User Manual for the LPA Simulator

by Robert A. Desharnais, Ph.D.

1. Overview

The LPA Simulator is a web site that allows one to run ecological simulations for the LPA and discrete-time Ricker population models. One can look at time series plots of the output from either model. Simulations of the LPA model can also be examined in three-dimensional phase space. The user can vary model parameter values and initial conditions and examine the effects on the model predictions.

Sections 1–5 and describe the models and each of the simulators. Interesting examples are provided in sections 6 and 7 for the Ricker and LPA models, respectively.

Figures are created using the Plotly javascript library. Plots can be manipulated interactively using operations such as pan, zoom, and rotate. Data points can be read directly off the plots. Figures can be saved and downloaded as images in the PNG graphics format. These features are described in section 8 on Plotly graph controls.

2. Ricker Simulator

The discrete-time Ricker population model describes changes in population size as a function of time. It is one of the simplest ecological models that allows for nonlinear population growth.

The equation for the discrete-time Ricker population model can be written as

$$N(t+1) = N(t)\exp\left(r\left(\frac{K-N(t)}{K}\right)\right), \tag{1}$$

where $N(t)$ is the size of the population at time t, r is the *intrinsic rate of increase* for the population, and K is the population *carrying capacity*. The parameter r represents the exponential rate of increase at low population densities. Population growth is *density-dependent*; that is, the effects of crowding decreases the rate of population growth as a result of limited resources. Parameter K is the size of the population that the environment can support.

The Ricker Time Series Simulator allows you to modify the population's intrinsic rate of increase and carrying capacity to see the effects on population growth. Changing K has the effect of the scaling the population size. Changes in r affect qualitative aspects of the population growth curve and its long-term dynamics. Interesting illustrative examples are provided in section 6. You can also vary the initial population size and the number of time intervals (iterations) plotted on the x-axis.

Clicking the **Run** button starts the simulation at time zero using the parameter values and initial condition specified in the form fields to the left of the plotting area. If you want to continue the simulation for additional time intervals, click the **More** button. The **Reset** button will reload the web page restore the default values to the form fields. (Some versions of the Firefox browser do not restore the parameter values.)

3. LPA Model

Flour beetles of the genus *Tribolium* have a long tradition of use in ecology dating back to Chapman (1928). Populations are cultured in the laboratory and, at regular intervals, the numbers of insects in the various life stages are counted and returned to fresh media. Despite this simple experimental protocol, *Tribolium* have been used to study a variety of phenomena in ecology including species competition and nonlinear population dynamics. Reviews of the research involving *Tribolium* can be found in the papers by King and Dawson (1972), Mertz (1972), and Costantino *et al.* (2005) and the books by Costantino & Desharnais (1991) and Cushing *et al.* (2002).

One of the most compelling reasons for using *Tribolium* in the study of populations is that it provides a fascinating example of nonlinear demographic dynamics. Laboratory populations maintained under constant environmental conditions usually exhibit dramatic fluctuations in density and age structure. These fluctuations are the result of strong behavioral interactions among the life stages—the most important being cannibalism.

The life-stage interactions that drive the dynamics of *Tribolium* populations are summarized in Figure 1. The open arrows represent the life cycle, which, for *T. castaneum* at 34° C, has a duration of approximately 28 days. The single arrows represent the interactions. The arrows labeled c_{ea} and c_{pa} represent the cannibalism of eggs and pupae, respectively, by adults. The arrow labeled c_{el} represents the cannibalism of eggs by larvae. The effects of these cannibalistic behaviors on the survival of eggs and pupae can be modeled using negative exponential functions.

The LPA population model describes changes in the numbers of larvae, pupae, and adults as a function of time. The model given by the following three equations:

$$\begin{aligned} L(t+1) &= \exp\left(-c_{el}L(t) - c_{ea}A(t)\right), \\ P(t+1) &= L(t)\left(1-\mu_l\right), \\ A(t+1) &= P(t)\exp\left(-c_{pa}A(t)\right) + A(t)\left(1-\mu_a\right). \end{aligned} \tag{2}$$

The first equation is for the number of feeding larvae (referred to as the L-stage), the second is for the number of large larvae, non-feeding larvae, pupae and callow adults (called the P-stage), and the third is for the number of sexually mature adults (A-stage animals). The unit of time is two weeks and is, approximately, the average amount of time spent in the feeding larval stage under experimental conditions. The time unit is also approximately the average duration of the P-stage. The quantity $b > 0$ is the number of larval recruits per adult per unit of time in the absence of cannibalism. The fractions μ_l and μ_a are the larval and adult rates of mortality in one time unit. The exponential functions account for the cannibalism of eggs by both larvae and adults and the cannibalism of pupae by adults. The fractions $\exp(-c_{el}L(t))$ and $\exp(-c_{ea}A(t))$ are

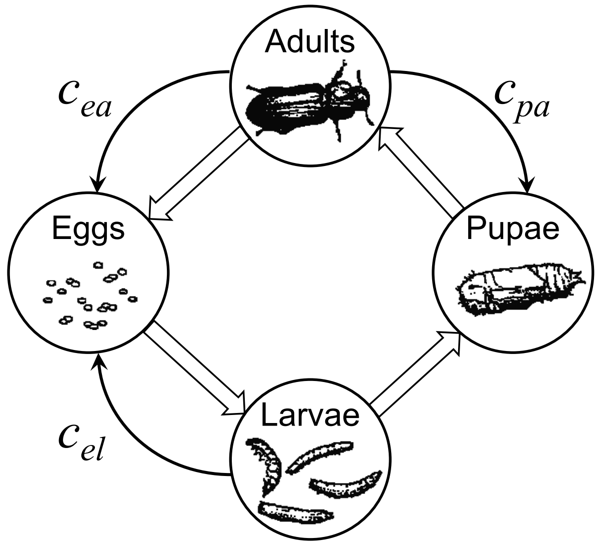

Figure 1. The *Tribolium* life cycle and life-stage interactions.

the probabilities that an egg is not eaten in the presence of $L(t)$ larvae and $A(t)$ adults in one time unit. The fraction $\exp(-c_{pa}A(t))$ is the survival probability of a pupa in the presence of $A(t)$ adults in one time unit. These equations form the basis of the LPA simulator.

4. LPA Time Series Simulator

The LPA Time Series Simulator allows you to modify the six parameters in the LPA model (2). You can also vary the initial numbers of L-stage, P-stage, and A-stage insects and the number of time intervals (iterations) plotted on the x-axis. The LPA model can exhibit a variety of population dynamics. Interesting examples are given in section 8. The default parameter values and initial conditions were estimated from a *Tribolium* experimental treatment designed to exhibit chaotic dynamics (Dennis *et al.* 2001).

Clicking the **Run** button starts the simulation at time zero using the parameter values and initial condition specified in the form fields to the left of the plotting area. If you want to continue the simulation for additional time intervals, click the **More** button. The **Reset** button will reload the web page restore the default values to the form fields. (Some versions of the Firefox browser do not restore the parameter values.)

5. LPA Phase Space Simulator

Ecologists are often interested in the long-term dynamical behavior of a population. After a period of initial transient behavior, the population “forgets” the initial conditions and approaches a long term solution called an *asymptotic attractor*, such as an equilibrium or cycle. In populations with more than one age class, the attractor can be visualized by plotting the different age classes against one another. This is called a *phase space* plot. For discrete-time models, populations can be envisioned as jumping through phase space towards the attractor. The type of attractor will vary depending on the model parameters.

Since the LPA model (2) consists of three life stages, one can view phase space as a three-dimensional plot. The LPA Phase Space Simulator plots the values of the L-stage, P-stage, and A-stage for every time value as points in phase space. This simulator allows you to modify the six parameters in the LPA model (2). You can also vary the initial numbers of L-stage, P-stage, and A-stage insects.

In some cases, you may only want to view the points close to the asymptotic attractor. The LPA Phase Space Simulator allows you to run model for many iterations before you begin plotting. The number of unplotted "transient" iterations can be varied in the **Initial** form field under "Iterations." The number iterations to be plotted can be varied in the **Plot** form field under "Iterations." If you want to plot all the model output, you can set the value for **Initial** to zero. The size of the plotting symbol can be varied in the **Symbol** field. Use small values such as 0.1 if the attractor consists of many points. Use a larger value such as 3 if you want to view the attractor for an equilibrium or a cycle. Checking the **Lines** option connects the model points with a line to indicate the time sequence as the population jumps through phase space.

Clicking the **Run** button starts the simulation at time zero using the parameter values and initial condition specified in the form fields to the left of the plotting area. If you want to continue the simulation for additional time intervals, click the **More** button. Since the simulator may take some time to generate the many points and plot them in three-dimensions, a "Working…" message will appear while the simulator is running. The **Reset** button will reload the web page restore the default values to the form fields. The default parameter values and initial conditions are the same as for the LPA Time Series Simulator. (Some versions of the Firefox browser do not restore the parameter values.)

6. Examples for the Ricker Model

Despite its simplicity, the discrete-time Ricker population model can exhibit a variety of qualitatively different dynamics, depending on the value of the intrinsic rate of increase. Below is a list of examples.

Table 1. Examples for the Discrete-Time Ricker Model

r	Attractor	Comments
0.2	equilibrium	Equilibrium is approached smoothly.
1.9	equilibrium	Equilibrium is approached with damped oscillations.
2.4	2-cycle	Equilibrium loses stability and bifurcates into a cycle with period 2.
2.6	4-cycle	2-cycle loses stability and bifurcates into a cycle with period 4.
2.68	8-cycle	A period doubling cascade of cycles continues as r is increased.
2.85	chaos	Aperiodic fluctuations with a sensitivity to initial conditions.

2.9	chaos	Aperiodic fluctuations with a sensitivity to initial conditions.
2.92	5-cycle	Cycle inside of a period-locking interval for r.
2.95	chaos	Back to chaos on the other side of the period-locking interval.

7. Examples for the LPA Model

The LPA model can produce a wide variety of dynamics depending on the values of the model parameters. The following examples focus on the effect of changing the pupal cannibalism rate by adults, c_{pa}, and the adult mortality rate, μ_a. These two parameters where manipulated experimentally in the studies by Costantino *et al.* (1995, 1997). Other examples can be explored by manipulating the other parameters.

In addition to the values for c_{pa} and μ_a, the table below also suggests settings for the symbol size and the option for lines. For these examples, all other parameter values and options should be left at the default values.

On time series plot, use the **More** button to make sure the asymptotic dynamics are seen. On the phase space plot, if the symbol size is 0.1, click the **More** button several times to get a better visualization of the attractor.

Table 2. Examples for the LPA Model

c_{pa}	μ_a	Symbol	Lines	Attractor	Comments
0.01	0.01	3	no	equilibrium	Costantino *et al.* (1997) control
0.01	0.50	3	yes	2-cycle	Costantino *et al.* (1995) treatment
0.01	0.96	0.1	no	invariant loop	Costantino *et al.* (1995) treatment
0.00	0.96	0.1	no	double loop	Costantino *et al.* (1997) treatment
0.05	0.96	0.1	no	chaos	Costantino *et al.* (1997) treatment
0.10	0.96	3	yes	26-cycle	Costantino *et al.* (1997) treatment
0.25	0.96	3	yes	8-cycle	Costantino *et al.* (1997) treatment
0.35	0.96	0.1	no	chaos	Costantino *et al.* (1997) treatment
0.50	0.96	3	yes	3-cycle	Costantino *et al.* (1997) treatment
1.00	0.96	3	yes	6-cycle	Costantino *et al.* (1997) treatment

8. Plotly Graph Controls

The LPA Simulator uses the Plotly javascript graphics library. Graphs generated using this library can be manipulated. When the mouse pointer is placed inside the graph area a horizontal menu appears at the top of the view. The following table summarizes the various options provided by Plotly:

Table 3. Plotly Menu Options

The options below are available in all plots:		
Icon	**Option**	**Description**
	Download plot	A copy of the plot is downloaded as a PNG graphics file.
	Zoom	Use the mouse to zoom in on an area of the plot.
	Pan	Use the mouse to pan the plot. (Best used after zoom.)
	Reset axes	Reset the plot to the default axes.
	Closest hover	Hover the mouse close to a point to view the data value.
	Plotly logo	Click to go to the Plotly web site.
The options below are only available in the time series plots:		
Icon	**Option**	**Description**
	Box select	Used to select a region of the plot. (No function for LPA Simulator.)
	Lasso select	Used to select a region of the plot. (No function for LPA Simulator.)
	Zoom in	Zooms in on the center of the plot. (Plot can then be panned.)
	Zoom out	Zooms out from the center of the plot.
	Autoscale	Rescales the plot. (It is better to use Reset Axes.)
	Spike lines	Toggles spike lines to the x and y axes when hovering near a point.
	Compare data	Shows all data values for a point on the x-axis. (LPA Time Series only.)
The options below are only available in the phase space plot:		
Icon	**Option**	**Description**
	Orbital rotation	Use mouse to orbitally rotate the 3D plot.
	Turntable rotation	Use mouse to do a turntable rotation of the 3D plot.

	Reset camera	Resets the “camera viewpoint” of the 3D plot. (Similar to Reset Axes.)

In addition, on the LPA Time Series plot, you can click on a life stage in the legend at the top of the graph to hide or show that life stage. Double-clicking on a life stage with show only that life stage.

9. References

Chapman, R.N. 1928. Quantitative analysis of environmental factors. *Ecology* **9**: 111–122.

Costantino, R. F., and Desharnais, R. A. 1991. *Population Dynamics and the Tribolium Model: Genetics and Demography*. Springer-Verlag, New York.

Costantino, R. F., Cushing, J. M., Dennis, B., and Desharnais, R. A. 1995. Experimentally induced transitions in the dynamic behaviour of insect populations. *Nature* **375**: 227–230.

Costantino, R. F., Desharnais, R. A., Cushing, J. M., and Dennis, B. 1997. Chaotic dynamics in an insect population. *Science* **275**: 389–391.

Costantino, R. F., Desharnais, R. A., Cushing, J. M., Dennis, B., Henson, S. M., and King, A. A. 2005. Nonlinear stochastic population dynamics: The flour beetle *Tribolium* as an effective tool of discovery. *Advances in Ecological Research* **37**: 101–141

Cushing, J. M., Costantino, R. F., Dennis, B., Desharnais. R. A., and Henson, S. M. 2002. *Chaos in Ecology: Experimental Nonlinear Dynamics*. Academic Press, San Diego.

Dennis, B., Desharnais, R. A., Cushing, J. M., Henson, S. M., and Costantino. R. F. 2001. Estimating chaos and complex dynamics in an insect population. *Ecological Monographs* **71**: 277–303.

King, C. E., and Dawson, P. S. 1972. Population biology and the *Tribolium* model. *Evolutionary Biology* **5**: 133–227.

Mertz, D. B. 1972. The *Tribolium* model and the mathematics of population growth. *Annual Review of Ecology and Systematics* **3**: 51–78.

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