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# 675

# The Lotka-Volterra Predator-Prey Model

James Morrow

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| INTERMODULAR DESCRIPTION SHEET: | UMAP Unit 675 |
| TITLE: | THE LOTKA-VOLTERRA PREDATOR-PREY MODEL |
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| MATHEMATICAL FIELD: | Precalculus |
| APPLICATION FIELD: | Biology |
| TARGET AUDIENCE: | Students in a precalculus course |
| ABSTRACT: | This module describes and analyzes qualitatively a simplified version of the predator-prey model attributed to Lotka and Volterra. Deductions are made concerning the size of populations based on information about their percentage growth rates. The module describes a nonstandard and stimulating way of illustrating the power and utility of combining geometry and algebra. |
| PREREQUISITES: | 1. to solve a linear inequality<br>2. to graph a linear equation |
| STUDENT OBJECTIVES: | 1. to be able to sketch a plausible two-species population trajectory based on an algebraic description (of the Lotka-Volterra type described in the module) of the species' percentage growth rates;<br>2. to be able to sketch a population trajectory based on the population vs. time graphs for each of the two species;<br>3. to be able to express verbally the information conveyed by a two-species population trajectory and the value and limitations of such trajectories. |

# The Lotka-Volterra Predator-Prey Model

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## Modules and Monographs in Undergraduate Mathematics and Its Applications (UMAP) Project

The goal of UMAP was to develop, through a community of users and developers, a system of instructional modules in undergraduate mathematics and its applications to be used to supplement existing courses and from which complete courses may eventually be built.

The Project was guided by a National Advisory Board of mathematicians, scientists, and educators. UMAP was funded by a grant from the National Science Foundation and is now supported by the Consortium for Mathematics and Its Applications (COMAP), Inc., a nonprofit corporation engaged in research and development in mathematics education.

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# 1. The Lotka-Volterra Model

## 1.1 Introduction

In the 1920s A.J. Lotka developed a mathematical model for the interaction between two species [Lotka 1925]. This model was worked out independently and in more detail a short time later by the mathematician Vito Volterra. Lotka and Volterra wished to understand the population dynamics involved in a simple system that involves only a single predator species and a single prey species. By ignoring such things as the variability of individuals of each species, variation in the environment over time, and the effects of other species, they hoped to discover some of the essential properties of the interaction between the two species and to understand the mechanisms involved in the cyclical behavior of their population levels. While it is still an open question as to whether they achieved their goals, the mathematical approach that they took stimulated many investigators and has changed the way that ecological systems are studied.

***"...the mathematical approach that they took... has changed the way that ecological systems are studied."***

In this module we shall examine the assumptions and conclusions of a slightly modified version of the Lotka-Volterra model. A subsequent related module contains a model that describes the dynamics of competing species.

Before reading on, take a few minutes to jot down some ideas and questions you have about a predator-prey model. For example, you might make a preliminary decision about what variables should be included; you might decide on what you hope the model would accomplish; and you might ask why one would try to form such a model.

## 1.2 Examples and Notation

Some examples of predator-prey systems that might be described by the Lotka-Volterra model include the hawk-sparrow, lynx-hare, wolf-caribou, pitcher plant-fly, and squirrel-acorn systems. The variety of examples to be described by a single mathematical model indicates how ambitious that model is. To make the ideas a little more concrete, we shall assume that the prey is a population of hare and the predators are Canadian lynx. A wealth of data has been collected, primarily from the pelt counts of human predation, which could provide a way of validating the Lotka-Volterra model [Elton and Nicholson 1942].

***"The variety of examples to be described by a single mathematical model indicates how ambitious that model is."***

Out of the complexity of the population dynamics of the real predator-prey system, the model abstracts in an explicit way only four variable quantities: the number of predators, the number of prey, and the percentage growth rates of each. We use the following notation.

| | |
|---|---|
| Prey (hare): | population size $= H$ |
| | percentage growth rage $= r_H$ |
| Predator (lynx): | population size $= L$ |
| | percentage growth rage $= r_L$ |

There is another variable quantity that enters the model implicitly: time. The model assumes that time is independent of the population sizes and rates and that it "flows along" in a continuous way. The preceding four explicitly labeled quantities represent variables that are assumed to change over time, and hence describe how the population sizes change with time. It is assumed that each can be specified at each point in time and thus is dependent (although in an implicit way) on time. Section 1.5 contains a bit more discussion of this point.

How does this choice of quantities compare with your ideas about a predator-prey system? Many different approaches to a model are possible, so don't be discouraged if your ideas seem radically different from those presented here.

## 1.3 Description of Growth Rates

The growth of populations can be described in several ways. For example, one reads that the world population in the mid-1960s was growing at an absolute rate of 180,000 people per day, or that world population grew by 1.7% per year from 1950 to 1960. The latter way of describing a rate of growth differs from the former not only in the unit of time used (day in the former case and year in the latter), but more fundamentally, in the use of a percentage rate rather than an absolute rate.

*Question:* If a certain population grows at a rate of 1.7% per year for a year, how many additional mouths are there to feed at the end of the year?

The idea that a population is growing at 1.7% per year cannot alone determine the additional number of people each year. To determine that additional number requires the use of a base population figure. Thus a population of 1,000 will grow to 1,017 in a year's time, while a population of 2,000 will grow to 2,034—each at a rate of 1.7% per annum. Percentage rates of growth are used for populations because they have generally been more stable figures than absolute rates of growth. A constant, positive percentage rate describes a changing (increasing) absolute rate of growth. Even percentage rates change—it is estimated that up to 1750, world population grew at 0.1% per year, from 1750 to 1900 at 0.5% per year, from 1900 to 1950 at 1.0% per year, and from 1950 to 1960 at 1.7% per year [Young 1968]. The corresponding absolute rates changed even more dramatically.

## 1.4 Assumptions of the Model

We first consider the situation of the hare without any lynx to prey on them. We assume that the hare population, in the absence of lynx, will grow with a constant, positive percentage rate. Symbolically, $r_H = a$, where $a$ is a positive constant (this is termed the "intrinsic" percentage rate—it applies only in the absence of lynx). More specifically, $r_H = 0.05$ means that the intrinsic growth rate is 5% per year. Rather than choosing a *specific* number to represent the growth rate, the constant $a$ is used so that the model can be more widely applied, and also so that general conclusions may be drawn which are independent of the particular value that $a$ may have.

We also assume that the lynx will have the effect of decreasing the intrinsic percentage growth rate in direct proportion to the lynx population size. Combining the intrinsic growth rate with the effect of the predation of the lynx population, we assume that

$$r_H = a - b * L, \tag{1}$$

where $a$ and $b$ are positive constants. (The symbol "$*$" is used to denote multiplication.) The symbol $b$ represents the constant of proportionality involved in the lynx's effect on the growth rate of the hare population. More precisely, $b$ is the percentage kill rate of hare per lynx, and $b * L$ is the percentage kill rate of hare. It should be noted that the more effective the lynx are in killing the hare, the larger the value of $b$ is. If we knew more about the rate at which lynx killed hare, we would be able to replace $b$ by some specific number. On the other hand, the model has more generality by using the unknown but fixed constant $b$.

In a parallel way, we assume that the lynx will die out in the absence of hare in such a way that their percentage growth rate is a negative constant: specifically, $r_L = -c$, where $c$ is a positive constant (the "intrinsic" percentage death rate—it applies only in the absence of the lynx' food source, the hare).

The presence of hare, however, will increase the intrinsic percentage growth rate, it is assumed, in direct proportion to their population size, so that

$$r_L = -c + d * H, \qquad (2)$$

where $c$ and $d$ are positive constants. Just as $b$ represents how effectively the lynx kill the hare, $d$ represents how effective the lynx' predation is in increasing the lynx population size.

***"... the parameters describe certain characteristics of the populations, which vary from one predator-prey system to another."***

Equations (1) and (2) describe our assumptions about the lynx-hare system in a precise mathematical way. The symbols $L$, $H$, $r_L$, and $r_H$ all represent variables which change over time, while the symbols $a$, $b$, $c$, and $d$ represent constants, numbers that are fixed but unknown. These constants are called the parameters of the model. Just as the *variables* describe the population sizes and rates of growth, which vary with time, the *parameters* describe certain characteristics of the populations, which vary from one predator-prey system to another. Thus, for example, the greater the intrinsic percentage growth rate of a prey population, the greater the value of the parameter $a$. How does the intrinsic death rate of lynx vary with the values of the parameter $c$?

## 1.5 Conclusions of the Model

We have tried to make a case for the plausibility of the assumptions made in the previous section. Perhaps you have some difficulties with them. Well, you're not alone! Nearly everyone would agree that those simple assumptions capture only a small part of a complex world. As a measure of how far off those assumptions might be, we shall now examine some mathematical conclusions that can be drawn from them.

***"What are the long-term tendencies for the 'hare' and 'lynx' populations?"***

What are these conclusions? Keep in mind that we are not asking the question of what happens to actual populations of hare and lynx, but, rather, about the theoretical population sizes symbolized by $H$ and $L$. What are the long-term tendencies for the "hare" and "lynx" populations? To answer these questions it is critical to know when the percentage growth rates are positive and when they are negative, for this will determine whether the populations are increasing or decreasing.

Rather than considering the model in complete generality, let us first look at a specific case. This will help us to see the general pattern. Suppose that the predator-prey system is governed by the equations: $r_H = 0.05 - 0.001 * L$; $r_L = -0.03 + 0.0002 * H$.

In addition, let us suppose that at a certain point in time there are 40 lynx and 250 hare. Then $r_H = 0.05 - 0.001 * 40 = 0.01$; and $r_L = -0.03 + 0.0002 * 250 = 0.02$.

What is most important to note is that both $r_H$ and $r_L$ are positive at these population levels. Also note that the percentage growth rate for lynx is double that for hare. We will try to guess what happens to each population over time. Since they both have positive rates of growth, both populations tend to increase in size. Since both populations are increasing in size, let us suppose, hypothetically, that they happen to grow to a point where there are 45 lynx and 265 hare. Then $r_H = 0.05 - 0.001 * 45 = 0.005$; and $r_L = -0.03 + 0.0002 * 265 = 0.023$.

We see that at these population levels the growth rates are still positive for each population, with the hare population growth slowing and the lynx increasing even faster. Let us try to trace what may happen a little further. Suppose, again hypothetically, that the lynx population reaches size 50 and the hare population reaches a size of 275. Then $r_H = 0.05 - 0.001 * 50 = 0.00$; and $r_L = -0.03 + 0.0002 * 275 = 0.025$.

At these population levels the percentage growth rate of the hare population reaches zero, while the lynx population still has a positive growth rate. It is the *lynx* population reaching a size of 50 that forces the *hare* growth rate to zero. Since the lynx population still has a positive growth rate, let us suppose that there are 51 lynx (and 275 hare). Checking the basic equations (1) and (2) again, we see that $r_H = -0.001$ and $r_L = 0.025$. Thus any time the lynx population exceeds 50, the hare population is forced to decline in number.

Rather than continue to play this "numbers" game, consider the whole process from a geometric point of view. There are three variables: the number of hare $H$, the number of lynx $L$, and time. We shall use a two-dimensional rectangular coordinate system, with $L$ plotted on the horizontal axis and $H$ plotted on the vertical axis. The variation over time will be shown by movement in this coordinate plane. What is critical to determine is where each of the two populations reaches a zero growth rate. We have already seen that the hare population reaches zero growth when the lynx number 50. When will the lynx population have a zero growth rate?

By solving the equation $-0.03 + 0.0002 * H = 0$ for $H$, it can be seen that when there are 150 hare, the lynx growth rate is zero. These two pieces of information are noted by drawing two dashed lines: the vertical one to represent $L = 50$ and the horizontal one to represent $H = 150$. The coordinate plane is divided into four regions:

In **Figure 1** the coordinate system appears, along with the critical lines; while in **Figure 2** the scenario that was just described in words is depicted geometrically. Each single point plotted represents a possible combination of lynx-hare population levels, and the arrow attached to each point indicates the growth tendency at those population levels. (Up is positive growth for hare and right is

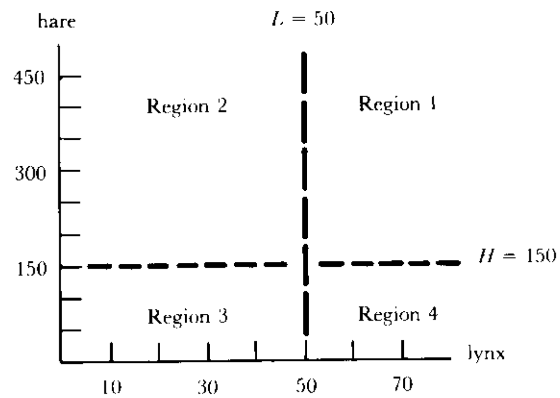



Figure 1.

positive growth for lynx.) Each of the four regions of the coordinate plane can be checked numerically to see what growth tendency is present. For example, in Region 4, where $L > 50$ and $H < 150$, we have $r_H < 0.00$ and $r_L < 0.00$; hence in Region 4 both populations are on the decline. Some typical growth tendencies are depicted in **Figure 3**.

Imagine now what may happen over time. A population pair starting at the point $A$ pictured in **Figure 3** will tend to move upward and to the right. As it moves in this direction, the hare *rate* of growth tends to decrease (though it is still positive), and the lynx *rate* of growth tends to increase, which makes it seem likely that the population pair will eventually hit the line $L = 50$. If the pair reaches the vertical line $L = 50$, it then begins to move downward and to the right. During this period of time the hare population increased until the lynx population hit 50 and then decreased, while the lynx population was steadily increasing. The population pair continues to move downward and to the right until the hare popula-

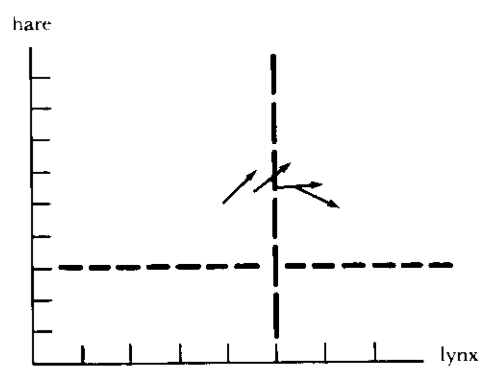



Figure 2.

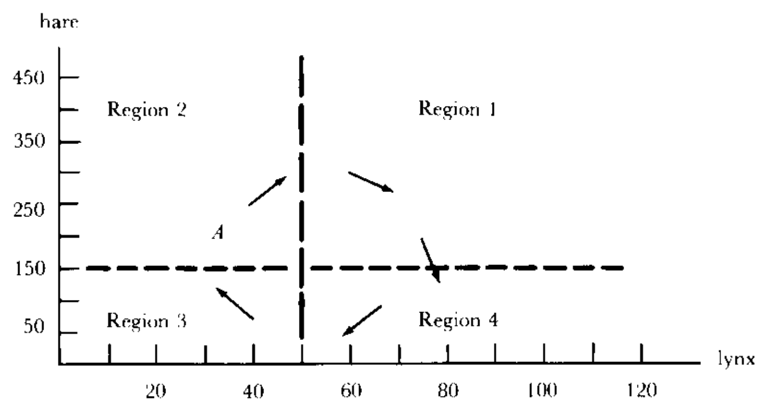



Figure 3.

tion reaches a size of 150, when it begins to move back to the left (corresponding to the now decreasing lynx population) while continuing down.

How long will the two populations continue to decrease in number? Although this question can't be answered in terms of time, it can be answered in the following way: the downward and leftward movement will continue until the lynx population size reaches 50 again (or until the hare population reaches zero—if the hare population ever reaches zero, the lynx population will also die out, since for $H = 0$, $r_L = -0.03$), at which time the motion changes to one of upward (increasing numbers of hare) and to the left. It is easy to guess what happens beyond this point; such a growth tendency persists until the hare population size reaches 150 once again (or until the lynx population reaches zero—see **Exercise 8**), at which point the situation is similar to that at point $A$, and the "cycle" is repeated. This wordy description of population dynamics is depicted very simply in **Figure 4**.

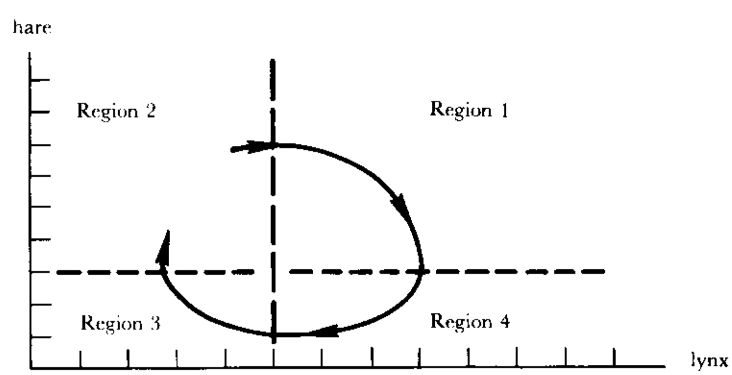



Figure 4.

The curve drawn in **Figure 4** illustrates the behavior resulting from the self-regulatory nature of the predator-prey relation modeled by the Lotka-Volterra equations. In "good" times for both species, both their numbers are increasing (Region 2). Eventually there are so many lynx that the hare population begins to decline (Region 1). For a while there are still enough hare left for the lynx population to continue to grow, but eventually there are few enough hare so that the lynx population begins to decline as well (Region 4). In time the lynx population becomes small enough so that once again the hare population begins to increase (Region 3), and eventually this increase in hare is enough to enable the lynx population to increase again (Region 2 again).

Let us return to the general situation. We have:

$$r_H = a - b * L \qquad \mathbf{(1')}$$

and

$$r_L = -c + d * H, \qquad \mathbf{(2')}$$

rather than the very specific

$$r_H = 0.05 - 0.001 * L \qquad \mathbf{(1)}$$

and

$$r_L = -0.03 + 0.0002 * H. \qquad \mathbf{(2)}$$

Thus where before the hare population growth rate was positive for $L < 50$ (and negative for $L > 50$), now $r_H$ is positive for $L < a/b$. This new, and more general, inequality is obtained by solving the inequality $a - b * L > 0$ for $L$. In the special case, the lynx population growth rate $r_L$ was positive for $H > 150$, while in the general case $r_L$ is positive when $H$ is greater than the quantity $c/d$. (Solve $-c + d * H > 0$ for $H$.) We proceed as before with a rectangular coordinate system, this time drawing the dashed vertical line $L = a/b$ and the dashed horizontal line $H = c/d$. (Of course we don't actually assign specific values to the parameters $a$, $b$, $c$, and $d$, so our placement of these critical lines is rather arbitrary. No matter—the value of the pictures is of a *qualitative* rather than quantitative nature.) See **Figure** 5.

The geometric analysis of the general case is also easy, now that the four critical regions of the plane have been identified. The population pair moves upward and to the right in Region 2, downward and to the right in Region 1, downward and to the left in Region 4, and upward and to the left in Region 3. The only thing different about the general case is the precise position of the critical

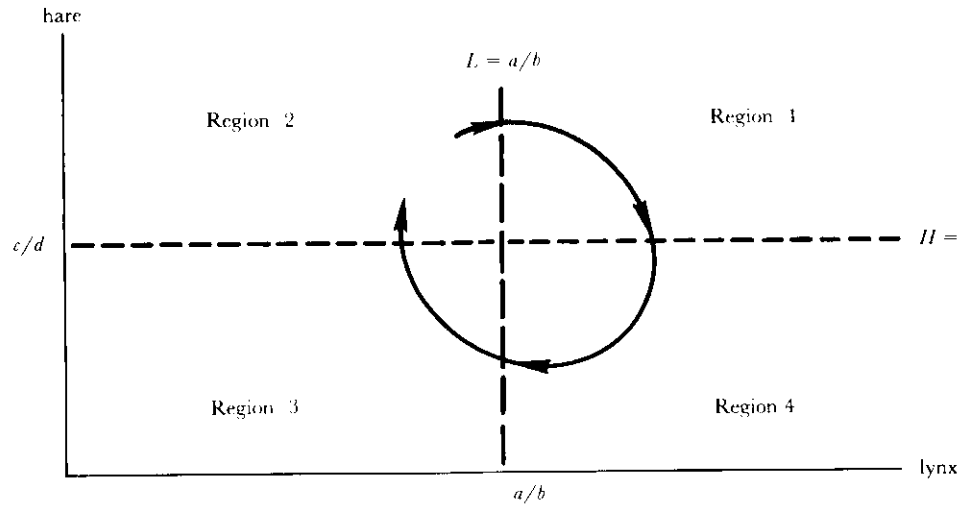



Figure 5.

dashed lines that divide up the plane. The qualitative nature of both is the same. The curve traced out over time by the population pair is called the population *trajectory*.

One of the subtle points about the model described here concerns the use of the term "percentage growth rate." Volterra and Lotka meant by this term an instantaneous rate, one that changes from instant to instant, rather than a rate that is obtained by averaging the changes in population levels over time. Such an instantaneous rate is modeled mathematically by the concept of derivative of a function, which may be studied in a calculus course. Using the "instantaneous" meaning of percentage growth rate and methods of differential calculus, Lotka and Volterra showed that the kind of smooth trajectory described above actually does result from the more sophisticated assumptions of their model. What is more striking is that they also showed that the trajectory is a *closed* curve in the plane. What this means is that the curve doesn't spiral around, but comes back around to itself, and then repeats. Thus the model results in a cyclical kind of behavior for each species which closely matches some natural predator-prey systems.

## 1.6 Concluding Remarks

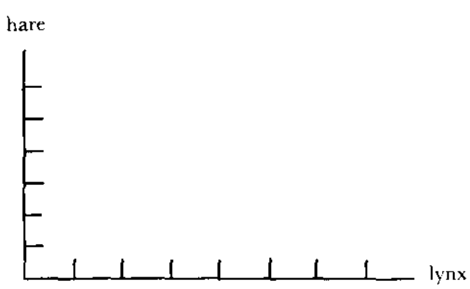
In mathematical terms, the (modified) Lotka-Volterra model presented in this module illustrates the fruitful interaction of algebraic and geometric methods. The form of the model's assumptions is algebraic; and the description of zero, positive, and negative percentage growth is also algebraic, being in the form of an algebraic equation or inequality. When these equations and inequalities are considered geometrically, and the pair of populations is looked at as a point in the plane, a powerful tool develops—for then we "see" how the populations must vary over time if they are to satisfy the assumptions of the model. Such variation over time is seen in the form of a curve being traced out in a coordinate plane.

In ecological terms, the model provides a beginning for a quantitative analysis of natural systems. Such a simple model might best be considered as a basis for deeper understanding. Its value lies in whatever questions, ideas, and experiments it may stimulate and in the simple picture that we may carry around in our mind to remind us of our ideas about a system of interacting species. The interested reader can find many variations on the theme of the Lotka-Volterra model in [May 1976; Pielou 1969; and Wilson and Bossert 1971].

# 2. Exercises

1. What features are omitted from the Lotka-Volterra model that you think might be important? What quantities do you think might be included to make the model closer to the reality of a natural system involving a predator species and its prey species? Why do you think Lotka and Volterra failed to include such quantities?

2. Consider the predator-prey system $r_H = 0.08 - 0.002 * L$; $r_L = -0.04 + 0.0002 * H$.
   a. Determine the number of lynx for which the percentage growth rate of hare is zero.
   b. Determine the number of hare for which the percentage growth rate of lynx is zero.
   c. On the graph below, draw the critical lines that divide the lynx-hare plane into critical regions such as those described in the module.



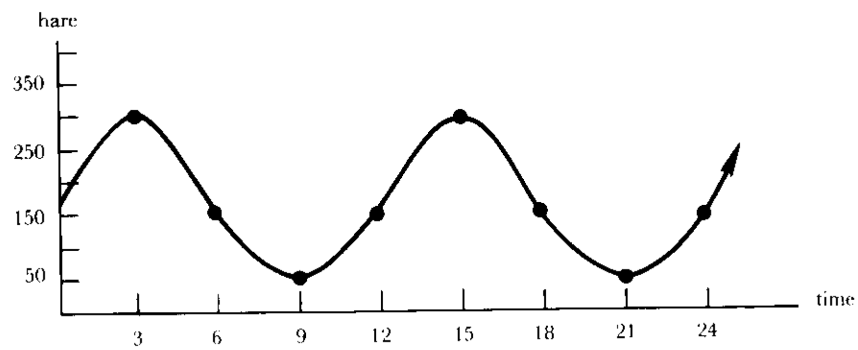

Graph for **Exercise 2**

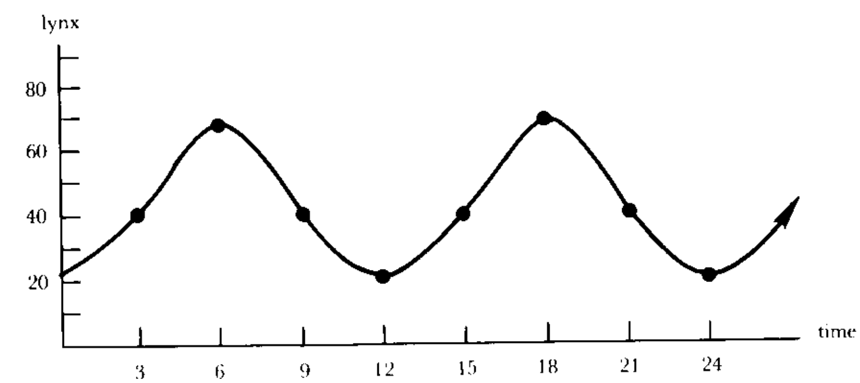

Graph for **Exercise 3**

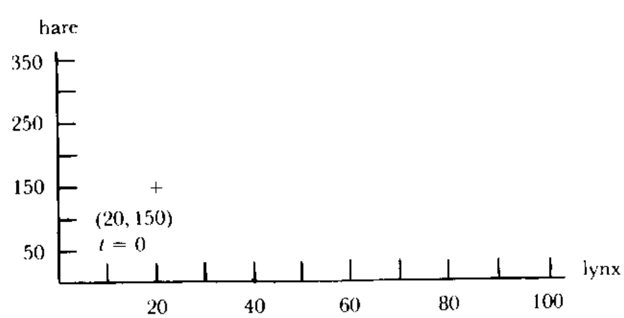
**d.** Plot the point in the plane corresponding to 35 lynx and 150 hare. Is the hare population growing or declining at that point? Is the lynx population growing or declining at that point?

3. Repeat **Exercise** 2 for the system $r_H = 0.05 - 0.002 * L$; $r_L = -0.03 + 0.0001 * H$.

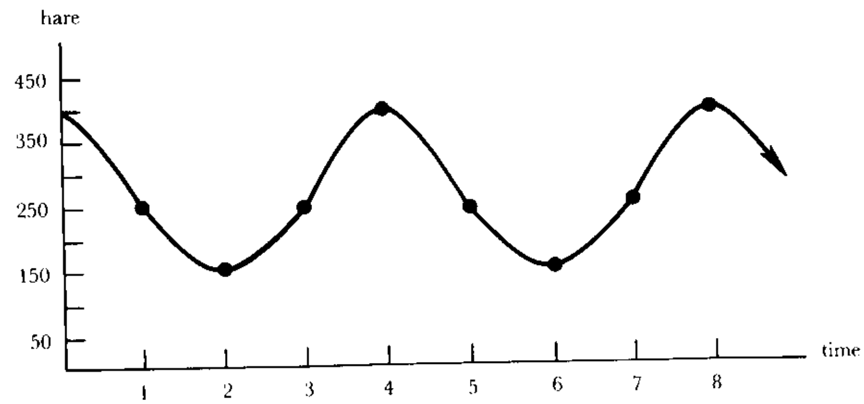
4. The two graphs below plot a prey species $H$ against time and a predator species $L$ against time. Draw a rough graph of the corresponding population trajectory of prey against predator.

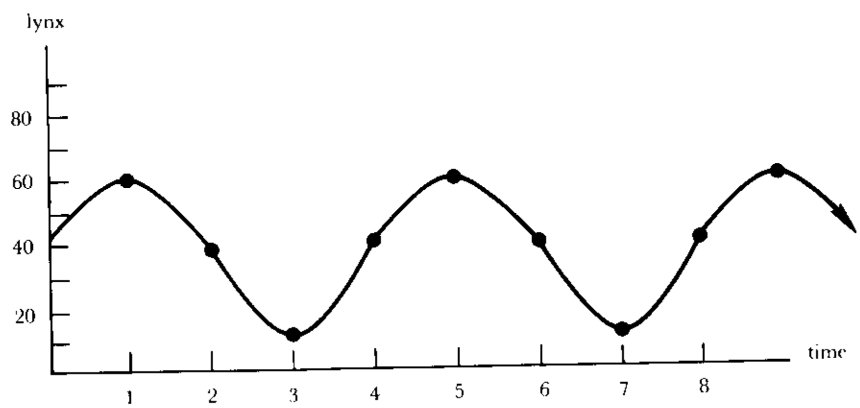


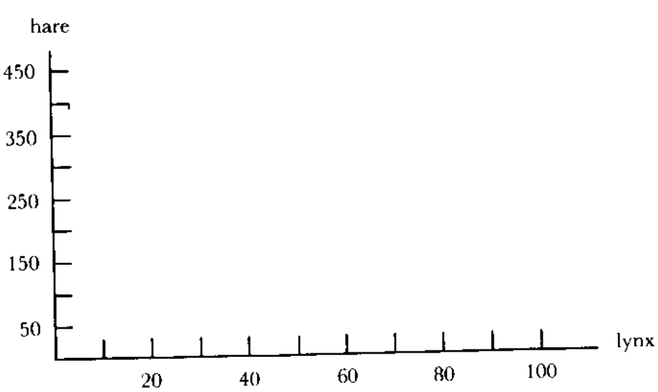



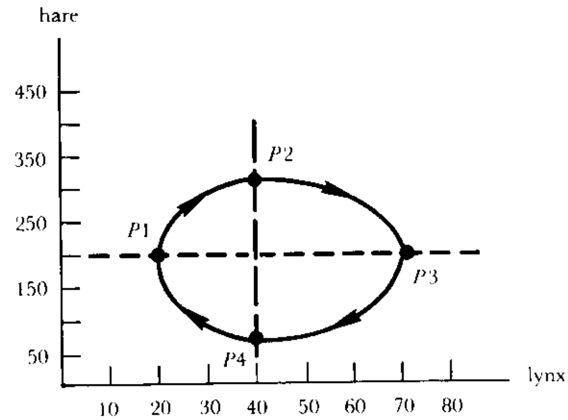
5. Repeat **Exercise 4** for the two time graphs drawn below.



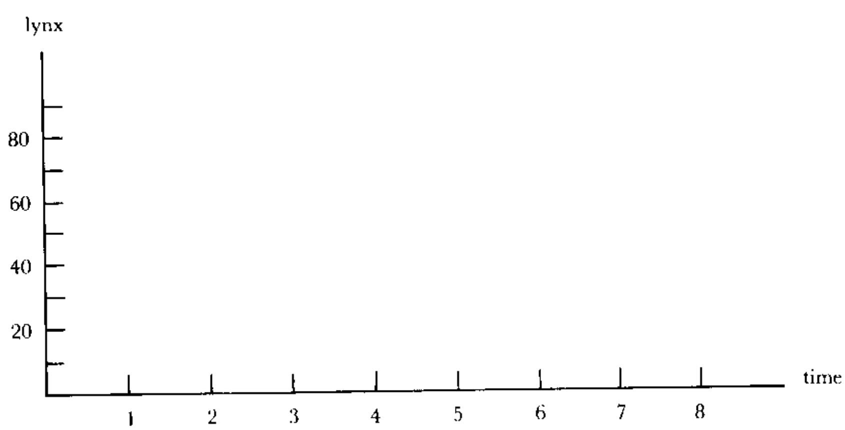



6. The figure below gives a possible population trajectory corresponding to the system of **Exercise 2**.



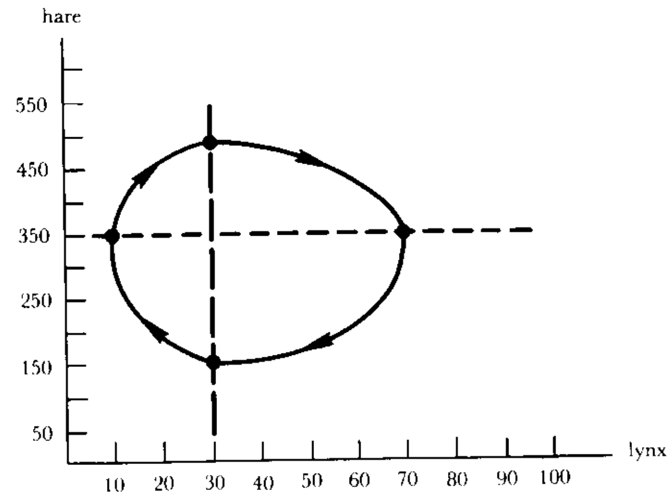

Draw a rough graph of the number of lynx against time. (Assume that the population pair is at point $P1$ at time $t = 0$ and that it takes the same amount of time for the pair to travel from $P1$ to $P2$ as from $P2$ to $P3$, as from $P3$ to $P4$, as from $P4$ to $P1$.)

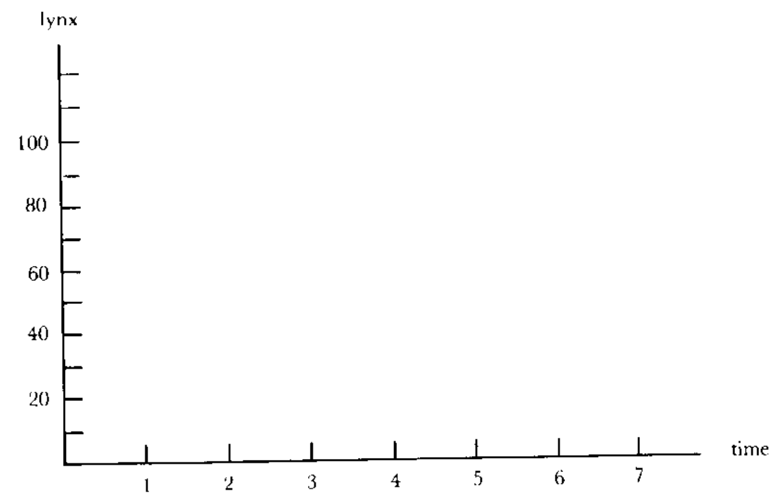



7. Repeat **Exercise 6** for the population trajectory that follows.

8. What happens to the hare population if the lynx population size ever reaches zero?

9. Put yourself in the place of a wildlife manager. Try to determine whether it is possible, according to the Lotka-Volterra model, to




attain each of the management objectives listed below, considered separately, by removing lynx:

**a.** to increase the maximum size of the hare population.

**b.** to increase the minimum size of the hare population.

**c.** to decrease the maximum size of the lynx population.

**10.** Describe what it might mean for the value of the parameter $b$ to increase. First consider the effect mathematically, then what the mathematical effect might stem from in terms of hare and lynx population characteristics.

11. Suppose there is a predator-prey system in which each of the populations grows by fairly distinct generations, most of the population change occurring in a short span of time. Then we might want to restrict our model to just the discrete points in time: an initial point in time, the time when the first generation is born, the time when the second generation is born, and so on. To make things as simple as possible we could assume that both populations have their new generations born at the same time, so that we could let $H(0)$ and $L(0)$ represent the initial populations; $H(1)$ and $L(1)$ represent the population sizes when the first generation is born; and, more generally, $H(n)$ and $L(n)$ represent the population sizes when the $n$th generation is born.
    a. Use the above notation to express the *actual increase* in the two population sizes as they go from their *initial population size* to the population size when the *first generation* is born.
    b. Use the above notation to express the *actual increase* in the two population sizes as they go from the time when the *nth generation* is born to the time when the $(n + 1)$*th generation* is born.
    c. Use the above notation to express the *percentage increase* in the two population sizes as they go from their *initial population* size to the population size when the *first generation* is born.
    d. Use the above notation to express the *percentage increase* in the two population sizes as they go from the time when the *nth generation* is born to the time when the $(n + 1)$*th generation* is born.
    e. Propose equations (a model) that describe how percentage increases in each population might be related to the actual population sizes.
    f. Write a computer program to test the equations you wrote in part e. above. You will need to use specific values for any parameters you introduced into the equation in part e.

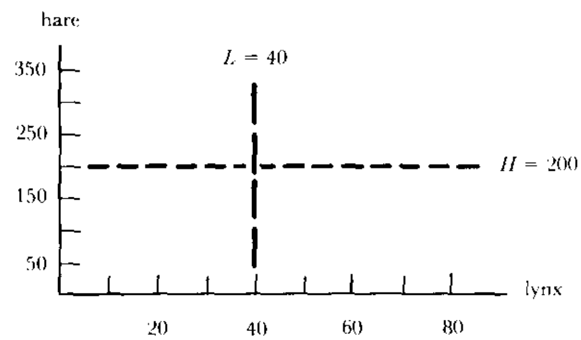
# 3. Solutions to Selected Exercises

1. In addition to the variability of individuals, variation over time, and the effect of other species mentioned in the first paragraph of the module, one might try to take into account the distribution of species in space, variation in the behavior of individuals, food available (other than hare!), and the different age groups within a population. Without trying to change the essential characteristics of the model too much, I might try to include the variables time and amount of food available to the hare as a specific function of time. What is unfortunate is that the more realistic the number of factors considered and the more realistic the hypotheses are, the more difficult it is to draw any conclusions at all mathematically. This is the sort of trade-off that Lotka and Volterra faced (and that anyone trying to make a mathematical model faces). The mathematical difficulty introduced by the inclu-

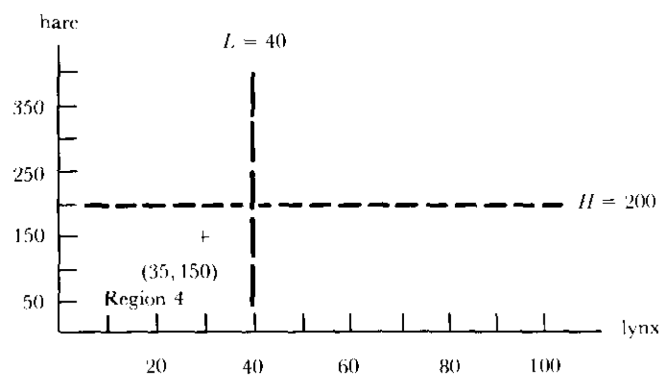
sion of additional variables may account for Lotka and Volterra's failure to include such quantities as those listed here.

2. a. *Set the growth rate for hare, $r_H$, equal to zero; i.e., consider $0.08 - 0.002 * L = 0$.* Solving for $L$ yields $L = 40$. Thus the hare growth rate is zero when there are 40 lynx.
   b. Similarly to part a., one sets $-0.04 + 0.0002 * H = 0$, and solves for $H$ to get $H = 200$. When there are 200 hare, the growth rate of the lynx population is zero.

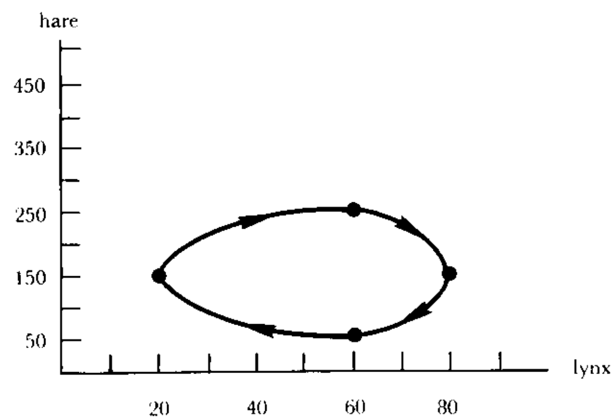
   c.



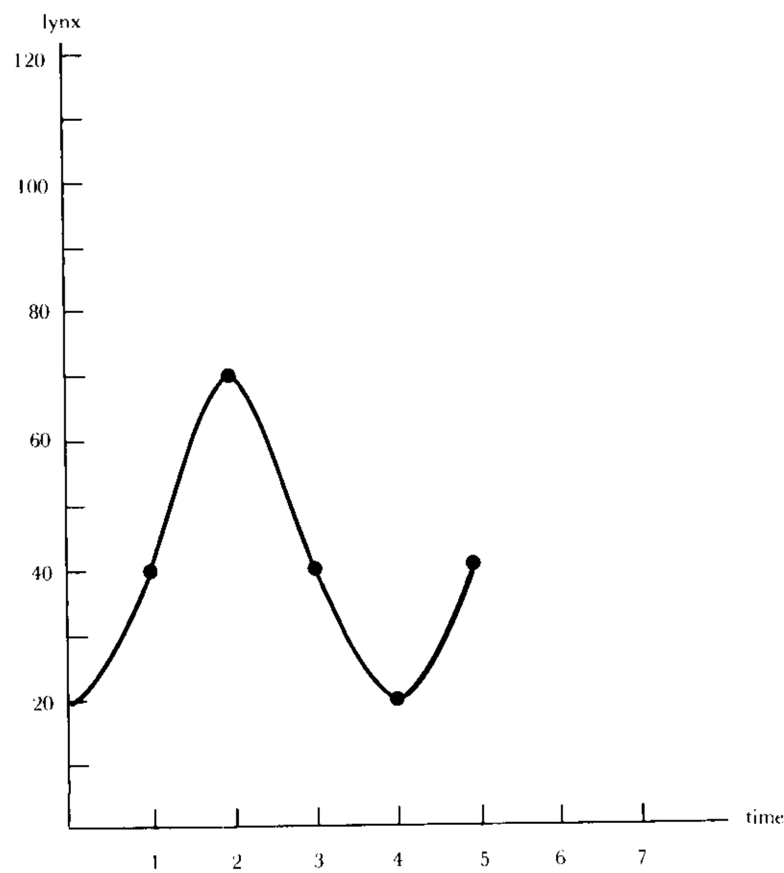

   d. For $L = 35$, $r_H = 0.08 - 0.002 * 35 = 0.01$, so the number of hare is increasing. For $H = 150$, lynx growth $= -0.04 + 0.0002 * 150 = -0.01$, so the number of lynx is decreasing.




4. A beginning to the solution is given in the statement of the exercise: the point (20,150), which describes the population pair when $t = 0$, has been plotted. Reading the lynx and hare populations from the two graphs at times $t = 3, 6, 9,$ and 12, we get the points (60,250), (80,150), (60,50), and (20,150), respectively. Filling in with a "smooth" curve, we get the picture as follows:




6. Since we are concerned with only the lynx we shall read off only the first coordinates of the points $P1$, $P2$, $P3$, and $P4$ (those that correspond to the lynx in the $(L, H)$ pair). We get 20, 40, 70, and 40 for $P1$, $P2$, $P3$, and $P4$, respectively, which correspond to the times $t = 0$, 1, 2, and 3, respectively. Since the first coordinate of the population pair represents the number of lynx, we read only the



first coordinate of the points $P1$, $P2$, $P3$, and $P4$ as those corresponding to times $t = 0$, 1, 2, and 3 (with some time unit attached). We then fill in with a curve motivated by the results of the Lotka-Volterra model.

# 4. References

Eisen, Martin. 1981. Graphical analysis of some difference equations in biology. UMAP Modules in Undergraduate Mathematics and Its Applications: Module 553. Arlington, MA: COMAP, Inc.

Uses only precalculus mathematics to consider a discrete model of the predator-prey interaction.

Elton, Charles, and Mary Nicholson. 1942. The ten-year cycle in numbers of the lynx in Canada. *Journal of Animal Ecology* 11:215–244.

This nonmathematical paper presents material from the archives of the Hudson's Bay Company. It contains fur returns over approximately 100 years, starting in 1821. The data are presented in graphical form that shows the great cyclical regularity and large (but varying) amplitude in a 10-year cycle. The relation of lynx to snowshoe hare is discussed.

Frauenthal, James C. *Introduction to Population Modeling*. The UMAP Expository Monograph Series. Boston: Birkhäuser.

Giordano, Frank R., and Stanley C. Leja. 1983. Competitive hunter models. UMAP Modules in Undergraduate Mathematics and Its Applications: Module 628. Arlington, MA: COMAP, Inc.

What if the two species are not predator and prey but both compete for the same food source? This module uses elementary concepts from calculus to examine this situation.

Lotka, A.J. 1925. *Elements of Physical Biology*. Baltimore, MD: Williams and Wilkins.

May, Robert M., editor. 1976. *Theoretical Ecology*. New York: Saunders.

This text contains articles that are much more sophisticated mathematically than the present paper. Chapter 6, written by M.P. Hassell, might be perused for its discussion of examples and the ideas of handling time of a prey by a predator and the probability of discovery of a prey by a predator. Hassell uses a discrete, rather than continuous, time variable.

Pielou, E.C. 1969. *An Introduction to Mathematical Ecology*. New York: Wiley.

Chapter 6 contains material on predation, much of which is difficult to follow without some guidance through the notation of differential equations. However, pp. 74–75 contain some interesting remarks concerning spatial heterogeneity, age distribution, and other nonuniformities, as well as some insights into the general process of mathematical modeling.

Wilson, Edward O., and William H. Bossert. 1971. *A Primer of Population Biology*. Sunderland, MA: Sinauer Associates.

Very useful information concerning the quantitative approach to biology and the formation of mathematical models is contained in Chapter 1. Although calculus notation is used, there is a helpful, informal, and intuitive explanation of such notation. Chapter 3 deals with predation and explains the Lotka-Volterra equations in much more depth than the present paper.

Young, Louise B. 1968. *Population in Perspective*. New York: Oxford University Press.

This is a collection of nonmathematical articles, starting with Malthus's seminal work on human population growth, and including Margaret Sanger on birth control and Sally Corrighar's research on crowding and stress.

# About the Author

James Morrow studied mathematics at Miami University and at Florida State University, where he obtained his Ph.D. in 1976. His interests are currently focused on the ways that people learn mathematics. He and Charlene Morrow direct Mount Holyoke College's program for high school-age women, SummerMath.