Background:

The interaction between predators and prey is of great interest to ecologists. In the 1920s, Alfred Lotka and Vito Volterra independently derived a pair of equations, called the Lotka-Volterra predatory-prey model, that have since been used by ecologists to describe the interactions of predators and prey. These equations, as you will see, can produce cyclical rise and fall in the abundance of predators and prey. These cycles have been observed in many predator-prey systems, including the famous example of Canadian lynx and snowshoe hares (Figure [PHOTO]). In lynx and snowshoe hare population trajectories reconstructed from trapping records (REF, Figure X), both lynx and hare numbers appear to rise and fall (cycle), with the lynx numbers beginning to decline after the number hares (their primary food source) declines.

![--- PHOTO (MAYBE) OF LYNX CAPTURING HARE ---]

Figure 1: Reconstructed population trajectories for Canadian lynx (*Lynx canadensis*) and snowshoe hares (*Lepus americanus*) from [REF].

This area of inquiry is even more important today as ecologists and conservation biologists consider the role of predators in ecosystems and the consequences of their extirpation. Recent research has emphasized the importance of predators in many ecosystems (for example, the reintroduction of wolves in Yellowstone National Park).
The purpose of this learning module is to explore deterministic and stochastic versions of the Lotka-Volterra predator-prey equations. For a given set of initial conditions (say, the number of predators and the number of prey at the time the model begins) and model parameters, deterministic models yield the same results each time the model is run. However, we do not understand all of the processes that affect the behavior of predators and prey (or other systems), so we often include some randomness in the models to account for this uncertainty. Models that contain such randomness are called “stochastic models,” and yield different results each time they are run even if the initial conditions and parameters are the same.

In this learning module, you will be able to explore deterministic and stochastic versions of four variations of the Lotka-Volterra predator-prey model using a computer program designed for this purpose.

**The Model:**

With the Lotka-Volterra predator-prey model, we model the change in the number of predators ($P$) and number prey ($V$) in continuous time via a system of two ordinary differential equations. In the equations, $dV/dt$ represents the change in the number of prey at an instant in time, and $dP/dt$ represents the change in the number of predators at an instant in time. Each term in the equations has a biological interpretation which I will give.

The predators have a death rate ($q$) which controls the rate of exponential decline of the predator population ($P$) in the absence of prey. Prey on the other hand, have a growth rate ($r$) which controls the rate at which the prey population ($V$) grows in the absence of predators (for the exponential Models 1 and 2). With respect to prey, models 1 and 2 are “exponential models” for population growth. In models 3 and 4 we include another term, $(-r/K)V^2$, which causes the prey growth rate to decline as the number of prey increases. This is called a “logistic model” for population growth. The logistic models include a second parameter, the carrying capacity ($K$), which limits the size the prey population can attain.

In order for the predator population to grow, predators must consume prey. This interaction is modeled by the last term in the $dV/dt$ equation and the first term in the $dP/dt$ equation. This term involves a functional response, which models the rate at which predators capture and consume prey. For models 1 and 3, the functional response is $aV$. This is a Type I functional response in which the rate of prey capture and consumption by each predator increases linearly with the number of prey. In this model, prey are converted to predators by the first term in the $dP/dt$ equation as $bV$, where $b$ is called the “conversion efficiency.” However, it might be unrealistic to assume that there is no limit to the number of prey a predator may consume, so models 2 and 4 use a Type II functional response, in which the rate of prey capture and conversion to predators increases non-linearly with the number of prey. The formulation for each of the four Lotka-Volterra predator-prey models is:

**Model 1:** Exponential prey growth and a Type I functional response.

\[
\begin{align*}
  \frac{dV}{dt} &= rV - aVP \\
  \frac{dP}{dt} &= bVP - qP
\end{align*}
\]
**Model 2**: Exponential prey growth and a Type II functional response.
\[
\begin{align*}
\frac{dV}{dt} &= rV - aVP/(1 + ahV) \\
\frac{dP}{dt} &= bVP/(1 + ahV) - qP
\end{align*}
\]

**Model 3**: Logistic prey growth and a Type I functional response.
\[
\begin{align*}
\frac{dV}{dt} &= rV - (r/K)V^2 - aVP \\
\frac{dP}{dt} &= bVP - qP
\end{align*}
\]

**Model 4**: Logistic prey growth and a Type II functional response.
\[
\begin{align*}
\frac{dV}{dt} &= rV - (r/K)V^2 - aVP/(1 + ahV) \\
\frac{dP}{dt} &= bVP/(1 + ahV) - qP
\end{align*}
\]

**Deterministic Models**: In the deterministic models, the number of prey \((V)\) and predators \((P)\) is treated as a continuous quantity. The program uses the equations above, initial values for \(V\) and \(P\), and numerical methods to produce the deterministic population trajectories.

**Stochastic Models**: In the stochastic models, the number of prey \((V)\) and predators \((P)\) is treated as a discrete (whole number) quantity. It is beyond the scope of this introduction to fully explain how the stochastic models work, so here I will give a brief explanation. In each of the two equations, the sum of the terms with positive signs can be thought of as the rate at which individuals are added to the population, and the sum of the absolute values of the terms with the negative signs can be thought of as the rate at which individuals are removed from the population. From these rates we determine a length of time to the next event, and which type of event occurs. The possible events are:
- birth of a prey, in which case \(V\) increases by 1
- death of a prey, in which case \(V\) decreases by 1
- birth of a predator, in which case \(P\) increases by 1
- death of a predator, in which case \(P\) decreases by 1

From this process, we simulate the stochastic population trajectories. In the absence of extinction of predators or prey, the stochastic versions will, on average produce behavior similar to the deterministic models (but notice what happens if the predators become extinct).

**The Program**:

When the program is started, two windows are displayed. The first is a Control Panel (Figure 1) and the second is a Population Trajectory panel (Figure 2 and 3). The Control Panel allows you to select the version of the model to run, set all of the parameters and initial conditions for the model, the number of time steps, reset the model, run stochastic versions, and quit the program. The Population Trajectory panel displays the number of predators (in red) and prey (in blue) over time. If stochastic simulations are run (by clicking the “STOCHASTIC” button, which can be done repeatedly), the number of predators are displayed in light red and the number of prey in light blue.
Figure 2: The Control Panel.
Figure 3: The Population Trajectory panel displaying deterministic trajectories.

Figure 4: The Population Trajectory panel displaying deterministic and stochastic trajectories.
The program is started by double clicking the PredPreySim.jar file under Windows or calling the PredPreySim.sh BASH shell script from a command-line terminal in Linux or Mac OS. In order to run the program you must have the Java Virtual Machine (JVM) properly installed and on your computer’s search path. If you do not have the JVM installed on your computer, you can download it for free from the Sun Microsystems website (http://www.java.com/en/download/index.jsp).

Once the program is running, deterministic predator and prey population trajectories will be displayed for the default parameters. If you change parameters, click the “RESET” button and then “RESUME.” To plot stochastic population trajectories, click the “STOCHASTIC” button.

**Note, however, that stochastic simulations can take a very long time for exponential models, especially for long time steps or if the prey intrinsic rate of increase is high.**

**Exercises:**

**Investigation 1:** What happens if there are no predators? Set the predator slider to 0 and lower the time steps slider to about 20. Run each of the four models, and vary the prey rate of increase and carrying capacity.

**Investigation 2:** Now add predators to the system. What happens to the number of prey? Explore the behavior of the model by varying the following parameters:

- Model 1 – vary prey rate of increase, predator death rate, the encounter rate, and conversion efficiency.
- Model 2 – vary prey rate of increase, predator death rate, the encounter rate, conversion efficiency, and prey handling time.
- Model 3 – vary prey rate of increase, prey carrying capacity, predator death rate, the encounter rate, and conversion efficiency.
- Model 4 – vary prey rate of increase, prey carrying capacity, predator death rate, the encounter rate, conversion efficiency, and prey handling time.

The initial number of predators and prey can also be changed.

What different behaviors are produced by the model? How do the deterministic and stochastic model results differ?

Based on your explorations on one version of the model, write a 1 – 2 page description of (a) the model, (b) the basic kinds of behaviors it can produce, (c) how each of the model parameters affects the behavior of the model, and (d) the outcome of stochastic versions of the model and how they compare to the deterministic version.