4

Interactions Between Organisms and Their Environment

Introduction

This chapter is a discussion of the factors that control the growth of populations of organisms.

Evolutionary fitness is measured by the ability to have fertile offspring. Selection pressure is due to both biotic and abiotic factors and is usually very subtle, expressing itself over long time periods. In the absence of constraints, the growth of populations would be exponential, rapidly leading to very large population numbers. The collection of environmental factors that keep populations in check is called *environmental resistance*, which consists of density-independent and density-dependent factors. Some organisms, called r-strategists, have short reproductive cycles marked by small prenatal and postnatal investments in their young and by the ability to capitalize on transient environmental opportunities. Their numbers usually increase very rapidly at first, but then decrease very rapidly when the environmental opportunity disappears. Their deaths are due to climatic factors that act independently of population numbers.

A different lifestyle is exhibited by K-strategists, who spend a lot of energy caring for their relatively infrequent young, under relatively stable environmental conditions. As the population grows, density-dependent factors such as disease, predation, and competition act to maintain the population at a stable level. A moderate degree of crowding is often beneficial, however, allowing mates and prey to be located. From a practical standpoint, most organisms exhibit a combination of r- and K-strategic properties.

The composition of plant and animal communities often changes over periods of many years, as the members make the area unsuitable for themselves. This process of succession continues until a stable community, called a *climax community*, appears.

4.1 How Population Growth Is Controlled

In Chapter 3, *we saw that uncontrolled growth of a biological population is exponential. In natural populations, however, external factors control growth. We can distinguish two extremes of population growth kinetics, depending on the nature of*

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*these external factors, although most organisms are a blend of the two. First, r-*strategists *exploit unstable environments and make a small investment in the raising of their young. They produce many offspring, which often are killed off in large numbers by climatic factors. Second, K-*strategists *have few offspring, and invest heavily in raising them. Their numbers are held at some equilibrium value by factors that are dependent on the density of the population.*

An organism's environment includes biotic and abiotic factors.

An *ecosystem* is a group of interacting living and nonliving elements. Every real organism sits in such a mixture of living and nonliving elements, interacting with them all at once. A famous biologist, Barry Commoner, has summed this up with the observation that "Everything is connected to everything else." Living components of an organism's environment include those organisms that it eats, those that eat it, those that exchange diseases and parasites with it, and those that try to occupy its space. The nonliving elements include the many compounds and structures that provide the organism with shelter, that fall on it, that it breathes, and that poison it. (See [1, 2, 3, 4] for discussions of environmental resistance, ecology, and population biology.)

Density-independent factors regulate r-strategists' populations.

Figure 4.1.1 shows two kinds of population growth curves, in which an initial increase in numbers is followed by either a precipitous drop (curve (a)) or a period of zero growth (curve (b)). The two kinds of growth curves are generated by different kinds of environmental resistance.[1]

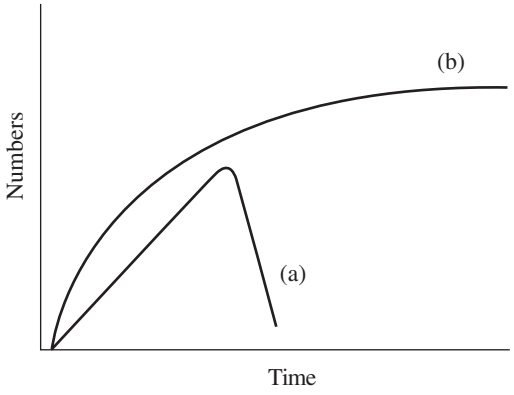

Fig. 4.1.1. A graph of the number of individuals in a population vs. time for (a) an idealized *r*-strategist and (b) an idealized *K*-strategist. *r*-strategists suffer rapid losses when density-independent factors like the weather change. *K*-strategists' numbers tend to reach a stable value over time because density-dependent environmental resistance balances birth rate.

[1] Note that the vertical axis in Figure 4.1.1 is the total number of individuals in a population; thus it allows for births, deaths, and migration.

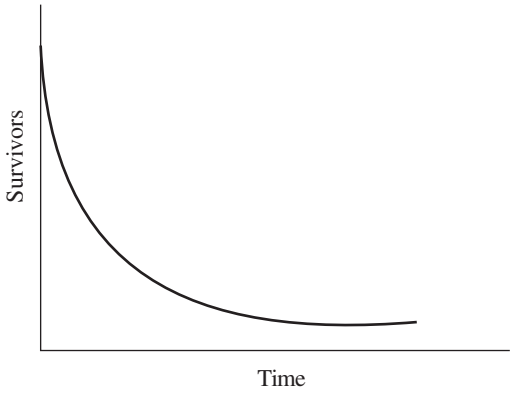

Fig. 4.1.2. An idealized survivorship curve for a group of r-strategists. The graph shows the number of individuals surviving as a function of time, beginning with a fixed number at time $t = 0$. Lack of parental investment and an opportunistic lifestyle lead to a high mortality rate among the young.

Organisms whose growth kinetics resemble curve (a) of Figure 4.1.1 are called *r-strategists*, and the environmental resistance that controls their numbers is said to be *density-independent*.[2] This means that the organism's numbers are limited by factors that do not depend upon the organism's population density. Climatic factors, such as storms or bitter winters, and earthquakes and volcanoes are density-independent factors in that they exert their effects on dense and sparse populations alike.

Two characteristics are helpful in identifying r-strategists:

1. *Small parental investment in their young.* The concept of "parental investment" combines the energy and time dedicated by the parent to the young in both the prenatal and the postnatal periods. Abbreviation of the prenatal period leads to the birth of physiologically vulnerable young, while abbreviation of postnatal care leaves the young unprotected. As a result, an r-strategist must generate large numbers of offspring, most of whom will not survive long enough to reproduce themselves. Enough, however, will survive to continue the population. Figure 4.1.2 is a *survivorship curve* for an r-strategist; it shows the number of survivors from a group as a function of time.[3] Note the high death rate during early life.

Because of high mortality among its young, an r-strategist must produce many offspring, which makes death by disease and predation numerically unimportant, inasmuch as the dead ones are quickly replaced. On the other hand, the organism's short life span ensures that the availability of food and water do not become limiting factors either. Thus density-dependent factors such as predation and resource availability do not affect the population growth rates of r-strategists.

[2] The symbol r indicates the importance of the rate of growth, which is also symbolized by r.

[3] Note that the vertical axes in Figures 4.1.2 and 4.1.4 are the numbers of individuals surviving from an initial, fixed group; thus they allow only for deaths.

2. *The ability to exploit unpredictable environmental opportunities rapidly.* It is common to find *r*-strategists capitalizing on transient environmental opportunities. The mosquitoes that emerge from one discarded, rain-filled beer can are capable of making human lives in a neighborhood miserable for months. Dandelions can quickly fill up a small patch of disturbed soil. These mosquitoes and dandelions have exploited situations that may not last long; therefore, a short, vigorous reproductive effort is required. Both organisms, in common with all *r*-strategists, excel in that regard.

We can now interpret curve (a) of Figure 4.1.1 by noting the effect of *environmental resistance*, i.e., density-independent factors. Initial growth is rapid and it results in a large population increase in a short time, but a population "crash" follows. This crash is usually the result of the loss of the transient environmental opportunity because of changes in the weather: drought, cold weather, or storms can bring the growth of the mosquito or dandelion population to a sudden halt. By this time, however, enough offspring have reached maturity to propagate the population.

Density-dependent factors regulate the populations of K-strategists.

Organisms whose growth curve resembles that of curve (b) of Figure 4.1.1 are called *K-strategists*, and their population growth rate is regulated by population *density-dependent* factors. As with *r*-strategists, the initial growth rate is rapid, but as the density of the population increases, certain resources such as food and space become scarce, predation and disease increase, and waste begins to accumulate. These negative conditions generate a feedback effect: Increasing population density produces conditions that slow down population growth. An equilibrium situation results in which the population growth curve levels out; this long-term, steady-state population is the *carrying capacity* of the environment.

The carrying capacity of a particular environment is symbolized by *K*; hence the name "*K*-strategist" refers to an organism that lives in the equilibrium situation described in the previous paragraph. The growth curve of a *K*-strategist, shown as (b) in Figure 4.1.1, is called a *logistic curve*. Figure 4.1.3 is a logistic curve for a more realistic situation.

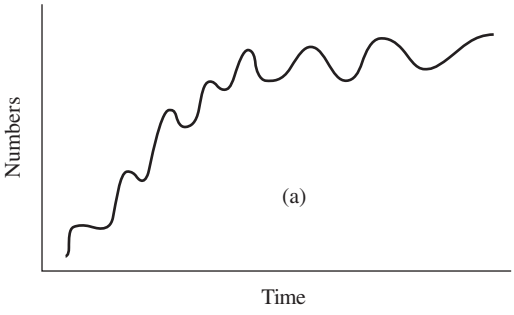

Fig. 4.1.3. A more realistic growth curve of a population of *K*-strategists. The numbers fluctuate around an idealized curve, as shown. Compare this with Figure 4.1.1(b).

Two characteristics are helpful in identifying K-strategists:

1. *Large parental investment in their young.* K-strategists reproduce slowly, with long gestation periods, to increase physiological and anatomical development of the young, who therefore must be born in small broods. After birth, the young are tended until they can reasonably be expected to fend for themselves. One could say that K-strategists put all their eggs in one basket and then watch that basket very carefully.

Figure 4.1.4 is an idealized survivorship curve for a K-strategist. Note that infant mortality is low (compared to r-strategists—see Figure 4.1.2).

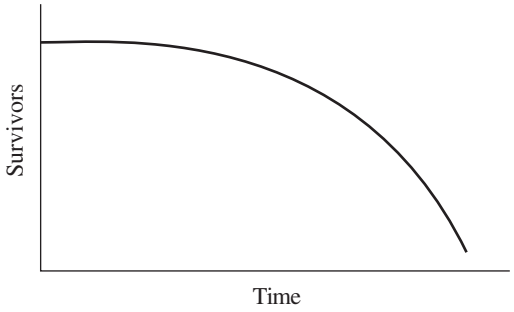

Fig. 4.1.4. An idealized survivorship curve for a group of K-strategists. The graph shows the number of individuals surviving as a function of time, beginning with a fixed number at time $t = 0$. High parental investment leads to a low infant mortality rate.

2. *The ability to exploit stable environmental situations.* Once the population of a K-strategist has reached the carrying capacity of its environment, the population size stays relatively constant. This is nicely demonstrated by the work of H. N. Southern, who studied mating pairs of tawny owls in England [5]. The owl pairs had adjacent territories, with each individual pair occupying a territory that was its own and which was the right size to provide it with nesting space and food (mainly rodents). Every year some adults in the area died, leaving one or more territories that could be occupied by new mating pairs. Southern found that while the remaining adults could have more than replaced those who died, only enough owlets survived in each season to keep the overall numbers of adults constant. The population control measures at work were failure to breed, reduced clutch size, death of eggs and chicks, and emigration. These measures ensured that the total number of adult owls was about the same at the start of each new breeding season.

As long as environmental resistance remains the same, so will population numbers. But if the environmental resistance changes, the carrying capacity of the environment will, too. For example, if the amount of food is the limiting factor, a new value of K is attained when the amount of food increases. This is shown in Figure 4.1.5.

The density-dependent factors that, in conjunction with the organism's reproductive drive, maintain a stabilized population are discussed in the next section. In a later

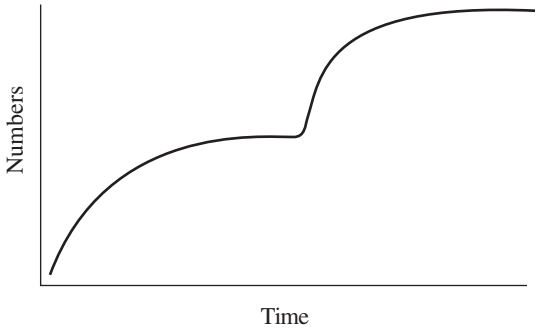

Fig. 4.1.5. The growth of a population of animals, with an increase in food availability midway along the horizontal axis. The extra food generates a new carrying capacity for the environment.

section, we will discuss some ways that a population changes its own environment, and thereby changes that environment's carrying capacity.

Some density-dependent factors exert a negative effect on populations and can thus help control K-strategists.

Environmental factors that change with the density of populations are of many kinds. This section is a discussion of several of them.

Predation. The density of predators, free-living organisms that feed on the bodies of other organisms, would be expected to increase or decrease with the density of prey populations. Figure 4.1.6 shows some famous data, the number of hare and lynx pelts brought to the Hudson Bay Company in Canada over a period of approximately 90 years. Over most of this period, changes in the number of hare pelts led to changes in the number of lynx pelts, as anticipated. After all, if the density of hares increased we would expect the lynx density to follow suit. A detailed study of the data, however, reveals that things were not quite that simple, because in the cycles beginning in 1880 and 1900 the lynxes led the hares. Analysis of this observation can provide us with some enlightening information.

Most importantly, prey population density may depend more strongly on its own food supplies than on predator numbers. Plant matter, the food of many prey species, varies in availability over periods of a year or more. For example, Figure 4.1.7 shows how a tree might partition its reproductive effort (represented by nut production) and its vegetative effort (represented by the size of its annual tree rings). Note the cycles of abundant nut production (called *mast years*) alternating with periods of vigorous vegetative growth; these alternations are common among plants. We should expect that the densities of populations of prey, which frequently are herbivores, would increase during mast years and decrease in other years, independently of predator density (see [2]).

There are some other reasons why we should be cautious about the Hudson Bay data: First, in the absence of hares, lynxes might be easier to catch because, being hungry, they would be more willing to approach baited traps. Second, the naive

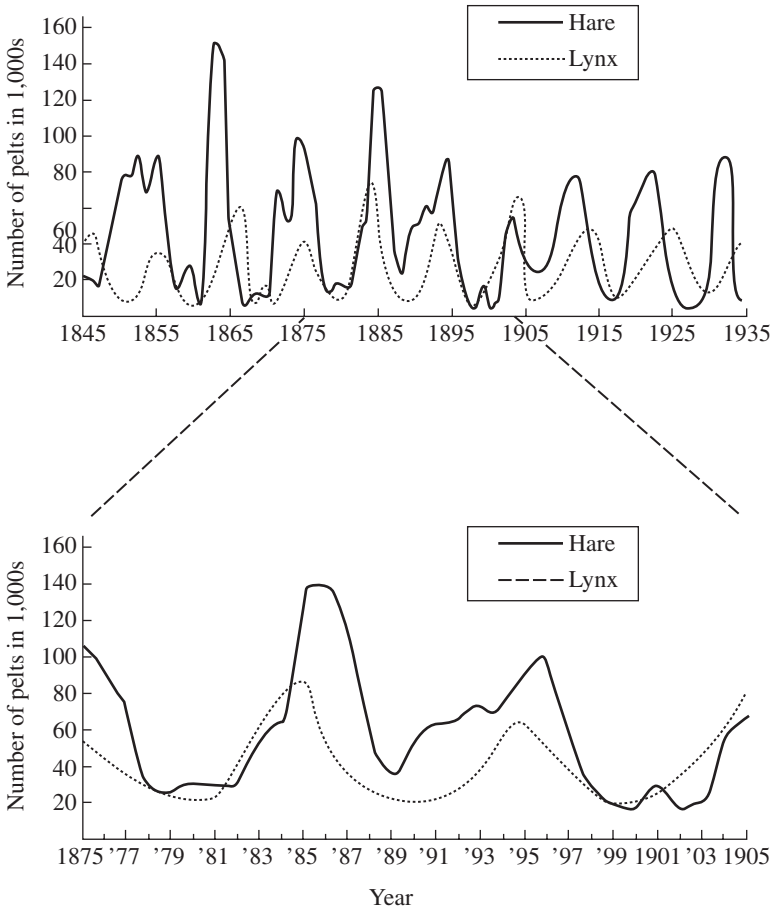

Fig. 4.1.6. The Hudson's Bay Company data. The curve shows the number of predator (lynx) and prey (hare) pelts brought to the company by trappers over a 90-year period. Note that from 1875 to 1905, changes in the lynxes sometimes precede changes in the hares. (Redrawn from D. A. McLulich, Sunspots and abundance of animals, *J. Roy. Astronom. Soc. Canada*, **30** (1936), 233. Used with permission.)

interpretation of Figure 4.1.6 assumes equal trapping efficiencies of prey and predator. Third, for the data to be interpreted accurately, the hares whose pelts are enumerated in Figure 4.1.6 should consist solely of a subset of all the hares that could be killed by lynxes, and the lynxes whose pelts are enumerated in the figure should consist solely of a subset of all the lynxes that could kill hares. The problem here is that very young and very old lynxes, many of whom would have contributed pelts to the study, may not kill hares at all (e.g., because of infirmity they may subsist on carrion).

Parasitism. Parasitism is a form of interaction in which one of two organisms benefits and the other is harmed but not generally killed. A high population density

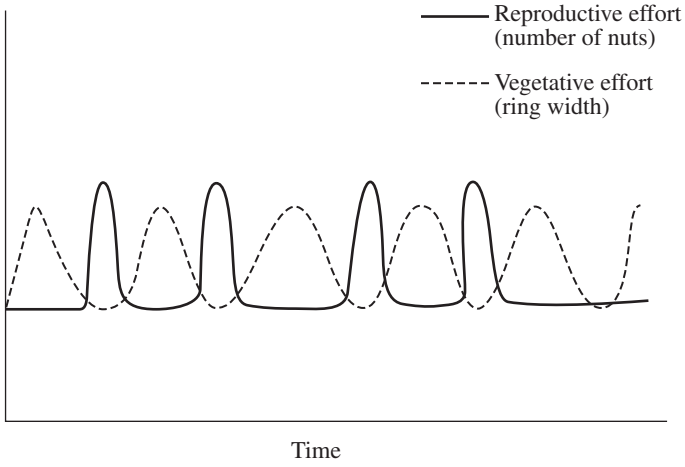

Fig. 4.1.7. This idealized graph shows the amount of sexual (reproductive) effort and asexual (vegetative) effort expended by many trees as a function of time. Sexual effort is measured by nut (seed) production and asexual effort is measured by tree ring growth. Note that the tree periodically switches its emphasis from sexual to asexual and back again. Some related original data can be found in the reference by Harper [2].

would be unfavorable for a parasite's host. For example, many parasites, e.g., hookworms and roundworms, are passed directly from one human host to another. Waste accumulation is implicated in both cases because these parasites are transmitted in fecal contamination. Other mammalian and avian parasites must go through intermediate hosts between their primary hosts, but crowding is still required for effective transmission.

Disease. The ease with which diseases are spread will go up with increasing population density. The spread of colds through school populations is a good example.

An important aggravating factor in the spread of disease is the accumulation of waste. For example, typhoid fever and cholera are easily carried between victims by fecal contamination of drinking water.

Interspecific competition. Every kind of organism occupies an *ecological niche*, which is the functional role that organism plays in its community. An organism's niche includes a consideration of all of its behaviors, their effects on the other members of the community, and the effects of the behaviors of other members of the community on the organism in question.

An empirical rule in biology, *Gause's law*, states that no two species can long occupy the same ecological niche. What will happen is that differences in fitness, even very subtle ones, will eventually cause one of the two species to fill the niche, eliminating the other species. This concept is demonstrated by Figure 4.1.8. When two organisms compete in a uniform habitat, one of the two species always becomes extinct. The "winner" is usually the species having a numerical advantage at the outset of the experiment. (Note the role of luck here—a common and decisive variable in

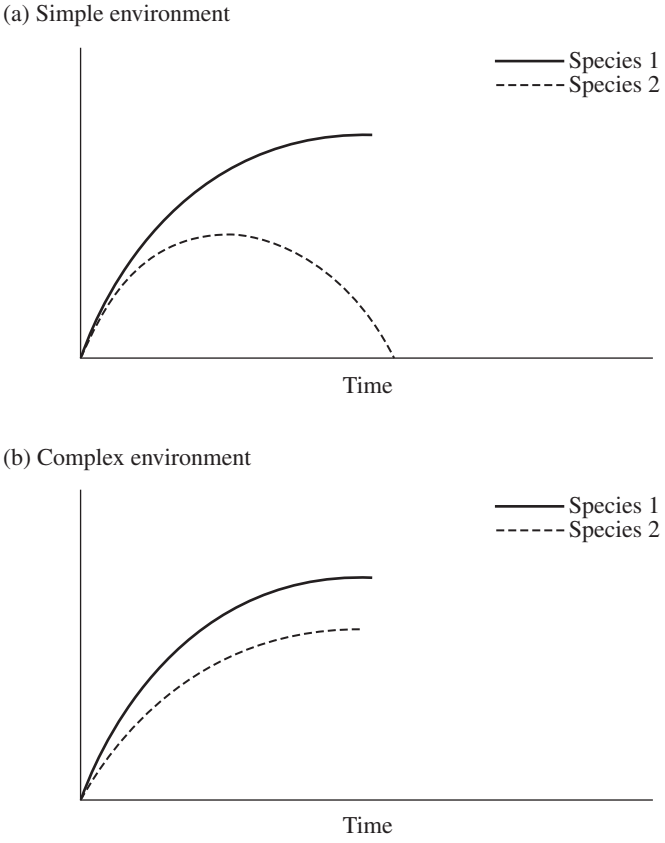

Fig. 4.1.8. Graphs showing the effect of environmental complexity on interspecies relationships. The data for (a) are obtained by counting the individuals of two species in a pure growth medium. The data for (b) are obtained by counting the individuals of the two species in a mechanically complex medium where, for example, pieces of broken glass tubing provide habitats for species 2. The more complex environment supports both species, while the simpler environment supports only one species.

Darwinian evolution.) On the other hand, when the environment is more complex, both organisms can thrive because each can fit into its own special niche.

Intraspecific competition. As individuals die, they are replaced by new individuals who are presumably better suited to the environment than their predecessors. The general fitness of the population thus improves because it becomes composed of fitter individuals.

The use of antibiotics to control bacterial diseases has contributed immeasurably to the welfare of the human species. Once in a while, however, a mutation occurs in a bacterium that confers on it resistance to that antibiotic. The surviving bacterium can then exploit its greater fitness to the antibiotic environment by reproducing rapidly, making use of the space and nutritional resources provided by the deaths of the

antibiotic-sensitive majority. Strains of the bacteria that cause tuberculosis and several sexually transmitted diseases have been created that are resistant to most of the available arsenal of antibiotics. Not unexpectedly, a good place to find such strains is in the sewage from hospitals, from which they can be dispersed to surface and ground water in sewage treatment plant effluent.

This discussion of intraspecific competition is not complete without including an interesting extension of the notion of *biocides*, as suggested by Garrett Hardin. Suppose the whole human race practices contraception to the point that there is zero population growth. Now suppose that some subset decides to abandon all practices that contribute to zero population growth. Soon that subset will be reproducing more rapidly than everyone else, and will eventually replace the others. This situation is analogous to that of the creation of an antibiotic-resistant bacterium in an otherwise sensitive culture. The important difference is that antibiotic resistance is genetically transmitted and a desire for population growth is not. But—as long as each generation continues to teach the next to ignore population control—the result will be the same.

Some density-dependent factors exert positive effects on populations.

The effect of increasing population density is not always negative. Within limits, increasing density may be beneficial, a phenomenon referred to as the *Allee effect*.[4] For example, if a population is distributed too sparsely, it may be difficult for mates to meet; a moderate density, or at least regions in which the individuals are clumped into small groups, can promote mating interactions (think "singles bars").

An intimate long-term relationship between two organisms is said to be *symbiotic*. Symbiotic relationships require at least moderate population densities to be effective. Parasitism, discussed earlier, is a form of symbiosis in which one participant benefits and the other is hurt, although it would be contrary to the parasite's interests to kill the host. The closeness of the association between parasite and host is reflected in the high degree of parasite–host specificity. For instance, the feline tapeworm does not often infect dogs, nor does the canine tapeworm often infect cats.

Another form of symbiosis is *commensalism*, in which one participant benefits and the other is unaffected. An example is the nesting of birds in trees: The birds profit from the association, but the trees are not affected.

The third form of symbiosis recognized by biologists is *mutualism*, in which both participants benefit. An example is that of termites and certain microorganisms that inhabit their digestive systems. Very few organisms can digest the cellulose that makes up wood; the symbionts in termite digestive systems are rare exceptions. The termites provide access to wood and the microorganisms provide digestion. Both can use the digestive products for food, so both organisms profit from the symbiotic association.

It would be unexpected to find a pure K-strategist or a pure r-strategist.

The discussions above, in conjunction with Figure 4.1.1, apply to idealized K- or

[4] Named for a prominent population biologist.

r-strategists. Virtually all organisms are somewhere in between the two, being controlled by a mixture of density-independent and density-dependent factors. For example, a prolonged drought is nondiscriminatory, reducing the numbers of both mosquitoes and rabbits. The density of mosquitoes might be reduced more than that of rabbits, but both will be reduced to some degree. On the other hand, both mosquitoes and rabbits serve as prey for other animals. There are more mosquitoes in a mosquito population than rabbits in a rabbit population, and the mosquitoes reproduce faster, so predation will affect the rabbits more. Still, both animals suffer from predation to some extent.

Density-independent factors may control a population in one context and density-dependent factors may control it in another context. A bitter winter could reduce rodent numbers for a while and then, as the weather warms up, predators, arriving by migration or arousing from hibernation, might assume control of the numbers of rodents. Even the growth of human populations can have variable outcomes, depending on the assumption of the model (see [6]).

The highest sustainable yield of an organism is obtained during the period of most rapid growth.

Industries like lumbering or fishing have, or should have, a vested interest in sustainable maintenance of their product sources. The key word here is "sustainable." It is possible to obtain a very high initial yield of lumber by clear-cutting a mature forest or by seining out all the fish in a lake. Of course, this is a one-time event and is therefore self-defeating. A far better strategy is to keep the forest or fish population at its point of maximal growth, i.e., the steepest part of the growth curve (b) in Figure 4.1.1. The population, growing rapidly, is then able to replace the harvested individuals. Any particular harvest may be small, but the forest or lake will continue to yield products for a long time, giving a high long-term yield. The imposition of bag limits on duck hunters, for instance, has resulted in the stable availability of wild ducks, season after season. Well-managed hunting can be viewed as a density-dependent population-limiting factor that replaces predation, disease, and competition, all of which would kill many ducks anyway.

4.2 Community Ecology

There is a natural progression of plant and animal communities over time in a particular region. This progression occurs because each community makes the area less hospitable to itself and more hospitable to the succeeding community. This succession of communities will eventually stabilize into a climax community that is predictable for the geography and climate of that area.

Continued occupation of an area by a population may make that region less hospitable to them and more hospitable to others.

Suppose that there is a *community* (several interacting populations) of plants in and

around a small lake in north Georgia. Starting from the center of the lake and moving outward, we might find algae and other aquatic plants in the water, marsh plants and low shrubs along the bank, pine trees farther inland, and finally, hardwoods well removed from the lake. If one could observe this community for a hundred or so years, the pattern of populations would be seen to change in a predictable way.

As the algae and other aquatic plants died, their mass would fill up the lake, making it hostile to those very plants whose litter filled it. Marsh plants would start growing in the center of the lake, which would now be boggy. The area that once rimmed the lake would start to dry out as the lake disappeared, and small shrubs and pine trees would take up residence on its margins. Hardwoods would move into the area formerly occupied by the pine trees. This progressive change, called *succession*, would continue until the entire area was covered by hardwoods, after which no further change would be seen. The final, stable, population of hardwoods is called the *climax community* for that area. Climax communities differ from one part of the world to another, e.g., they may be rain forests in parts of Brazil and tundra in Alaska, but they are predictable.

If the hardwood forest described above is destroyed by lumbering or fire, a process called *secondary succession* ensues: Grasses take over, followed by shrubs, then pines, and then hardwoods again. Thus both primary and secondary succession lead to the same climax community.

Succession applies to both plant and animal populations, and as the above example demonstrates, it is due to changes made in the environment by its inhabitants. The drying of the lake is only one possible cause of succession; for instance, the leaf litter deposited by trees could change the pH of the soil beneath the trees, thus reducing mineral uptake by the very trees that deposited the litter. A new population of trees might then find the soil more hospitable, and move in. Alternatively, insects might drive away certain of their prey, making the area less desirable for the insects and more desirable for other animals.

4.3 Environmentally Limited Population Growth

Real populations do not realize constant per capita growth rates. By engineering the growth rate as a function of the population size, finely structured population models can be constructed. Thus if the growth rate is taken to decrease to zero with increasing population size, then a finite limit, the carrying capacity, is imposed on the population. On the other hand, if the growth rate is assigned to be negative at small population sizes, then small populations are driven to extinction.

Along with the power to tailor the population model in this way comes the problem of its solution and the problem of estimating parameters. However, for one-variable models, simple sign considerations predict the asymptotic behavior and numerical methods can easily display solutions.

Logistic growth stabilizes a population at the environmental carrying capacity.

As discussed in Sections 3.1 and 4.1, when a biological population becomes too large,

the per capita growth rate diminishes. This is because the individuals interfere with each other and are forced to compete for limited resources. Consider the model, due to Pierre Verhulst in 1845, wherein the per capita growth rate decreases linearly with population size y:

$$\frac{1}{y}\frac{dy}{dt} = r\left(1 - \frac{y}{K}\right). \tag{4.3.1}$$

The profile of the right-hand side is depicted in Figure 4.3.1.

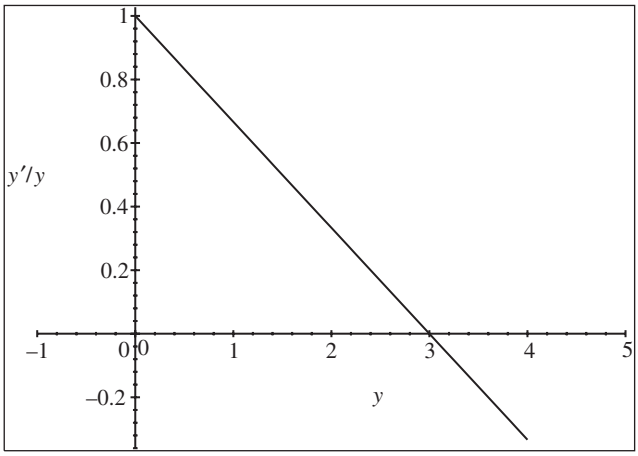

Fig. 4.3.1. Linearly decreasing per capita growth rate ($r = 1$, $K = 3$).

This differential equation is known as the *logistic* (*differential*) *equation*; two of its solutions are graphed later in Figure 4.3.2. Multiplying (4.3.1) by y yields the alternative form

$$\frac{dy}{dt} = ry\left(1 - \frac{y}{K}\right). \tag{4.3.2}$$

From this equation we see that the derivative $\frac{dy}{dt}$ is zero when $y = 0$ or $y = K$. These are the *stationary points* of the equation (see Section 2.4). The stationary point $y = K$, at which the per capita growth rate becomes zero, is called the *carrying capacity* (of the environment).

When the population size y is small, the term $\frac{y}{K}$ is nearly zero and the per capita growth rate is approximately r as in exponential growth. Thus for small population size (but not so small that the continuum model breaks down), the population increases exponentially. Hence solutions are repelled from the stationary point $y = 0$. But as the population size approaches the carrying capacity K, the per capita growth rate decreases to zero and the population ceases to change in size. Further, if the population size ever exceeds the carrying capacity for some reason, then the per capita growth rate will be negative and the population size will decrease to K. Hence solutions are globally attracted to the stationary point $y = K$.

From the form (4.3.2) of the logistic equation we see that it is nonlinear, with a quadratic nonlinearity in y. Nevertheless, it can be solved by separation of variables (see Section 2.4). Rewrite (4.3.1) as

$$\frac{dy}{y\left(1-\frac{y}{K}\right)} = r\,dt.$$

The fraction on the left-hand side can be expanded by *partial fraction decomposition* and written as the sum of two simpler fractions (check this by reversing the step)

$$\left(\frac{1}{y} + \frac{\frac{1}{K}}{\left(1-\frac{y}{K}\right)}\right) dy = r\,dt.$$

The solution is now found by integration. Since the left-hand side integrates to

$$\int \left(\frac{1}{y} + \frac{\frac{1}{K}}{\left(1-\frac{y}{K}\right)}\right) dy = \ln y - \ln\left(1-\frac{y}{K}\right),$$

we get

$$\ln y - \ln\left(1-\frac{y}{K}\right) = rt + c, \tag{4.3.3}$$

where c is the constant of integration. Combining the logarithms and exponentiating both sides, we get

$$\frac{y}{1-\frac{y}{K}} = Ae^{rt}, \tag{4.3.4}$$

where $A = e^c$, and A is not the $t = 0$ value of y. Finally, we solve (4.3.4) for y. First, divide numerator and denominator of the left-hand side by y and reciprocate both sides; this gives

$$\frac{1}{y} - \frac{1}{K} = \frac{1}{Ae^{rt}},$$

or, isolating y,

$$\frac{1}{y} = \frac{1}{Ae^{rt}} + \frac{1}{K}. \tag{4.3.5}$$

Now reciprocate both sides of this and get

$$y = \frac{1}{\frac{1}{Ae^{rt}} + \frac{1}{K}},$$

or equivalently,

$$y = \frac{Ae^{rt}}{1 + \frac{A}{K}e^{rt}}. \tag{4.3.6}$$

Equation (4.3.6) is the solution of the logistic equation (4.3.1). To emphasize that it is the concept of "logistic growth" that is important here, not these solution techniques, we show how a solution for (4.3.1) can be found (symbolically) by the computer algebra system. The initial value is taken as $y(0) = y_0$ in the following:

```
MAPLE
> dsolve({diff(y(t),t) = r*y(t)*(1-y(t)/k),y(0)=y0},y(t));
```

The output of this computation is

$$y(t) = \frac{k}{1 + \frac{e^{-rt}(k - y_0)}{y_0}}.$$

Clearing the compound denominator easily reduces this computer solution to

$$y(t) = \frac{ke^{rt}y_0}{y_0(e^{rt} - 1) + k}.$$

Three members of the family of solutions (4.3.6) are shown in Figure 4.3.2 for different starting values y_0. We take $r = 1$ and $K = 3$ and find solutions for (4.3.2) with $y_0 = 1$, or 2, or 4.

Logistic parameters can sometimes be estimated by least squares.

Unfortunately, the logistic solution (4.3.6) is not linear in its parameters A, r, and K. Therefore, there is no straightforward way to implement least squares. However, if the data values are separated by fixed time periods, τ, then it is possible to remap the equations so least squares will work.

Suppose the data points are $(t_1, y_1), (t_2, y_2), \ldots, (t_n, y_n)$ with $t_i = t_{i-1} + \tau$, $i = 2, \ldots, n$. Then $t_i = t_1 + (i - 1)\tau$ and the predicted value of $\frac{1}{y_i}$, from (4.3.5), is given by

$$\frac{1}{y_i} = \frac{1}{Ae^{rt_1}e^{(i-1)r\tau}} + \frac{1}{K} = \frac{1}{e^{r\tau}}\left[\frac{1}{Ae^{rt_1}e^{(i-2)r\tau}} + \frac{e^{r\tau}}{K}\right]. \tag{4.3.7}$$

But by rewriting the term involving K as

$$\frac{1}{K} + \frac{e^{r\tau} - 1}{K},$$

and using (4.3.5) again, (4.3.7) becomes

$$\frac{1}{y_i} = \frac{1}{e^{r\tau}}\left[\frac{1}{y_{i-1}} + \frac{e^{r\tau} - 1}{K}\right].$$

Now put $z = \frac{1}{y}$, and we have

$$z_i = e^{-r\tau}z_{i-1} + \frac{1 - e^{-r\tau}}{K}, \quad \text{where } y = \frac{1}{z}. \tag{4.3.8}$$

A least squares calculation is performed on the points $(z_1, z_2), (z_2, z_3), \ldots, (z_{n-1}, z_n)$ to determine r and K. With r and K known, least squares can be performed on, say (4.3.5), to determine A.

In the exercises we will illustrate this method and suggest another for U.S. population data.

```
MAPLE
> r:=1;k:=3;
> dsolve({diff(y(t),t)=r*y(t)*(1-y(t)/k),y(0)=1},y(t));
  y1:=unapply(rhs(%),t);
> dsolve({diff(y(t),t)=r*y(t)*(1-y(t)/k),y(0)=2},y(t));
  y2:=unapply(rhs(%),t);
> dsolve({diff(y(t),t)=r*y(t)*(1-y(t)/k),y(0)=4},y(t));
  y4:=unapply(rhs(%),t);
> plot({y1(t),y2(t),y4(t)},t=0..5,y=0..5);
```

```
MATLAB
% solve the logistic eqn for starting values y0=1, y0=2, y0=4
% Make up an m-file, fig432.m, as follows:
%   function yprime = fig432(t,y) % with r=1 and K=3
%   r=1; K=3; yprime=y.*r.*(1-y./K);
> tspan=[0 5];
> [t1,y1]=ode23('fig432',tspan,1);
> [t2,y2]=ode23('fig432',tspan,2);
> [t4,y4]=ode23('fig432',tspan,4);
> plot(t1,y1,t2,y2,t4,y4)
```

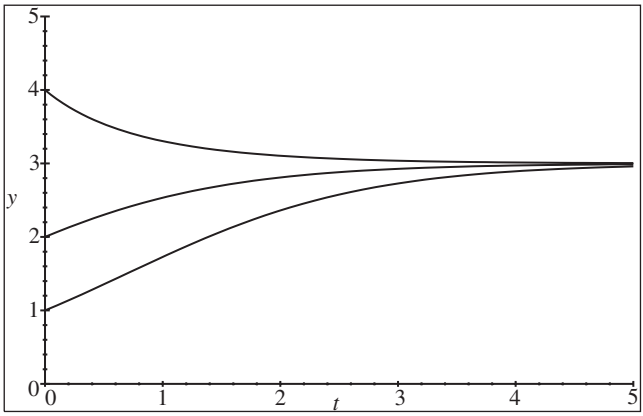

Fig. 4.3.2. Solutions for (4.3.1).

The logistic equation has a discrete analogue.

The corresponding discrete population model to (4.3.2) is

$$y_{t+1} - y_t = \rho y_t \left(1 - \frac{y_t}{K}\right). \tag{4.3.9}$$

By transposing y_t, we get an equivalent form,

$$y_{t+1} = y_t \left(1 + \rho - \frac{\rho y_t}{K}\right) = (1+\rho) y_t \left(1 - \frac{\rho}{1+\rho}\frac{y_t}{K}\right). \tag{4.3.10}$$

Recall that we encountered a similar recurrence relation, (2.5.11), in Section 2.5. From that discussion, we suspect that some values of ρ may lead to chaos. In fact, with $K = 1$ and $\rho = 3$, we get the population behavior shown in Figure 4.3.3.

```
MAPLE
> K:=1;
> rho:=3.0;
> c:= (rho/K)/(1+rho):
> y[0]:=1/48.0;
> for i from 1 to 60 do y[i]:=(1+rho)*y[i-1]*(1-c*y[i-1]);
> od;
> pts:=[seq([i,y[i]],i=0..60)];
> plot(pts);

MATLAB
> K=1; rho=3; c=(rho/K)/(1+rho); y(1)=0.05; t=[1:60];
> for i = 2:60 y(i)=(1+rho)*y(i-1)*(1-c*y(i-1));
  end
> plot(t,y)
```

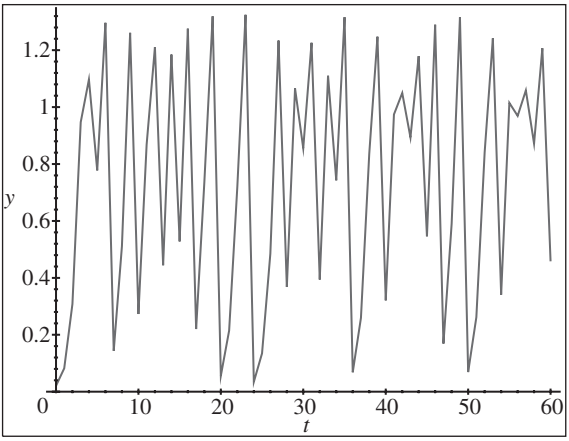

Fig. 4.3.3. Logistic growth, discrete model, ρ large.

Does the chaos phenomenon extend to the continuous model too? Not strictly, according to the Verhulst equation (4.3.2). This is because as y increases continuously, $\frac{y}{K}$ will increase to 1 without overshooting. Then continued population growth will stop, since $\frac{dy}{dt}$ will then be 0. However, if population increases are based not on the present population size but on the population size in the previous generation, say, then instability and chaos is possible.

In fact, real populations are sometimes chaotic. An unwelcome example is in the sardine population off the coast of California. In this case, the cause appears to be the practice of harvesting too many big fish. For details, see [12].

Nonlinear per capita growth rates allow more complicated population behavior.

Real populations are in danger of extinction if their size falls to a low level. Predation might eliminate the last few members completely, finding mates becomes more difficult, and lack of genetic diversity renders the population susceptible to epidemics. By constructing a per capita growth rate that is actually negative below some critical value θ, there results a population model that tends to extinction if population size falls too low. Such a per capita growth rate is given as the right-hand side of the

following modification of the logistic equation:

$$\frac{1}{y}\frac{dy}{dt} = r\left(\frac{y}{\theta} - 1\right)\left(1 - \frac{y}{K}\right), \tag{4.3.11}$$

where $0 < \theta < K$. This form of the per capita growth rate is pictured in Figure 4.3.4 using the specific parameters $r = 1$, $\theta = \frac{1}{5}$, and $K = 1$. It is sometimes referred to as the *predator pit*.

We draw the graph in Figure 4.3.4 with these parameters:

MAPLE
```
> restart
> r:=1; theta:=1/5; K:=1;
> plot([y,r*(y/theta-1)*(1-y/K),y=0..1],-.2..1,-1..1);
```

MATLAB
```
> r=1; theta=0.2; K=1; y=0:0.05:1; f=r.*(y/theta - 1).*(1-y/K);
> plot(y,f); hold on
> xaxis = zeros(size(y));
> plot(y,xaxis)
```

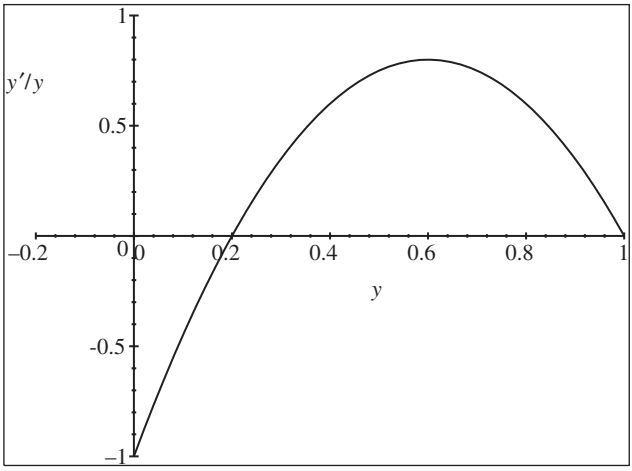

Fig. 4.3.4. The predator pit per capita growth rate function.

The stationary points of (4.3.11) are $y = 0$, $y = \theta$, and $y = K$. Unlike before, now $y = 0$ is asymptotically stable; that is, if the starting value y_0 of a solution is near enough to 0, then the solution will tend to 0 as t increases. This follows because the sign of the right-hand side of (4.3.11) is negative for $0 < y < \theta$, causing $\frac{dy}{dt} < 0$. Hence y will decrease. On the other hand, a solution starting with $y_0 > \theta$ tends to K as t increases. This follows because when $\theta < y < K$, the right-hand side of (4.3.11) is positive, so $\frac{dy}{dt} > 0$ also and hence y will increase even more. As before, solutions starting above K decrease asymptotically to K.

Some solutions to (4.3.11) are shown in Figure 4.3.5 with the following syntax:

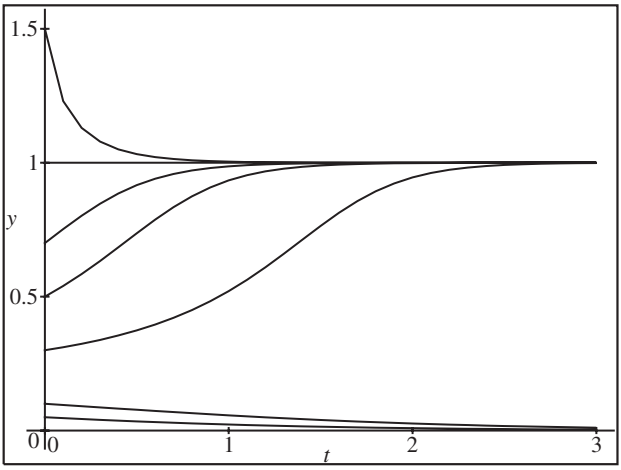

Fig. 4.3.5. Some solutions to the predator pit equation.

MAPLE

```
> r:=1; theta:=1/5; K:=1;
> inits:={[0,.05],[0,.1],[0,0.3],[0,.5],[0,1],[0,0.7],[0,1.5]};
> with(DEtools): DEplot(diff(y(t),t)=r*y(t)*(y(t)/theta-1)*(1-y(t)/K),y(t),t=0..3,inits, arrows=NONE,stepsize=0.1);
```

MATLAB

```
% Make up an m-file, fig434.m:
%   function yprime = fig434(t,y)
%   with r=1, theta=.2, and K=1.
%   r=1; theta=0.2; K=1;
%   yprime = y.*r.*(1-y./K).*(y/theta-1);
> tspan=[0 3];
> [t05,y05]=ode23('fig434',tspan,.05);
> [t1,y1]=ode23('fig434',tspan,.1);
> [t3,y3]=ode23('fig434',tspan,.3);
> [t5,y5]=ode23('fig434',tspan,.5);
> [t7,y7]=ode23('fig434',tspan,.7);
> [t15,y15]=ode23('fig434',tspan,1.5);
> plot(t05,y05,t1,y1,t3,y3,t5,y5,t7,y7,t15,y15)
```

As our last illustration, we construct a population model that engenders little population growth for small populations, rapid growth for intermediate sized ones, and low growth again for large populations. This is achieved by the quadratic per capita growth rate and given as the right-hand side of the differential equation

$$\frac{1}{y}\frac{dy}{dt} = ry\left(1 - \frac{y}{K}\right). \tag{4.3.12}$$

Exercises/Experiments

1. At the meeting of the Southeastern Section of the Mathematics Association of America, Terry Anderson presented a MAPLE program that determined a logistic fit for the U.S. population data. His fit is given by

$$\text{U.S. population} \approx \frac{\alpha}{1 + \beta e^{-\delta t}},$$

where $\alpha = 387.9802$, $\beta = 54.0812$, and $\delta = 0.0270347$. Here population is measured in millions and t = time since 1790. (Recall the population data of Example 3.5.1.)

(a) Show that the function given by the Anderson fit satisfies a logistic equation of the form

$$\frac{dy}{dt} = \delta y(t)\left(1 - \frac{y(t)}{\alpha}\right),$$

with

$$y(0) = \frac{\alpha}{1+\beta}.$$

(b) Plot the graphs of the U.S. population data and this graph superimposed. Compare the exponential fits from Chapter 3.

(c) If population trends continue, what is the long-range fit for the U.S. population level?

MAPLE

```
> Anderfit:=t->alpha/(1+beta*exp(-delta*t));
> dsolve({diff(y(t),t)-delta*y(t)*(1-y(t)/alpha)=0, y(0)=alpha/(1+beta)},y(t));
> alpha:=387.980205; beta:=54.0812024; delta:=0.02270347337;
> J:=plot(Anderfit(t),t=0..200):
> tt:=[seq(i*10,i=0..20)];
> pop:=[3.929214, 5.308483, 7.239881, 9.638453, 12.866020, 17.069453, 23.191876,
        31.433321, 39.818449, 50.155783, 62.947714, 75.994575, 91.972266, 105.710620,
        122.775046, 131.669275, 151.325798, 179.323175, 203.302031, 226.545805,
        248.709873];
> data:= [seq([tt[i],pop[i]],i=1..21)];
> K:=plot(data,style=POINT):
> plots[display]({J,K});
> expfit:= t->exp(0.02075384393*t+1.766257672);
> L:=plot(expfit(t),t=0..200):
> plots[display]({J,K,L});
> plot(Anderfit(t-1790),t=1790..2150);
```

MATLAB

```
> tt=0:10:200;
> pop=[3.929214, 5.308483, 7.239881, 9.638453, 12.866020, 17.069453, 23.191876,...
       31.433321, 39.818449, 50.155783, 62.947714, 75.994575, 91.972266, 105.710620,...
       122.775046, 131.669275, 151.325798, 179.323175, 203.302031, 226.545805,...
       248.709873];
> plot(tt,pop,'x'); hold on;
> alpha=387.980205; beta=54.0812024; delta=0.02270347337;
> Anderfit=alpha./(1+beta*exp(-delta*tt));
> plot(tt,Anderfit)
```

2. Using the method of (4.3.8), get a logistic fit for the U.S. population. Use the data in Example3.5.1.

3. Suppose that the spruce budworm, in the absence of predation by birds, will grow according to a simple logistic equation of the form

$$\frac{dB}{dt} = rB\left(1 - \frac{B}{K}\right).$$

Budworms feed on the foliage of trees. The size of the carrying capacity, K, will therefore depend on the amount of foliage on the trees; we take it to be constant for this model.

(a) Draw graphs for how the population might grow if r were 0.48 and K were 15. Use several initial values.

(b) Introduce predation by birds into this model in the following manner: Suppose that for small levels of worm population there is almost no predation, but for larger levels, birds are attracted to this food source. Allow for a limit to the number of worms that each bird can eat. A model for predation by birds might have the form

$$P(B) = a\frac{B^2}{b^2 + B^2},$$

where a and b are positive (see [7]). Sketch the graph for level of predation of the budworms as a function of the size of the population. Take a and b to be 2.

(c) A model for the budworm population size in the presence of predation could be modeled as

$$\frac{dB}{dt} = rB\left(1 - \frac{B}{K}\right) - a\frac{B^2}{b^2 + B^2}.$$

To understand the delicacy of this model and the implications for the care that needs to be taken in modeling, investigate graphs of solutions for this model with parameters $r = 0.48$, $a = b = 2$, and $K = 15$ or $K = 17$.

(d) Verify that in one case, there is a positive steady-state solution and in the other, the limit of the budworm population is zero.

The significance of the graph with $K = 17$ is that the worm population can rise to a high level. With $K = 15$, only a low level for the size of the budworms is possible. The birds will eat enough of the budworms to save the trees!

Here is the syntax for making this study with $K = 15$:

MAPLE

```
> K:= 15;
> h:=(t,B)–>.48*B*(1-B/K)-2*B^2/(4+B^2);
> plot(h(0,B),B=0..20);
> inits:={[0,1], [0,2], [0,4], [0,5], [0,6], [0,8], [0,10], [0,12], [0,14], [0,16]};
> with(DEtools);
> DEplot(diff(y(t),t)=h(t,y(t)),y(t),t=0..30,inits,arrows=NONE,stepsize=0.1);
```

MATLAB

```
% make an m-file, exer43.m
%   function Bprime=exer43(t,B); r=.48; K=15; a=2; b=2; Bprime=r*B.*(1-B/K)-a*B.^2./(b^2+B.^2);
> K=15; a=2; b=2; r=.48;
> B=0:.1:20; Bprime=exer43(0,B); plot(B,Bprime)
> [t,y1]=ode23('exer43',[0 30],1);plot(t,y1)
> hold on
> [t,y2]=ode23('exer43',[0 30],2);plot(t,y2)
> [t,y4]=ode23('exer43',[0 30],4);plot(t,y4)
> [t,y5]=ode23('exer43',[0 30],5);plot(t,y5)
> [t,y6]=ode23('exer43',[0 30],6);plot(t,y6)
> [t,y8]=ode23('exer43',[0 30],8);plot(t,y8)
> [t,y10]=ode23('exer43',[0 30],10);plot(t,y10)
> [t,y12]=ode23('exer43',[0 30],12);plot(t,y12)
> [t,y14]=ode23('exer43',[0 30],14);plot(t,y14)
> [t,y16]=ode23('exer43',[0 30],16);plot(t,y16)
```

4. The following is a logistic adaptation of Code 3.5.1. Experiment with the parameter r and observe the behavior of the population size. Is the size chaotic for some values of r? It might be necessary to decrease delT (by increasing N to, say, 20) to get valid results.

```
  MAPLE
> N:=10: delT:=1/N:
  #t is now linked to index i by t=-1+(i-1)*delT
> for i from 1 to N+1 do f[i]:=1:
  od:
> #work from t=0 in steps of delT
> tfinal:=10: #end time tfinal, end index is n
> n:=(tfinal+1)*N+1:
> K:=3; r:=1.2;
> for i from N+1 to n-1 do t:=-1+(i-1)*delT:
    delY:=r*f[i-N]*(1-f[i-N]/K)*delT: #N back=delay of 1
    f[i+1]:=f[i]+delY: #Eulers method
> od;
> pts:=[seq([i,f[i]],i=0..n)];
> plot(pts);

  MATLAB
  % make an m-file, delayFcn0.m:
  %   function y=delayFcn0(t)
  %   y = 1;
> N=10; % steps per unit interval
> delT=1/N; % so delta t=0.1
  % t is now linked to index i by t=-1+(i-1)*delT
  % set initial values via delay fcn f0
> for i=1:N+1
>    t=-1+(i-1)*delT; f(i)=delayFcn0(t);
> end
  % work from t=0 in steps of delT
  tfinal=10; % end time tfinal, end index is n
  % solve tfinal=-1+(n-1)*delT for n
> n=(tfinal+1)*N+1;
> K=3; r=1.2;
> for i=N+1:n-1
>    t=-1+(i-1)*delT;
>    delY=r*f(i-N)*(1-f(i-N)/K)*delT; % N back=delay of 1
>    f(i+1)=f(i)+delY; % Eulers method
> end
> t=-1:delT:tfinal; plot(t,f);
```

4.4 A Brief Look at Multiple Species Systems

Without exception, biological populations interact with populations of other species. Indeed, the web of interactions is so pervasive that the entire field of Ecology is devoted to it. Mathematically, the subject began about 70 *years ago with a simple two-species, predator–prey differential equation model. The central premise of this Lotka–Volterra model is a mass action–interaction term. While community differential equation models are difficult to solve exactly, they can nonetheless be analyzed by qualitative methods. One tool for this is to linearize the system of equations about their stationary solution points and to determine the eigenvalues of the resulting interaction, or community, matrix. The eigenvalues in turn predict the stability of the web. The Lotka–Volterra system has neutral stability at its nontrivial stationary*

point, which, like Malthus's unbounded population growth, is a shortcoming that indicates the need for a better model.

Interacting population models utilize a mass action–interaction term.

Alfred Lotka (1925) and, independently, Vito Volterra (1926) proposed a simple model for the population dynamics of two interacting species (see [8]). The central assumption of the model is that the degree of interaction is proportional to the numbers, x and y, of each species and hence to their product, that is,

$$\text{degree of interaction} = (\text{constant})xy.$$

The Lotka–Volterra system is less than satisfactory as a serious model because it entails neutral stability (see below). However, it does illustrate the basic principles of multispecies models and the techniques for their analysis. Further, like the Malthusian model, it serves as a point of departure for better models. The central assumption stated above is also used as the interaction term between reactants in the description of chemical reactions. In that context it is called the *mass action principle*. The principle implies that encounters occur more frequently in direct proportion to their concentrations.

The original Lotka–Volterra equations are

$$\begin{aligned} \frac{dx}{dt} &= rx - axy, \\ \frac{dy}{dt} &= -my + bxy, \end{aligned} \tag{4.4.1}$$

where the positive constants r, m, a, and b are parameters. The model was meant to treat predator–prey interactions. In this, x denotes the population size of the prey, and y the same for the predators. In the absence of predators, the equation for the prey reduces to $\frac{dx}{dt} = rx$. Hence the prey population increases exponentially with rate r in this case; see Section 3.5. Similarly, in the absence of prey, the predator equation becomes $\frac{dy}{dt} = -my$, dictating an exponential decline with rate m.

The sign of the interaction term for the prey, $-a$, is negative, indicating that interaction is detrimental to them. The parameter a measures the average degree of the effect of one predator in depressing the per capita growth rate of the prey. Thus a is likely to be large in a model for butterflies and birds but much smaller in a model for caribou and wolves. In contrast, the sign of the interaction term for the predators, $+b$, is positive, indicating that they are benefited by the interaction. As above, the magnitude of b is indicative of the average effect of one prey on the per capita predator growth rate.

Besides describing predator–prey dynamics, the Lotka–Volterra system describes to a host–parasite interaction as well. Furthermore, by changing the signs of the interaction terms, or allowing them to be zero, the same basic system applies to other kinds of biological interactions as discussed in Section 4.1, such as mutualism, competition, commensalism, and amensalism.

Mathematically, the Lotka–Volterra system is not easily solved. Nevertheless, solutions may be numerically approximated and qualitatively described. Since the system has two dependent variables, a solution consists of a pair of functions $x(t)$ and $y(t)$ whose derivatives satisfy (4.4.1). Figure 4.4.1 is the plot of the solution to these equations with $r = a = m = b = 1$ and initial values $x(0) = 1.5$ and $y(0) = 0.5$. The figure is drawn with the following syntax:

```
MAPLE
> predprey:=diff(x(t),t)=r*x(t)-a*x(t)*y(t), diff(y(t),t)=-m*y(t)+b*x(t)*y(t);
> r:=1; a:=1; m:=1; b:=1;
> sol:=dsolve({predprey,x(0)=3/2,y(0)=1/2}, {x(t),y(t)},type=numeric, output=listprocedure);
> xsol:=subs(sol,x(t)); ysol:=subs(sol,y(t));
> plot([xsol,ysol],0..10,-1..3);

MATLAB
% make an m-file named predPrey44.m with:
%   function Yprime=predPrey44(t,x)
%   r=1; a=1; m=1; b=1;
%   Yprime=[r*x(1)-a*x(1).*x(2); -m*x(2)+b*x(1).*x(2)];
> [t,Y]=ode23('predPrey44',[0 10],[1.5;0.5]); % ; for column vector
> plot(t,Y) % both curves as the columns of Y vs. t
```

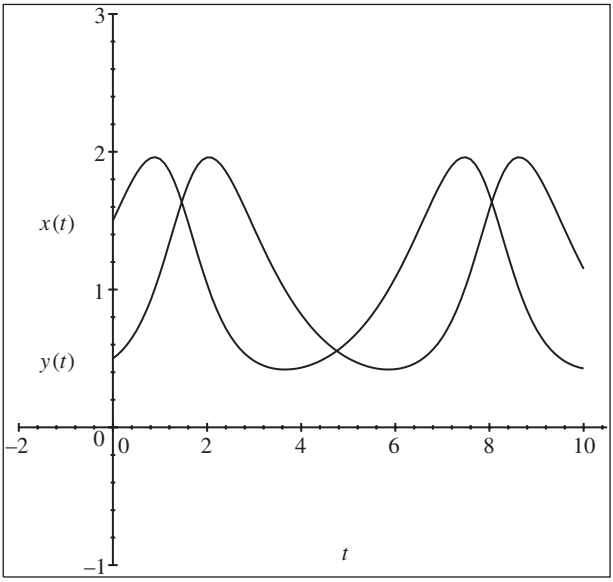

Fig. 4.4.1. Graphs of $x(t)$ and of $y(t)$, solutions for (4.4.1).

Notice that the prey curve leads the predator curve.[5] We discuss this next.

Although there are three variables in a Lotka–Volterra system, t is easily eliminated by dividing $\frac{dy}{dt}$ by $\frac{dx}{dt}$; thus

[5] In Section 4.1, we have discussed a number of biological reasons why in a real situation, this model is inadequate.

MAPLE
```
> with(plots): with(DEtools):
> inits:={[0,3/2,1/2],[0,4/5,3/2]};
> phaseportrait({predprey},[x,y],t=0..10,inits,stepsize=.1);
```

MATLAB
```
> x=Y(:,1); y=Y(:,2); plot(x,y)
```

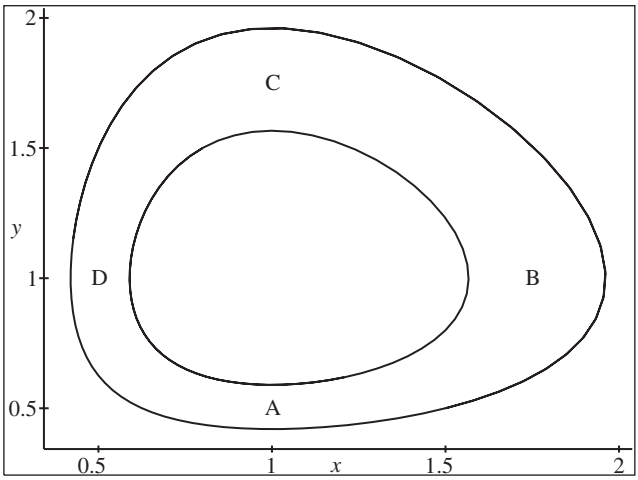

Fig. 4.4.2. A plot of two solutions of (4.4.1) in the (x, y)-plane.

$$\frac{dy}{dx} = \frac{-my + bxy}{rx - axy}.$$

This equation does not contain t and can be solved exactly as an implicit relation between x and y:[6]

MAPLE
```
> dsolve(diff(y(x),x)=(-y(x)+x*y(x))/(x-x*y(x)),y(x),implicit);
```

$$-\ln(y(x)) + y(x) - \ln(x) + x = C.$$

This solution gives rise to a system of closed curves in the (x, y)-plane called the *phase plane* of the system. These same curves, or *phase portraits*, can be generated from a solution pair $x(t)$ and $y(t)$ as above by treating t as a parameter. In Figure 4.4.2, we show the phase portrait of the solution pictured in Figure 4.4.1.

Let us now trace this phase portrait. Start at the bottom of the curve, region A, with only a small number of prey and predators. With few predators, the population size of the prey grows almost exponentially. But as the prey size becomes large, the interaction term for the predators, bxy, becomes large and their numbers y begin to grow. Eventually, the product ay first equals and then exceeds r, in the first equation of (4.4.1), at which time the population size of the prey must decrease. This takes us to region B in the figure.

[6] *Implicit* means that neither variable x nor y is solved for in terms of the other.

However, the number of prey is still large, so predator size y continues to grow, forcing prey size x to continue declining. This is the upward and leftward section of the portrait. Eventually, the product bx first equals and then falls below m in the second equation of (4.4.1), whereupon the predator size now begins to decrease. This is point C in the figure.

At first, the predator size is still at a high level, so the prey size will continue to decrease until it reaches its smallest value. But with few prey around, predator numbers y rapidly decrease until finally the product ay falls below r. Then the prey size starts to increase again. This is region D in the figure. But the prey size is still at a low level, so the predator numbers continue to decrease, bringing us back to region A and completing one cycle.

Thus the phase portrait is traversed counterclockwise, and as we have seen in the above narration, the predator population cycle qualitatively follows that of the prey population cycle but lags behind it.

Of course the populations won't change at all if the derivatives $\frac{dx}{dt}$ and $\frac{dy}{dt}$ are both zero in the Lotka–Volterra equations (4.4.1). Setting them to zero and solving the resulting algebraic system locates the stationary points,

$$\begin{aligned} 0 &= x \cdot (r - ay), \\ 0 &= y \cdot (-m + bx). \end{aligned}$$

Thus if $x = \frac{m}{b}$ and $y = \frac{r}{a}$, the populations remain fixed. Of course, $x = y = 0$ is also a stationary point.

Stability determinations are made from an eigenanalysis of the community matrix.

Consider the stationary point $(0, 0)$. What if the system starts close to this point, that is, y_0 and x_0 are both very nearly 0? We assume that these values are so small that the quadratic terms in (4.4.1) are negligible, and we discard them. This is called *linearizing the system* about the stationary point. Then the equations become

$$\begin{aligned} \frac{dx}{dt} &= rx, \\ \frac{dy}{dt} &= -my. \end{aligned} \tag{4.4.2}$$

Hence x will increase and y will further decrease (but not to zero) and a phase portrait will be initiated as discussed above. The system will *not*, however, return to $(0, 0)$. Therefore, this stationary point is unstable.

We can come to the same conclusion by rewriting the system (4.4.2) in matrix form and examining the eigenvalues of the matrix on the right-hand side. This matrix is

$$\begin{bmatrix} r & 0 \\ 0 & -m \end{bmatrix}, \tag{4.4.3}$$

and its eigenvalues are $\lambda_1 = r$ and $\lambda_2 = -m$. Since one of these is real and positive, the conclusion is that the stationary point $(0, 0)$ is unstable.

Now consider the stationary point $x = \frac{m}{b}$ and $y = \frac{r}{a}$ and linearize about it as follows. Let $\xi = x - \frac{m}{b}$ and $\eta = y - \frac{r}{a}$. In these new variables, the first equation of the system (4.4.1) becomes

$$\frac{d\xi}{dt} = r\left(\xi + \frac{m}{b}\right) - a\left(\xi + \frac{m}{b}\right)\left(\eta + \frac{r}{a}\right) = -\frac{am}{b}\eta - a\xi\eta.$$

Again discard the quadratic term; this yields

$$\frac{d\xi}{dt} = -\frac{am}{b}\eta.$$

The second equation of the system becomes

$$\begin{aligned}\frac{d\eta}{t} &= -m\left(\eta + \frac{r}{a}\right) + b\left(\xi + \frac{m}{b}\right)\left(\eta + \frac{r}{a}\right),\\ \frac{d\eta}{dt} &= \frac{br}{a}\xi + b\xi\eta.\end{aligned}$$

And discarding the quadratic term gives

$$\frac{d\eta}{dt} = \frac{br}{a}\xi.$$

Thus the equations in (4.4.1) become

$$\begin{aligned}\frac{d\xi}{dt} &= -\frac{am}{b}\eta,\\ \frac{d\eta}{dt} &= \frac{br}{a}\xi.\end{aligned} \tag{4.4.4}$$

The right-hand side of (4.4.4) can be written in matrix form:

$$\begin{bmatrix} 0 & -\frac{am}{b} \\ \frac{br}{a} & 0 \end{bmatrix}\begin{bmatrix}\xi\\ \eta\end{bmatrix}. \tag{4.4.5}$$

This time the eigenvalues of the matrix are imaginary, $\lambda = \pm i\sqrt{mr}$. This implies that the stationary point is *neutrally stable*.

Determining the stability at stationary points is an important problem. Linearizing about these points is a common tool for studying this stability, and has been formalized into a computational procedure. In the exercises, we give more applications that utilize the above analysis and that use a computer algebra system. Also, we give an example in which the procedure incorrectly predicts the behavior at a stationary point. The text by Steven H. Strogatz [9] explains conditions under which the procedure is guaranteed to work.

To illustrate a computational procedure for this predator–prey model, first create the vector function V:

```
MAPLE
> restart:
> with(LinearAlgebra):with(VectorCalculus):
> V:=Vector([r*x-a*x*y,-m*y+b*x*y]);

MATLAB
% We must compute derivates numerically
% make an m-file predPrey44.m with:
%   function Yprime=predPrey44(t,x);
%   r=1; a=1; m=1; b=1;
%   Yprime=[r*x(1)-a*x(1).*x(2); -m*x(2)+b*x(1).*x(2)];
```

Find the critical points of (4.4.1) by asking where this vector-valued function is zero (symbolically):

```
MAPLE
> solve({V[1]=0,V[2]=0}, {x,y});
```

This investigation provides the solutions $\{0, 0\}$ and $\{\frac{m}{b}, \frac{r}{a}\}$, as we stated above. We now make the linearization of V about $\{0, 0\}$ and about $\{\frac{m}{b}, \frac{r}{a}\}$:

```
MAPLE
> Jacobian(V,[x,y]);
> subs({x=0,y=0},%);
> subs({x=m/b,y=r/a},%%);

MATLAB
% eps is matlab's smallest value; by divided difference
% find the derivatives numerically; first at (0,0)
> M1=(predPrey44(0,[eps 0]) - predPrey44(0,[0 0]))/eps;
% this is the first column of the Jacobian at x=y=0, i.e., derivatives with respect to x
> M2=(predPrey44(0,[0 eps]) - predPrey44(0,[0 0]))/eps;
% the derivatives with respect to y
> M=[M1 M2]; % the Jacobian
% calculate its eigenvalues
> eig(M) % get 1 and -1, +1 means unstable at (0,0)
```

Note that in matrix form,

$$\begin{pmatrix} \frac{dx}{dt} \\ \frac{dy}{dt} \end{pmatrix} = \begin{pmatrix} r & 0 \\ 0 & -m \end{pmatrix} \begin{pmatrix} x-0 \\ y-0 \end{pmatrix} + \begin{pmatrix} -a \\ b \end{pmatrix} (x-0)(y-0)$$

for linearization about $(0, 0)$ and

$$\begin{pmatrix} \frac{dx}{dt} \\ \frac{dy}{dt} \end{pmatrix} = \begin{pmatrix} 0 & -\frac{am}{b} \\ \frac{br}{a} & 0 \end{pmatrix} \begin{pmatrix} x-\frac{m}{b} \\ y-\frac{r}{a} \end{pmatrix} + \begin{pmatrix} -a \\ b \end{pmatrix} \left(x-\frac{m}{b}\right) \left(y-\frac{r}{a}\right)$$

for linearization about $(\frac{m}{b}, \frac{r}{a})$. Finally, we compute the eigenvalues for the linearization about each of the critical points:

```
MAPLE
> Eigenvalues(%%); Eigenvalues(%%);

MATLAB
% now linearize at x=m/b=1, y=r/a=1
> M1=(predPrey44(0,[1+eps 1])-predPrey44(0,[1 1]))/eps;
> M2=(predPrey44(0,[1 1+eps])-predPrey44(0,[1 1]))/eps;
> M=[M1 M2];
> eig(M) % get +/-I (I=sqrt(-1)), so neutrally stable
```

The result is the same as that from (4.4.5).

Exercises/Experiments

1. The following *competition model* is provided in [9]. Imagine rabbits and sheep competing for the same limited amount of grass. Assume a logistic growth for the two populations, that rabbits reproduce rapidly, and that the sheep will crowd out the rabbits. Assume that these conflicts occur at a rate proportional to the size of each population. Further, assume that the conflicts reduce the growth rate for each species, but make the effect more severe for the rabbits by increasing the coefficient for that term. A model that incorporates these assumptions is

$$\frac{dx}{dt} = x(3 - x - 2y),$$
$$\frac{dy}{dt} = y(2 - x - y),$$

where $x(t)$ is the rabbit population and y is the sheep population. (Of course, the coefficients are not realistic but are chosen to illustrate the possibilities.) Find four stationary points and investigate the stability of each. Show that one of the two populations is driven to extinction.

2. Imagine a *three-species predator–prey problem* that we identify with grass, sheep, and wolves. The grass grows according to a logistic equation in the absence of sheep. The sheep eat the grass and the wolves eat the sheep. (See McLaren [10] for a three-species population under observation.) We model this with the equations that follow. Here x represents the wolf population, y represents the sheep population, and z represents the area in grass:

$$\frac{dx}{dt} = -x + xy,$$
$$\frac{dy}{dz} = -y + 2yz - xy,$$
$$\frac{dz}{dt} = 2z - z^2 - yz.$$

What would be the steady state of grass with no sheep or wolves present? What would be the steady state of sheep and grass with no wolves present? What is the revised steady state with wolves present? Does the introduction of wolves benefit the grass? This study can be done as follows:

MAPLE

```
> restart:
> rsx:=-x(t)+x(t)*y(t);
> rsy:=-y(t)+2*y(t)*z(t)-x(t)*y(t);
> rsz:= 2*z(t)-z(t)^2-y(t)*z(t);
```

MATLAB

```
% make an m-file, exer442.m
%   function Yprime=exer442(t,Y); % Y(1)=x, Y(2)=y, Y(3)=z;
%   Yprime=[-Y(1)+Y(1).*Y(2); -Y(2)+2*Y(2).*Y(3)-Y(1).*Y(2); 2*Y(3)-Y(3).*Y(3)-Y(2).*Y(3)];
```

For just grass:

```
MAPLE
> sol:=dsolve({diff(x(t),t)=rsx,diff(y(t),t)=rsy,diff(z(t),t)=rsz,x(0)=0,y(0)=0,z(0)=1.5},{x(t),y(t),z(t)},
                type=numeric,output=listprocedure);
> zsol:=subs(sol,z(t)); zsol(1);
> plot(zsol,0..20,color=green);

MATLAB
% grass
> [t,Y]=ode23('exer442',[0 200],[0; 0; 1.5]);
> plot(t,Y(:,3))
```

For grass and sheep:

```
MAPLE
> sol:=dsolve({diff(x(t),t)=rsx,diff(y(t),t)=rsy,diff(z(t),t)=rsz,x(0)=0,y(0)=.5,z(0)=1.5},{x(t),y(t),z(t)},
                type=numeric,output=listprocedure);
> ysol:=subs(sol,y(t));zsol:=subs(sol,z(t));
> plot([ysol,zsol],0..20,color=[green,black]);

MATLAB
% grass and sheep
> [t,Y]=ode23('exer442',[0 200],[0; .5; 1.5]);
> plot(t,Y)
```

For grass, sheep, and wolves:

```
MAPLE
> sol:=dsolve({diff(x(t),t)=rsx,diff(y(t),t)=rsy,diff(z(t),t)=rsz,x(0)=.2,y(0)=.5,z(0)=1.5},{x(t),y(t),z(t)},
                type=numeric,output=listprocedure);
> xsol:=subs(sol,x(t));
> ysol:=subs(sol,y(t));
> zsol:=subs(sol,z(t));
> plot([xsol,ysol,zsol],0..20,color=[green,black,red]);

MATLAB
% all three
> [t,Y]=ode23('exer442',[0 200],[.2; .5; 1.5]);
> plot(t,Y(:,3),'g') % grass behavior
> hold on
> plot(t,Y(:,2),'b') % sheep behavior
> plot(t,Y(:,1),'r') % wolf behavior
```

3. J. M. A. Danby [11] has a collection of interesting population models in his delightful text. The following *predator–prey model with child care* is included. Suppose that the prey $x(t)$ is divided into two classes, $x_1(t)$ and $x_2(t)$, of young and adults. Suppose that the young are protected from predators $y(t)$. Assume that the young increase in proportion to the number of adults and decrease due to death or to moving into the adult class. Then

$$\frac{dx_1}{dt} = ax_2 - bx_1 - cx_1.$$

The number of adults is increased by the young growing up and decreased by natural death and predation, so that we model

$$\frac{dx_2}{dt} = bx_1 - dx_2 - ex_2y.$$

Finally, for the predators, we take

$$\frac{dy}{dt} = -fy + gx_2y.$$

Investigate the structure for the solutions of this model. Parameters that might be used are

$$a = 2, \qquad b = c = d = \frac{1}{2}, \quad \text{and} \quad e = f = g = 1.$$

4. Show that the linearization of the system

$$\frac{dx}{dt} = -y + ax(x^2 + y^2),$$
$$\frac{dy}{dt} = x + ay(x^2 + y^2)$$

predicts that the origin is a center for all values of a, whereas, in fact, the origin is a stable spiral if $a < 0$ and an unstable spiral if $a > 0$. Draw phase portraits for $a = 1$ and $a = -1$.

5. Suppose there is a small group of individuals who are infected with a contagious disease and who have come into a larger population. If the population is divided into three groups—the susceptible, the infected, and the recovered—we have what is known as a classical S–I–R problem. (We take up such problems again in Section 11.4.) The susceptible class consists of those who are not infected, but who are capable of catching the disease and becoming infected. The infected class consists of the individuals who are capable of transmitting the disease to others. The recovered class consists of those who have had the disease, but are no longer infectious.

A system of equations that is used to model such a situation is often described as follows:

$$\frac{dS}{dt} = -rS(t)I(t),$$
$$\frac{dI}{dt} = rS(t)I(t) - aI(t),$$
$$\frac{dR}{dt} = aI(t)$$

for positive constants r and a. The proportionality constant r is called the infection rate and the proportionality constant a is called the removal rate.

(a) Rewrite this model as a matrix model and recognize that the problem forms a closed compartment model. Conclude that the total population remains constant.

(b) Draw graphs for solutions. Observe that the susceptible class decreases in size and that the infected size increases in size and later decreases.

MAPLE

```
> r:=1; a:=1;
> sol:=dsolve({diff(SU(t),t)=-r*SU(t)*IN(t),diff(IN(t),t)=r*SU(t)*IN(t)-a*IN(t),diff(R(t),t)=a*IN(t),
              SU(0)=2.8,IN(0)=0.2,R(0)=0},{SU(t),IN(t),R(t)},type=numeric,output=listprocedure):
> f:=subs(sol,SU(t)): g:=subs(sol,IN(t)): h:=subs(sol,R(t));
> plot({f,g,h},0..20,color=[green,red,black]);
```

```
MATLAB
% contents of the m-file exer445a.m:
%   function SIRprime=exer445a(t,SIR); % S=SIR(1), I=SIR(2), R=SIR(3);
%   r=1; a=1;
%   SIRprime=[-r*SIR(1).*SIR(2); r*SIR(1).*SIR(2)-a*SIR(2);a*SIR(2)];
> r=1; a=1;
> [t,SIR]=ode45('exer445a',[0 20], [2.8; .2; 0]);
> plot(t,SIR)
```

(c) Suppose now that the recovered do not receive permanent immunity. Rather, we suppose that after a delay of one unit of time, those who have recovered lose immunity and move into the susceptible class. The system of equations changes to the following:

$$\frac{dS}{dt} = -rS(t)I(t) + R(t-1),$$
$$\frac{dI}{dt} = rS(t)I(t) - aI(t),$$
$$\frac{dR}{dt} = aI(t) - R(t-1).$$

Draw graphs for solutions to this system. Observe the possibility of oscillating solutions. How do you explain these oscillations from the perspective of an epidemiologist? (Note: The following has a long run time.)

```
MAPLE
> restart:with(plots):
> N:=5;
> f[0]:=t->2.8; g[0]:=t->0.2*exp(-t^2); h[0]:=t->0;
> P[0]:=plot([[t,f[0](t),t=-1..0],[t,g[0](t),t=-1..0],[t,h[0](t),t=-1..0]],color=[green,red,black]):
> for n from 1 to N do
> sol:=dsolve({diff(SU(t),t)=-SU(t)*IN(t)+h[n-1](t-1),diff(IN(t),t)=SU(t)*IN(t)-IN(t),
                diff(R(t),t)=IN(t)-h[n-1](t-1),SU(n-1)=f[n-1](n-1),IN(n-1)=g[n-1](n-1),
                R(n-1)=h[n-1](n-1)},{SU(t),IN(t),R(t)},numeric,output=listprocedure,known=h[n-1]):
> f[n]:=subs(sol,SU(t)); g[n]:=subs(sol,IN(t));
> h[n]:=subs(sol,R(t)):
> P[n]:=plot([[t,f[n](t),t=n-1..n],[t,g[n](t),t=n-1..n],[t,h[n](t),t=n-1..n]],color=[green,red,black]):
> od:
> n:='n';
> J:=plot([t,1,t=0..N],color=blue):
> display([J,seq(P[n],n=0..N)]);
> for n from 1 to N do
> Q[n]:=spacecurve([f[n](t),g[n](t),h[n](t)],t=n-1..n,axes=normal,color=black):
> od:
> PP:=pointplot3d([1,1,1],axes=normal,symbol=diamond,color=green):
> display([PP,seq(Q[n],n=1..N)]);

MATLAB
> N=100; % number steps per unit interval
> delT=1/N; % so delta t=0.01
  % t is now linked to index i by t=-1+(i-1)*delT, where i=1,2,...,nFinal
  % and the final index nFinal is given by solving tFinal = -1+(nFinal-1)*delT.
> tFinal=5; nFinal=(tFinal+1)*N+1;
  % set up the initial values of R on -1 to 0
> for i=1:N
> R(i)=0; S(i)=0; I(i)=0;
> end
  % work from t=0 in steps of delT
> S(N+1)=2.8; I(N+1)=0.2; R(N+1)=0;
> for i=N+1:nFinal-1
> delY=delT*[-r*S(i)*I(i)+R(i-N); r*S(i)*I(i)-a*I(i); a*I(i)-R(i-N)]; S(i+1)=S(i)+delY(1);...
  I(i+1)=I(i)+delY(2); R(i+1) = R(i)+delY(3);
```

```
> end
  % graph it
> t=-1:delT:tFinal;
> plot(t,S,t,I,t,R) % S blue, I green, R red
```

Questions for Thought and Discussion

1. Name and discuss four factors that affect the carrying capacity of an environment for a given species.
2. Draw and explain the shape of survivorship and population growth curves for an r-strategist.
3. Draw and explain the shape of survivorship and population growth curves for a K-strategist.
4. Define carrying capacity and environmental resistance.
5. Discuss the concept of parental investment and its role in r- and K-strategies.

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