

VARIABILITY IN PREDATOR-PREY EXPERIMENTS: SIMULATION USING A STOCHASTIC MODEL

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ABSTRACT

Simulation of several actual predator-prey experiments was carried out, using a stochastic version of the Lotka-Volterra equations. Great variability was found from run to run, with occasional extinction of either predator or prey with the same parameters. It is suggested that single experimental runs are very unreliable for parameter estimation, multiple replicates of experiments being necessary. It was not found necessary to postulate such mechanisms as hiding places for most experimental results, the discrete stochastic equations being adequate for this purpose.

INTRODUCTION

The mechanism of interaction between predator and prey first received serious consideration in the works of Lotka (1925) and Volterra (1931). In separate works, each used a continuous deterministic model consisting of differential equations describing the rates of change of predator and prey with respect to time. Solution of these equations indicates that both populations should oscillate—a condition perhaps to be expected from the interaction between predator and prey. At high prey densities the predators have plenty to eat and multiply rapidly, subsequently decreasing the prey density while their own density increases. Eventually a turning point is reached when the prey density becomes low enough to cause predators to starve. As a consequence of the lowered predator density, the prey begin to multiply more rapidly and the above sequence repeats itself.

In spite of the apparent appropriateness of the above model, Gause (1934) and other researchers found that their experimental predator-prey populations usually failed to exhibit oscillatory behavior, with one or the other species becoming extinct. Many modifications and much intense mathematical investigation of the Lotka-Volterra equations ensued. Several variations of the original Lotka-Volterra equations are given by Rosenzweig (1971).

The Pearl-Verhulst logistic model reflects the fact that an environment will support some maximum number of animals. This condition is generally applied to prey birth rate. Gause's experimental data on *Paramecium Caudatum* appears to support the Pearl-Verhulst version fairly accurately.

Another condition which may modify the Volterra model is the decrease in the predator's voracity as the number of prey increases. Gause (1934) first modelled this phenomenon; Rosenzweig (1971) lists this and other similar models.

Several models seek to reconcile the discrepancy between experimental behavior and Volterra's equation by introducing more animals of the almost extinct species, thereby producing the desired oscillation. Immigration is one such mechanism and has been studied experimentally by Gause (1934) and modelled by Bartlett (1960). Huffaker (1970) reports experiments, dealing with dispersion, which allow the depleted prey a chance to multiply elsewhere and then migrate into the depleted area. Similarly, Gause's (1934) use of hiding places for the prey effectively prevents the prey population from crashing.

An approach used by Bartlett (1960) involves bringing the experimental data

into compliance with deterministic theory by the introduction of time lags, representing gestation time of prey and predator. The first attempt to formulate the stochastic version of the deterministic model was made by Feller (1939), who considered the problem intractable. Chiang (1954) formulated the difference equations and obtained the system of differential equations for the joint probability function, but was unable to obtain the solution for the partial differential equation for the probability generating function.

With the advent of computers, Bartlett (1960) and Leslie and Gower (1960) approached the Volterra equations via simulation, and appear to have attacked the root of the discrepancy between animal behavior and the Lotka-Volterra model--that failure to oscillate is predominantly a result of the stochastic nature of the real life situation. The element of chance can divert the interaction of predator and prey sufficiently far from its deterministic path to cause extinction of either species. For "laboratory-size" populations, experience with simulation soon leads one to realize that sustained oscillation appears to be virtually impossible if the initial numbers of predator and prey are not near the equilibrium state described by Volterra in his analysis of the deterministic model.

This paper seeks to make comparisons between simulation results based on a discrete stochastic version of Volterra's differential equations and some of the data obtained from literature. Since great variability is found upon repetition of a simulation, using the same parameters, an attempt has been made to quantitate this inherent variability by reporting means, variances and ranges of the number of predators and prey present at each time point.

METHODS

The simulation program was written in FORTRAN and run on the IBM 370 computer. The basic formulas underlying the simulation are a modification of Volterra's differential equations. To formulate the difference equations we will define the operator R as follows: $M R X$ is the number of random numbers (uniformly distributed between 0 and 1) out of a total of X random numbers which are less than M . Then:

$$\text{prey}(t + \Delta t) - \text{prey}(t) = (C\Delta t) R \text{prey}(t) - (D \text{pred}(t)\Delta t) R \text{prey}(t)$$

$$\text{pred}(t + \Delta t) - \text{pred}(t) = -(B\Delta t) R \text{pred}(t) + \frac{A(\text{prey eaten})\Delta t}{\text{pred}(t)} R \text{pred}(t) \text{ where:}$$

A = efficiency of predator

B = death rate of predator

C = birth rate of prey

D = encounter rate between predator and prey

$\text{prey eaten} = (D \text{pred}(t)\Delta t) R \text{prey}(t)$

t = time

Δt = time interval in which one event occurs

$C\Delta t \doteq$ probability of prey birth in Δt per prey

$D \text{pred}(t)\Delta t \doteq$ probability of pred-prey encounter resulting in prey being eaten, in Δt , per prey

$B\Delta t \doteq$ probability of pred death, in Δt , per pred

$\frac{A(\text{prey eaten})\Delta t}{\text{pred}(t)} \doteq$ probability of pred birth in Δt , per pred

these approximations being valid if t is sufficiently small, so that the probabilities $\ll 1$.

The random-number-generating subroutine employs the Taussky-Todd multiplicative congruence method and generates uniformly-distributed floating point pseudo-random numbers between 0 and 1.

The probabilities above are kept smaller than .05 by a subroutine which repetitively halves the time interval. Thus the probability of two events occurring in one time interval is less than .0025 and we may neglect this possibility. To provide for computing efficiency, another subroutine doubles Δt if the probabilities all become smaller than .02. Doubling the time interval when possible saves a considerable amount of looping.

Equation (2) was revised for greater realism and to increase efficiency by using the following "lumped" version:

$$\text{pred}(t + \Delta t) - \text{pred}(t) = \frac{(A (\text{prey eaten}) - B \Delta t) R \text{pred}(t)}{\text{pred}(t)}$$

Although this form displayed less variability than the previous, its qualitative behavior remained the same. Biologically, prey eaten goes into maintenance of the predators, largely resulting in a decreased predator death rate, lending biological justification for lumping predator birth and death probabilities.

The most recent version modifies the encounter probability as a function of prey density:

$$\text{Prey}(t+\Delta t) - \text{Prey}(t) = (C \left[\frac{1 - \text{prey}(t)}{\text{PYMAX}} \right] \Delta t) R \text{prey}(t) - \left[\frac{D}{1 + \frac{\text{prey}(t)}{E}} \right] \text{pred}(t) \Delta t R \text{prey}(t)$$

The expression $\frac{D}{1 + \frac{\text{prey}(t)}{E}}$ attempts to deal with the fact that predator voracity decreases as the prey density increases. This function was chosen mainly for the following desirable properties:

1. It is a monotone decreasing function of $\text{prey}(t)$ having range $(0, D)$ for $\text{prey}(t) \geq 0$.
2. The constant E has the effect of modifying the speed with which the function decreases with increasing prey. E may be interpreted by letting $\text{prey}(t) = E$ and observing that the function value is $D/2$; i.e., E is the number of prey present when the predator's voracity is half that of starvation.

Parameter Estimation

Accurate parameter estimation is extremely difficult. The following (fairly crude) methods were used as a starting point and parameters were then adjusted by observing results of the simulation.

The birth rate of the prey is the starting point. Most researchers start cultivating the prey a few time intervals before the predator is introduced and one can attempt to determine the birth rate from this time period using the formula

$$\frac{d \text{prey}}{dt} = C \text{prey} \quad \text{whose solution is} \quad C = \frac{1}{t} \ln \frac{\text{prey}(t)}{\text{prey}(t_0)}$$

The values for C found by taking different t 's may vary considerably, but one can approximate upper and lower boundaries, which are helpful.

If the data of the experiment show one or more cycles, B may be estimated by using the formula for the period of the deterministic form, $T = \frac{2\pi}{\sqrt{BC}}$. Rearranging,

$$\text{we may then calculate } B = \frac{4\pi^2}{T^2 C}$$

To set parameters A and D , one may use the maximum prey and predator values, with the corresponding first time derivatives being zero, in the following manner:

$$\frac{d \text{ prey}}{dt} = (c - D \text{ pred}) \text{ prey} = 0, \text{ or } D = \frac{C}{\text{PRED}} \quad \text{and}$$

$$\frac{d \text{ pred}}{dt} = (AD \text{ prey} - B) \text{ pred} = 0, \text{ or } A = \frac{B}{D \text{ PREY}}$$

where PRED = number of predators at prey maximum and PREY = number of prey at predator maximum.

PYMAX is sometimes experimentally determined, or can sometimes be estimated by observing the greatest number of prey when few predators are present. E may be estimated roughly by observing the change in predators relative to the number of prey.

RESULTS

Simulation of experiments from the literature is limited by experimental conditions such as too many animals for economical computing; reporting of animal density rather than total number of animals; and limitations created by biological complexity of the animals selected, as in the case of egg laying insects which introduce time lags.

The first simulation results are from data taken from Gause's experiments using *Paramecium Caudatum* as prey and *Didinium Nasutum* as predator. He mentions that growth rates under different conditions are not comparable since growth rates of predator and prey vary not only with the number of bacteria serving as nutrient for the prey, but also with pH and the medium used. Computer runs support the fact that growth rates are subject to change from one experiment to the next, as is seen in the following two experiments from Gause.

Experiment 1: Data of Gause (1934) p. 118. (See page 7)

Prey birth rate was calculated from data on prey growth in the absence of predators to be approximately 1.7. Scrutiny of the data indicates that the encounter rate must be much less for 118 prey than it is for 30, since the predators increase more for prey = 30 than for prey = 118. Hence, 125 seems a reasonable value for the half kill rate. Gause indicates that 375 is the maximum number of prey to be supported by the environment.

The best simulation obtained resulted from a prey birth rate of 1.5. Introduction of the predator could influence prey birth rate by changing the age distribution of the prey population. Results are shown in Figure 1. Simulation data are means of 5 runs. Data for predators lags the simulation; this is probably the effect of time delays in predator death.

Experiment 2: Data of Gause (1934) p. 119. (See page 7)

This simulation was attempted with the parameters of the preceding experiment, but gave no success; in fact the predators crashed first in the simulation, but the prey crashed first in the experiment. With revised parameters, better results were obtained. The prey growth rate was held at the "experiment 1" value. The effect of a time lag on predator death was simulated by setting the predator death rate to zero over the short time period of this experiment. The encounter rate and efficiency were roughly tripled. Results of the simulation are shown in Figure 2; the data are well fitted. However, considerable run to run variability was observed.

Experiment 3: Data of Gause (1934), p. 126. (See page 8)

In this experiment, Gause obtained 2 oscillations, and introduced a very small number of prey and predators, (1 each) at several points, thus simulating the effect of immigration. Since such a tiny number of animals was introduced, a simulation was

attempted without introducing animals, to see if oscillations could be observed in the absence of immigration. Computer runs which approximated the first experimentally observed predator and prey peaks almost always crashed without exhibiting the second oscillation. One simulation out of ten yielded two oscillations, and is shown in Figure 2.

Experiment 4: Data of Huffaker (1958). (See page 8.)

To obtain a simulation on an experiment exhibiting some oscillatory behavior, Huffaker's data on orange mites were used. In dealing with various dispersions of predator and prey, he essentially is adjusting encounter rate, and his final experiment gave 3 oscillations over a period of 207 days, where upon the predator died. Judging from computer runs, Huffaker was relatively lucky to obtain these results - one simulation in ten using the parameters given resulted in 3 oscillations as pictured in Figure 4.

DISCUSSION

In the absence of a likelihood function, fitting a stochastic model to experimental data is a difficult and parlous process. In this case, the severe nonlinearity of the model greatly restricts its potential qualitative behavior, and qualitative or semi-quantitative fitting may yield information as to the model's validity (or lack of it).

The results given here might well be improved upon, since in effect we are working with an eight-parameter stochastic surface to find a best simulation. Of these eight parameters, two are known: the original number of predators and prey. Three more may be estimated from the data; at least, we may put boundaries on their values. These are the maximum number of animals supported by the environment, the number of prey present when the predator's voracity is half that of starvation, and prey birth rate. This problem could be solved by an optimization routine, but the amount of computer time required is prohibitive at present.

The Lotka-Volterra equations, then, remain an extremely sturdy model for predator-prey interaction if they are modified to a stochastic form. A little experience with the results of simulation leads to the general conclusion that the closer the parameters are to the steady state point of the deterministic form ($\frac{d \text{ prey}}{dt} = \frac{d \text{ pred}}{dt} = 0$), the longer oscillation will be sustained. Most of the research attempting to produce oscillation with experimental populations amounts to changing parameters to a more favorable position. Changes in nutrient represent changes in predator death and prey birth; changes in viscosity represent changes in encounter rate and different animals have different rates.

In a sense, it will be much harder to obtain oscillation in a lab than in nature, since the lab experiment usually represents a limited population, which is fairly likely to crash, while nature represents a composite of many such experiments, which is far less likely to crash.

The basic qualitative behavior of most experiments may be obtained using a discrete stochastic form of the Lotka-Volterra equations; one does not need limitation of the number of animals in the environment, hiding places, or adjusting of the predator's voracity to have simulated populations crash.

A quantitative approximation of laboratory behavior, however, does require the above adjustments, and possibly more depending on the experiment. More experimental data on predator voracity would probably yield a more appropriate function for adjusting this variable with respect to prey density. Time lags involved in birth and starvation should be considered, and, as understanding of

simulation behavior increases, more adjustments yet may be necessary to yield simulations worthy of statistical comparison with the experimental data. The amount of stochastic fluctuation among simulation runs strongly indicates that several replicate experimental runs should be made in laboratory investigations of predator-prey interactions.

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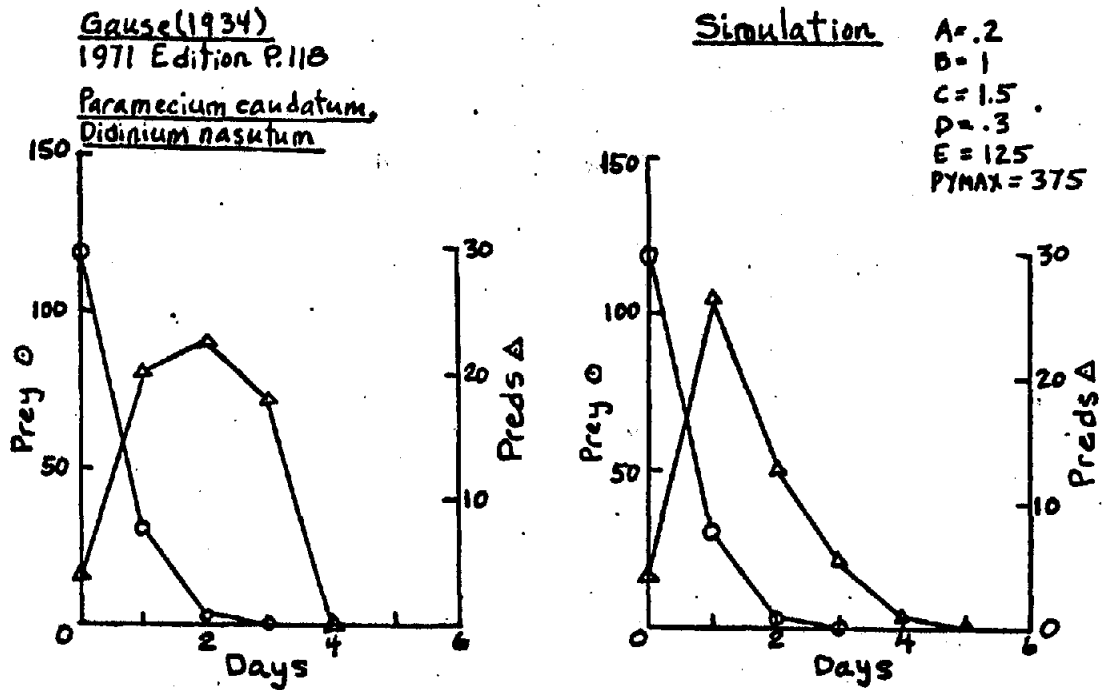


Figure 1

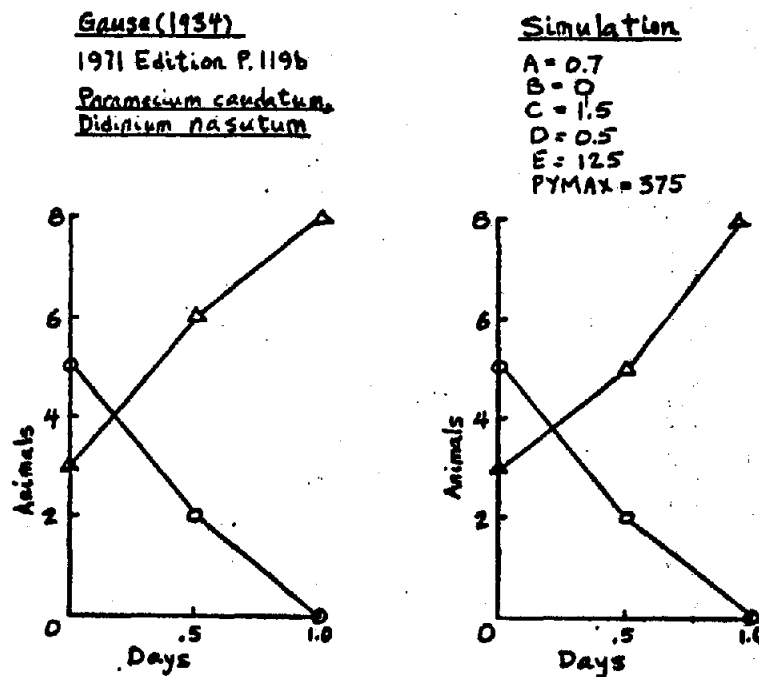


Figure 2

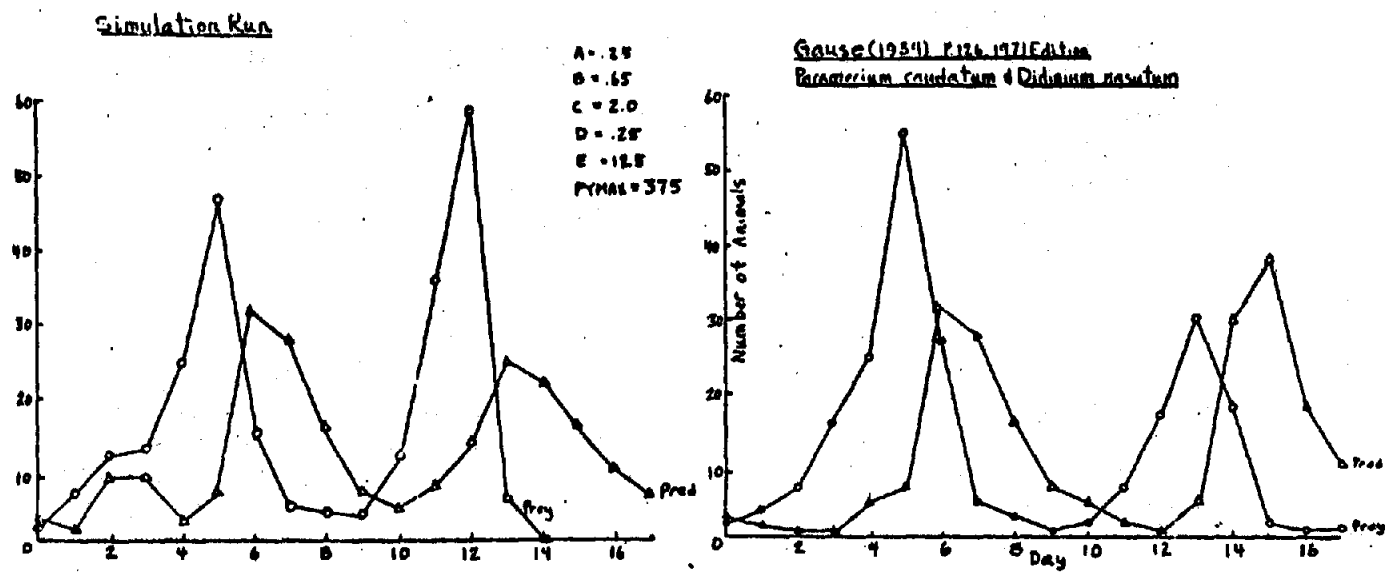


Figure 3

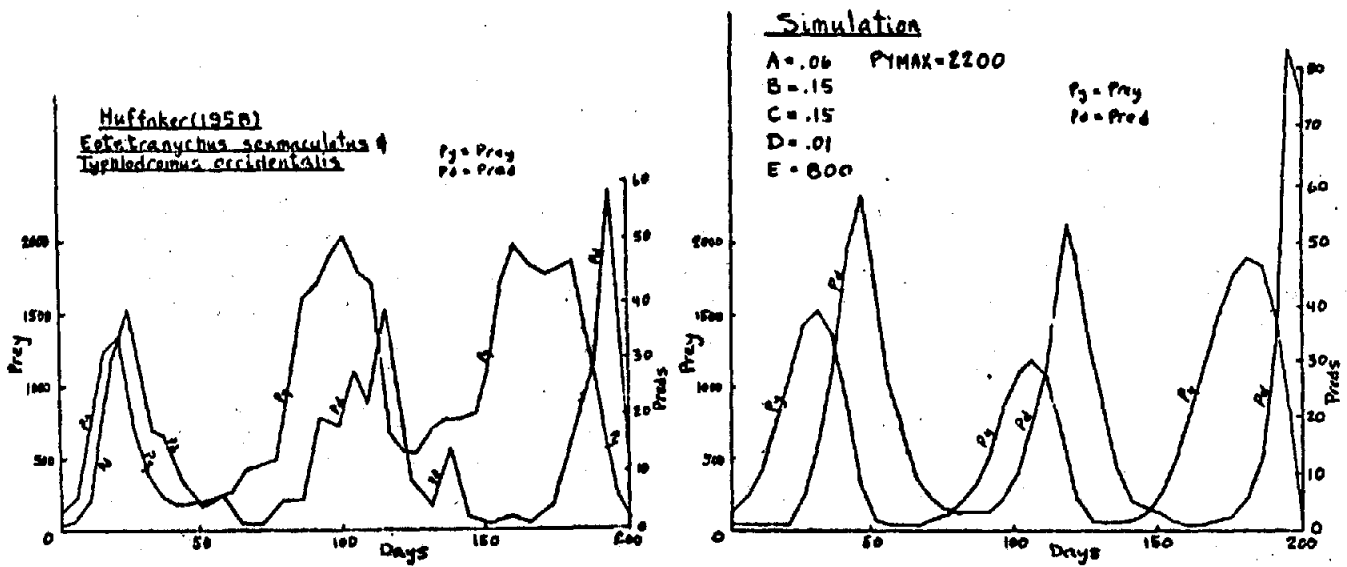


Figure 4