next two Figures, 10 and 11, indicate parameters used to generate Figures 5-9 using NetLogo simulation control window. One can set many different parameters and create very complex ABM model. This is an advantage of ABM compared to simpler mathematical LVM. On the flip side, we have no essential insight into what is happening "inside" ABM, whereas we do with LVM. Their combination, our Dual Approach, may be a winning strategy in general. Figure 10 shows rate of food consumption by fish population, and Figure 11 rate of fish consumption by predators.

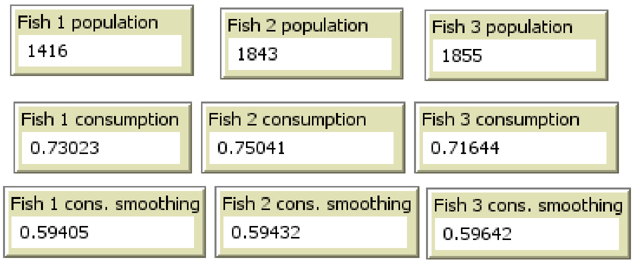


Figure 10. Rate of food consumption by fish population

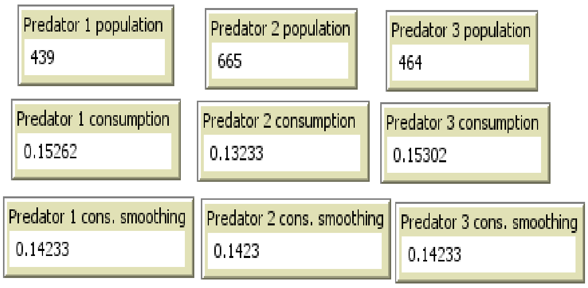


Figure 11. Rate of fish consumption by predators

4.4 NetLogo ABM (3+3) Unstable Model Simulation

One of the key features of predators-prey system is its stability properties. In the next set of Figures we have predator and prey numbers for an unstable system.

Example 1. In Figures 12 and 13 we have a summary of parameters used to generate unstable system of Figure 14. At first it appears as if the system is stable.

When we look into specific prey numbers shown in Figure 15, we see that one of the prey species indeed goes into instability, i.e. its numbers are rising steadily. One prey species is unstable and two are stable. That is hidden in Figure 14 which shows total prey and predator numbers.

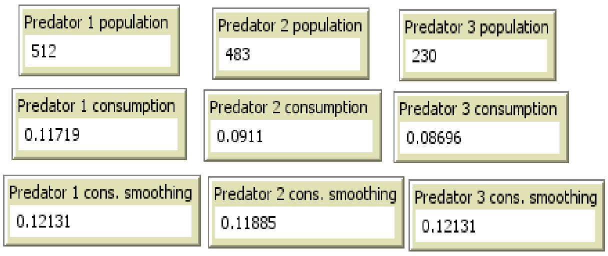


Figure 12. Unstable system predator parameters

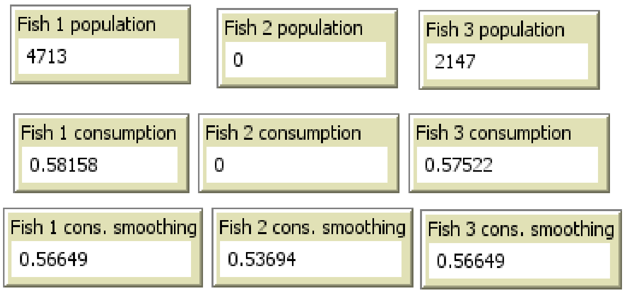


Figure 13. Unstable system pray parameters

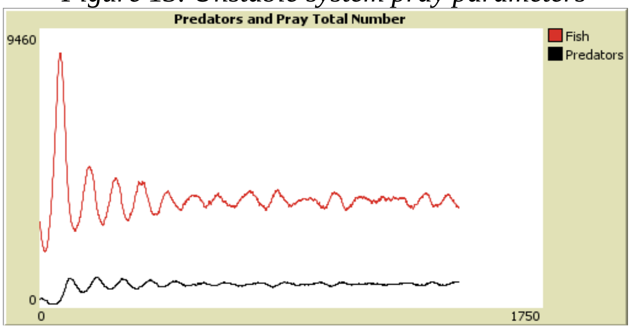


Figure 14. Unstable predator-prey system

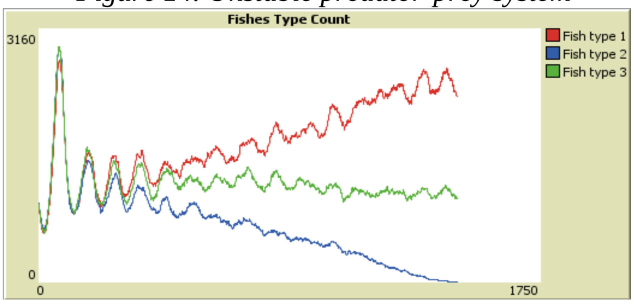


Figure 15. Unstable system detailed count of preys

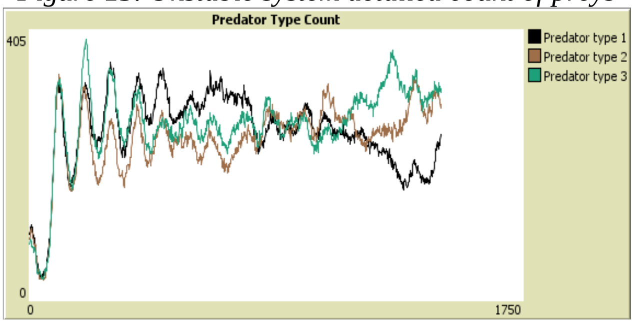


Figure 16. Unstable system detailed count of predators

Finally, in Figures 17 and 18 we summarize predators elimination rate and preys consumption by predators rate, respectively, for the unstable system. All figures in Example 1 indicate how various ABM features can be set and played With. Eventually in our follow up work we will use this for the benefit of LVM model, in particular to fine tune various Community Matrix parameters. As the number of species and complexity of the models grow this will be important to get reliable and predictable mathematically tractable LVM formulas.

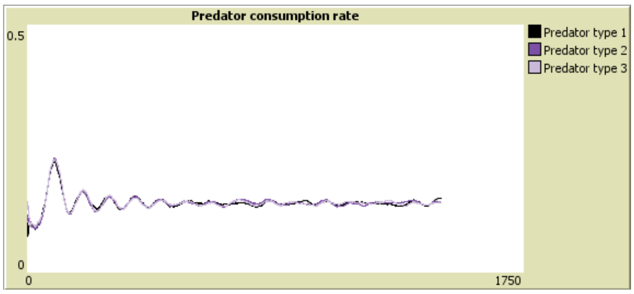


Figure 17. Predators elimination rate, unstable system

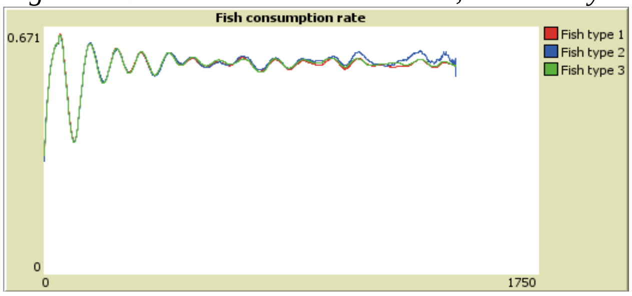


Figure 18. Preys consumption rate by predators

Example 2. In this example number of preys and predators are changed, as well as other parameters, per Figure 19. All other figures grouped together into Figure 20 summarize various details similar as in Example 1.

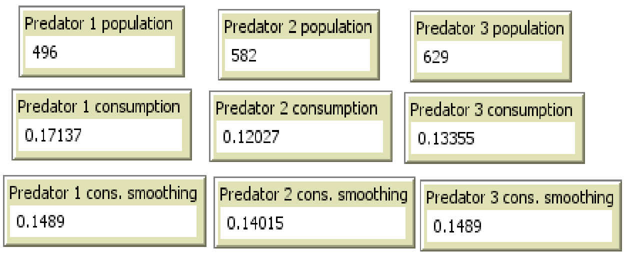
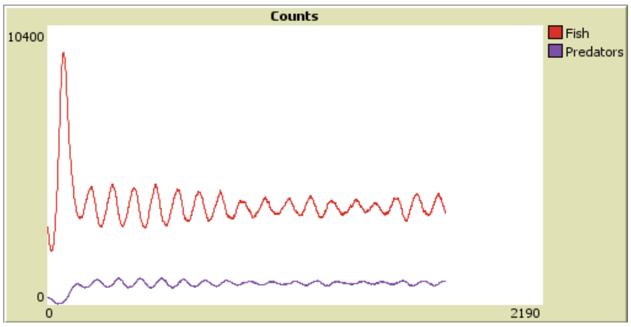
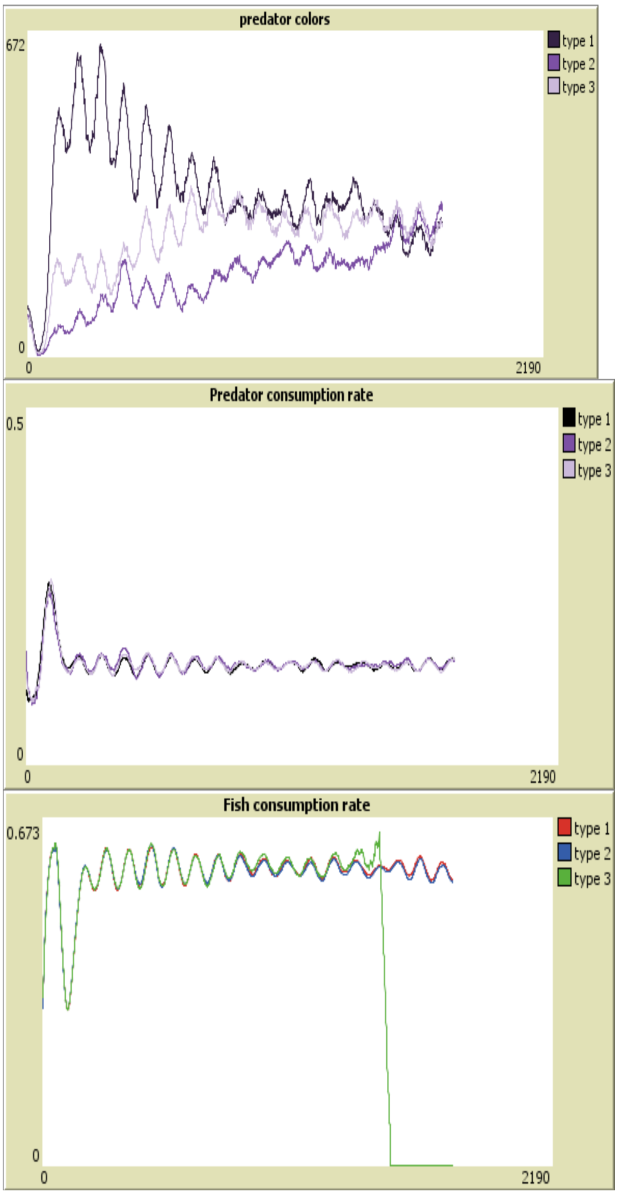


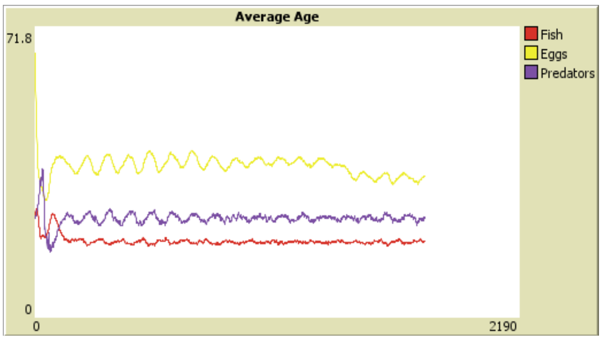
Figure 19. Unstable system predator parameters





Figures 20. Results for Example 2 unstable system

We conclude Example 2 with Figure 21 which has average age of preys, predators and "eggs" which "produce" preys.



Figures 21. Example 2 average age, preys, predators

5. CONCLUSION

In this paper we continue research started in [1] on dual model approach for complex predator-prey models. We present Single Prey Single Predator as well as Multiple Prey Multiple Predator LVM models. ABM simulation using NetLogo environment illustrates three predator-prey examples, one stable and oscillatory, the other two unstable with different count of 3+3 species involved. Our main goal is to show how ABM can mimic LVM formulas which allows to fine tune LVM. ABM can produce very complex simulations. On the other hand, LVM, which is based on mathematical equations models predator-prey behavior via its Community Matrix with certain number of elements. In this paper we used 6 species which results in 6x6=36 parameters. Typically not all the species are connected hence there are less than 36 parameters to consider. Once we establish reliable ABM, we can use it to fine tune these LVM parameters. With this paper we made another step in that direction with building complex ABM. This approach aims to produce results which can be used in practical ecological problems, and potentially assist in better understanding of classic multi-species issues, as (i) Paradox of the Plankton and of the Enrichment, (ii) Oksanen's description and tropic levels, and other general paradigms such as (iii) Adaptivity and (iv) Emergence.

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