Using Spreadsheets To Model Population Growth, Competition & Predation in Nature

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The most basic definition of ecology is the study of populations in nature. The most general attribute that a population has is its size, consequently this is the focus of many ecological models. This paper will introduce discrete (that is, measured once per generation instead of continuously) models for population growth as presented by Robert Ricklefs (1993). Starting with a simple exponential growth model for one species, we will build up to a model that considers two competing herbivore species and a predator species that preys on them both.

The equations considered can be placed into a spreadsheet that performs the calculations quickly and easily. Spreadsheet programs can graph columns of values and we will graph the populations of each species over time to observe the effects of the population interactions. I do assume minimal experience with spreadsheets, nothing more than defining equations, referencing cells and generating plots—all of which can be learned and taught in a matter of minutes.

The models and spreadsheets will encourage students to make the connection between a purely mathematical model and the real population it represents. Students will consider the qualitative effects of changing a value in equations, and their spreadsheets will present the quantitative effects. Environmental issues can be discussed by their effects on the equations and predicting or observing the resulting population crashes or booms (seen from the graphs of the populations over time).

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Population Equations

If we start with a population of size N and an intrinsic rate of population growth (r) in percent (r = .04 is 4% increase per generation), we can calculate N′ (the next population size) from r and N. The discrete exponential equation for a population of N organisms is:

$$N' = N + rN$$

You can see from this equation that the population will grow exponentially without bound until the entire earth would be covered (Figure 1 shows the case with a 5% growth rate, r = 0.05 and an initial population of 20). This is clearly unrealistic; the students may wish to offer their opinions as to what is wrong. What the equation is lacking is a notion of a maximum sustainable population size that can be supported in an environment (carrying capacity).

This notion of an environment's carrying capacity was used by Raymond Pearl and L. J. Reed (1920) in their equations to explain the population growth of early America. The discrete version of the logistic equation they proposed for population growth in a population of N organisms and a carrying capacity k is:

$$N' = N + rN\left(\frac{k - N}{k}\right)$$

From this equation you can see that when $N < k$ the population would grow until $k - N = 0$. At that point the second term is zero so that $N' = N$ and the population stops increasing. Likewise if the population were above the carrying capacity for some reason, $N > k$ and the second term is negative and $N' < N$, the population starts to decrease. Figures 2 and 3 demonstrate the shape of these two cases; the flattened s-shaped curve in Figure 2 is a sigmoid curve that is the hallmark of the logistic equation. This model seems more realistic, but treats the organism as if it is alone and is the only organism that is consuming resources in the environment.

The notion of competition was introduced by A. J. Lotka (1932) and G. F. Gause (1934) in the following way. For

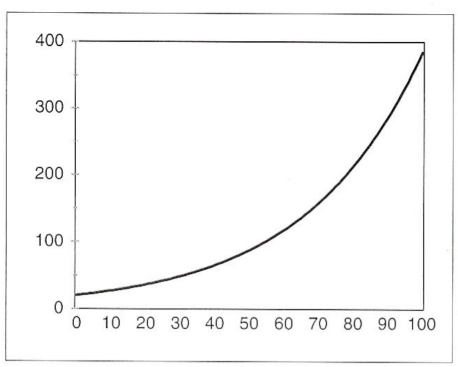

Figure 1. Example of exponential growth with r = 0.05 from an initial N = 20.

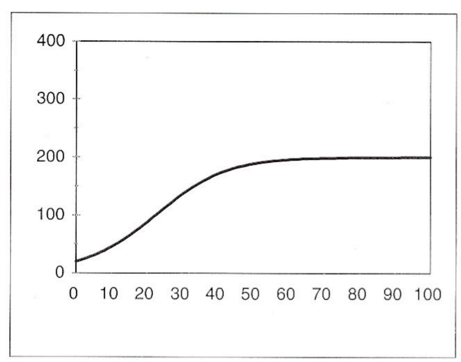

Figure 2. Example of logistic growth with r = 0.1, k = 200 from an initial N= 20.

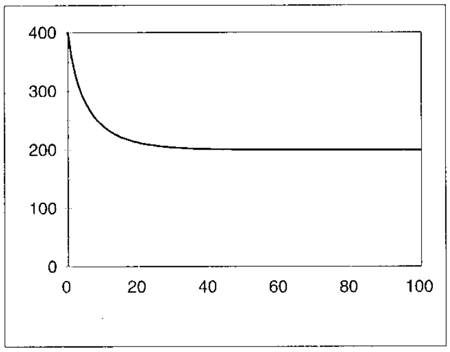

Figure 3. Example of logistic decline with r = 0.1, k = 200 from an initial N = 400.

a pair of competing organisms the appropriate equations would be:

$$N_1' = N_1 + r_1N_1\left(\frac{k_1 - N_1 - \alpha_2N_2}{k_1}\right)$$

$$N_2' = N_2 + r_2N_2\left(\frac{k_2 - N_2 - \alpha_1N_1}{k_2}\right)$$

The subscripts indicate which population the r, N and k values would correspond to if they were modeled alone as in the previous paragraph. The α_1 and α_2 values show the impact of the other population on the resources that the given population uses. The α_2N_2 and α_1N_1 values represent competing organisms expressed as equivalent organisms of the original species. For example if $\alpha_2 > 1$, that means that each individual of population 2 consumes more of population 1's resources than an individual of population 1 does, depressing population 1's growth greatly. Similarly if $\alpha_2 < 1$, individuals of population 2 consume less of population 1's resources than each member of population 1 does. The students may wish to consider factors such as organism size and food preference overlap that determine α_1 and α_2.

Predation was independently considered by A.J. Lotka and Vito Volterra (1926). This final case is a discrete version of a model combining their work with the results above, considering one population of predators (P) consuming two populations of herbivores (H_1 and H_2). The appropriate equations for this would be:

$$H_1' = H_1 + r_1H_1\left(\frac{k_1 - H_1 - \alpha_2H_2}{k_1}\right) - \gamma_1H_1P$$

$$H_2' = H_2 + r_2H_2\left(\frac{k_2 - H_2 - \alpha_1H_1}{k_2}\right) - \gamma_2H_2P$$

$$P' = \gamma_1H_1P\epsilon_1 + \gamma_2H_2P\epsilon_2 - DP$$

Where γ indicates the rate of a successful kill per encounter (the number of which are expressed by H*P) between the two organisms. The ϵ's represent the conversion ratio between successful kills and new predators. D is the death rate of the predators. The form of these equations can lead to discussions about what the factors really mean, for example would a larger body size for H_1 increase or decrease ϵ_1? (Increase.) If H_2 gets faster what would happen to γ_2? (Decrease.)

Setting Up Spreadsheet Models

Apart from discussing the equations in general terms, these equations can be programed onto a spreadsheet that will allow the students to set values and watch the populations of the organisms thrive or die. The spreadsheet program I have used to model the equations and to generate the figures is Corel® Quattro® Pro 7.0. I will describe the modeling of the two herbivores/one predator case because other cases are simplified versions of this and easily modeled if this example is understood. When being taught to students it is probably best to present the models in the order above, especially if the students are unfamiliar with spreadsheets.

Figure 4 shows a setup for the calculations. The cells are identified by their coordinates (for example, in Figure 4, cell B5 is 0.1). Rows 2–8 contain the labels for the constants or the constants themselves as defined in the equations above: r1 and r2 represent r_1 and r_2, k1 and k2 represent k_1 and k_2, a1 and a2 represent α_1 and α_2, g1 and g2 represent γ_1 and γ_2, e1 and e2 represent ϵ_1 and ϵ_2, and finally D represents D. Row 9 contains labels for each column below. Row 10 contains the generation number in column A and the starting population of each organism in B10, C10 and D10. Row 11 is where the calculations begin.

In cell B11 the equation is: B10+$B$3*B10*(($B$4-B10-$D$5*C10)/$B$4)-$B$6*B10*D10 which corresponds to the equation shown earlier. The dollar signs are used to prevent the cell references from changing when the cell is dragged down (to form the long columns). In cell C11 the equation is: C10+$D$3*C10*(($D$4-C10-$B$5*B10)/$D$4)-$D$6*C10*D10. In cell D11 the equation is: D10+$B$6*B10*D10*$B$7+$D$6*C10*D10*$D$7-$B$8*D10. Once all the equations are entered, all you need do is drag the cells down to generate a series of cells that re-evaluate the equations with each generation using the population values from the previous one.

The graph can be generated simply by highlighting the population columns (I recommend creating the graphs out of at least 100 generations in order to see long-term changes) and clicking the graph icon above the spreadsheet. Adding the generation column as a series for x-values gives a good x-axis.

Experiments with the Spreadsheet

Once a spreadsheet and linked graph have been set up, the students can experiment by changing the values of the constants and starting popula-

	A	B	C	D
1				
2		H1		H2
3	r1=	0.4	r2=	0.1
4	k1=	1000	k2=	400
5	a1=	0.1	a2=	0.3
6	g1=	0.005	g2=	0.001
7	e1=	0.15	e2=	0.3
8	D=	0.2		
9	Generation	H1	H2	P
10	0	100	100	2
11	1	133.8	107.05	1.81
12	2	177.2293	114.3382	1.687762
13	3	231.6297	121.8042	1.632443
14	4	297.5444	129.3713	1.649197
15	5	374.0763	136.9485	1.751398
16	6	458.3103	144.4341	1.964441
17	7	545.17	151.7236	2.331915
18	8	628.0716	158.7192	2.925141
19	9	700.3622	165.3368	3.857295
20	10	756.9012	171.5037	5.303289
21	11	794.8542	177.1459	7.526041
22	12	813.2715	182.162	10.90737
23	13	811.8849	186.3919	15.97496
24	14	789.9674	189.5847	23.40063
25	15	745.9344	191.3771	33.91572

E F G H I

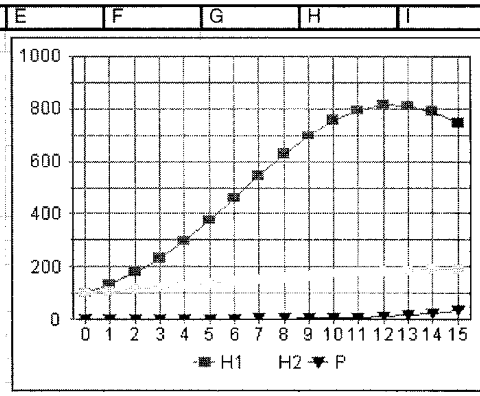

Figure 4. Example of a spreadsheet setup to demonstrate population growth.

tions. Once a block of cells and graph are linked, the graph should automatically change when the values in the block do. The students should consider what characteristics the organisms would have to change in order to change the values. Would a larger γ mean that the organism was better or worse at escaping predators? (Worse.) Would a smaller, shorter-lived organism have: a larger r? (Yes), smaller ϵ? (yes), larger γ? (maybe), etc. The goal is for the students to be able to make the connection between the mathematical model and the reality it represents.

Figure 5 shows 100 generations using the same values as in Figure 4. From these values perhaps herbivore 1 is small (rabbit) and herbivore 2 is larger (moose) and the predator is a wolf. Note that cycling of population size is common for models with predators and quickly reproducing prey. Note that the more quickly reproducing organisms (larger r) cycle more severely with the predator.

If there are no predators, we set the initial value of P to zero (with the same values we have been using for the other constants as in Figure 4) and get Figure 6. This represents pure competition without predation. The final populations of the herbivores can be seen to be below their individual carrying capacities (k) due to their competition with each other. Changing the values of α_1 and α_2 would result in different final proportions of the populations. We can also see the effects that the predator in Figure 5 had on the final populations of the herbivores.

We could model the introduction of a new predator or herbivore by setting

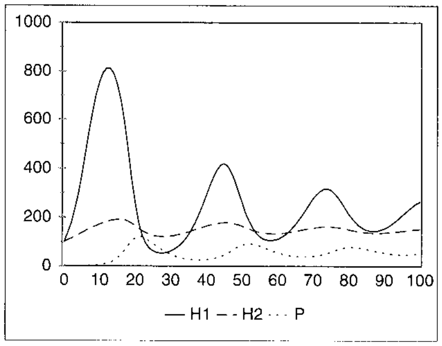

Figure 5. 100 generations using values from Figure 4. Note cycling of predator and herbivore populations.

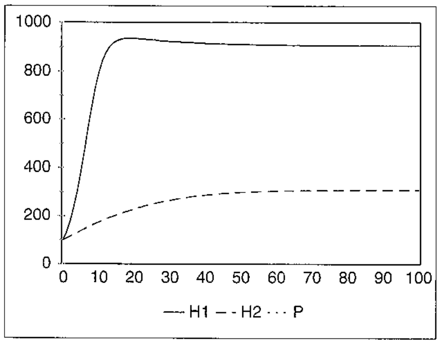

Figure 6. Example of pure competition. Note that H_1 and H_2 do not reach their individual carrying capacities of 1000 and 400 respectively.

the initial value of the species to be introduced to zero and inserting a value at some later generation to represent the introduction. Figure 7 shows the introduction of 2 predators (at generation 50) into the competition situation in Figure 6. We can see the

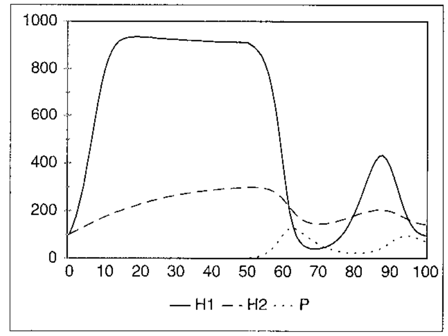

Figure 7. The introduction of two predators at generation 50 into a pure competition situation as in Figure 6. Note the drastic decline in herbivore 1, almost driving it to extinction.

drastic reduction in the number of organisms in this ecosystem. In fact, herbivore 1 comes close to extinction. This is an example of what can happen when humans are careless and introduce unsuitable species into new environments.

I would encourage the students to explore many situations and values for the mathematical constants. There are many different looking graphs that can arise out of this model and each makes a different statement about what happens to these organisms in their shared ecosystem. It is actually surprising how many situations are unstable; perhaps this is a testament to the fragility of nature. The students could prepare reports about the shape of the graphs for different values. They could try to predict the shape of the graphs for certain values of r, ϵ, γ, etc., and then accept or reject these hypotheses. If the graphs do not meet their expectations they may want to explain why they think they were mistaken.

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