

2.6 A Predator-Prey Model: the Lotka–Volterra System

A struggle for existence inevitably follows from the high rate at which all organic beings tend to increase. Every being, which during its natural lifetime produces several eggs or seeds, must suffer destruction during some period of its life, and during some season or occasional year; otherwise, on the principle of geometrical increase, its numbers would quickly become so inordinately great that no country could support the product. Hence, as more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with the individuals of distinct species, or with the physical conditions of life. It is the doctrine of Malthus applied with manifold force to the whole animal and vegetable kingdoms; for in this case there can be no artificial increase of food, and no prudential restraint from marriage. Although some species may be now increasing, more or less rapidly, in numbers, all cannot do so, for the world would not hold them. . . .

The amount of food for each species of course gives the extreme limit to which each can increase; but very frequently it is not the obtaining food, but the serving as prey to other animals, which determines the average numbers of a species.⁵

Charles Darwin

In 1926, Humberto D’Ancona, an Italian biologist, completed a statistical study of the changing populations of various species of fish in the northern reaches of the Adriatic Sea. His estimates of the populations during the years 1910 to 1923 were based on the numbers of each species sold at the fish markets of the three ports Trieste, Fiume, and Venice. D’Ancona assumed, as we will, that the numbers of the various species in the markets reflected the relative abundance of the species in the Adriatic. A part of the data is given in Table 2.6.1.

TABLE 2.6.1 Percentages of Predators in the Total Catch (Predators + Prey)

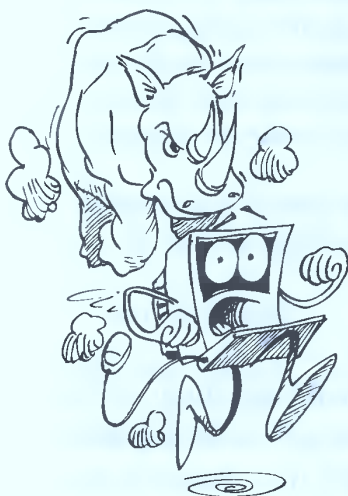
Port	1914	1915	1916	1917	1918	1919	1920	1921	1922	1923
Fiume	12%	21%	22%	21%	36%	27%	16%	16%	15%	11%
Trieste	14%	7%	16%	15%	—	18%	15%	13%	11%	10%

As often happens, the data do not provide overwhelming support for any particular theory of changing fish populations. D’Ancona observed, however, that the percentages of predator species were generally higher during and immediately after World War I (1914–1918). Fishing was drastically curtailed during the war years as fishermen abandoned their nets to fight in the war, and D’Ancona concluded that the decline in fishing caused the change in the proportions of predator to prey. He formulated the hypothesis that during the war the predator-prey community was close to its natural state of a relatively high proportion of predator fish, while the more intensive fishing

⁵From Charles Darwin, “Struggle for Existence,” *The Origin of Species*, new ed., Chap. 3 (from 6th English ed.) (New York: Appleton, 1882). He was not a mathematician, but his insight as a modeler was profound.

of the prewar and postwar years disturbed that equilibrium to the advantage of the prey species. Unable to give a reason for the phenomenon, D'Ancona asked his father-in-law, the noted Italian mathematician Vito Volterra (1860–1940), whether there was a mathematical model that might cast some light on the matter. Within a few months, Volterra had outlined a series of models for the interactions of two or more species. Alfred Lotka independently created similar mathematical models.⁶

Building the Predator-Prey Model



The simplest model of predator and prey association includes only natural growth or decay and the predator-prey interaction itself. We assume all other relationships to be negligible. We will assume that the prey population grows according to a first-order rate law in the absence of predators, while the predator population declines according to a first-order rate law if the prey population is extinct. The following principle gives us a way to convert species interactions into terms in a mathematical model.

Population Law of Mass Action. 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 .

Now let's apply the Balance Law to each population:

Net rate of change of a population = Rate in – Rate out

Denoting the predator population at time t by $x(t)$, the prey population at time t by $y(t)$, and using the Balance Law and the Population Law of Mass Action, we see that the *predator-prey* (or *Lotka–Volterra*) model is the *autonomous system*

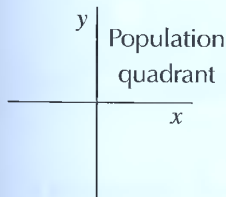
$$\begin{aligned}x' &= (-a + by)x = -ax + bxy \\ y' &= (c - kx)y = cy - kxy\end{aligned}\tag{1}$$

where the rate constants a, b, c, k are positive. The linear rate terms $-ax$ and cy model the natural decay and growth, respectively, of the predator and the prey population as if each were isolated from the other (so y would no longer be the food supply for x). The quadratic terms $+bxy$ and $-kxy$ model the effects of mass action on the rates of



Vito Volterra

⁶Volterra eventually wrote a book on his theories, *Leçons sur la théorie mathématique de la lutte pour la vie* (Paris: Gauthier-Villars, 1931; reproduced by University Microtexts, Ann Arbor, Mich., 1976). The Soviet biologist G. F. Gause (or Gauze) tested Volterra's theories by carrying out numerous laboratory experiments with various competing and predatory microorganisms. He published his results in *The Struggle for Existence* (Baltimore: Williams & Wilkins, 1934; reissued by Hafner, New York, 1964). D'Ancona defended Volterra's work in a book that again used the memorable phrase of Malthus and Darwin, *The Struggle for Existence* (Leiden: E. J. Brill, 1954). A. J. Lotka, an American biologist and, later in life, an actuary, arrived at many of the same conclusions independently of Volterra; see his book *Elements of Physical Biology* (Baltimore: Williams & Wilkins, 1925); reprinted as *Elements of Mathematical Biology* (New York: Dover, 1956).



change of the two species: food promotes the predator population's growth rate, while serving as food diminishes the prey population's growth rate.

Constant solutions of an autonomous system are *equilibrium solutions*. The corresponding point orbits in the xy -plane are *equilibrium points*. We find the coordinates of the equilibrium points of system (1) by solving the equations $-ax + bxy = 0$, $cy - kxy = 0$. The equilibrium points are the origin and the point $(c/k, a/b)$, which is inside the *population quadrant* (that part of the xy -plane with $x \geq 0$, $y \geq 0$). As we shall see later, the autonomous system (1) has a unique orbit through each point (x_0, y_0) . Moreover, that orbit does not depend on when the clock is started, but only on the solve time. It follows that two distinct orbits of system (1) can not intersect (for if they did intersect at a point p , then start the clock on both orbits at p and the uniqueness result implies that the orbits coincide). Now the positive x -axis is an orbit of the system. To see this, observe that on the x -axis system (1) becomes $x' = -ax$, $y' = 0$. This system has the solution $x = x_0 e^{-at}$, $y = 0$, where $(x_0, 0)$ is any point on the positive x -axis. In the same way we see that the positive y -axis is an orbit. So an orbit originating inside the population quadrant stays inside. An orbit of an autonomous system that intersects itself repeats the same path forever and hence arises from a periodic solution (just restart the clock at the intersection period to see that the closed orbit is repeated forever). So orbits of an autonomous system that arise from periodic solutions are closed curves. These closed curves are *cycles*.

EXAMPLE 2.6.1

See the Library entry under Population Models.

The amplitude of a population curve is its maximal distance from the equilibrium value.

ODEA Predator-Prey Orbits and Component Graphs

Figures 2.6.1 and 2.6.2 show orbits and component graphs of the system

$$x' = -x + xy/10, \quad y' = y - xy/5$$

with equilibrium points $(0, 0)$ and $(5, 10)$. In Figure 2.6.1 the numerically computed orbits through the points $(5, 20)$, $(5, 30)$, and $(5, 40)$ seem to be closed curves (i.e., *cycles*) that turn clockwise around the equilibrium point $(5, 10)$. The component graphs of Figure 2.6.2 suggest that the solutions are indeed periodic, that predator peaks lag behind prey peaks (is that what you would expect?), and that the larger the amplitude of a population curve, the longer the period.

Do these computational results have anything to do with real species?

Volterra's Laws

Volterra summarized his conclusions about the solutions of system (1) in the form of three laws.

THEOREM 2.6.1

The Law of the Periodic Cycle (Volterra's First Law)

The fluctuations of the populations of the predator and its prey are periodic. The period depends on the values of the rate coefficients of system (1) and on the initial data. The period increases with the amplitude of the corresponding cycle.

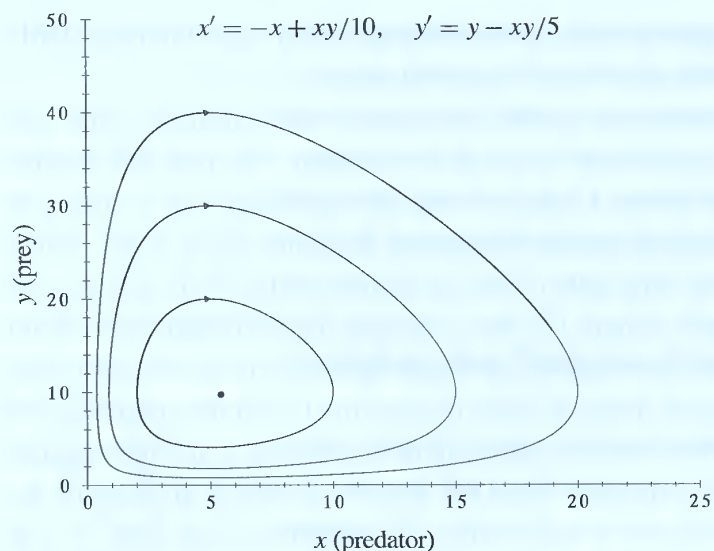


FIGURE 2.6.1 Some closed orbits of a predator-prey system. (Example 2.6.1).

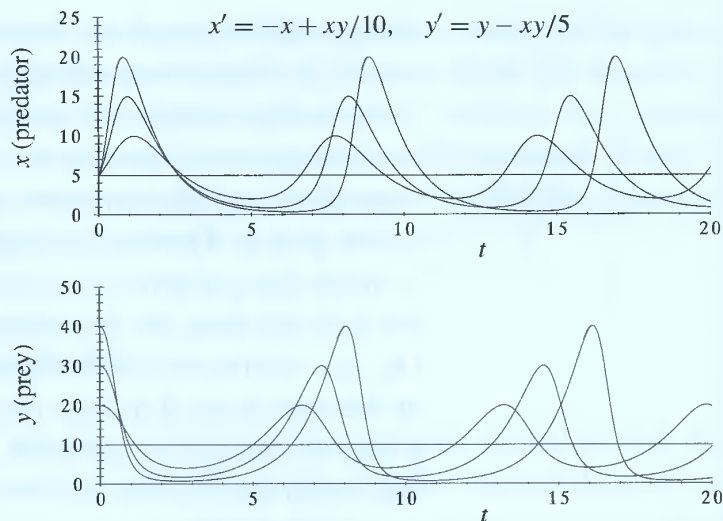


FIGURE 2.6.2 The component graphs for orbits of Figure 2.6.1 (Example 2.6.1).

Proof. Divide the second rate equation of system (1) by the first and obtain

$$\frac{dy}{dx} = \frac{cy - kxy}{-ax + bxy} = \left(\frac{y}{-a + by} \right) \left(\frac{c}{x} - k \right) \quad (2)$$

Separating the variables in ODE (2), we get

$$\left(\frac{c}{x} - k \right) dx + \left(\frac{a}{y} - b \right) dy = 0 \quad (3)$$

Antidifferentiating each term in (3), we see that an equation for an orbit in the population quadrant is the level curve

$$(c \ln x - kx) + (a \ln y - by) = C \quad (4)$$

where C is a constant. If we want the equation of the orbit through the point (x_0, y_0) , where x_0 and y_0 are positive, then we evaluate C as follows:

$$(c \ln x_0 - kx_0) + (a \ln y_0 - by_0) = C \quad (5)$$

Use the value of C given in (5) and exponentiate each side of (4) (recall that $e^{A+B} = e^A e^B$, $e^{\alpha \ln \beta} = e^{\ln(\beta^\alpha)} = \beta^\alpha$):

$$\begin{aligned} (e^{c \ln x - kx}) (e^{a \ln y - by}) &= (e^{c \ln x_0 - kx_0}) (e^{a \ln y_0 - by_0}) \\ (e^{c \ln x} e^{-kx}) (e^{a \ln y} e^{-by}) &= (e^{c \ln x_0} e^{-kx_0}) (e^{a \ln y_0} e^{-by_0}) \\ (x^c e^{-kx}) (y^a e^{-by}) &= (x_0^c e^{-kx_0}) (y_0^a e^{-by_0}) \end{aligned} \quad (6)$$

Formula (6) defines a simple closed curve (i.e., a cycle) for each $(x_0, y_0) \neq (c/k, a/b)$ inside the population quadrant (see Problem 11). So the corresponding solution $x = x(t)$, $y = y(t)$ of system (1) is indeed periodic. ■

The periods of the cycles increase with the amplitudes of the cycles. The computed orbits of Figure 2.6.1 show some of the cycles; we can estimate the corresponding periods from the population curves in Figure 2.6.2.

Remarkably, the average population of each species over a cycle is a fixed constant that is independent of the particular cycle.

THEOREM 2.6.2**The Law of Averages (Volterra's Second Law)**

In system (1), the average predator and prey populations over the period of every cycle are, respectively, c/k and a/b .

Proof. Suppose that $x = x(t)$, $y = y(t)$ is a nonconstant solution that defines a cycle of period T . The average populations \bar{x} and \bar{y} over one period are

$$\bar{x} = \frac{1}{T} \int_0^T x(t) dt, \quad \bar{y} = \frac{1}{T} \int_0^T y(t) dt \quad (7)$$

To show that $\bar{x} = c/k$ rearrange the second ODE of system (1),

$$x(t) = \frac{c}{k} - \frac{1}{k} \frac{y'(t)}{y(t)} \quad (8)$$

Then integrate each side of (8) from 0 to T , divide by T , use (7), and integrate:

$$\begin{aligned} \bar{x} &= \frac{1}{T} \int_0^T x(t) dt = \frac{1}{T} \int_0^T \frac{c}{k} dt - \frac{1}{T} \int_0^T \frac{1}{k} \frac{y'(t)}{y(t)} dt \\ &= \frac{c}{k} - \frac{1}{T} \cdot \frac{\ln y(T) - \ln y(0)}{k} = \frac{c}{k} \end{aligned}$$

since $y(T) = y(0)$. A similar argument shows that $\bar{y} = a/b$. ■

The Law of Averages brings us closer to the actual data given earlier for the fish catches, because that data consists of averages. For example, look at the entry in Table 2.6.1 for the port of Fiume for 1919. According to the table, the population x of predator species comprises 27% of the total fish population $x + y$. Since 27% is an average over the year 1919, let's assume we can replace x and y with their respective averages \bar{x} and \bar{y} over one period, and so

$$0.27 = \frac{\bar{x}}{\bar{x} + \bar{y}} = \frac{c/k}{c/k + a/b}$$

where the last equality follows from the Law of Averages. Since $(c/b, a/k)$ is the equilibrium population point of the predator-prey system (1), we see a direct connection between the data of Table 2.6.1 and the parameters in Volterra's model.

Now to put the fishermen into the picture.



Why Harvesting Hurts the Predator and Helps the Prey

The simplest harvesting model is *constant-effort harvesting*, in which the amount caught per unit of time is proportional to the population:

$$\begin{aligned}x' &= -ax + bxy - H_1x = (-a - H_1 + by)x \\y' &= cy - kxy - H_2y = (c - H_2 - kx)y\end{aligned}\quad (9)$$

The nonnegative numbers H_1 and H_2 are the harvesting coefficients. When harvesting occurs, the equilibrium point lying inside the population quadrant shifts to the left and upward from $x = c/k$, $y = a/b$ to the point

$$x = (c - H_2)/k, \quad y = (a + H_1)/b \quad (10)$$

Assume that $H_2 < c$. If $H_2 \geq c$, then the heavy harvesting of the prey species y doesn't leave enough food for the predator x , so the predator species heads toward extinction (modeled by a nonpositive x -coordinate for the equilibrium point given in (10)).

By the Law of Averages, the population averages around any cycle are given by the coordinates of the equilibrium point. Since harvesting causes the equilibrium point to move up and to the left of the original position in the population quadrant, harvesting raises the average prey population but lowers the average predator population.

THEOREM 2.6.3

The Law of Harvesting (Volterra's Third Law)

Constant-effort harvesting raises the average number of prey per cycle and lowers the average number of predators.

Before we can compare the data of Table 2.6.1 with the predictions of the Law of Harvesting, we must reformulate that law in terms of percentages, rather than averages.

THEOREM 2.6.4

The Percentage Law of Harvesting

Constant-effort harvesting raises the average percentage of prey per cycle in the total fish population and lowers the average percentage of predators per cycle.

Proof. The verification of Theorem 2.6.4 is in Problem 7. ■


If the harvesting coefficients in system (9) are too large, the internal equilibrium point $((c - H_2)/k, (a + H_1)/b)$ crosses the positive y -axis, and one (or both) species becomes extinct, as we see in the next example.

EXAMPLE 2.6.2

The Effect of Constant Effort Harvesting

Let's consider the IVP with equal harvesting coefficients $H_1 = H_2 = H$:

$$\begin{aligned}x' &= -x + xy/10 - Hx, & x(0) &= 8 \\y' &= y - xy/5 - Hy, & y(0) &= 16\end{aligned}\quad (11)$$

 In addition to the point (8,16), all these orbits seem to pass through another point. Is this a computational artifact, or does it really happen?

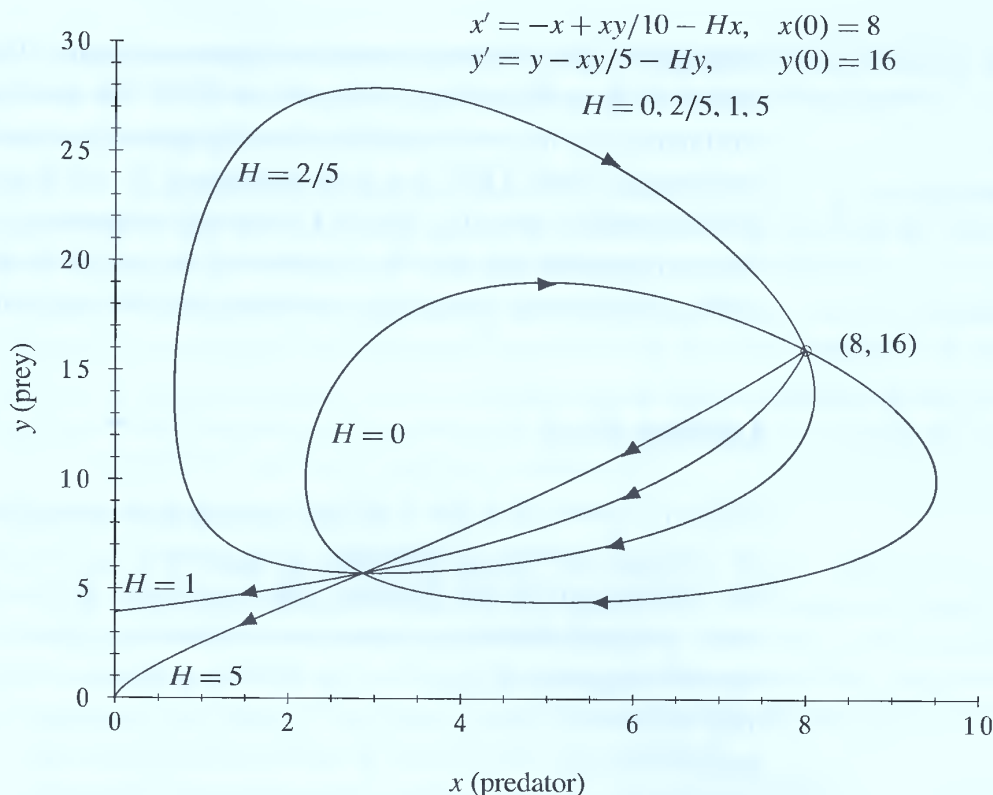


FIGURE 2.6.3 The effects of harvesting (Example 2.6.2).

Figure 2.6.3 shows orbits for IVP (11) with four different values for the harvesting coefficient: $H = 0$ (no harvesting), $2/5$ (light harvesting), 1 (critical harvesting), and 5 (heavy harvesting). Two of the orbits in Figure 2.6.3 suggest that with no harvesting or with only light harvesting both species survive. If the harvesting is critical ($H = 1$), then only the prey species survives. If H exceeds 1 , then both predator and prey become extinct.

The Percentage Law of Harvesting Theorem 2.6.4 answers D’Ancona’s question. A *decrease* in the harvesting rate leads to an *increase* in the predator percentage, while an increase in the harvesting rate causes a decrease in the predator percentage. Now look again at Table 2.6.1. As the harvesting rate fell during the war years and then increased during the postwar years, the predator percentage increased and then dropped, just as Volterra’s model predicts.

Validity of Volterra’s Law of Harvesting

Mathematicians have both challenged and supported Volterra’s models many times in the years since their formulation, but the model continues to be the starting point for most serious attempts to understand just how predator-prey communities evolve with or without harvesting.

One dramatic confirmation of the general validity of Volterra’s Law of Harvesting occurred when farmers applied the insecticide DDT to control the cottony cushion

scale insect that infested American citrus orchards. The scale insect had been accidentally introduced from Australia in 1868. Its numbers were controlled (but not eliminated) by importation of the insect's natural predator, a particular kind of ladybird beetle. When DDT was first introduced, it was hoped that the scale insect could be completely wiped out. But DDT acts indiscriminately, killing all insects it touches. The consequence was that the numbers of the ladybirds dropped, while the population of the scale insects, freed from extensive ladybird predation, increased.

Looking Back

Darwin's observation that it is "the serving as prey to other animals which determines the average numbers of a species" is supported by Volterra's model and by the data of the fish harvests in the Adriatic. The model has its flaws: no account is taken of the delay in time between an action and its effect on population numbers, the averaging over all categories of age, fertility, and sex is dubious, and the parameters of the model may very well change over time. In addition, examination of Figure 2.6.1 shows that large-amplitude orbits of the Lotka–Volterra model are squeezed together close to the axes and the origin during the course of each cycle. A small disturbance in that region might lead to the extinction of one or both species.

Nonetheless, *Occam's Razor* applies: "what can be accounted for by fewer assumptions is explained in vain by more."⁷

PROBLEMS

Lotka–Volterra Systems. Which is the predator and which is the prey? Find the average predator and prey populations. Do the population cycles turn clockwise or counterclockwise around the equilibrium point in the first quadrant? [Hint: use Theorem 2.6.2. To determine cycle orientation, find the sign of x' if on the positive x -axis and the sign of y' on the positive y -axis.]

1. $x' = -x + xy$, $y' = y - xy$ 2. $x' = 0.2x - 0.02xy$, $y' = -0.01y + 0.001xy$
3. $x' = (-1 + 0.09y)x$, $y' = (5 - x)y$



Estimating the Periods of Cycles. Plot slope fields, the equilibrium point, and the cycles that pass through the points (5, 10) and (10, 5) for the given systems. Plot component graphs for the orbits, and use these graphs to estimate periods.

4. Problem 1 5. Problem 2 6. Problem 3

Harvesting Strategies.

7. *Law of the Percentages* Verify Theorem 2.6.4 for the predator percentages. [Hint: the harvested system is $x' = -ax + bxy - H_1x$, $y' = cy - kxy - H_2y$, with $H_2 < c$. Explain why the predator fraction F of the total average catch is

$$F = \left[1 + \frac{k(a + H_1)}{b(c - H_2)} \right]^{-1}$$

Explain why F decreases as H_1 and H_2 increase.]

⁷William of Occam (1285–1349) was an English theologian and philosopher who applied the Razor to arguments of every kind. The principle is called the Razor because Occam used it so often and so sharply.

8. *Harvesting a Predator-Prey Community to Extinction* High harvesting coefficients H_1 and H_2 may lead to the extinction of the species. This problem explores what happens.

(a) Explain the graphs in Figure 2.6.3.

(b) Set H_1 at a fixed positive value in system (9). Show that as $H_2 \rightarrow c^-$, the equilibrium point inside the population quadrant approaches the point $(0, (a + H_1)/b)$ on the y -axis and that if $H_2 = c$, all points on the y -axis are equilibrium points of system (9).

(c) Let $H_2 = c$ in system (9). Show that $dy/dx = (kxy)((a + H_1)x - bxy)^{-1}$. Separate the variables, solve, and find x as a function of y and the initial data x_0, y_0 , where $x_0 > 0, y_0 > 0$.



(d) What do you think happens to the harvested species as time increases for the case $H_2 = c$? Give an informal explanation, but with reasons for your conclusions. As an aid, set $a = b = c = k = 1, H_1 = 0.1$, and plot a direction field and orbits.

Properties of the Predator-Prey System.



9. *Linearizing to Estimate the Periods of Cycles* To linearize a planar system $x' = f(x, y), y' = g(x, y)$ about an equilibrium point (x_0, y_0) , expand each rate function in a Taylor series about (x_0, y_0) and discard all terms higher than first-order. The result is the *linearization* of the original system at (x_0, y_0) . Apply this process to the predator-prey rate equations $x' = -ax + bxy, y' = cy - kxy$ in order to estimate the periods of the population cycles near the equilibrium point $(c/d, a/b)$ inside the population quadrant.

(a) Show that the linearized rate equations about the equilibrium point $(c/k, a/b)$ form the linear system $x' = bcy/k - ac/k, y' = -akx/b + ac/b$.

(b) Show that, for certain values of ω, A , and B , the functions $x = c/k + A \cos \omega t, y = a/b + B \sin \omega t$ solve the linearized system in (a). What are the values of A/B and ω ?



(c) Set $a = b = c = k = 1$ and plot orbits and component graphs of the nonlinear and the linearized systems, using the common initial data $x_0 = 1, y_0 = 1, 1.1, 1.3, 1.5, 1.9$. Plot over $0 \leq t \leq 20$. Explain the graphs and compare the periods of the cycles of the two systems using common initial points.



10. Suppose that system (9) models a predator-prey system and that you are the harvester. Suppose we require $0 < x_m \leq x(t) \leq x_M$ and $0 \leq y_m \leq y(t) \leq y_M$ for all t , where the positive population bounds x_m, x_M, y_m, y_M are given. Suppose also that $x(0) = c/k, y(0) = a/b$.

- Describe how you would choose the positive coefficients H_1 and H_2 to maintain each species within the prescribed bounds. Justify your arguments.
- High harvesting rates can be maintained if the harvesting season is short. Construct and justify your own strategy for maximizing the yield by imposing a limit on the harvest season, while still maintaining the populations within reasonable bounds.

Orbits of the Lotka–Volterra System Are Cycles.

11. Follow the steps below to show that for $0 < K \leq K_0 = c^c(ke)^{-c}a^a(be)^{-a}$ the graph of the orbit defined by the equation $x^c e^{-kx} y^a e^{-by} = K$ is a simple closed curve (i.e., a cycle) in the interior of the population quadrant. The only exception occurs for $K = K_0$ when the graph is the equilibrium point $(c/k, a/b)$.

(a) Show that $f(x) = x^c e^{-kx}$ is defined for $x \geq 0$, rises from the value of 0 at $x = 0$ to its maximum value of $M_1 = c^c(ke)^{-c}$ at $x = c/k$, falls as x increases beyond c/k , and $f(x) \rightarrow 0$ as $x \rightarrow +\infty$. Show that the function $g(y) = y^a e^{-by}$ rises from the value of 0 at $y = 0$ to its maximum value $M_2 = a^a(be)^{-a}$ at $y = a/b$, and then decays to 0 as $y \rightarrow +\infty$.

(b) Show that no nonnegative values of x and y satisfy the equation $x^c e^{-kx} y^a e^{-by} = K$ if $K > M_1 M_2$. Show that equation $x^c e^{-kx} y^a e^{-by} = K$ has the unique solution $x = c/k, y = a/b$ if $K = M_1 M_2$.

(c) Suppose that γ is any positive number, $\gamma < M_1$. Show that $f(x) = \gamma$ has two solutions, x_1 and x_2 , where $x_1 < c/k < x_2$. Show that the equation $g(y) = \gamma M_2/f(x)$ has no solution y if $x > x_2$ or $x < x_1$; exactly one solution, $y = a/b$, if $x = x_2$ or if $x = x_1$; and two solutions, $y_1(x) < a/b$ and $y_2(x) > a/b$, if $x_1 < x < x_2$. Show that $y_1(x) \rightarrow a/b$ and $y_2(x) \rightarrow a/b$ if $x \rightarrow x_1$ or $x \rightarrow x_2$.

(d) Explain why the equation $x^c e^{-kx} y^a e^{-by} = K$ defines a cycle inside the population quadrant if $0 < K < M_1 M_2$.

2.7 Extension of Solutions: Long-Term Behavior

The definition of a solution of an ODE is a bit redundant. If $y(t)$, defined on a t -interval I , is a solution of an ODE, then $y(t)$, restricted to any subinterval of I , is also a solution. It is not useful to distinguish between these solutions since they are all pieces of the original solution $y(t)$ on I . What if there is a solution $z(t)$ on a *larger* interval with $y(t) = z(t)$ if t is restricted to I ? In this case the solution $z(t)$ is an *extension* of the solution $y(t)$.

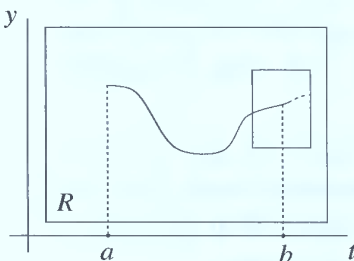
The Existence and Uniqueness Theorem is vague about the length of the time intervals on which the solutions are defined, but our numerical solver ignores this. We just tell the solver to plot the solution of an IVP over larger and larger time intervals, and the resulting solution curve appears to extend itself until it eventually exits the screen at the sides, the top or the bottom, or else the solution curve stops abruptly. By rescaling our screen, we can see what happens to solution curves far into the future, if the solution lives that long.

Computers are bound by the realities of finite time and finite space, but theory allows us to contemplate the infinite. Can a solution live forever; that is, can the solution be extended to the entire t -axis? Can a solution become infinite in a finite stretch of time? Can a solution just suddenly “die” and not be extendable any further in time? Let’s construct the background needed to begin to answer these questions.



Maximally Extended Solutions

Can a solution of the ODE $y' = f(t, y)$ be extended? With no solution formula in hand, here is how we answer that question. Suppose that the rate function $f(t, y)$ and the partial derivative $\partial f/\partial y$ are continuous on a closed rectangle R in the ty -plane (think of R as the portion of the ty -plane displayed on your computer screen). Now suppose that $y(t)$, $a \leq t \leq b$, defines a solution curve of $y' = f(t, y)$, a curve that lies entirely in R . If the endpoint $(b, y(b))$ of the curve is inside R (see margin figure), then the Existence and Uniqueness Theorem implies that the unique solution $z(t)$ to the IVP



$$z' = f(t, z), \quad z(b) = y(b)$$