Exploring Sustainability through the Lens of the Lotka-Volterra Model in Population Ecology

N. Karjanto* and A. Peng

Abstract

The Lotka-Volterra equations, a cornerstone of predator-prey modeling, provide a valuable framework for understanding sustainable population dynamics. This chapter explores how these equations, through analysis of dynamic equilibrium and stability, illuminate sustainability principles within ecological systems. By analyzing predator-prey interactions, we gain important insights into population management, resource conservation, and the delicate balance of ecosystems. Furthermore, we discuss the broader implications of the Lotka-Volterra model, highlighting its potential to inform our understanding of complex systems dynamics in various fields. These include their relevance to educational frameworks, where the model can enhance student engagement with sustainability concepts and foster a deeper understanding of systems thinking.

Keywords: Predator-prey model, Lotka-Volterra equations, stability analysis, dynamic equilibrium, education and sustainability.

1 Introduction

Antelopes and lions, foxes and rabbits, lynx and hares, owls and mice, ladybirds and aphids, dragonflies and mosquitoes–these are just some of the predator-prey pairs commonly found in nature. Each of these relationships is more than a simple predator-prey interaction. The populations of each species are intricately linked, demonstrating the diversity and complexity of ecological interactions.

While this list includes pairs of animals interacting in natural cycles, it often overlooks the most formidable predator of all–humans. Our relentless pursuit for food and resources places us at the top of the predatory chain, with practices like fishing and hunting exerting unparalleled pressure on ecosystems and threatening the balance that sustains them. This raises not only ethical and moral questions about our responsibilities but also sustainability concerns: Can we fish sustainably without depleting marine ecosystems? How might understanding predator-prey dynamics contribute to sustainable resource management? As human activities significantly alter natural ecosystems, understanding these interactions is critical for promoting sustainability both in the wild and in human-modified systems such as agriculture and fisheries.

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To answer these sustainability questions, we turn to mathematical modeling, which provides structured insights into predator-prey dynamics. While mathematics excels at revealing systematic patterns, it also has limitations in capturing the full complexity of ecological systems.

In ecology, the interaction between predator and prey falls under the concept of *biocoenosis*. Also often referred as *life assemblage* or *biotic community*, it refers to an association of different species cohabiting in the same area, which we refer to as a *biotope*, at the same period (von Bertalanffy 1968). In general, many species interact with each other to form structurally complex web of communities, primarily for the purpose of nutrition and survival. A *trophic web*, or *food web*, represents this complex network of energy flow between organisms in an ecosystem, highlighting the interdependence among species (Murray 2007).

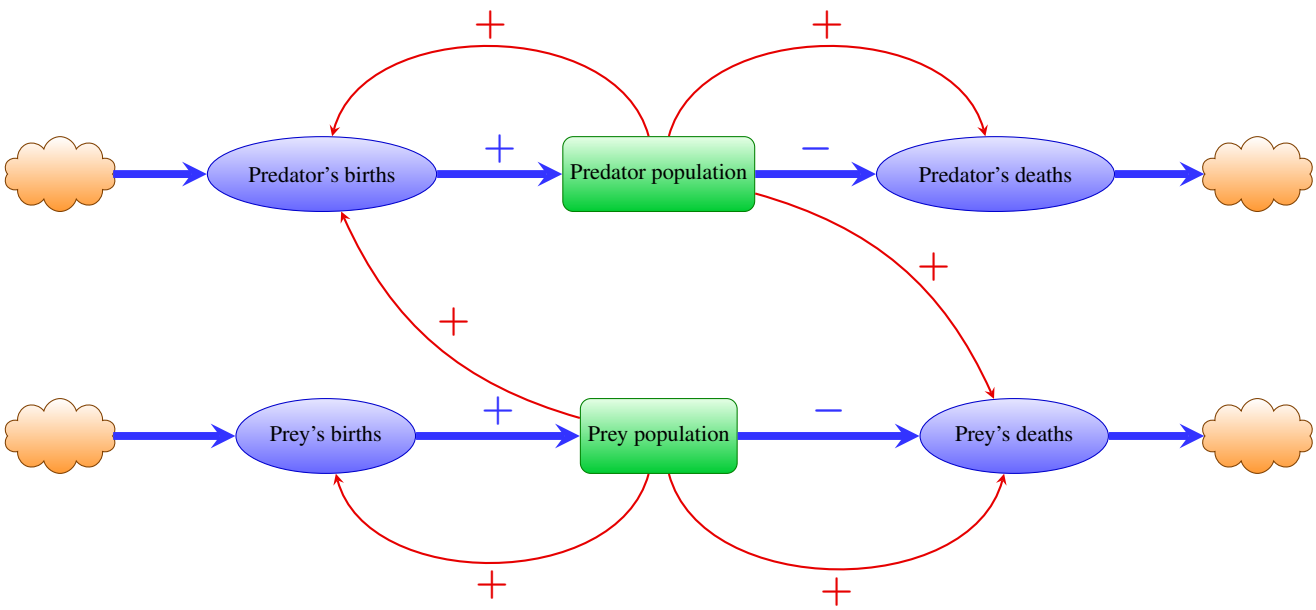

Figure 1: An interaction between predator and prey populations depicted as a stock-flow diagram.

Using a stock-flow diagram, we can visualize the dynamics of predator-prey interactions, as illustrated in Figure 1 (Roe et al. 2018). In this diagram, green rectangles represent stocks, denoting the predator and prey populations, while blue ovals indicate the inflows (birth rates) and outflows (death rates) affecting each population.

The straight blue arrows indicate inflow and outflow rates, with positive arrows for births and negative arrows for deaths. The clouds at both ends of the flow represent sources and sinks, assuming infinite capacity, which ensures no external constraints affect the flow.

The inflow rate of natality and the outflow rate of mortality for each species are affected by an amplifying and stabilizing feedback loops, respectively. These are indicted by the curved red arrows with positive sign that emerge from the stock of predator and prey populations to the inflow of birth rates and the outflow of death rates. Additionally, there are positive control effects of the prey population on the predator's natality rate and the predator's population on the prey's mortality rate. These feedback loops play a crucial role in sustainability studies, as they enable us to predict how changes in one population affect the entire ecosystem.

A mathematical model for the predator and prey relationship has been long known, the notable one being the Lotka-Volterra equations. This model describes how predator and prey populations interact over time. The equations capture the growth of the prey population and the dependency of the predator population on prey availability, leading to cyclical population dynamics.

This model was proposed by a Polish-American mathematician Alfred James Lotka in the 1910s and 1920s (Lotka 1920, Lotka 1925). In 1926, an Italian mathematician Vito Volterra published the same set of equations and credited Lotka's earlier work (Volterra 1926a, Volterra 1926b, Volterra 1928, Volterra 1931). The model that involves two species became known as the "classical Lotka-Volterra model" since then. This model can help us to understand the dynamics of predator-prey populations and how they oscillate and evolve over time. However, real ecosystems often involve complex food webs with multiple species interactions. This model, while foundational, may oversimplify these dynamics, limiting its applicability to more intricate ecosystems (Brauer 2012, Hannon and Ruth 2014).

In this chapter, we will discuss how this predator-prey model helps us to understand sustainability and promote sustainable ecology. This chapter is organized as follows. After this introduction, Section 2 describes the mathematical aspect of the Lotka-Volterra predator-prey model. It shows how to find a family of exact solutions and discusses its properties. It also explains the population equilibria and their characteristics. Section 3 explores how this predator-prey model can help us to understand sustainability, and how can we achieve that through the teaching and learning of mathematical modeling. Finally, Section 4 summarizes and concludes our discussion.

2 Lotka-Volterra Model

The classical Lotka-Volterra equations consist of a system of first-order nonlinear ordinary differential equations (ODEs) that describes the interaction of two species, one being a predator, whereas the other as prey in a biocoenotic system. Let $N(t)$ be the prey population and $P(t)$ be the predator population, then in the absence of predators, the prey population grows exponentially according to the following equation:

$$\frac{dN}{dt} = \alpha N, \qquad \alpha > 0.$$

Without prey, the predator population declines at a rate proportional to itself, that is

$$\frac{dP}{dt} = -\gamma P, \qquad \gamma > 0.$$

The positive constants α and γ are called *natural growth* and *natural decay coefficients*, respectively (Borrelli and Coleman 2004).

With both species present, the principle cause of death among the preys is being eaten by a predator. And similarly, the birth and survival rates of the predators depends on their available food supply, i.e., the prey. Assume also that the two species encounter each other at a rate that is proportional to both populations: $\sim NP$. The term $-\beta NP$, $\beta > 0$, decreases the natural growth rate of the prey, whereas the term $+\delta NP$, $\delta > 0$, increases the natural growth rate of the predator. The coefficients β and δ measure the likelihood that a predator-prey encounter removes prey and predator efficiency in converting food into fertility, respectively.

This assumption follows the *Population Law of Mass Action*, which states that at time t, the rate of change of one population due to interaction with another is proportional to the product of the two populations at that time t (Borrelli and Coleman 2004). Furthermore, by incorporating these interaction terms and applying the Balance Law to each population, i.e., the net rate of change of a population = rate in − rate out, we obtain the *predator-prey* (or *Lotka-Volterra*) model, given as follows:

$$\frac{dN}{dt} = N(\alpha - \beta P),$$
$$\frac{dP}{dt} = P(-\gamma + \delta N).$$

Observe also that this Lotka-Volterra model obeys an *autonomous system* of first-order differential equations, where the independent variable t does not appear explicitly on the right-hand side of each ODE (Zill 2023a, Zill 2023b). The model is also nonlinear, thanks to the interactions between the predator and prey.

Because there are no external factors that influence the predator and prey populations, the Lotka-Volterra model is an example of a *closed system*. This means that everything that affects the system is contained in the system. On the other hand, in an *open system*, external factors can affect the dynamics of the variables. In this context, the predator and prey populations could rise or fall because of those external factors (Brown 2007).

Furthermore, although we could, we do not impose any initial conditions to the system because our purpose is not to seek a particular solution but a general solution instead. Additionally, understanding global dynamics would be more interesting than focusing to a single dynamic of the solution.

2.1 Exact solution and its properties

In this subsection, we are using normalized variables to solve the system of ODEs. By scaling the independent variable and both dependent quantities, we reduce the number of parameters to only one. The equations become simpler, make it easier to analyze, and we can focus on the underlying dynamics of the model.

By introducing the following variables:

$$x(t) = \frac{\delta}{\gamma} N(t), \qquad y(t) = \frac{\beta}{\alpha} P(t), \qquad \tau = \alpha t, \qquad \text{and} \qquad \omega = \sqrt{\frac{\gamma}{\alpha}},$$

we obtain the normalized Lotka-Volterra equations:

$$\frac{dx}{d\tau} = x(1-y), \tag{1}$$
$$\frac{dy}{d\tau} = \omega^2 y(x-1). \tag{2}$$

By eliminating the temporal variable τ, we obtain a separable first-order ODE for the solution curves. By writing $y = y(x)$ and deducing using the chain rule, the ODE is given as follows:

$$\frac{dy}{dx} = \frac{dy}{dt}\left(\frac{dx}{dt}\right)^{-1} = \omega^2 \frac{(x-1)\,y}{x\,(1-y)}.$$

By separating the variables, that is, bring over all the y and x variables to the left and right sides of the equations, respectively, integrating both sides of the equation, we obtain a general solution of the normalized Lotka-Volterra equations:

$$\int \left(\frac{1}{y} - 1\right) dy = \omega^2 \int \left(1 - \frac{1}{x}\right) dx,$$
$$\ln y - y = \omega^2 (x - \ln x) + C_0, \qquad C_0 \in \mathbb{R}.$$

We can also express this exact solution in the following implicit form (Teschl 2012):

$$g(y) + \omega^2 g(x) = C_0, \tag{3}$$

where

$$g(x) = \ln x - x.$$

Another possible expression takes the following form (Olinick 2014):

$$\left(x^{\omega^2} e^{-\omega^2 x}\right)\left(y e^{-y}\right) = K_0, \qquad K_0 = e^{-C_0},$$

where it is obtained by exponentiating each side of equation (3). In all cases, the expressions are implicit rather than explicit.

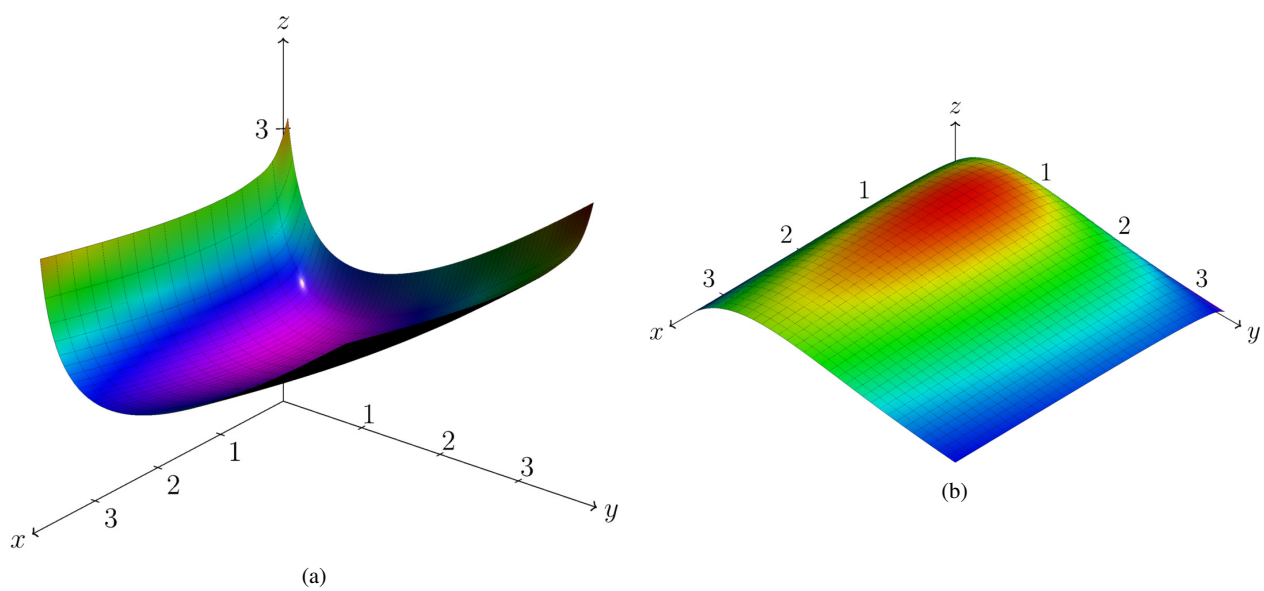

Figure 2: Three-dimensional renderings of the surface (a) $h(x,y) = g(y) + \omega^2 g(x)$ where the equilibrium point $(1,1)$ gives a local minimum value of $h(1,1) = 1 + \omega^2$, and (b) $f(x,y) = x^{\omega^2} e^{-\omega^2 x} y e^{-y}$ where the equilibrium point $(1,1)$ gives a local maximum value of $e^{-(1+\omega^2)}$. In both cases, we take $\omega = 0.5$, and hence the local minimum and local maximum values are $5/4$ and $e^{-5/4}$, respectively.

We have the following theorem regarding the solution function. This theorem confirms that the population equilibrium at $(1,1)$ is a local minimum, implying that both populations tend to oscillate around this balanced state.

Theorem 1. *Consider a two-variable function*

$$f(x,y) = x^{\omega^2} e^{-\omega^2 x} y e^{-y}, \tag{4}$$

then $f(x,y)$ has a local maximum at $(x,y) = (1,1)$ with the local minimum value of $e^{-\left(1+\omega^2\right)}$.

Proof. The first-order partial derivatives of f are given by

$$\begin{aligned} f_x &= \omega^2 \left(\frac{1}{x} - 1\right) x^{\omega^2} e^{-\omega^2 x} y e^{-y}, \\ f_y &= (1-y)\, e^y x^{\omega^2} e^{-\omega^2 x}. \end{aligned}$$

Equating both partial derivatives to zero, we obtain the critical values of f, i.e., $(0,0)$ and $(1,1)$.

The second-order partial derivatives of f are given as follows:

$$\begin{aligned} f_{xx} &= \omega^2 \left[\omega^2 \left(1 - \frac{1}{x}\right)^2 - \frac{1}{x^2}\right] x^{\omega^2} e^{-\omega^2 x} y e^{-y}, \\ f_{xy} &= \omega^2 \left(\frac{1}{x} - 1\right) x^{\omega^2} e^{-\omega^2 x} (1-y)\, e^{-y} = f_{yx}, \\ f_{yy} &= (y-2)\, e^{-y} x^{\omega^2} e^{-\omega^2 x}. \end{aligned}$$

The Hessian matrix H of f is given by

$$\begin{aligned} H(x,y) &= \begin{bmatrix} f_{xx} & f_{xy} \\ f_{yx} & f_{yy} \end{bmatrix} \\ &= x^{\omega^2} e^{-\omega^2 x} e^{-y} \begin{bmatrix} \omega^2 \left[\omega^2 \left(1 - \frac{1}{x}\right)^2 - \frac{1}{x^2}\right] y & -\omega^2 \left(1 - \frac{1}{x}\right)(1-y) \\ -\omega^2 \left(1 - \frac{1}{x}\right)(1-y) & y-2 \end{bmatrix}, \end{aligned}$$

and its determinant $\mathscr{D}$ is given by

$$\mathscr{D}(x,y) = \omega^2 \left\{ \omega^2 \left(1 - \frac{1}{x}\right)^2 \left[y - (1-y)^2\right] - \frac{y}{x^2} \right\} x^{2\omega^2} e^{-2\omega^2 x} e^{-2y}.$$

We observe that neither H nor $\mathscr{D}$ is defined for the trivial critical point $(x,y) = (0,0)$, and thus we focus on the nontrivial critical point $(x,y) = (1,1)$. By applying the Second Derivative Test for two-variable functions, we observe that

$$\begin{aligned} f_{xx}(1,1) &= -\omega^2 e^{-\left(1+\omega^2\right)} < 0, \\ \mathscr{D}(1,1) &= -\omega^2 e^{-2\left(1+\omega^2\right)} < 0. \end{aligned}$$

Because both values are negative, f has a local maximum at $(x,y) = (1,1)$ with the local maximum value of $f(1,1) = e^{-(1+\omega^2)}$.

Alternatively, we observe that the Hessian matrix at the nontrivial critical point is given by

$$H(1,1) = e^{-(1+\omega^2)} \begin{bmatrix} -\omega^2 & 0 \\ 0 & -1 \end{bmatrix}.$$

The eigenvalues of $H(1,1)$ are $\lambda_1 = -\omega^2 e^{-(1+\omega^2)}$ and $\lambda_2 = -e^{-(1+\omega^2)}$. Because both eigenvalues are negative, $H(1,1)$ is a negative definite matrix. The Hessian matrix's negative definiteness indicates that the function's critical point is a local maximum. Thus, indeed that f attains an isolated local maximum at $(x,y) = (1,1)$. This completes the proof. □

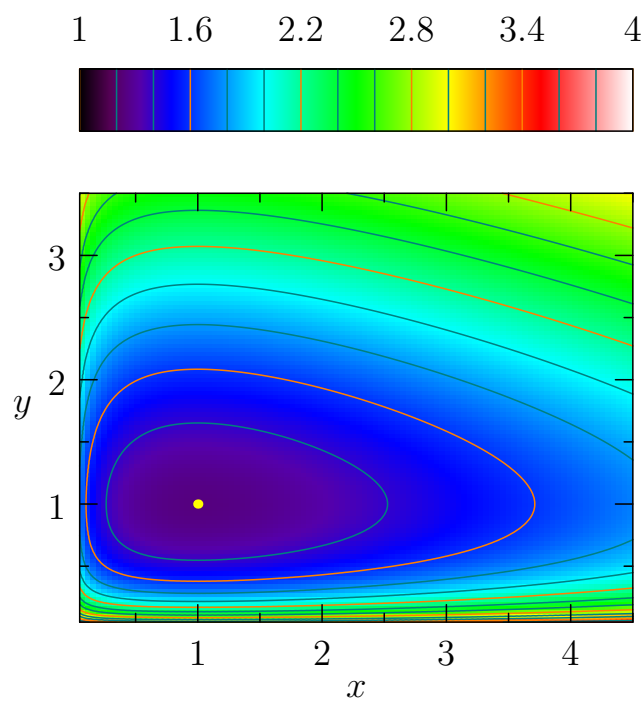

Figure 3: Contour plots of the surface $h(x,y) = g(y) + \omega^2 g(x)$ for $\omega = 0.5$. The critical point $(x,y) = (1,1)$ is shown as a yellow dot.

Remark 1. The choice for the two-variable function $f(x,y)$ as in (4) is far from unique to understand the characteristics of the exact solution of the Lotka-Volterra equation. If we choose another function, let say, $h(x,y) = \ln f(x,y)$, that is, the left side of equation (3), we would obtain different Hessian matrix, its determinant, its associated eigenvalues, and its local maximum value even though the nontrivial critical point remain the same. Furthermore, we can also consider the negative of either $f(x,y)$ or $h(x,y)$, for which the function admits a local minimum value instead of a local maximum value. In this case, the Hessian matrix at the critical point is positive definite because its eigenvalues are both positive.

To investigate the direction of the contour plots, observe again the normalized Lotka-Volterra equations (1)–(2) and divide the population quadrant into four subquadrant regions along the lines $x = 1$ and $y = 1$, which makes the critical point as the center of these regions. See the left panel of Figure 4. Using the values of x and y in each of these subquadrants, we can investigate whether the value of $\dot{x} = dx/d\tau$ or $\dot{y} = dy/d\tau$ is positive or negative, and hence determine the direction of phase trajectories in each region, which is shown on the right panel of Figure 4. The result is summarized in Table 1.

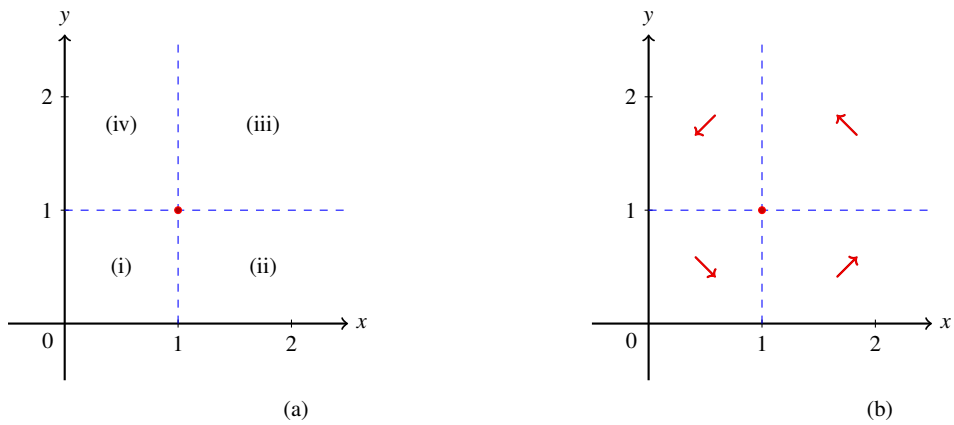

Figure 4: (a) The population quadrant is divided into four subquadrants with the center at $(1,1)$. The naming of the region proceeds in the counterclockwise direction, which starts at the bottom left subquadrant and ends at the top left region. (b) The direction of phase trajectories in each of the region.

Table 1: The value of derivatives $\dot{x}$ and $\dot{y}$ for each of the four regions depicted in Figure 4 and the direction of the phase trajectories in that particular subquadrant.

Region	Range of x	Range of y	Value of derivatives	Direction of phase trajectories	
(i)	$0 < x < 1$	$0 < y < 1$	$\dot{x} > 0, \dot{y} < 0$	$\searrow$	(South East)
(ii)	$x > 1$	$0 < y < 1$	$\dot{x} > 0, \dot{y} > 0$	$\nearrow$	(North East)
(iii)	$x > 1$	$y > 1$	$\dot{x} < 0, \dot{y} > 0$	$\nwarrow$	(North West)
(iv)	$0 < x < 1$	$y > 1$	$\dot{x} < 0, \dot{y} < 0$	$\swarrow$	(South West)

2.2 Population equilibrium and its stability

Population equilibrium occurs when the growth rates of both species stabilize, resulting in no net change in population levels. In this state, the predator and prey populations reach a dynamic balance. These constant solutions of an autonomous system are called *equilibrium solutions*. Mathematically, they are given as follows:

$$\begin{aligned} x(1-y) = 0 \quad &\Longrightarrow \quad x = 0 \quad \text{or} \quad y = 1, \\ \omega^2 y(x-1) = 0 \quad &\Longrightarrow \quad y = 0 \quad \text{or} \quad x = 1. \end{aligned}$$

The corresponding point orbits in the xy-plane are called the *equilibrium points*, which are located at the *population quadrant*, that is, the first quadrant of the xy-plane with $x \geq 0$ and $y \geq 0$. It follows that there are two equilibrium points:

$$(x,y) = (x_0, y_0) = (0,0) \qquad \text{and} \qquad (x,y) = (x_1, y_1) = (1,1).$$

These equilibrium points are also called *critical points* or *fixed points* in the literature.

On the one hand, the first equilibrium solution effectively represents the extinction of both species. If both populations are at 0 level, then they will continue to be so indefinitely. On the other hand, the second equilibrium solution represents a fixed point at which both populations sustain their current, non-zero numbers, indefinitely.

To assess the stability of equilibrium points, we can analyze small perturbations around these points using the *Jacobian matrix*, which represents the sensitivity of each species' growth rate to changes in population size. Let

$$\begin{aligned} \frac{dx}{d\tau} &= F(x,y), \\ \frac{dy}{d\tau} &= G(x,y), \end{aligned}$$

be a system of ODEs. Let $(x,y) = (\xi_0, \zeta_0)$ be an equilibrium point of the system, then by Taylor-expanding the expressions on the right-side about the equilibrium point, we obtain

$$\begin{aligned} F(x,y) &= F(\xi_0,\zeta_0) + \frac{\partial F}{\partial x}(\xi_0,\zeta_0)(x-\xi_0) + \frac{\partial F}{\partial y}(\xi_0,\zeta_0)(y-\zeta_0) + \varepsilon_1(x,y), \\ G(x,y) &= G(\xi_0,\zeta_0) + \frac{\partial G}{\partial x}(\xi_0,\zeta_0)(x-\xi_0) + \frac{\partial G}{\partial y}(\xi_0,\zeta_0)(y-\zeta_0) + \varepsilon_2(x,y). \end{aligned}$$

Let $\widehat{x} = x - \xi_0$ and $\widehat{y} = y - \zeta_0$, then the associated linearized system can be written as

$$\frac{d}{d\tau}\begin{bmatrix}\widehat{x}\\ \widehat{y}\end{bmatrix} = J(\xi_0,\zeta_0)\begin{bmatrix}\widehat{x}\\ \widehat{y}\end{bmatrix} + \begin{bmatrix}\varepsilon_1(\widehat{x},\widehat{y})\\ \varepsilon_2(\widehat{x},\widehat{y})\end{bmatrix}, \qquad \det J(\xi_0,\zeta_0) \neq 0.$$

In this expression, the matrix J is called the *Jacobian* or *community matrix* (Kot 2001, Murray 2007), and is defined as follows:

$$J(x,y) = \begin{bmatrix} \dfrac{\partial F}{\partial x} & \dfrac{\partial F}{\partial y} \\ \dfrac{\partial G}{\partial x} & \dfrac{\partial G}{\partial y} \end{bmatrix}.$$

In particular, the Jacobian associated with the Lotka-Volterra model is given by

$$J(x,y) = \begin{bmatrix} 1-y & -x \\ \omega^2 y & \omega^2(x-1) \end{bmatrix},$$

which can be easily obtained by taking partial derivatives of $F(x,y) = x(1-y)$ and $G(x,y) = \omega^2 y(x-1)$ with respect to x and y.

The Jacobian matrix provides insight into the local behavior of the system near equilibrium points, playing an essential role in determining stability and system response to small perturbations. Having identified equilibrium points, we now explore their stability, starting with the extinction equilibrium point.

2.2.1 Extinction equilibrium point

Let us consider the equilibrium point at the origin $(x_0, y_0) = (0,0)$, which is called the *extinction equilibrium point*. The associated community matrix J_0 is given by

$$J_0 = J(0,0) = \begin{bmatrix} 1 & 0 \\ 0 & -\omega^2 \end{bmatrix},$$

with eigenvalues

$$\lambda_1 = 1 > 0 \qquad \text{and} \qquad \lambda_2 = -\omega^2 < 0.$$

This equilibrium point is a saddle point, and hence unstable. If it were stable, nonzero populations might be attracted towards it. Such dynamics might lead towards the extinction of both species for many cases of initial population levels.

2.2.2 Oscillation equilibrium point

In a predator-prey system, populations typically do not stabilize at a single value but instead oscillate around equilibrium points. Prey populations tend to rise and fall, followed by similar oscillations in predator populations, with a slight delay due to their dependency on prey availability.

In this subsubsection, we investigate the characteristics of the *oscillation equilibrium point* at $(x_1, y_1) = (1,1)$. The associated community matrix J_1 is given by

$$J_1 = J(1,1) = \begin{bmatrix} 0 & -1 \\ \omega^2 & 0 \end{bmatrix},$$

with both eigenvalues are purely imaginary and conjugate to each other:

$$\lambda = \lambda_{1,2} = \pm\, \omega\, i.$$

For this case, the equilibrium point must either be a center for a closed orbit or a spiral point. It turns out that $(x_1, y_1) = (1,1)$ is a stable center equilibrium point. Both predator and prey populations oscillate indefinitely around this equilibrium point.

To find out the trajectory of the closed orbit around this equilibrium point, consider again the linearized system. From

$$\frac{d\widehat{x}}{d\tau} = -\widehat{y},$$
$$\frac{d\widehat{y}}{d\tau} = \omega^2\, \widehat{x},$$

we obtain

$$\frac{d\widehat{y}}{d\widehat{x}} = -\omega^2 \frac{\widehat{x}}{\widehat{y}}.$$

Separating the variables and integrating both sides of the equation, we acquire a family of ellipses centered at $(1,1)$:

$$(x-1)^2 + \frac{(y-1)^2}{\omega^2} = \kappa^2, \qquad 0 < \kappa < 1.$$

If $0 < \omega^2 < 1$, the ellipses are elongated somewhat in the horizontal direction. Furthermore, for $\kappa \to 0$, the ellipse shrinks to the equilibrium point $(1,1)$, whereas for $\kappa \to 1$, the value of x may become zero, which is a contradiction with the assumption that $x > 0$.

Figure 5 shows a family of ellipses centered at the oscillation equilibrium point $(x,y) = (1,1)$ for a particular value of ω and several values of κ. It satisfies Volterra's First Law, which states that if the system is undisturbed, the duo predator and prey populations would evolve and stay on their orbit. For a particular initial condition, the orbit would be traced counterclockwise. The situation also occurs for the nonlinearized Lotka-Volterra system for which its contour plots were depicted in Figure 3.

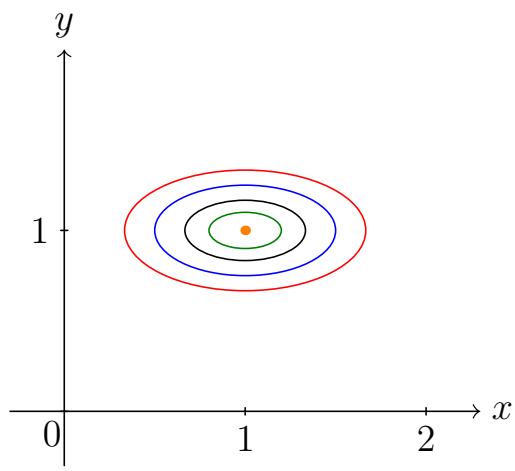

Figure 5: A family of ellipses centered at $(x,y) = (1,1)$ (shown as the orange dot) for $\omega = 0.5$ and several values of κ: $\kappa = 0.2$ (green), $\kappa = \frac{1}{3}$ (black), $\kappa = 0.5$ (blue), and $\kappa = \frac{2}{3}$ (red). The trajectories trace in the counterclockwise direction, as explained in Table 1 and Figure 4.

To express an explicit solution for the linearized system for the oscillation fixed point, we first need to calculate the eigenvectors. For $\lambda_1 = \omega i$ and $\lambda_2 = -\omega i$, the associated eigenvectors $\mathbf{u}_1$ and $\mathbf{u}_2$ are given as follows:

$$\mathbf{u}_1 = \begin{bmatrix} -1 \\ \omega i \end{bmatrix}, \qquad \text{and} \qquad \mathbf{u}_2 = \begin{bmatrix} 1 \\ \omega i \end{bmatrix}.$$

The solution to the linearized system is then given by:

$$\begin{bmatrix} x-1 \\ y-1 \end{bmatrix} = c_1 \begin{bmatrix} -1 \\ \omega i \end{bmatrix} e^{\omega i \tau} + c_2 \begin{bmatrix} 1 \\ \omega i \end{bmatrix} e^{-\omega i \tau}, \qquad c_1, c_2 \in \mathbb{C}.$$

Or, by defining the complex constants c_1 and c_2, we can express the solutions with real-valued constants:

$$x(\tau) = 1 + A\cos(\omega\tau) - B\sin(\omega\tau) = 1 + C\cos(\omega\tau + \phi),$$
$$y(\tau) = 1 + \omega B\cos(\omega\tau) + \omega A\sin(\omega\tau) = 1 + C\,\omega\sin(\omega\tau + \phi),$$

where the constant C and phase ϕ are determined by the initial conditions, and the following relations are hold:

$$C^2 = A^2 + B^2, \qquad \tan\phi = \frac{B}{A}, \qquad A, B \in \mathbb{R},$$
$$A = c_2 - c_1, \qquad B = i(c_1 + c_2).$$

From the obtained solutions, we can observe the following characteristics:

- The average populations are $\overline{x} = 1$ and $\overline{y} = 1$.
- The sizes of the predator and prey populations vary sinusoidally with period $2\pi/\omega$, independent of the initial conditions.
- The predator and prey populations are out of phase by one-quarter of a cycle. The prey leads and the predator lags.

Figure 6 depicts the graphs of the solution of the linearized Lotka-Volterra system for a selected value of parameters, showing the periodic nature of both predator and prey populations.

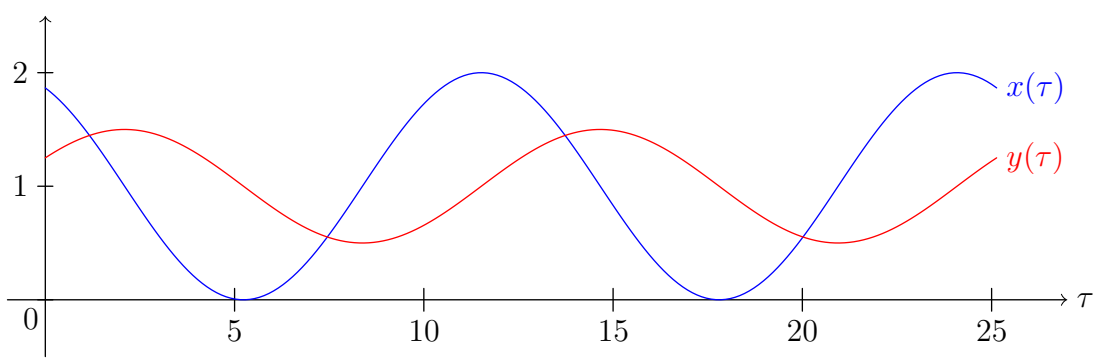

Figure 6: The solutions of the linearized system for $C = 1$, $\omega = 0.5$, and $\phi = \pi/3$. The normalized prey x and predator y variables are depicted in blue and red curves, respectively.

While the classical Lotka-Volterra model offers valuable insights, it has limitations. A modified version of the Lotka-Volterra model is that the prey population follows the logistic model instead of exponential model, in addition to its loss due to kills by the predator (Baker 2016, Brown 2007, Conrad 2003, Noonburg 2014, Olinick 2014, MacCluer et al. 2019). Incorporating environmental variables such as habitat quality or climate conditions makes the model more adaptable to real-world ecosystems under stress, which is essential for sustainability planning.

3 Understanding sustainability through modeling education

While the previous section discusses the mathematical properties and solutions of the Lotka-Volterra model, it is essential to recognize the broader implications of these findings for sustainability education. We understand that the Lotka-Volterra model provides critical insights into the dynamics of predator-prey relationships, which are essential for achieving sustainability in ecological systems. This section explores how the Lotka-Volterra model can serve as a powerful educational tool, enhancing students' understanding of sustainability concepts and their applications in real-world scenarios.

The Lotka-Volterra model not only provides valuable insights into fundamental interactions within ecosystems but also serves as a critical framework for understanding sustainability from a mathematical perspective. The insights gained from this model can significantly impact sustainable development across various domains, including environmental, social, and economic contexts, where the principles of predator-prey dynamics are applicable.

From a mathematical perspective, our earlier discussion on the solution of the Lotka-Volterra model suggests that sustainability between predators and prey could entail over time when the interaction between predators and prey leads to stable coexistence or oscillatory behavior, which is shown in Figure 6. Stable coexistence is an indication of sustainability, as both predators and prey can persist over time. This balance is often achieved through a combination of factors such as birth rates, death rates, and the efficiency of predation.

For example, if prey have a high reproductive rate and predators are not overly efficient at catching prey, a stable coexistence may be possible (as illustrated in Figure 1). Oscillatory behavior may indicate a less stable system, but it can still be sustainable if the oscillations are within certain limits (see Figure 6). However, if oscillations become too extreme or unpredictable, it can disrupt the stability of the ecosystem and lead to a decline in sustainability.

By analyzing the equilibrium points of the Lotka-Volterra equations, we can determine the stable states of a model of a system from different applications. These equilibrium points represent situations where the various elements of the system are in balance and can provide insights into the conditions necessary for sustainable development. Studies in different ecosystem scenarios have been conducted in this line of direction.

For instance, in fisheries management, the assumptions of the Lotka-Volterra model are utilized to determine maximum sustainable yields, thereby optimizing resource use while ensuring ecological balance (Basir et al. 2023). Additionally, in the medical area, (Gao et al. 2025) introduced the dynamics of infectious diseases in predator and prey populations and established essential criteria for the system's decline and sustainability.

As the Lotka-Volterra model is a classical model that is presented in nearly every differential equations text and mathematical biology text (Czocher et al. 2024), and sustainability is a crucial concept and an important issue in our current world, the Lotka-Volterra model could provide numerous opportunities to develop students' knowledge of sustainability and their awareness of sustainable development with appropriate teaching design. Integrating the Lotka-Volterra model into educational curricula can foster a deeper understanding of sustainability among students, equipping them with the tools to analyze complex ecological interactions. Here are a few suggestions.

Firstly, when introducing the Lotka-Volterra model, we encourage not only to mention its popularity in ecosystems but also its utility in broad competitive phenomena such as in political, social, and business fields, whose nature of the competitive interactions can be modeled by using the Lotka-

Volterra model (Avetisyan 2024, Marino et al. 2023, Kawira et al. 2020). In such ways, it may prompt students to reflect on how to make a balance in different competitive scenarios and maintain a common sustainable development.

Secondly, in a mathematical modeling class, we would encourage students to pose mathematical questions related to sustainability in different phases of the cyclic process of mathematical modeling by using the Lotka-Volterra model. For instance, in the phase of formulating the mathematical model, students are encouraged to pose questions such as how sustainability could be related to a mathematical model; during solving the Lotka-Volterra model, students are encouraged to pose questions such as the connection of specific meaning of sustainability and the solution of equilibrium points; in the phase of using the Lotka-Volterra model to represent the real-world scenario, students are encouraged to pose questions such as how to contribute to achieving the Sustainable Development Goals (SDGs) set for 2030 by UNESCO from the perspective of the predator-prey system.

In such ways, students are expected to develop a holistic perspective of things and system thinking and make better decisions in management or conservation issues in the complex social and natural world toward sustainable development.

4 Conclusion

In this chapter, we explored the classic Lotka-Volterra predator-prey model as a tool for understanding ecological dynamics and its implications for sustainability. The model provides insights into population equilibrium, stability, and the oscillatory nature of population cycles, highlighting the balance between species and sustainable population management. It demonstrates how predator and prey populations can exhibit stable, repeating patterns while avoiding extinction or uncontrolled growth under ideal conditions—key to maintaining ecosystem stability.

Moreover, the model emphasizes the importance of feedback loops, where predator and prey populations influence each other's growth and survival. These dynamics reflect broader ecological principles, such as the role of resource availability and natural constraints on species populations. By understanding these principles, we can apply mathematical insights to address real-world sustainability challenges, including natural resource management and biodiversity conservation.

Finally, integrating the Lotka-Volterra model into educational settings offers a valuable approach to teaching sustainability through mathematical modeling. Engaging students with such models fosters a deeper understanding of ecological balance and encourages systems thinking. Through continued study of predator-prey dynamics, their adaptations, and human impacts, we can develop innovative strategies for sustainable resource management, environmental preservation, and ecosystem conservation. Future research and educational efforts can build upon this model to explore complex ecological interactions and support sustainability in natural and human-modified systems.

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