

reasons: first, a competitor would be the demographic, actuarial calculations made by the Romans in the third century CE (though they focused on mortality, not reproduction; see Hutchinson (1978) for further description). Secondly, it was simply a single problem in a book of solved algebraic word problems, and was not really intended to explain population dynamics. Publications in mathematics at that time consisted of books full of worked problems using the Arabic decimal number system (instead of Roman numerals) for ease of calculations, and the rabbit problem was one of those problems (Devlin, 2011). The development of calculus and the other kinds of mathematics used in the population dynamics of this book did not begin for another four centuries.

The rabbit problem appears near the end of Leonardo's book in a section called *paria coniculatorum* ("pairs of rabbits"). It is stated as

How many pairs of rabbits can be bred from one pair in one year? A man has one pair of rabbits at a certain place entirely surrounded by a wall. We wish to know how many pairs can be bred from it in one year, if the nature of these rabbits is such that they breed every month one other pair and begin to breed in the second month after their birth. Let the first pair breed a pair in the first month, then duplicate it and there will be 2 pairs in a month. From these pairs one, namely the first, breeds a pair in the second month, and thus there are 3 pairs in the second month . . . (emphasis ours)

The calculations carry on as shown in Table 2.1. The time series of the total number of adult pairs is the well-known Fibonacci series, which appears in many areas in biology and elsewhere (Edelstein-Keshet, 2005). In addition to describing this as the first population model, we could get carried away with identifying the origin of ideas and wonder whether the stipulation that the population be surrounded by a wall shouldn't also be considered the first example of a boundary condition.

Table 2.1 Calculations for Leonardo of Pisa's rabbit problem. Each month, m , all rabbits born in $m - 1$ become juveniles, and all juveniles in $m - 1$ become adults, and then all adults spawn new pairs. The series of pairs born is known as the Fibonacci series.

Month	Adult pairs	Juvenile pairs	Pairs born
1	1	0	1
2	1	1	1
3	2	1	2
4	3	2	3
5	5	3	5
6	8	5	8
7	13	8	13
8	21	13	21
9	34	21	34
10	55	34	55
11	89	55	89
12	144	89	144

algebra, and the concept of zero to Europe from Islamic countries, where they had been preserved.

2.1 The first population model—the rabbit problem

Leonardo of Pisa was one of the first mathematicians of the Middle Ages. We know him today as Fibonacci (“son of Bonacci”), which has much greater name recognition than Leonardo of Pisa. This is perhaps the reason that the statue identified only as Leonardo of Pisa draws little attention in among many other medieval relics in the Campo Santo Memoriale in the grounds of the cathedral in Pisa, famous for the leaning tower (Fig. 2.1). You can visit it yourself, without fear of running into crowds of tourists (or most likely, even anyone who knows who Leonardo of Pisa was).

In Leonardo’s 1202 book, *Liber Abaci* (*Book of Calculation*; a recent translation is by Sigler, 2002), the first chapter begins with the phrase, “The nine Indian figures are: 9, 8, 7, 6, 5, 4, 3, 2, and 1. With these nine figures, and with the sign 0, which in Arabic is called zephir, any number whatsoever can be written, as is demonstrated below.” This introduced thirteenth-century merchants and others to the inclusion of zero, a vital step in European

Box 2.1 CONTINUOUS VERSUS DISCRETE

Mathematical models of dynamic behavior all describe the changes in a system's state as time progresses, but they describe time in one of two different ways: continuous time and discrete time. Continuous-time models keep track of the state of a system at every instant of time (Figure 2.2a). Solutions are referred to as continuous functions, and the fundamental mathematical tools used are from calculus. We write these models as differential equations expressing rates of change of the state variables. For a single-state variable $x(t)$ this would be the statement that the rate of change of variable x with respect to time is a function of the value of x at time t ,

$$\frac{dx}{dt} = f(x). \quad (\text{B2.1-1})$$

The function could also contain a dependence on values of x in the past, e.g. $x(t - \tau)$.

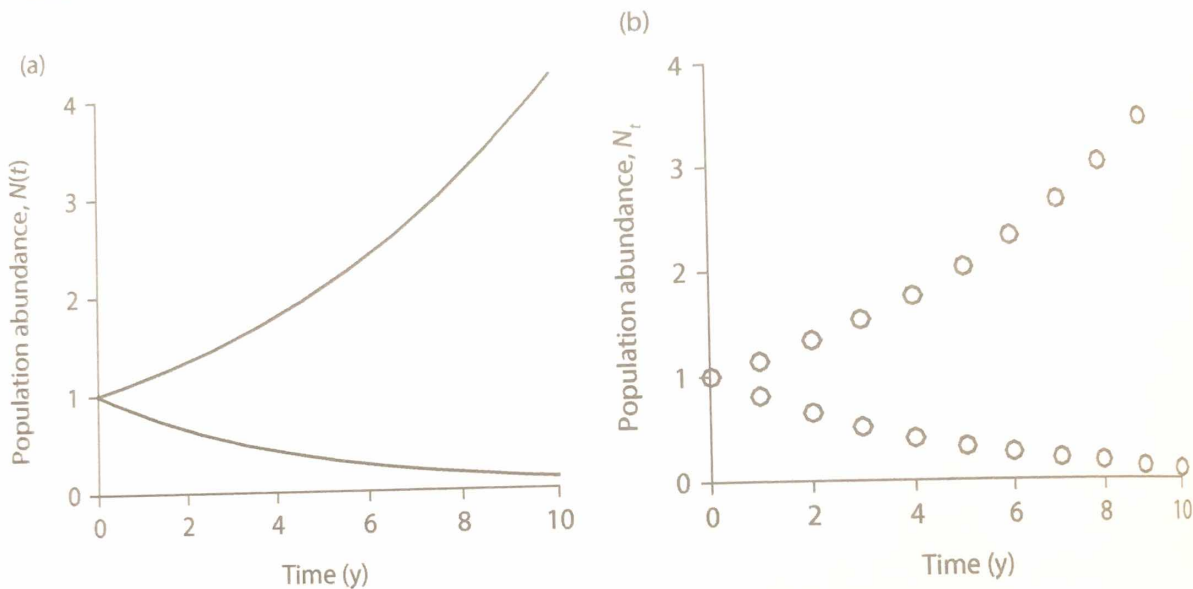


Fig. 2.2 The distinction between (a) continuous-time models (Eq. (2.1)) and (b) discrete-time models (Eq. (2.3)). In this example, the time interval $\Delta t = 1$ year. In (a), $r = 0.14 \text{ y}^{-1}$ (increasing) or -0.22 y^{-1} (decreasing); in (b) $\lambda = 1.15$ and 0.8 , respectively. Note that in both the increasing and the decreasing cases, $\lambda = e^r$, so the continuous and discrete models are equivalent.

Discrete-time models, by contrast, keep track of the state of a system at a series of times, separated by a certain time interval Δt (Figure 2.2b), and the fundamental mathematical tools are those of difference equations. We write difference equations in terms of how the state variable at time t depends on its value at previous times. For example, for a single state variable at time t , X_t :

$$X_t = F[X_{t-1}, X_{t-\tau}], \quad (\text{B2.1-2})$$

where the integer τ is a constant time interval. For discrete-time models, time is frequently, but not always, written as a subscript rather than in parentheses.

For population biology, models in discrete time would be most applicable to situations in which reproduction occurs once per year over a small time period. This would be more appropriate for populations in the seasonal environments of high latitudes. Models in continuous time are more appropriate for populations that do not experience strong seasonality, or for which the time scale of reproduction is fast relative to environmental variability (e.g. microbial populations).

Box 2.3 ... to lead to the population being ... *overcompensatory*. Similarly, a weak density-dependent ... population to a point greater than its original density is *undercompensatory*. Finally, density-dependent effects that increase reproduction or survival in response to an increase in density are termed *depensatory* (or sometimes, *inversely density dependent*). Examples of the latter are Allee effects at low population densities, in which reductions in density lead to lower birth rates and lower survival, perhaps because it is harder to find mates or participate in collective defenses against predators.

2.2 Simple linear models (exponential or geometric growth)

The simple model for exponential growth was the first population model developed to explore future population behavior. However, populations were described in terms of a related concept, doubling times, as far back as the seventeenth century (Hutchinson, 1978). The first major formal use was by Thomas Malthus in 1798 (reprinted as Malthus, 1960), who was concerned that the population of the British Isles was growing exponentially, while the resources it required were growing only linearly. Since the rate of growth is continually increasing in exponential growth, he feared that at some point the population would outstrip its required food resources (see Malthus (1960) and Hutchinson (1978) for further historical details).

The basic form of the exponential model in continuous time (see Box 2.1) gives the rate of change of the number of individuals in the population, $N(t)$, in the form of a differential equation,

$$\frac{dN(t)}{dt} = rN(t), \quad (2.1)$$

where r is a constant called the per capita rate of increase (or the intrinsic rate of increase). The units of r are simply time^{-1} , which allows the units of dN/dt to be individuals/time, as one would expect. Note that this differential equation is a linear system (Box 2.2). At the individual level it can be derived by expressing dN/dt as the difference between total birth rate (bN) and total mortality (death) rate (dN), resulting in $r = b - d$. This equation can be solved to obtain an expression for $N(t)$ by the method of separation of variables (i.e. get all of the N 's on one side of the equals sign and all of the t 's on the other side, then integrate each side; see Box 2.4), to obtain

$$N(t) = N_0 e^{rt}. \quad (2.2)$$

Box 2.4 SOLVING A DIFFERENTIAL EQUATION BY SEPARATION OF VARIABLES

We will solve Eq. (2.1) for the more general case in which r is allowed to vary with time. To solve an equation of the form

$$\frac{dX}{ds} = r(s)X, \quad (\text{B2.4-1})$$

The astute reader might have noticed that we have ignored the cases where $r = 0$ or $L = 1$. These values provide the dividing line between the two kinds of behavior of increase and decline. We will return later to a further understanding of the meaning of this particular growth rate, though here we note that explaining steady state behavior of a population with a linear model would require the growth rate to be precisely zero, which essentially can never happen.

Before moving on to nonlinear, logistic-type models, we can evaluate the usefulness of the exponential/geometric models. In terms of realism, at the individual level, all individuals are assumed to be identical, hence both reproductive and mortality rates are proportional to total numbers. In most biological populations, the mere presence or absence of an individual is not a good i -state description; we need to know age, at least, to be able to specify current reproduction and mortality. Because of this, simple exponential and geometric growth models do not allow a very realistic portrayal of the contributions of individuals to population behavior. Single-celled organisms such as microbes or phytoplankton might be the exception in which all individuals are essentially identical from the perspective of reproduction and mortality rates.

At the population level, the resulting behavior is exponential or geometric increase, which is only observed in specific situations. In the exponential and geometric growth models, the overall population growth rate is a constant proportion of the current population size; there is no density dependence. In actual populations, density dependence typically arises as populations grow large, intensifying competition for resources. Thus, we might expect to see geometric or exponential growth in situations where abundance is low, such as in recent introductions or in populations declining to extinction. An example of the former is the initial growth of the ring-necked pheasant (*Phasianus colchicus*) introduced to Protection Island in the Strait of Juan de Fuca (Fig. 2.3). An example of

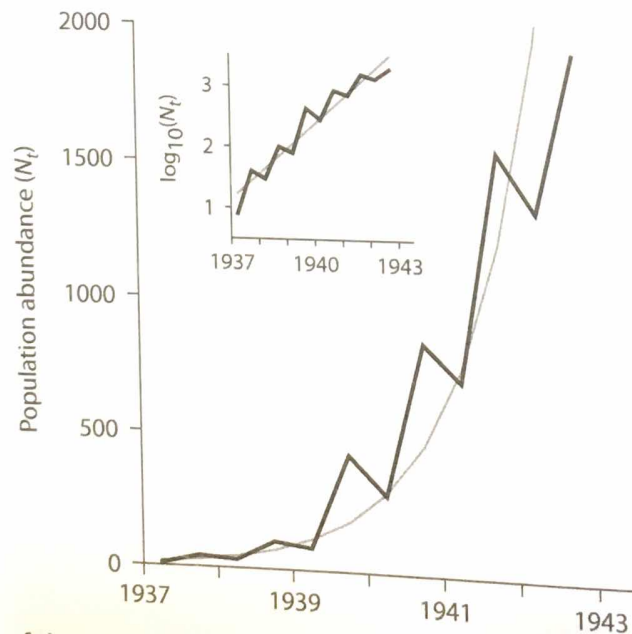


Fig. 2.3 Initial growth of the ring-necked pheasant (*Phasianus colchicus*) population introduced on to Protection Island in the Strait of Juan de Fuca, Washington, USA in 1937. Main plot shows the semiannual inventory of total birds (cocks, hens, and unclassified). Inset plot shows the same data on growth rate; the gray curve is a linear regression fitted to the semilog data. In the main plot, the gray curve is a discrete-time exponential model (Eq. 2.3) using the value of $\lambda = 2.58$ obtained from the semilog plot. Data from Einarsen (1945).

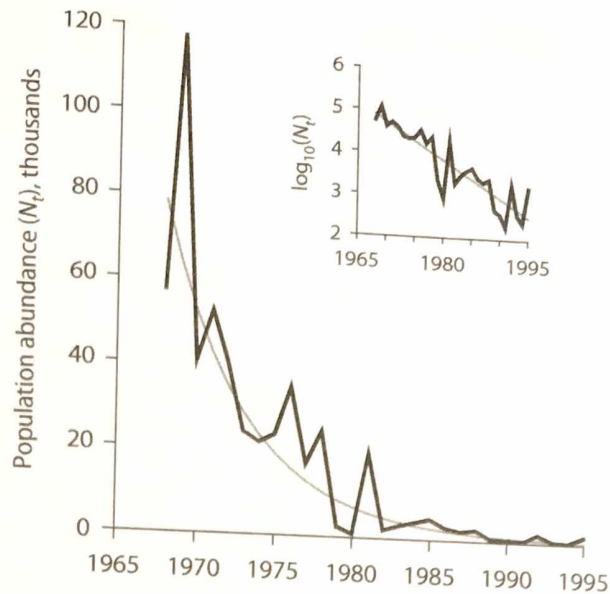


Fig. 2.4 Decline of the winter run of chinook salmon (*Oncorhynchus tshawytscha*) in the Sacramento River, California. Main plot shows the count of salmon traversing the Red Bluff Diversion Dam. Inset plot shows the same data on semilogarithmic axes, illustrating how the slope of decrease can be used to estimate $\log_{10}(\lambda)$, the geometric growth rate; the gray curve is a linear regression fitted to the semilog data. In the main plot, the gray curve is a discrete-time exponential model (Eq. (2.3)) using the value of $\lambda = 0.82$ obtained from the semilog plot. Redrawn from Botsford and Brittnacher (1998).

the latter is the decline of the winter run of chinook salmon (*Oncorhynchus tshawytscha*) in the Sacramento River in California (Fig. 2.4). The insets in each of these examples show the quick and easy way of estimating the per capita growth rate from an abundance time series: when plotted on a semilogarithmic plot, the exponential (or geometric) growth trajectory becomes a straight line, and the slope is r (or $\log[L]$).

In terms of pedagogical value, we have learned that constant per capita rates yield a population whose chief characteristic is that the larger the population, the faster total numbers will grow. Geometric (or exponential) growth is quite relevant to one ecologically important animal population, the population of humans on Earth. The fact that the human population of the world is not only growing at an exponential rate, but that the growth rate $r(t)$ is actually increasing with time is a critical problem (Cohen, 1995). The growing human population—although not the focus of this book—probably influences most of the problems we discuss in the population dynamics of resource management.

Exponential and geometric models also illustrate another point of practical value: that linear models will be of little use in determining optimal harvest (i.e. how much to harvest and when, in order to maximize the total harvest). If the population is declining ($r < 0$ for continuous time or $L < 1$ in discrete time) the population should be completely harvested right away, before it disappears. If the population is growing ($r > 0$ for continuous time or $L > 1$ in discrete time) for a completely unconstrained optimal harvest problem, the solution is to wait until the population is infinitely large, then harvest all of it. This clearly does not make sense.

A more meaningful formulation would be to maximize harvest over a limited time span. However, the answer in this case is similar: for a growing population, the optimal harvest is to wait until just before the end of the time span, then harvest everything. One could possibly find a cost function that leads to a more meaningful solution, but because the standard ways of formulating the optimal harvest problem lead to the problems just stated,

and because the model is not considered to be a realistic portrayal of population dynamics, the optimal harvest problem is not approached using this model. See Mendelsohn (1976) for a discussion of this point in the context of age-structured models. We will revisit optimal harvesting with more appropriate models at the end of this chapter, and then in more depth in Chapter 11.

2.3 Simple nonlinear models (logistic-type models)

The simple logistic model (and similar logistic-type models) has been the workhorse of both theoretical and applied population biology. It has been the most commonly used model of population dynamics in population and community theories, and forms the basis of management of many populations, especially in fisheries (Chapter 11; Graham, 1935; Schaefer, 1954; Gulland, 1983). It was originally developed in the early nineteenth century in response to the observation that models with geometric or exponential increase did not hold for some populations of laboratory animals and some human populations. In these, the population growth rate declined at high abundance, thus exhibiting density dependence (Box 2.3). The form we now use most commonly was developed by Verhulst (1838) as the simplest way of modifying the exponential model to produce an upper limit to abundance (see Hutchinson (1978) for further historical information).

Note that the rationale in the modeling efforts associated with the logistic model is basically inductive curve fitting of population-level data. That is, the functional form and parameter values are phenomenological, chosen to mimic trends in population abundance as closely as possible, with (almost) no attempt to represent the individual level mechanism(s) that actually cause changes in population growth rate.

2.3.1 Continuous-time logistic models

Verhulst (1838) proposed that the model for exponential growth be modified to approach a constant level by multiplying the model for exponential growth (Eq. (2.1)) by a function that declined from one to zero, as abundance $N(t)$ increased from zero to a new constant, K , the carrying capacity. The basic form of the logistic equation in continuous time is

$$\frac{dN}{dt} = rN(t) [1 - N(t)/K], \quad (2.6)$$

where r is a constant, the same intrinsic rate of increase. We can obtain a solution for this equation (i.e. the value of $N(t)$ at any given time) fairly easily by separation of variables (Box 2.4),

$$\frac{K}{N(K-N)} dN = r dt \quad (2.7a)$$

followed by a partial fraction expansion,

$$\left[\frac{1}{N} + \frac{1}{K-N} \right] dN = r dt \quad (2.7b)$$

whose solution, integrated from 0 to t , is

$$\ln \frac{N}{K-N} - \ln \frac{N_0}{K-N_0} = r(t - t_0), \quad (2.7c)$$

which can be written

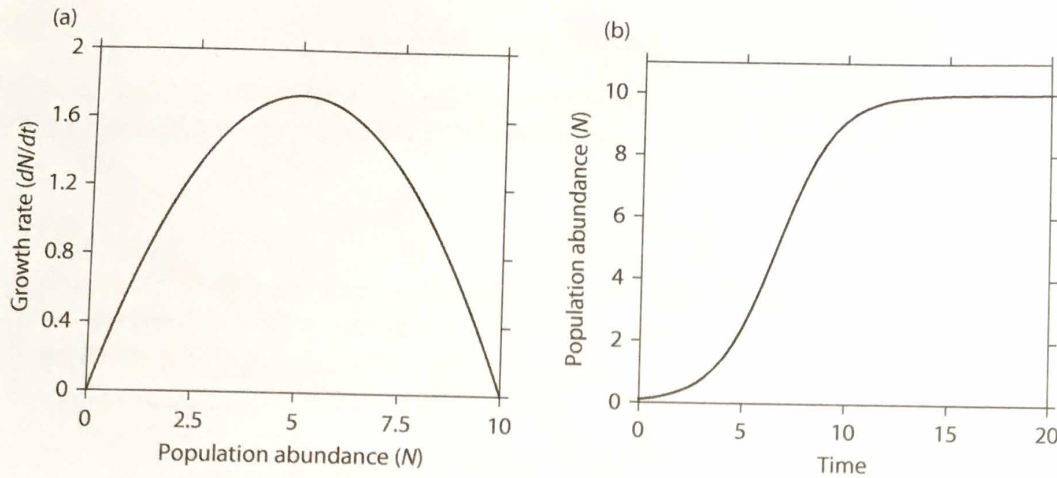


Fig. 2.5 Example of the logistic model (Eq. (2.6)), with intrinsic growth rate $r = 0.69$ and carrying capacity $K = 10$. Panel (a) shows the population growth rate dN/dt as a function of population abundance; note that the growth rate is a maximum at $N = K/2 = 5$. Panel (b) shows the abundance of the population increasing from a low value ($N = 0.1$) to the carrying capacity (Eq. (2.7d)).

$$N(t) = \frac{K}{1 + Ce^{-r(t-t_0)}}, \quad (2.7d)$$

where $C = (K - N_0)/N_0$. Letting t go to infinity, we can see that the solution approaches K asymptotically (Fig. 2.5b).

We can also write Eq. (2.6) in dimensionless form as

$$\frac{d\tilde{N}}{d\tilde{t}} = \tilde{N}(1 - \tilde{N}). \quad (2.8)$$

Here the tildes (e.g. \tilde{N}) indicate that we have rescaled the model by creating new variables or parameters that are combinations of the originals (notice that for simplicity we sometimes write these equations omitting the (t) after N , essentially assuming it is understood that N is the state variable that depends on time). In this case, $\tilde{t} = rt$ and $\tilde{N} = N/K$. In both cases the units cancel out in the new variable or parameter, so the model is now unitless (i.e. has been nondimensionalized). The step of making a model nondimensional often provides a clearer view of how it works, since the dynamical behavior of a model can only depend on nondimensional parameters. That is, the behavior of a model (whether it increases exponentially or reaches a stable equilibrium, for example) never depends on the units in which model parameters or variables are measured, but rather on their magnitude relative to one another. Here in Eq. (2.8) no parameters remain, so the value of this form for the logistic model is that it allows us to see that changes in K simply scale amplitude (i.e. the magnitude of N). Essentially K could be thought of simply as the units associated with population abundance, e.g. thousands of individuals, or population density (per unit area or volume), while changes in r simply scale time (i.e. r merely determines the time it takes the population to reach a particular fraction of K).

In somewhat of a mathematical digression to aid understanding of why some models are linear and some are nonlinear, we can compare how the definition of linear systems in Box 2.2 applies to the linear model of exponential growth (Eq. (2.1)) and the nonlinear model of logistic growth (Eq. (2.6)). For the first condition in Box 2.2, we ask whether $aN(t)$ is a solution of Eq. (2.1), given that $N(t)$ is a solution. That is, whether

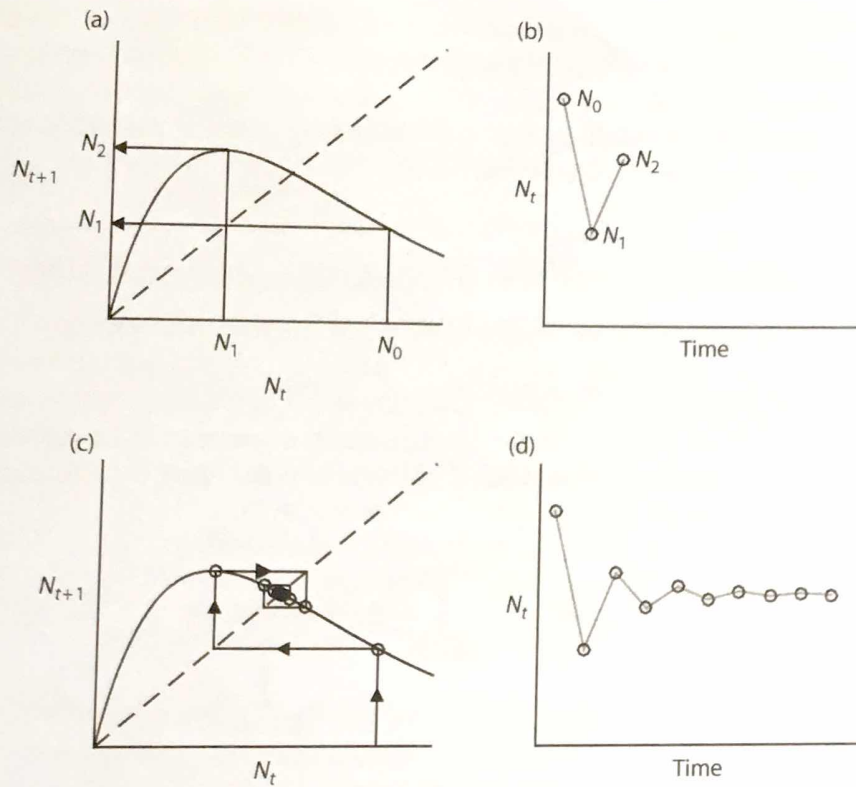


Fig. 2.9 Demonstration of the cobwebbing procedure. (a) The function $F(N)$ (solid curve) and the process of simply looking up the first two values of the next abundance. Also shown is the line of slope $= 1$ (dashed line), the "replacement line," used to identify the upper right-hand corner of the squares used to avoid looking up values on the horizontal axis. The resulting time series is shown in (b). The shortcut, cobwebbing process can be seen by following the arrows in (c). (d) The process is followed through to equilibrium, using the shortcut of only drawing horizontal lines to the replacement line, then vertical lines to the function.

2.4 Illustrating population concepts with simple models

While simple population models may lack the realism to reflect some important aspects of population dynamics, we can take advantage of their simplicity to introduce fundamental aspects of population behavior that we will be studying later. We first use the simple nonlinear model in discrete time to illustrate the concept of population stability, including stability about zero abundance, as a reflection of population persistence. The second application uses a simple linear model in discrete time (Eq. (2.3)) with random values of the L_t 's to illustrate the effects of randomness on population persistence and probability of extinction. The third example uses the continuous time logistic model to give a primitive view of how fishing and density dependence interact when trying to achieve sustainable fishing.

2.4.1 Illustrating dynamic stability with simple, linear, discrete-time models

Unlike the simple linear models, for more complex models with density dependence we often cannot write down an explicit formula giving the solution (N_t) as a function of time. Instead, we use stability analysis as a way of determining how a dynamic system will be expected to behave, without simulating each possible situation. Stability analysis

can determine what combinations of parameter values will tend to cause the population to increase, decrease, cycle with diminishing amplitude, cycle with increasing amplitude, persist at a constant equilibrium, or go extinct. We will begin by describing the *local stability* of deterministic populations that are responding to being perturbed away from a specific *equilibrium* abundance (See definition of local stability in Box 2.5).

Box 2.5 A GRAPHICAL DEFINITION OF EQUILIBRIA AND LOCAL STABILITY

We can get a clear sense of the mathematical definition of local stability by presuming that model solutions (i.e. the possible values of $N(t)$) define a topographical surface that may have various hills and valleys in it (e.g. Fig. 2.10). The shape of the landscape represents the dynamics of the model. Possible solutions to the model equations can be represented by the location of a ball on the surface. Figure 2.10 is an example of part of such a surface that includes a peak, a valley, and a flat region.

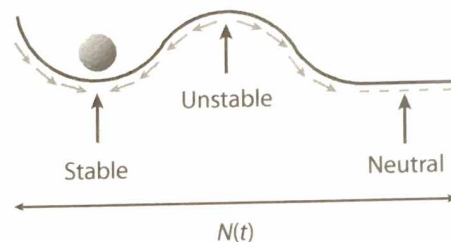


Fig. 2.10 A graphical illustration of dynamic stability. The black curve represents the range of possible model solutions (values of $N(t)$). The black arrows indicate three possible equilibria, i.e. places where $N(t)$ will remain constant unless perturbed. Gray arrows indicate what will happen if $N(t)$ is perturbed away from any of the equilibria: it will tend to be pushed back towards the stable equilibrium and pushed away from the unstable equilibrium. $N(t)$ will not tend to move in either direction if moved a short distance away from the neutral equilibrium point, it will just remain at the new location (thus the entire flat portion of the surface is comprised of neutral equilibria).

First we define an *equilibrium*, which is also referred to as a *fixed point*. It is a point on the surface at which the ball will stay if not perturbed. These are indicated by arrows in Fig. 2.10. The population can be either be locally stable or locally unstable about each equilibrium. It is defined to be locally stable if, when perturbed a little from the equilibrium (e.g. the ball is pushed gently), it tends to return to the equilibrium. If it tends to move away from the equilibrium when perturbed, it is locally unstable. Continuing the topographical metaphor, we refer to the “valley” surrounding an equilibrium as a *basin* of attraction. It is also possible (although probably rare in nature) to have neutral stability, which is represented by the flat surface in Fig. 2.10 (if the ball is pushed, it stays at the new location without rolling back or accelerating away).

A mathematical analysis of the dynamic stability of a system is equivalent to determining whether each equilibrium is on a hill or in a valley, and how steep the surrounding slopes are.

Before beginning our description of population stability, we must place our mathematical definitions in the context of the many uses of the term “stability” throughout ecology (see Table 2.3 for a summary of these definitions). When we describe issues associated with

To move incrementally toward more complex examples, we can analyze stability of another linear example, the rabbit problem from Section 2.1. Recall that in the Fibonacci series, which emerges from the rabbit problem, each entry is the sum of the previous two entries,

$$N_{t+1} = N_t + N_{t-1}. \quad (2.18a)$$

Once again there is one equilibrium, $N^* = 0$ (this is generally true for linear models). To analyze small deviations ΔN_t from N^* , we again substitute the expected solution to a linear equation, $\Delta N_t = \Delta N_0 \lambda^t$, to obtain

$$\lambda^{t+1} = \lambda^t + \lambda^{t-1}, \quad (2.18b)$$

which, dividing by λ^t and rearranging, becomes the characteristic equation

$$\lambda^2 - \lambda - 1 = 0, \quad (2.18c)$$

which can be solved using the quadratic formula. The characteristic equation for this linear model is of order 2 (i.e. the highest power of λ is 2), so there are two roots,

$$\lambda_1 = \frac{1 + \sqrt{5}}{2}; \lambda_2 = \frac{1 - \sqrt{5}}{2}. \quad (2.19)$$

Because there are two roots, the solution will be the sum of two terms, each of which is one of the roots of the characteristic equation to the t power, multiplied by a constant. Thus,

$$\Delta N_t = c_1 \left(\frac{1 + \sqrt{5}}{2} \right)^t + c_2 \left(\frac{1 - \sqrt{5}}{2} \right)^t, \quad (2.20)$$

where c_1 and c_2 are constants whose values are determined from the initial conditions (i.e. the starting values) of ΔN_t and ΔN_{t-1} . As time (t) increases the first term will be 1.618^t and the second will be $(-0.618)^t$, with the terms alternating in sign for the latter (because λ_2 is negative, the second term will be positive for even values of t but negative for odd t). Also, as t increases the value of the first term will eventually be much larger than the value of the second term, regardless of what the two constants are, so the value of λ_1 is more important to stability than the value of λ_2 . In this case $\lambda_1 > 1$, so the system is unstable at $N^* = 0$ and will increase away from zero without bound. This illustrates a general rule of analysis of stability of a linear system, that stability will be determined by the largest root of the characteristic equation.

These simple examples display the essence of the stability analyses we will employ throughout the book, with more complex models (basically actions at many more lags). For each model we will derive a characteristic equation and find its roots. We will then claim that we can write the solution to the model's equation as we did in Eq. (2.20), that is as the sum of n terms (where n is the order of the characteristic equation) that are each a constant times a root to the power t (for discrete-time models). We will then conclude that, in the long run, the behavior of the population will be determined by the largest root (sometimes the largest two or three roots), as we concluded from Eq. (2.20). Thus to know how a population will behave in future, we will not need to run many simulations, we need only to find the largest root(s) of the characteristic equation.

Stability analysis does not involve using Eq. (2.20) to calculate a solution. That is, we simply look at the values of the largest eigenvalues to determine if the system is stable, but we do not need to find out what ΔN_t will be for a particular value of t . However, some readers may be wondering if Eq. (2.20) is actually a solution. For this particular problem, we know how to generate a Fibonacci series (start with 1 and 1, then add each two values

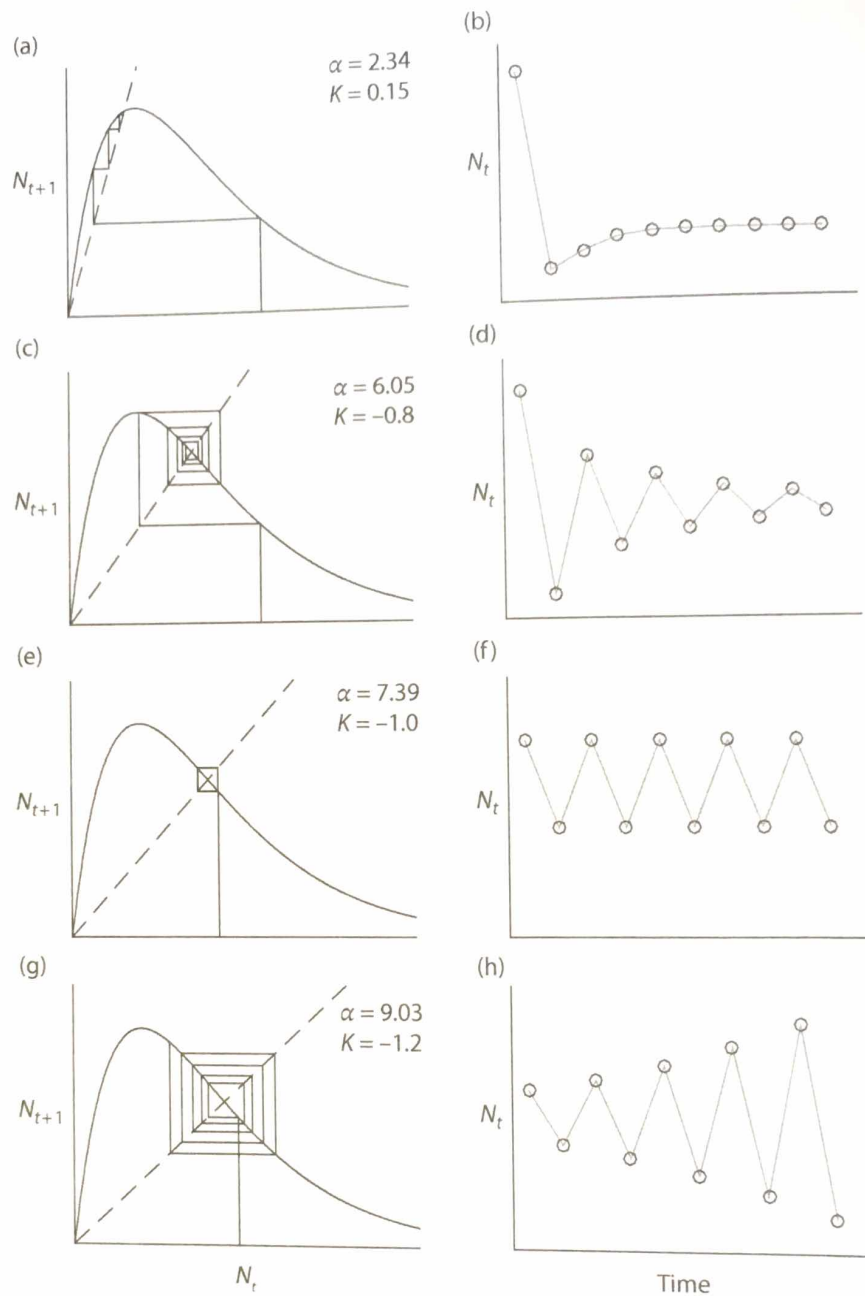


Fig. 2.12 Using cobwebbing to characterize stability of the Ricker model. As in Fig. 2.9, the black curve is $F(N)$, and the dashed line is the replacement line. The cobweb (a, c, e, g) and corresponding time series (b, d, f, h) are shown for a range of parameter values that lead to different dynamic stabilities. Parameter $\beta = 1$ in all panels, but parameter α (which determines the slope, K) varies as indicated. Note that the scale of the vertical axis in the left-hand panel varies in order to show the cobwebbing (the replacement line has slope 1 in all panels).

that the point at which the function $F(N)$ intersects the replacement line is an equilibrium (i.e. $F[N^*] = N^*$; in the Ricker model, $N^* = \ln[\alpha]/\beta$). To examine local stability about that point we define the slope of $F(N)$ at the equilibrium to be K . (This notation, using K as a normalized slope parameter, arises in the analysis of age-structured models. Be careful not to confuse it with carrying capacity. We will use this notation again in Chapter 7.) In the Ricker model, $F'(N) = K = 1 - \ln(\alpha)$. We can then graphically determine solutions for several values of K ; these correspond to the solutions we have just presented previously.

2.4.4 What does the simple logistic model tell us about managing for sustainable fisheries?

In the early twentieth century, concern arose among wildlife and fisheries biologists because harvested populations were declining. They wondered how much a population should be expected to decline in abundance with removals by harvesting, and whether there was an optimal level at which such extraction should be operated. Fortunately, mathematical ecology was developing in parallel, and researchers in these fields were well aware of each other. The idea of the logistic model was introduced into fisheries and management of other animal resources at that time as a way to represent the growing belief that the greatest yield could be obtained from populations not at their greatest possible abundance, but rather at some lower level. Hjort et al. (1933) described this concept in the context of whaling in the Barents Sea, but they also mentioned bear hunting in Norway. Graham (1935) was concerned with the increase then decline of fish catch in the eastern Atlantic, and he used data from the period of no fishing during the First World War as the basis for his logistic-type models. Both were aware of the parallel development of the logistic model in general ecology (see Chapter 6 in Smith (1994) for more of this history).

The version of the logistic model developed by Verhulst (Eq. 2.6) provided a framework for investigating the question of optimal harvest. One approach would be to assume that harvest exactly balanced the population growth rate, so that $dN/dt = 0$. That would represent the conditions under which yield could be removed from a population while maintaining it at a constant abundance. That consideration led to logistic models in fisheries being referred to as *surplus yield* models. There was naturally interest in determining the maximum yield that would satisfy that relationship. This could be obtained by taking the partial derivative of the expression for dN/dt in Eq. (2.6) with respect to N , and setting it equal to zero to find the maximum growth rate:

$$\frac{\partial}{\partial N} \left(rN - \frac{rN^2}{K} \right) = 0. \quad (2.31a)$$

Evaluating this derivative leads to

$$r - \frac{2rN}{K} = 0, \quad (2.31b)$$

which simplifies to

$$N = K/2. \quad (2.31c)$$

This implies that the growth rate (and thus the possible harvest rate) is at a maximum at $K/2$ (Fig. 2.5a). This characteristic of this simple model is the origin of the oft-quoted result that the best way to harvest a population is to harvest at a rate that reduces it to half of its carrying capacity. This is the point at which it is increasing the fastest (dN/dt is greatest), hence it can endure the greatest harvest without declining. Even in the early 1900s, while some viewed this approach as a universal law, few believed that the straight line representing the decline in dN/dt with N held in general. That motivated the search for other forms of the logistic mentioned earlier as logistic-type models (Section 2.3.1). The valuable lesson observed was that it was not necessarily optimal to keep the population at high abundance, rather that the optimal yield would be at more of a "middling" level. Schaefer (1954) applied the logistic model to management of several fisheries, and in Chapter 11 we describe how he added the assumption that abundance was proportional

to catch per unit fishing effort (CPUE), so that catch and effort data could be used to fit the model.

Maximizing harvest by maintaining the population near half of the carrying capacity and removing the annual growth each year became known as managing for *maximum sustainable yield*. It was a very influential idea that dominated fishery management globally through the 1980s, and is still currently used (see Botsford (2013) for a bibliography, and brief history). It is also used in the management of species other than fish. Examples include surplus yield curves for northwest Atlantic harp seals (*Pagophilus groenlandicus*) (Lett et al., 1981), a plot of the production of an unharvested species, grizzly bears (*Ursus arctos horribilis*) versus abundance (McCullough, 1981), a surplus production plot of life history information on gamebirds (Robertson and Rosenberg, 1988), and a demonstration that the maximum sustainable ivory yield for African elephants (*Loxodonta africana*) could be met by gathering tusks from natural mortality (Basson and Beddington, 1991). The logistic model continues to be used as a description of harvest of many kinds of animals (e.g. in a recent book on wildlife and climate change, the discussion of harvesting is based on the logistic model; Boyce et al., 2012).

2.5 What have we learned in Chapter 2?

Before moving on to Chapter 3, we can ask what we have learned in Chapter 2. First we learned some basic definitions regarding how we will represent time in population models (discrete and continuous) and the kind of equations used for each (Section 2.2). We also learned what linear versus nonlinear models are (Section 2.3), an important mathematical distinction with a parallel biological interpretation (nonlinear models contain density-dependent effects, while linear models do not). We learned some simple solutions to differential equation models (e.g. separation of variables), and a graphical solution to some nonlinear discrete-time models (cobwebbing).

The three illustrations with simple models of: (1) the determination of population stability (Sections 2.4.1 and 2.4.2) and (2) the effects of random variability in populations (Section 2.4.3) gave us a simple introduction to concepts we will be dealing with throughout the book. In the first illustration, introduction to stability analysis, we presented a useful way of describing general characteristics of behavior of models and populations. With simple linear, discrete time models (Section 2.4.1) we learned that we could propose solutions of the form $N_t = c\lambda^t$, and come up with an algebraic equation whose solution told us something about how the population would behave. We tried that approach with arguably the first population model, the rabbit problem, and saw that a weighted sum of two constants, each raised to t power, could reproduce the known behavior of the Fibonacci series. From Chapter 3 on, we will refer to these values of λ as eigenvalues, and this approach will underpin much of what we learn about population behavior. For simple, nonlinear, discrete-time models (Section 2.4.2) we saw that populations can have a nonzero equilibrium, and that we can form linear models of how the population behaves near those equilibria. We also learned some of the characteristics of that equilibrium that we will be interested in, such as local stability and cyclic behavior. The stability of a zero equilibrium was also of interest because it told us how populations can continue to persist (essentially the opposite of the topic in the second example, extinction).

In the second illustration (Section 2.4.3), we added the effects of the random environment to our consideration of the zero equilibrium. We learned that when we are interested in population extinction, we will most often be calculating quasi-extinction, rather than