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Using the Historical Development of Predator-Prey Models to Teach Mathematical Modeling

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1 Introduction

Many differential equations texts introduce the classic Lotka-Volterra predator-prey model as an application of coupled systems of differential equations. The model is based on a set of very simple premises:

- In the absence of predators, the prey population grows exponentially.
- Some fraction of predator-prey interactions end in death for prey.
- In the absence of prey, the predator population decreases exponentially.
- The predator birthrate is dependent on predators interacting with the prey (as the food source).

Using these assumptions as starting points for proportionality arguments, the four terms in the model (prey birth and death, predator birth and death) can be built in a variety of ways. The classic Lotka-Volterra form of the model can be written as a difference equation as:

$$\frac{\Delta x}{\Delta t} = ax - bxy$$

$$\frac{\Delta y}{\Delta t} = cxy - dy$$

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where x is the current prey population, y is the current predator population, and a, b, c, and d are constants of proportionality that can be interpreted as birth and death rates.

This model, first proposed in the 1920s, is the most famous of many models developed during the twentieth century. In attempts to correct the model's unnatural behavior (such as predators never becoming sated or prey growing without bound), scientists proposed alternatives to one or more of the four terms. Studying the historical development of these models, including variations and extensions proposed in the 1930s, 1950s, and 1970s, is an excellent way to introduce students to the issues associated with building mathematical models involving rates of change.

Access to technology such as computer algebra systems or spreadsheets makes these models accessible to students at a much lower level in the undergraduate curriculum, motivating the study of calculus and differential equations, rather than serving as an "afterthought" example.

2 The Historical Background

Before presenting the teaching sequences, a review of the historical development of the predator-prey equations is in order. This survey is by no means complete; the models chosen for discussion here have been selected because they are easily described as differential equations and because the rationales are understood by students with little experience in model development. For a more complete discussion of the mathematical evolution of predator-prey models, complete with suggestions for using the models with advanced students, see [9]. For a different point of view, including more historical information on the scientists involved in the lively development of the discipline of population ecology, see [3].

For all models, we will assume the following notation:

- $x(t)$: The size of the population of prey at time t, i.e., the number of individuals or some other measure of their biomass.
- $y(t)$: The size of the population of predators at time t, again either the number of individuals or some other measure of their biomass.

The most famous and the earliest model of interest to us is the Lotka-Volterra system, named for the two scientists who developed it independently, Alfred Lotka (1880-1949) publishing the equations in 1925 [6] and Vito Volterra (1860-1940) in 1926 [10]. The equations can be written in the form of difference equations, suitable for solution by spreadsheets or using system dynamics software such as Vensim:

$$\frac{\Delta x}{\Delta t} = ax - bxy$$

$$\frac{\Delta y}{\Delta t} = cxy - dy$$

for non-negative rate constants a, b, c, and d. There are several ways to justify the choices for the four functions, and it is interesting to look at how Lotka and Volterra each justified their choices.

First consider Lotka's argument concerning the prey increase term: In the absence of predators, the prey should increase without bound at a rate proportional to the current population level, hence the ax term. Likewise, Lotka assumed that in the absence of prey, the predators should decrease at a rate proportional to the current population level, hence the $-dy$ term. When the two species co-exist, Lotka used a chemical kinetics analogy to explain the change in the populations resulting from interactions: When a reaction occurs by mixing chemicals, the law of mass action states that rate of the reaction is proportional to the product of the quantities of the reactants.

If two quantities are denoted A and B, then the reaction rate would be proportional to AB. Using this as a rough analogy, Lotka argued that prey should decrease and predators should increase at rates proportional to the product of the number of prey and predators present, hence the terms -*bxy* for the prey decrease and *cxy* for the predator increase.

This analogy is not surprising, given Lotka's background. An American educated in Germany and France, Lotka had degrees in physics and chemistry and was extemely interested in the emerging field of physical chemistry, the application of physical principles, particularly thermodynamics, to chemistry. He believed that one could apply physical principles to biological systems as well, and his work on predator-prey interactions is just a small part of extensive work in this area, work he published in 1925 in the text, *Elements of Physical Biology* [6]. For more information on Lotka's contributions to population ecology, see chapter two in [3].

Volterra appears to have arrived at the interaction terms using somewhat different reasoning, namely a competition argument to suggest that in the presence of predators the prey's effective growth rate should be less than a, and how much less should depend on the predator population, giving

$$\frac{\Delta x}{\Delta t} = (a - by)x$$

A similar argument for the predator increase yields

$$\frac{\Delta y}{\Delta t} = (cx - d)y$$

As with Lotka's ideas, this approach is not surprising given Volterra's background and connections. Born and educated in Italy, Volterra was a physicist whose daughter and son-in-law were biologists. While looking for a mathematical explanation for a problem his son-in-law was working on, Volterra became very interested in interactions of species and spent the rest of his professional life looking for a mathematical theory of evolution. For more information on Volterra's work, including an account of the lively interplay between Lotka and Volterra, see chapters five and six in [3].

The Lotka and Volterra rationales yield models that are algebraically equivalent. For appropriate values of the rate constants, the solution of these equations leads to periodic behavior for both species. It is interesting to note that these continuous, quantitative attempts to explain species interaction were met with great skepticism by biologists of the day, but led to a huge increase in research related to the field of population dynamics by both physical and natural scientists as well as mathematicians.

An obvious limitation of these equations is the unrealistic behavior of the prey population in the absence of predators, so one of the first changes to the system proposed above was to limit the growth of the prey by incorporating a maximum sustainable population, M. One of the strongest proponents of the notion that intra-species competition is important was Alexander Nicholson (1895-1969), an Australian entomologist who studied predator-prey models applied to parasite-host relationships. Developed in the 1930s, his models were strictly discrete; we won't present them here. See chapter 5 of[3].

Adding intra-species competition to the prey equation can be accomplished using Belgian mathematician Pierre Verhulst's (1804-1849) notion that population growth should slow at a rate proportional to the ratio of the excess population to the total population. We can incorporate a birth slowing term into the prey equation, yielding with a little algebra the modified system

$$\frac{\Delta x}{\Delta t} = ax\left(1 - \frac{x}{M}\right) - bxy$$

$$\frac{\Delta y}{\Delta t} = cxy - dy$$

where M is the maximum number of prey that can be sustained in the system. This generalization appears to have arisen almost immediately after Lotka's and Volterra's work.

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References

[1] Bartlett, M. S. (1957) "On Theoretical Models for Competitive and Predatory Biological Systems," *Biometrica* Vol. 44, pp. 27-42.

[2] Gomatam, J. (1974) "A New Model for Interacting Populations – I: Two Species Systems," *Bulletin of Mathematical Biology* Vol. 36, pp. 347-353.

[3] King, S. E. (1988) *Modeling Nature, Episodes in the History of Population Ecology*, The University of Chicage Press, Chicago, pp. 98-134.

[4] Leslie, P. H. (1958) "A Stochastic Model for Studying the Properties of Certain Biological Systems by Numerical Methods," *Biometrica* Vol. 45, pp. 16-31.

[5] Leslie, P. H. and J. C. Gower (1960) "The Properties of a Stochas- tic Model for the Predator-Prey Type of Interaction Between Two Species," *Biometrica* Vol. 47, pp. 219-231.

[6] Lotka, A. J. (1925) *Elements of Physical Biology*, Williams and Wilkins Publishers, Baltimore.

[7] May, R. M. (1973) *Stability and Complexity in Model Ecosystems,* Princeton University Press, Princeton NJ.

[8] Smith, D. A. (1977) "Human Population Growth: Stability or Explosion?" *Mathematics Magazine* Vol. 80 No. 4, pp. 186-197.

[9] van der Vaart, H. R. (1976) "Some Examples of Mathematical Models for the Dynamics of Several-Species Ecosystems," in *Case Studies in Applied Mathematics,* Committee on the Undergraduate Program in Mathematics, Mathematical Association of America, pp. 186-290.

[10] Volterra, V (1926) "Variations and Fluctuations of the Number of Individuals in Animal Species Living Together," in *Animal Ecology*, R. Chapman, ed., McGraw-Hill, pp. 409-448.