

ist explanation for the maintenance of variability at the molecular level is presented in the book by Gillespie (1991).

The book *Evolution and the Theory of Games* by Maynard Smith (1982) gives a thorough treatment of ESS's. The book *Ecological Genetics* edited by Real (1994) has a series of overviews on topics in this important area.

4

Density-Dependent Population Growth

We now return to strictly ecological questions. We have remarked earlier that our models and common sense imply that exponential growth cannot continue forever. As illustrated by the growth of collared doves in Great Britain (Figure 2.3), growth of natural populations cannot be exponential forever, and eventually approaches zero. Similarly, the number of sheep in Tasmania increased after introduction in a fashion that could be considered exponential, but then the numbers reached an approximate equilibrium (Figure 4.1). In this chapter we return to the fundamental question of the causes and consequences of regulation of population growth.

4.1 Hypotheses for population regulation

What regulates the growth of the sheep population in Tasmania, or the growth of other populations? Many hypotheses have been proposed for the causes of regulation of populations:

- Populations are limited by density-independent factors such as changes in the weather.
- Populations are limited by their food supply.

Can you think of other factors that might regulate population growth?
How useful is it to think of a single factor, as opposed to a combination of factors, as the cause of population regulation?

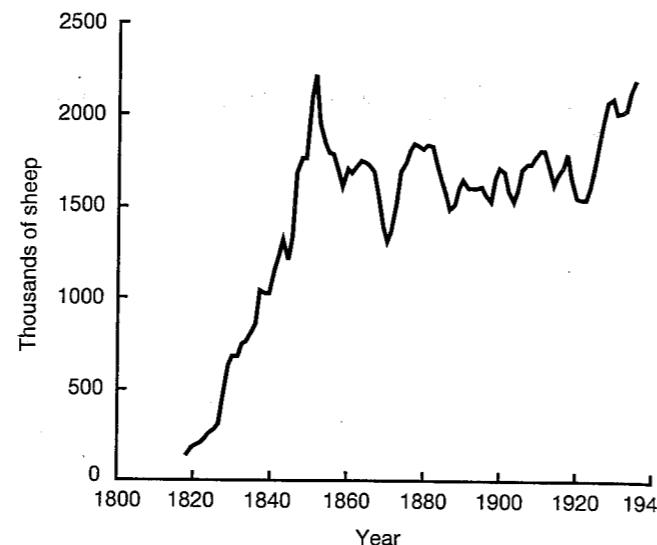


FIGURE 4.1. Dynamics of sheep numbers in Tasmania after introduction (data from Davidson, 1938).

- Populations regulate themselves through mechanisms such as territoriality or cannibalism.
- Populations are regulated through competition.
- Populations are regulated by predators.
- Populations are regulated by parasites or diseases.

We will explore some of these hypotheses in later chapters. Here we begin a discussion of the implications of regulation by limitations in the food supply, or more generally, density-dependent factors that operate within a single species. One of our eventual goals is to elucidate information about the causes of population regulation by examining the consequences of different forms of population regulation. Obviously, any of these factors would limit growth, so the important question is what in nature is actually the limiting factor for a particular population.

Density dependence here refers to processes whose effect changes as the number of individuals within the population changes. Thus regulation by food limitations is one example of a density-dependent factor. How might you experimentally determine the regulating factor in a natural population?

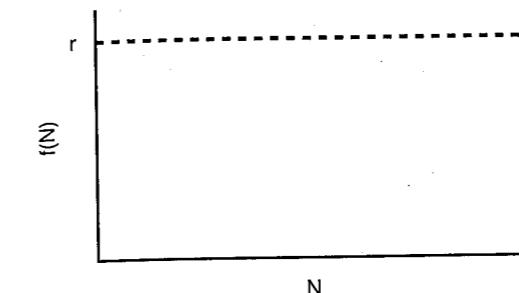


FIGURE 4.2. Per capita growth rate in a model without density dependence

4.2 Logistic model

Regulation by limitations in the food supply can be a difficult question to address through field studies, although much progress has been made recently. Laboratory studies by Gause (1934, 1935) and others demonstrated early in the twentieth century the dynamics of populations limited by their food supply. We will explore models that demonstrate the dynamics expected.

The basic model we will examine takes the form

$$\frac{dN}{dt} = Nf(N), \quad (4.1)$$

where $f(N)$ is the per capita growth rate. By writing the equation this way, we emphasize that the per capita growth rate may depend on the number of organisms in the population, thus providing one explanation for the cessation of exponential growth. In the simplest models that we explored earlier, the per capita growth rate $f(N)$ was a constant r and did not depend on the population density N , as shown in Figure 4.2.

We now change the form of the function $f(N)$ to include the effects of density dependence. What is the simplest function that changes with density so the per capita growth rate goes down as the density goes up? It is a straight line, as illustrated in Figure 4.3. We assume that when the population density is very small, the per capita growth rate is given by r , the ‘intrinsic rate of increase’. We denote by K the value of the population density at which the per capita growth rate is zero. This is known as the *carrying capacity*. Note that we have not specified the biological mechanism

We ignore here the consequences of age structure. Coupling age structure with density dependence is in fact a difficult problem that is the subject of much current research.

Here, the parameter r couples both births and deaths, which in fact causes some problems with biologically interpreting the parameter K in the logistic model.

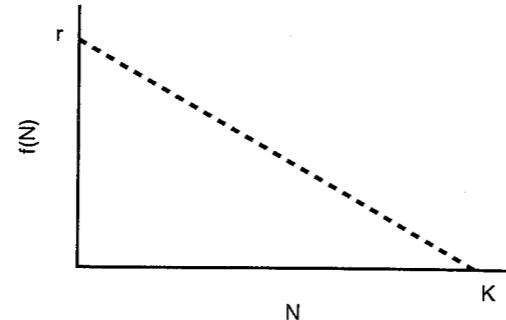


FIGURE 4.3. Per capita growth rate in a model with density dependence.

responsible for this dependence on density. What is the equation describing this line? We write it as

$$f(N) = r(1 - N/K). \quad (4.2)$$

It is easy to see that this is the equation of a straight line and that it satisfies the two conditions that $f(0) = r$ and that $f(K) = 0$. This model is known as the *logistic model*.

Explicit solution of the logistic model

This model is simple enough that we can find the explicit solution and determine the density N as a function of time. The method we use cannot be applied to more complex models, but is useful here. We begin with the model

$$\frac{dN}{dt} = rN(1 - N/K). \quad (4.3)$$

We then separate variables by writing all the terms with N on one side of the equation and all the terms with t on the other side:

$$\frac{dN}{N(1 - N/K)} = rdt. \quad (4.4)$$

We then integrate both sides of the equation from $t = 0$ to $t = T$:

$$\int_{N(0)}^{N(T)} \frac{dN}{N(1 - N/K)} = \int_0^T rdt. \quad (4.5)$$

To integrate the left-hand side of this equation, we use the technique of integration by parts, first writing

We are interested in the explicit solution because we compare it to data below. The answer here is more important than the technique, so if you have trouble following the steps, just concentrate on the final answer, equation (4.12).

Your calculus textbook has a section on integration by parts.

Here we first write

$\frac{1}{N(1 - N/K)} = \frac{a}{N} + \frac{b}{1 - N/K}$ and then

$$\frac{1}{N(1 - N/K)} = \frac{1}{N} + \frac{1/K}{1 - N/K}. \quad (4.6)$$

$$\int \frac{1/K}{1 - N/K} = -\ln(1 - N/K)$$

Then

$$\int_{N(0)}^{N(T)} \frac{1}{N} + \frac{1/K}{1 - N/K} = [\ln(N) - \ln(1 - N/K)]_{N(0)}^{N(T)} \quad (4.7)$$

$$= \ln(N(T)) - \ln(1 - N(T)/K) \\ - \ln(N(0)) + \ln(1 - N(0)/K). \quad (4.8)$$

The right-hand side of (4.5) is simply

$$\int_0^T rdt = rT. \quad (4.9)$$

Combining these last two equations, we see that

$$\ln(N(T)) - \ln(1 - N(T)/K) - \ln(N(0)) + \ln(1 - N(0)/K) = rt. \quad (4.10)$$

Taking the exponential of both sides, we find that

$$\frac{N(T)(1 - N(0)/K)}{(1 - N(T)/K)N(0)} = e^{rt}. \quad (4.11)$$

Solving this equation for $N(T)$, we find

$$N(T) = \frac{N(0)e^{rt}}{1 + N(0)(e^{rt} - 1)/K}. \quad (4.12)$$

What does this equation imply that $N(T)$ is (approximately) when T and $N(0)$ are small? What does $N(T)$ approach when T is large?

This solution is graphed in Figure 4.4.

Comparison with data

The very general result that we have just obtained, that the population first grows more rapidly and then approaches an equilibrium, is exactly what we have seen for collared doves (Figure 2.3) and sheep in Tasmania (Figure 4.1). We can now ask how exact are the predictions – is just the general feature of approach to an equilibrium correct, or does population growth really follow a logistic curve?

We can turn to simple laboratory experiments on microorganisms as studied by Gause (1934, 1935). As illustrated in Figure 1.1, the dynamics of the microorganism *Paramecium aurelia* show

Recall that $e^{a+b} = e^a e^b$ and that $e^{\ln(a)} = a$.

4. Density-Dependent Population Growth

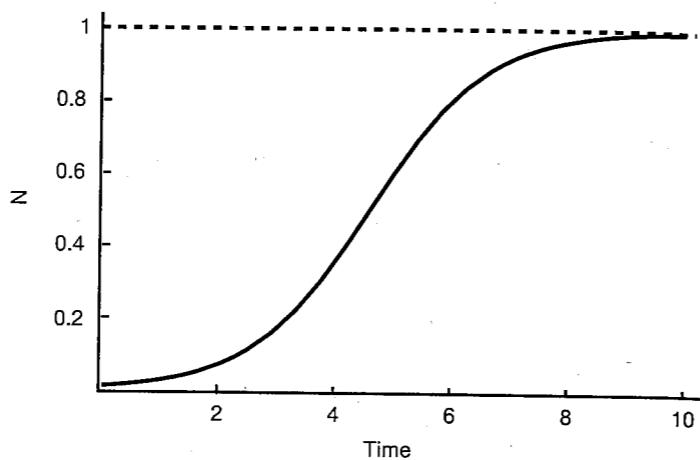


FIGURE 4.4. Explicit solution of the logistic model with $r = 1$, $K = 1$, and $N(0) = 0.01$.

what appears to be logistic growth during the first 10 days of the experiment. However, the population then declines and appears to approach a second equilibrium phase. Thus, even in the simplest setting, our model can be an oversimplification. We will now begin asking how to modify the simple model to make it more realistic.

We can also ask how good the quantitative fit of the model is to data; perhaps the logistic model describes the initial phase of population growth well. One way to do this is to find the best fit of the model to experimental data and ask how good the fit is. One way to find the best fit is to calculate the parameter values that minimize the sum of the squares of the deviations of the model from the experimental data points, where the sum is taken over the experimental data points. One example of this kind of approach is given in Figure 4.5, where the numerical fit is quite good. One should, however, exercise caution in taking fits like these as proof that the logistic model is a good description of population dynamics. Not only do we already have the example given in Figure 1.1, but we can use the following example as another cautionary tale.

A celebrated example demonstrating the quantitative failure of the logistic model is the growth of the human population in the United States (Figure 4.6). Pearl et al. (1940) fit a logistic curve to

Why do we say 'describe', rather than 'predict', population growth?

4.2 Logistic model

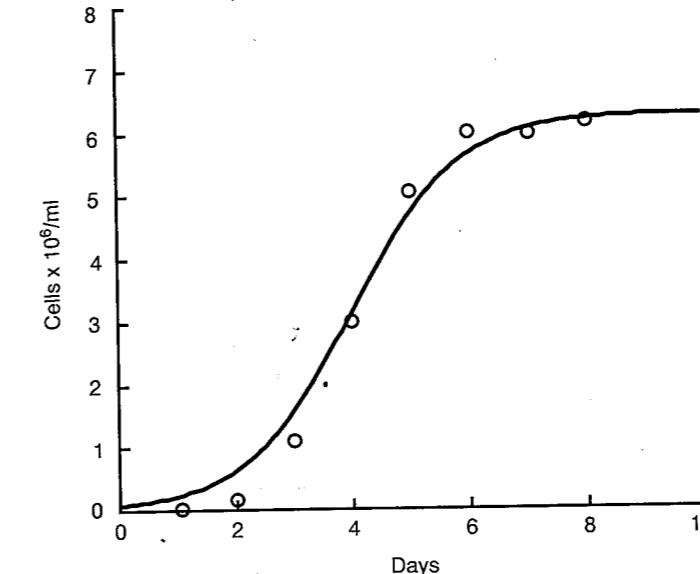


FIGURE 4.5. Plot of numbers of *Escherichia coli* versus time from an experiment of McKendrick and Pai (1911). The best fit of the logistic model is also drawn.

population censuses in the United States through 1940. Although the logistic model fit the data until 1940 very well, the fitted curve predicted that the population of the United States would level off, when in fact it has continued to rise. Thus, we are led to the conclusion that we should not try to make too much of the quantitative aspects of the logistic model.

Equilibrium analysis

We now outline how a qualitative analysis of the logistic model would proceed. Although we have solved the logistic model exactly, there are several reasons to go through this analysis. First, more complex models cannot be solved exactly, so it is useful to learn this technique. By beginning with the logistic model, which we already understand, we can see better how this technique works. Second, unlike the quantitative predictions of the logistic model, which we have indicated are unreliable, the qualitative predictions are *robust*. By robust, we mean that they hold even if we make changes in our model.

Why do you think the logistic model fit so well, but did not predict future population levels?

'Quantitative' here refers to numbers, while 'qualitative' would mean more general features, such as the prediction that the population reaches an equilibrium.

Robust models are very important in ecology because the models are typically quite crude – many simplifying and perhaps inaccurate assumptions are usually made.

4. Density-Dependent Population Growth

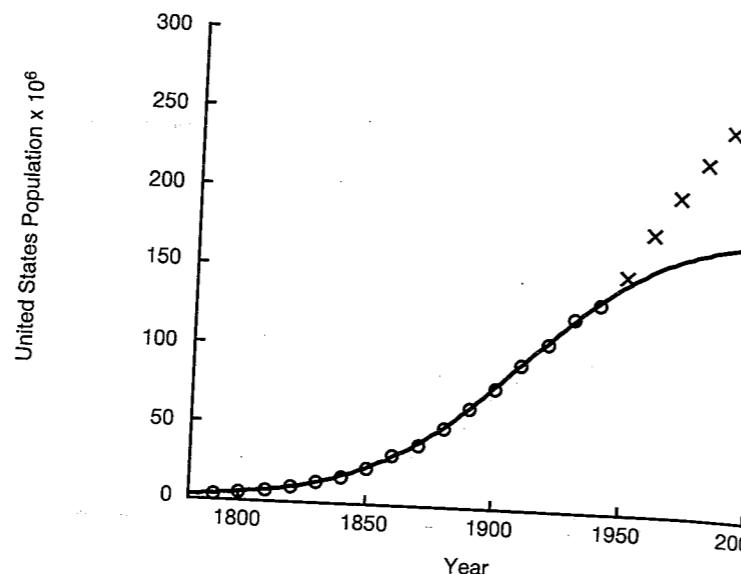


FIGURE 4.6. United States census figures from 1790 until the present. The best fit of the logistic model to the data from 1790 through 1940 (indicated on the graph by circles with the fit drawn as the curve) is astoundingly good, but the fit since that time is very poor (the data given by X's). This example, based on the fit to the data until 1940 by Pearl et al. (1940), is discussed in Hutchinson (1978).

We will outline the analysis as a series of steps:

- Determine the values of the population density, \hat{N} , which are equilibria. Set

$$\frac{dN}{dt} = 0 \quad (4.13)$$

to obtain

$$r\hat{N}(1 - \hat{N}/K) = 0 \quad (4.14)$$

which has the solutions

$$\hat{N} = 0 \text{ and } \hat{N} = K. \quad (4.15)$$

- Determine the behavior of solutions near equilibrium points. Near $\hat{N} = 0$, we see that $\frac{N}{K}$ is much smaller than 1. Thus, we neglect the term $\frac{N}{K}$ in (4.3) so

$$\frac{dN}{dt} \approx rN. \quad (4.16)$$

The details of the development of this procedure are not absolutely necessary to understand what follows. If particular steps are not clear, keep reading. The concepts and the summary in the box below are important.

4.2 Logistic model

- Because $r > 0$, and the solution of (4.16) is

$$N(t) = N(0)e^{rt}, \quad (4.17)$$

we conclude that solutions grow exponentially when N is small. This is confirmed by looking at the exact solution in Figure 4.4.

We now indicate a systematic way to arrive at this conclusion. We let n represent the deviation from the equilibrium, so

$$N = \hat{N} + n. \quad (4.18)$$

Then, in general, we are interested in finding how n changes with time. We observe that since \hat{N} is a constant

$$\frac{dN}{dt} = \frac{dn}{dt}. \quad (4.19)$$

So

$$\frac{dn}{dt} = F(N) \quad (4.20)$$

where

$$F(N) = rN(1 - N/K). \quad (4.21)$$

We need to approximate $F(N)$ near the equilibrium, \hat{N} . We use a Taylor series (Box 3.2) to see that

$$F(\hat{N} + n) \approx F(\hat{N}) + n \left. \frac{dF}{dN} \right|_{N=\hat{N}}. \quad (4.22)$$

We note that since \hat{N} is an equilibrium, $F(\hat{N}) = 0$. Thus we conclude that:

$$\frac{dn}{dt} \approx n \left. \frac{dF}{dN} \right|_{N=\hat{N}}. \quad (4.23)$$

In the logistic model with

$$F(N) = rN(1 - N/K) = rN - rN^2/K \quad (4.24)$$

we compute

$$\frac{dF}{dN} = r - 2rN/K. \quad (4.25)$$

The very beginning of population growth in Figure 4.5, the laboratory population of *E. coli*, also appears to be exponential.

Near the equilibrium $\hat{N} = 0$,

$$\frac{dn}{dt} \approx n(r - 2rN/K)|_{N=0} \quad (4.26)$$

$$= r. \quad (4.27)$$

We already see that some results about stability are robust, because they depend on the sign of the derivative dF/dN at equilibrium, and this sign will not be changed by small changes in the model. We observe that an equilibrium of the continuous time model will be stable (approached from nearby population levels) if increasing the density reduces the growth rate – that is, if there is negative density dependence.

This is the same conclusion we reached earlier.

Near the equilibrium $\hat{N} = K$,

$$\frac{dn}{dt} \approx ((r - 2rN/K)|_{N=K})n \quad (4.28)$$

$$= (r - 2r)n \quad (4.29)$$

$$= -rn. \quad (4.30)$$

Thus, if n represents the deviation from the equilibrium $\hat{N} = K$, we conclude that

$$n(t) = n(0)e^{-rt}. \quad (4.31)$$

Hence, solutions approach the equilibrium $\hat{N} = K$. The procedure we have gone through is outlined for general equations in Box 4.1.

The form of equation (4.31) indicates again the fact that the exact form of the per capita growth rate chosen for the logistic is not necessarily correct. There is no biological reason that the rate of return to the equilibrium $\hat{N} = K$ should be the same as the rate of exponential growth when the population is small. However, this is inherent in the logistic model. On the other hand, the basic conclusions from the qualitative analysis we have just performed do not depend on the exact form of the logistic. That the equilibrium with $\hat{N} = 0$ is unstable, and that the equilibrium with $\hat{N} = K$ is stable (where K is the population density at which the per capita growth rate is zero), is a feature of many similar models.

The θ -model described in Problem 4.1 is an example of one alternate model.

Graphical approach

One more way to look at the dynamics of a single species is to use a graphical approach. This approach has the advantage of displaying the dynamics for all values of the population density and of displaying easily the effects of small changes in the model.

Box 4.1. Qualitative analysis of a model with a single differential equation.

We consider a model of the form

$$dN/dt = F(N).$$

The first step in the analysis is to determine the equilibria. Do this by setting $dN/dt = 0$ to obtain an equation for \hat{N} :

$$0 = F(\hat{N}).$$

Then solve this equation for \hat{N} . Note that this may be impossible to do for some functions F .

The next step is to determine the stability of these equilibria by approximating F . We define the deviation from equilibrium, n , by letting $N = \hat{N} + n$ and compute

$$dn/dt \approx \lambda n,$$

where

$$\lambda = \left. \frac{dF}{dN} \right|_{N=\hat{N}}.$$

- The equilibrium is stable, and is approached if the system starts nearby, if λ for that equilibrium is negative.
- The equilibrium is unstable, and the system moves away from the equilibrium if the system starts nearby, if λ for that equilibrium is positive.

The rate of return to the equilibrium, or the rate at which the system moves away from the equilibrium, is determined by λ .

We graph the rate of change of the population, $\frac{dN}{dt}$, against the population size, N (Figure 4.7). From the figure we can easily find equilibria. From the figure we can also determine whether the population is increasing or decreasing for a given population size. This latter information lets us quickly determine stability, confirming our analytical results and further illustrating that small changes in the model do not lead to qualitative changes in behavior.

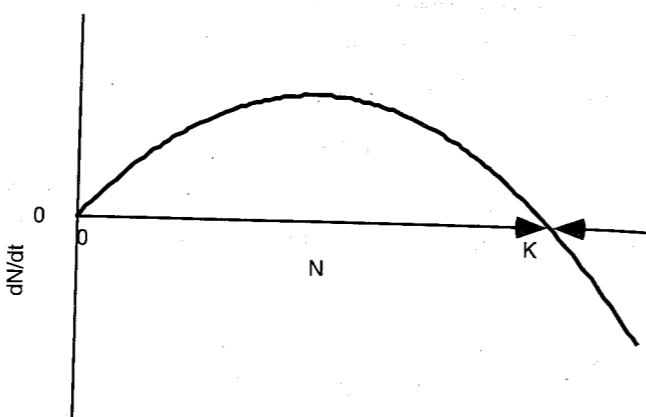


FIGURE 4.7. Plot of rate of change of population size against population size for the logistic model. When $\frac{dN}{dt} > 0$, N increases; when $\frac{dN}{dt} < 0$, N decreases. Along the N axis the direction of population change is indicated by the arrows. From the figure we easily see that the equilibrium $N = 0$ is unstable and the equilibrium $N = K$ is stable.

4.3 Lag time and density dependence

Testing the logistic model is quite difficult, and as we have already suggested, a quantitative test is probably not appropriate. Additionally, if we concentrate on the qualitative features rather than the quantitative ones, the prediction that there is a stable equilibrium is not easily proved or disproved for many examples, like the Tasmanian sheep illustrated in Figure 4.2.

However, a number of natural (and laboratory) populations such as lemmings (Shelford, 1943) show cyclic behavior, a qualitative behavior that cannot be explained by the logistic model. For example, the rotifer populations graphed in Figure 1.1 show strong evidence of cyclic dynamics. We will indicate how this behavior can be explained in general.

An analogy

The temperature in the room you are sitting in (unless you are outdoors) is probably controlled by a thermostat. If the temperature gets too low, the heat immediately goes on; if it gets too high the heat goes off. The temperature remains relatively constant. However, suppose that instead someone checked the tempera-

Cyclic behavior here means a population whose numbers increase and decrease in a relatively regular fashion.

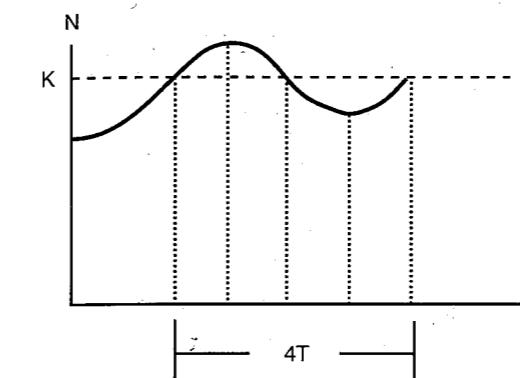


FIGURE 4.8. Qualitative behavior of the delayed logistic model.

ture only once per hour, and either turned off the heat if it was too hot, or turned on the heat if it was too cold. The temperature would almost certainly alternate between too hot and too cold. If the temperature was checked once a week instead, the fluctuations in the temperature would be much more severe. The fact that delayed regulation leads to oscillations is well known in engineering. We will indicate how this principle has been used as a general explanation for oscillations in population biology.

Logistic growth with lags

The simplest model incorporating delayed regulation is the equation

$$\frac{dN}{dt} = rN(t) \left[1 - \frac{N(t-T)}{K} \right], \quad (4.32)$$

originally introduced by Hutchinson (1948) and first carefully analyzed by Wangersky and Cunningham (1957). From the qualitative argument we have just made, we conclude that if the delay is long enough, then the model will exhibit oscillations.

We will now go through a qualitative argument leading to the conclusion that the period of the oscillations will be roughly $4T$, as indicated in Figure 4.8. Assume that first the population is below the carrying capacity. It will increase, and the per capita growth will be positive. The per capita growth rate will remain positive until T time units after the population rises above K . At

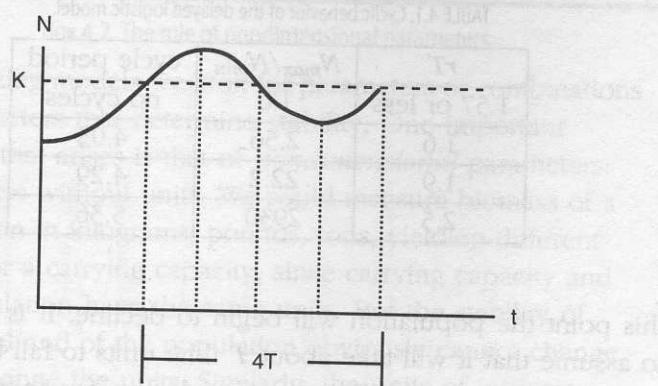


FIGURE 4.8. Qualitative behavior of the delayed logistic model.

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TABLE 4.1. Cyclic behavior of the delayed logistic model.

rT	N_{max}/N_{min}	cycle period
1.57 or less	1.0	no cycles
1.6	2.56	4.03
1.9	22.2	4.29
2.5	2930	5.36

this point the population will begin to decline. It is reasonable to assume that it will take about T time units to fall back to the carrying capacity. It will continue to decline for another T time units, and then start to rise again. Similarly, we conjecture that it will take about T time units for the population to rise again to the carrying capacity. Thus completion of the cycle takes roughly $4T$ time units.

Note also that in determining stability, we conjecture that the model is unstable if the delay is long enough. But the 'size' of T depends on the units we choose for time. The condition for stability should be independent of the units we use for measurements. Similarly, if the growth rate of the population is high enough, even a short delay may be enough to cause instability. Observe that the units of T are time and the units of r are per time (time^{-1}). Thus the quantity rT has no units; it is dimensionless. It is the size of rT that determines stability of the equilibrium point $\hat{N} = K$ in the delayed logistic model. The exact stability results are as indicated in Table 4.1. The general argument about nondimensional parameters is important, and too little used in ecology. The concept is summarized in Box 4.2.

Nicholson's blowflies

There have been a number of classical laboratory experiments that have been the subject of many modeling studies. One of the prime examples is Nicholson's (1957) blowfly experiment, which examined the dynamics of *Lucilia cuprina* over a long time. May (1975) fit the delayed logistic model to this data.

The logic of May's approach is as follows. There is only one nondimensional parameter combination, namely rT . The combi-

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Box 4.2. The role of nondimensional parameters.

In analyzing models we look for parameters or combinations of parameters that determine stability. One important concept that arises is that of *nondimensional* parameters: parameters without units. We could measure biomass of a population in kilograms, pounds, tons, yielding different values for a carrying capacity, since carrying capacity and the population have the same units. But the stability of the model and of the population obviously cannot change as we change the units. Similarly, the units of intrinsic rate of increase are inverse time units, and the stability of the population cannot depend on whether time is measured in weeks, years, or centuries. *Our conclusion is that stability can only depend on nondimensional groups of parameters, combinations for which all the units cancel.* For example, in the delay logistic model, the only nondimensional combination possible is the time delay multiplied by the intrinsic growth rate, and this is the combination that determines stability. One can often identify the stability-determining groups of parameters for a system by simply looking for nondimensional combinations.

nation rT is adjusted to fit the experimental curve. The parameter r is estimated from the life table data, allowing T to be estimated. This value of T is then compared to the observed egg-to-adult time at the experimental temperature.

The best fit to the data is obtained with $rT \approx 2.1$. This leads to a calculated value of $T \approx 9$ days, while the actual value of T is 11 to 14 days, which is a very good fit. This, however, cannot be taken as proof that the model is correct. In fact, some details of the dynamics are clearly not explained by this model, namely the tendency for the data to exhibit a double peak.

Explain why we have not proven that this model is correct.

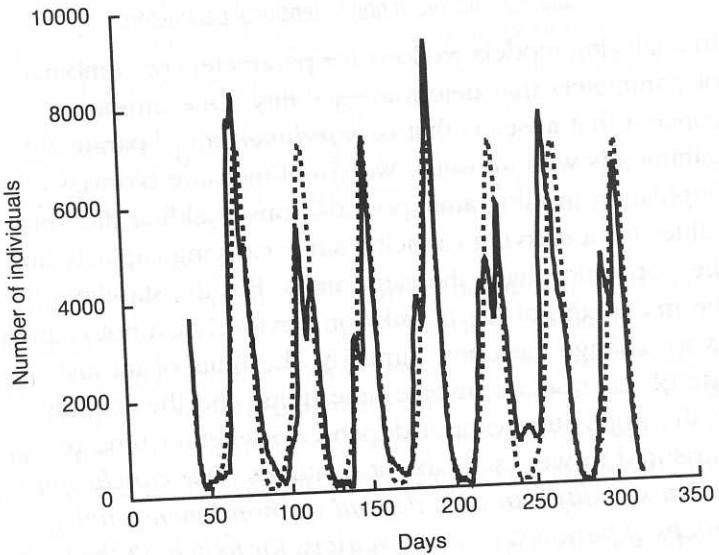


FIGURE 4.9. Plot of numbers of blowflies *Lucilia cuprina* and best fit from the delayed logistic versus time. The data (thick line) are from Nicholson (1957), and the fit (thin line) is by May (1975).

4.4 Discrete time density-dependent models

We have looked primarily at the effects of density dependence in continuous time models. However, as we discussed earlier discrete time models are much more appropriate for insects that breed once per year. The time-delayed logistic model led to oscillations, but even more complex behavior is possible for the equivalent models in discrete time. At the time that this book is being written, the importance of this complex behavior in describing natural populations is an open question.

A class of models appropriate for describing animals (or plants) that live 1 year, reproduce, and then die, takes the form

$$N_{t+1} = F(N_t), \quad (4.33)$$

where the function F gives the population numbers next year in terms of this year's numbers. This equation has an implicit time delay of 1 year, so we expect behavior at least as complex as

FIGURE 4.10.
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4.4 Discrete time density-dependent models

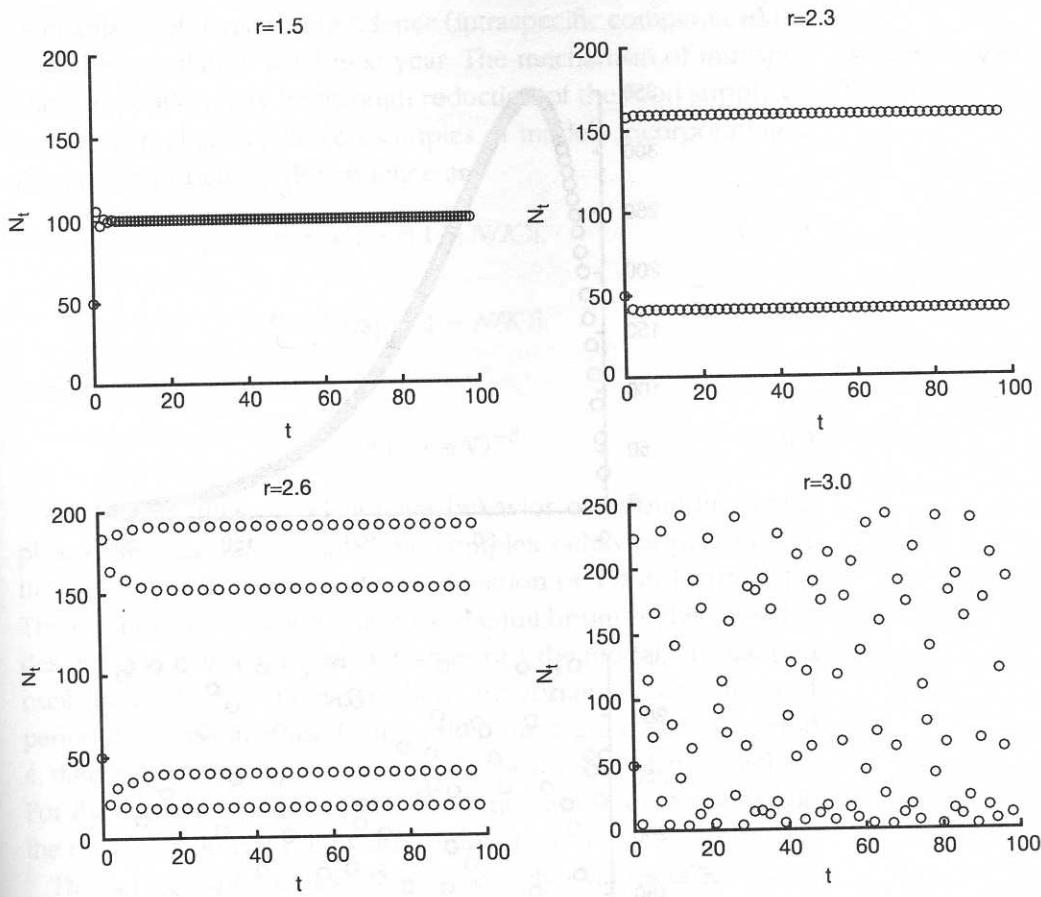


FIGURE 4.10. Dynamics of the Ricker model, which is given by equation 4.35, as a function of the parameter r . Each panel plots numbers against time, as found by solving the equation numerically. In each case the initial condition $N(0) = 50$, and the parameter $k = 100$. For $r = 1.5$ the population quickly approaches an equilibrium. As r is increased, the population has a 2-cycle at $r = 2.3$, a 4-cycle at $r = 2.6$, and chaos at $r = 3.0$.

for the time-delayed logistic. We will use computer simulations to understand the potentially complex behavior.

A number of models (e.g., May, 1974) describing the dynamics of populations in discrete time have been proposed, all sharing some qualitative features. The plot of the population next year versus the population this year has a single maximum. At low population levels, next year's population increases as a function of the current population, but at very high population levels,

4. Density-Dependent Population Growth

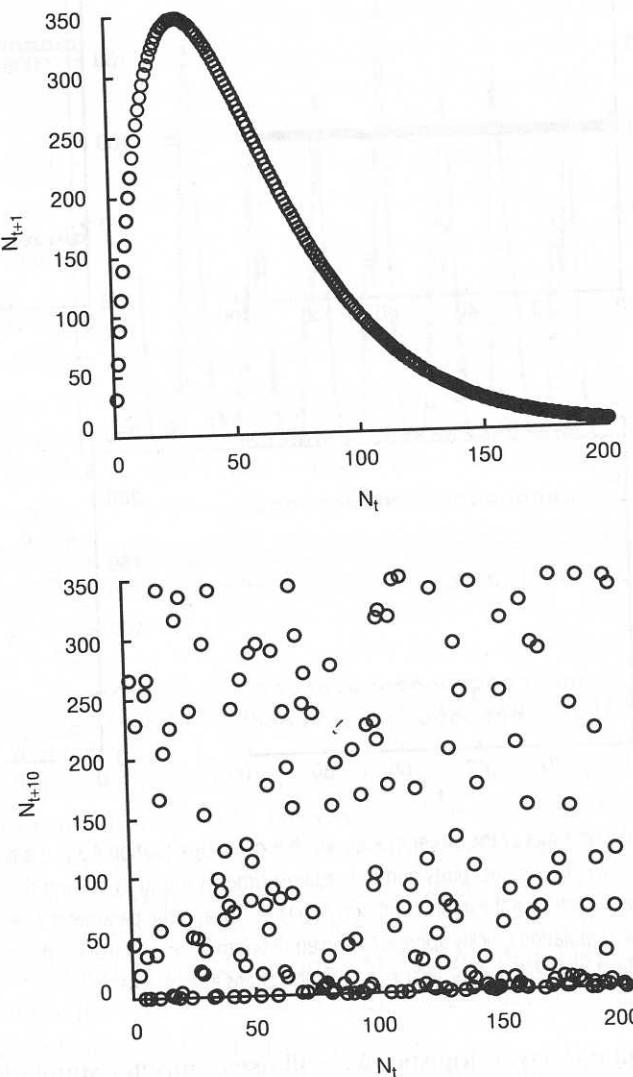


FIGURE 4.11. Dynamics of the Ricker model (equation 4.35) with $K = 100$ and $r = 3.5$. Population sizes after either 1 or 10 years are shown as a function of initial population sizes. In the top plot, one sees that it is easy to predict the population next year from the population this year. However, the bottom plot demonstrates that the population after 10 years is essentially impossible to predict from the population this year.

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mechanisms of density dependence (intraspecific competition) reduce the population level next year. The mechanism of intraspecific competition may be through reduction of the food supply or through cannibalism. Three examples of models incorporating a description of density dependence are

Cannibalism is actually very common in nature.

$$F = N[1 + r(1 - N/K)], \quad (4.34)$$

$$F = N \exp[r(1 - N/K)], \quad (4.35)$$

and

$$F = \lambda N(1 + \alpha N)^{-\beta}. \quad (4.36)$$

All three of these models have behavior of astounding complexity. We illustrate some of the complex behavior possible for the Ricker (1954) model given by equation (4.35) in Figure 4.10. The stability analysis of the nontrivial equilibrium of this model is described in Box 4.3. For small values of r the model has damped oscillations. As r is increased there are sustained oscillations of period 2. As r is increased still further, there are cycles of period 4, then 8, then 16, and so on until a critical value of r is reached. For these higher values of r there is no simple cyclic behavior; the dynamics do not follow any simple pattern.

The behavior of the model for these higher values of r is called *chaotic*, and some of the aspects of chaos can be seen by looking at Figure 4.11. By plotting the population level next year versus the population level this year we emphasize that the dynamics are in fact deterministic and simple. However, if we plot the population level after 10 years versus the population level this year, as in Figure 4.11, a very different picture emerges. Even a small change in the population level now typically leads to a very large change in the population level after 10 years. Thus, although in this model we can predict the population level after 1 year, we cannot predict the population level after 10 years because we can never know the current population level well enough. This ability to predict over short time scales coupled with an inability to predict over long time scales is one of the central features of chaos.

Although chaos is not possible in a simple one-species continuous time model, it is possible in multispecies models with at least three species.

What would be the implications if chaos turned out to be a common feature of natural populations?

Box 4.3. Stability analysis of a single species discrete time ecological model.
We proceed with an example, the Ricker model,

$$N_{t+1} = N_t \exp[r(1 - N_t/K)].$$

- Find the equilibria by setting $N_{t+1} = N_t = N$, and solving for N . From the equation

$$N = N \exp[r(1 - N/K)],$$

we see that $N = 0$ or

$$1 = \exp[r(1 - N/K)],$$

which implies (using $\exp[0] = 1$) that

$$0 = [r(1 - N/K)].$$

We focus attention on the nontrivial solution of equation (4.3), the equilibrium $N = K$.

- Determine the stability of the equilibria using the procedure from Box 3.3. Linearize the model by computing dF/dN , where F is given by equation (4.35), and evaluating the derivative at the equilibrium $N = K$. The derivative is

$$\begin{aligned} \frac{dF}{dN} &= \frac{d(N \exp[r(1 - N/K)])}{dN} \\ &= \exp[r(1 - N/K)] + N(-r/K) \exp[r(1 - N/K)]. \end{aligned}$$

We then evaluate the derivative at the equilibrium:

$$\begin{aligned} \left. \frac{dF}{dN} \right|_{N=K} &= \exp[r(1 - N/N)] \\ &\quad + N(-r/N) \exp[r(1 - N/N)] \\ &= 1 - r. \end{aligned}$$

The stability condition (see Box 3.3), that (a) be less than one in absolute value, is

$$|1 - r| < 1,$$

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4.5 Metapopulations

Box 4.3 (cont.)

which implies

$$0 < r < 2.$$

When $r > 2$, instability sets in because $\frac{dF}{dN} \Big|_{N=K}$ becomes less than -1 . Instabilities arising because the 'growth rate' of deviations from equilibrium becomes less than -1 lead to oscillations. At each time step, the deviation from equilibrium will change sign, but become larger in absolute value. That oscillations result is confirmed by the numerical solutions in Figure 4.10.

What is not known is how important chaotic dynamics are in understanding the dynamics of natural populations. The techniques for studying this question are beyond the scope of this book. However, the laboratory population of Nicholson's blowflies illustrated in Figure 4.9 is one example of a population that some authors have suggested is chaotic. (Although chaos cannot be detected 'by eye', the irregularities that indicate the possibility of chaos are the varying heights of the population peaks and the varying times between peaks.)

4.5 Metapopulations

One could describe a population not by its total size, but by the fraction of available habitat sites it occupies, p . What we will do is describe the dynamics of this *metapopulation* consisting of a number of subpopulations. This kind of approach has been recently used extensively to understand metapopulations (Gilpin and Hanski, 1991; Hastings and Harrison, 1994). At any one site or location, the species colonizes the empty habitat, and then at some later time goes extinct. This cycle can then repeat, with the colonizers coming from other occupied sites. The transitions at one location are illustrated in Figure 4.12.

In the simplest description (Levins, 1969), the rate at which a population goes extinct from sites as the result of random pro-

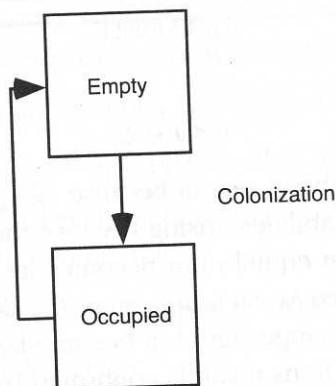


FIGURE 4.12. Transitions at one location in a simple model of a metapopulation.

cesses will just be proportional to the fraction of sites occupied ep , where e is a constant. (We choose the letter e to stand for extinction.) Similarly, the rate at which the population colonizes empty sites will be proportional to the product of the fraction of occupied sites times the fraction of empty sites, $mp(1 - p)$, where m is a constant. (We ignore any effect on colonization arising from different locations of suitable habitat.) The total rate of change of the fraction of occupied sites will then be

$$\frac{dp}{dt} = mp(1 - p) - ep. \quad (4.37)$$

The analysis of this model in the problems shows that a stable equilibrium arises (if colonization is large enough relative to extinction) at the metapopulation level, even though at the level of the subpopulation extinction is certain. This metapopulation concept has played a major role in conservation biology, even though its strict applicability has been questioned.

Conclusions

We have shown that the consequences of population regulation by factors operating within a single species can have very different consequences, depending on the time scale of regulation. If the regulation is instantaneous, the population reaches an equilibrium. Although we can numerically describe the population

The consequences for dynamics do not depend on the cause of regulation, which could be cannibalism, limited food supply, or some other factor operating within a single species.

dynamics in this case, we have shown that quantitative conclusions from these models are suspect, although the qualitative conclusions are likely to be robust.

In contrast, if regulation is delayed, as with organisms that reproduce once per year and then die, or organisms where the delay until sexual maturity is significant, the dynamics can be much more complex, with cycles and chaos.

Unfortunately, the search for evidence of density dependence in natural populations has not yielded clear answers. Results from the survey by Hassell et al. (1989) are typical in this regard. Complications making the detection of density dependence difficult that we have not discussed in this chapter include the influence of stochastic forces, such as the weather, and the difficulty of obtaining large enough data sets. Perhaps the most important issue is elucidating the appropriate spatial and temporal scales for determining density dependence.

Problems

1. The model

$$\frac{dN}{dt} = rN [1 - (N/K)^\theta] \quad (4.38)$$

(where θ is a positive parameter that depends on the organism) has been proposed as an alternative to the logistic model (Gilpin and Ayala, 1973).

- (a) Find the equilibria of the model, and determine their stability as described in Box 4.1.
- (b) Graph the per capita growth rate

$$\frac{dN/dt}{N} = r [1 - (N/K)^\theta] \quad (4.39)$$

against N , for several different values of θ . (Use a value less than 1, a value greater than 1, and 1.) Discuss how changes in the value of θ alter the behavior of the model.

- (c) Discuss briefly (one-half page) how you think this model may be superior to the logistic and to what taxa it

might apply for different choices of θ . You may have to do additional reading to answer this question.

2. Here we analyze the metapopulation model, equation (4.37).

(a) Find the equilibria of this model.

(b) What is the condition required for the model to have an equilibrium with $p > 0$, and does this condition make biological sense?

(c) Determine the stability of the equilibria in this model.

(d) How is this model related to the logistic model?

3. Often, when a population level is too low, the population will decline, an effect known as the *Allee effect*. This effect can be incorporated in a simple model of the form

$$\frac{dN}{dt} = rN(N - a)[1 - (N/K)] \quad (4.40)$$

where the positive parameter a is a threshold population level above which the population will grow.

(a) Find the equilibria of the model.

(b) Determine the stability of all the equilibria.

(c) Graph the per capita growth rate in this model against the population size N .

(d) Discuss the behavior of this model and contrast it with the behavior of the simple logistic model.

4. Variations in the simple logistic model have been used to study the effects of harvesting on the long-term dynamics of a species, for example, how many fish can be harvested without reducing the viability of the population. This situation can be described by a simple variation of the logistic model

$$\frac{dN}{dt} = rN[1 - (N/K)] - HN \quad (4.41)$$

where H is the harvest rate.

- (a) Find the non-zero equilibrium of this model, which will depend on the value of H . What restriction on H is

4.5 Metapopulations

necessary for this equilibrium to be positive? Discuss biologically why this condition makes sense.

- (b) What happens to the population if H is larger than the value determined in part a?
- 5. In the text, we examined the behavior of the discrete time Ricker model. We claimed that the surprising and complex behavior of this model did not depend on the exact form of the model used. To show that the behavior is in fact robust, look at the behavior of a version of a discrete time logistic model

$$N_{t+1} = rN_t(1 - N_t/K) \quad (4.42)$$

for different values of r . The value of K does not in fact affect the form of the dynamics, so for simplicity you can use the value 1 for K . Thus, you should always have N between 0 and 1. The parameter K is not in fact the carrying capacity here.

- (a) Construct a figure similar to Figure 4.10 using the values 1.5, 3.2, 3.5, and 3.9 for r .
- (b) Construct a figure similar to Figure 4.11 using the value 3.9 for r .

Suggestions for further reading

The early work of Gause (1934, 1935) provides a large number of wonderful examples of population dynamics of laboratory organisms. Hutchinson's 1978 book provides an extensive historical discussion of the logistic equation and density dependence.

The role of nondimensionalization is discussed in Nisbet and Gurney's 1982 book. A further look at Nicholson's blowflies is in Gurney et al. (1980).

The question of chaos in ecology is reviewed by Hastings et al. (1993), which provides numerous further references. The important early paper by May (1976) on chaos in simple models is worth reading. One recent paper of note, by Costantino et al. (1995), shows the presence of two-cycles as in the simple models

(although they in fact use a more complex model) in a laboratory population of flour beetles.

The early paper by Ricker (1954) on population regulation in fish is a classic in population ecology well worth reading. Crawley (1990) provides a detailed review of several studies of density-dependent population dynamics in plants. In the same symposium, Shepherd and Cushing (1990) review the more recent literature on population regulation in fish populations.

The metapopulation model discussed in the homework was originally introduced by Levins (1969). The metapopulation approach is extensively reviewed in both Gilpin and Hanski (1991) and Hastings and Harrison (1994).

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