

Elementary Population Dynamics

1

In 1960 the famous cyberneticist Heinz von Foerster and colleagues devised an equation predicting that the human population would become effectively infinite on Friday the 13th of November, 2026, meaning that at that point in time all humans would perish because the next individual to be born would crush everyone else—mass death due to squashation! In fact von Foerster and his colleagues were making a tongue-in-cheek argument to call attention to an issue they thought quite important. This was one, perhaps humorous, example of the application of simple quantitative principles of population dynamics to problems considered important.

Indeed there are many contexts in which it is important to understand the quantitative characteristics of single populations of organisms. In fisheries management, for example, the manager is interested in being able to predict the density of a fish population in the future under different management plans. An agronomist may wish to know the yield of a population of maize plants when planted at a particular density; an epidemiologist will want to know the density of disease-infected humans next month. Many other examples could be cited with clear practical importance. Of perhaps even more importance are theoretical applications that give us a more detailed understanding of more complex ecological systems. We might be interested in knowing the rate at which a population changes its density in response to selection pressure as part of a general program of understanding the consequences of natural selection under some hypothetical or real constraints. These topics, both applied and theoretical, are typical of the field called population ecology, and they all start with some basic ideas of what single populations of organisms do.

The unit of analysis is, not surprisingly, the “population,” a concept that is at once simple and complicated. The simple idea is that a population is simply a collection of individuals. But, as most ecologists intuitively know, the idea of a population is considerably more complex when one deals with it in any of

the applied or theoretical contexts alluded to above. To know what size limits one should place on a fish species one must know not only the number of fish in the population but the size distribution of that population and how that distribution relates to the population's reproductive effort. To decide when to take action on the emergence of pest species in an agricultural or forestry context, the distribution of individuals in various life stages must be known. In deciding whether a species is threatened with extinction, its distribution in space and movement among subpopulations (i.e., metapopulation dynamics) is far more important than simply its numerical abundance. And, to use the most frequently cited example, given the huge variation in the consumption of resources per person around the globe, the absolute numbers of the human population may be much less important than the activities undertaken by the members of that population—doomsday could be at hand well before 2026.

Thus the subject of population ecology can be a very complicated one indeed. But, as in the case of any science, we begin by assuming that it is rather simple. We eliminate the complications, make simplifying assumptions, and try, as much as possible, to develop general principles that might form a skeleton onto which the flesh of real-world complications might meaningfully be attached. In 2013 it seems that, unlike some other fields of biology, population ecology has a certain core subject matter that has come to be the “conventional wisdom.” That is, wherever a university course in population ecology is taught, pretty much the same material is covered, at least at the beginning of the course. This text is our attempt to present that core material precisely, and this chapter covers the first two essential ideas—the density independence and density dependence of population growth.

Density Independence: The Exponential Equation

It is often surprising how quickly a self-reproducing event becomes a big event. The classic story is this: suppose you have a pond with some lily pads in it, and suppose each lily pad replicates itself once per week. If it takes a year for half the pond to become covered with lily pads, how long will it take for the entire pond to become covered? If one does not think too long or too deeply about the question, the quick answer seems to be about another year. But with a moment's reflection one can retrieve the correct answer—only one more week.

This simple example has many parallels in real-world ecosystems. A pest building up in a field may not seem to be a problem until it is too late. A disease may seem much less problematical than it really is. The simple problem of computing the “action threshold” (the population density a pest must reach before you have to spray pesticide) requires the ability to predict how large a population will be based on its prior behavior. If half the plants in the field are attacked within three months, how long will it be before they are all attacked?

To understand even the extremely simple example of the lily pads, one constructs a mathematical model, usually quite informally, in one's head. If

all the lily pads on a pond replicate themselves once per week, in a pond half-filled with lily pads each one of those lily pads will replicate itself in the next week and thus the pond will be completely filled up. To make the solution to the problem general, we simply say the same thing, but instead of labeling the entities lily pads, we call them something general, say organisms. If organisms replicate themselves once per week, by the time the environment is half full, it will take only one week to become completely full. Implicitly, the person who makes such a statement is simply stating verbally the following equation:

$$N_{t+1} = 2N_t. \quad (1)$$

N is the number of organisms, in this case lily pads. Instead of N , say lily pads, and instead of t , say this week, and instead of $t + 1$, say next week, and equation 1 expresses simply, “The number of lily pads next week will be equal to twice the number this week.”

Writing down equation 1 is no different than making any of the statements that were made previously about it. But by making it explicitly a mathematical expression, we bring to our potential use all the machinery of formal mathematics. And that is actually good, even though beginning students sometimes don’t think so.

Using equation 1 we can develop a series of numbers that reflect the changes of population numbers over time. For example, consider a population of herbaceous insects. If each individual produces a single offspring once per week, and if those offspring mature and each produces an offspring within a week, we can apply equation 1 to see exactly how many individuals will be in the population at any point in time. Beginning with a single individual, we have, in subsequent weeks, 2, 4, 8, 16, 32, 64, 128, and so on. If we change the conditions such that the species replicates itself twice per week, equation 1 becomes

$$N_{t+1} = 3N_t \quad (2)$$

(with a 3 instead of a 2, because before we had the individual and the single offspring it produced but now we have the individual and the two offspring it produced). Now, beginning with a single individual, we have, in subsequent weeks, 3, 9, 27, 81, 243, and so on.

We can use this model in a more general sense to describe the growth of a population for any rate of production of offspring at all (not just 2 and 3 as above). That is, write

$$N_{t+1} = \lambda N_t \quad (3)$$

where λ can take on any value at all. λ is frequently called the finite rate of population growth (or the discrete rate).

It may have escaped notice in the above examples, but either of the series of numbers could have been written with a much simpler mathematical notation. For example, the series 2, 4, 8, 16, 32, is actually $2^1, 2^2, 2^3, 2^4, 2^5$, while the series 3, 9, 27, 81, 243 is actually $3^1, 3^2, 3^3, 3^4, 3^5$. So we could write

$$N_t = \lambda^t, \quad (4)$$

which is just another way of representing the facts described by equation 3. (Remember, we began with a single individual, so $N_0 = 1.0$.)

EXERCISES

- 1.1 Compute the expected number of individuals over time in a population growing according to equation 3 for $\lambda = 1.9$, $\lambda = 2.0$, and $\lambda = 2.1$, where λ is the finite rate of increase (it is convenient to begin with a single individual). Graph the results as a function of time.
- 1.2 Plot the numbers calculated in exercise 1.1 as $\ln(N)$ versus time. Sketch (by hand, by eye) the function that best approximates one of the data sets (try for $\lambda = 2$), and visually estimate what the parameters of that function might be. What is the nature of the function, and how do its parameters relate to the original construction of the set of numbers in exercise 1.1?

For further exposition we wish to express the constant λ in a different fashion. It is a general rule that any number can be written in a large number of ways. For example, the number 4 could be written as $8/2$ or $9 - 5$ or 2^2 or in many other ways. In a similar vein, an abstract number, say λ , could be written in any number of ways: $\lambda = 2^b$, where b is equal to $\lambda/2$, or $\lambda = 2^b$, in which case $b = \ln(\lambda)/\ln(2)$ (where \ln stands for natural logarithm). For reasons that will be obvious to the reader not too far removed from the elementary calculus class, if we represent λ as 2.7183^r , a powerful set of mathematical tools immediately becomes available. The number 2.7183 is Euler's constant, usually symbolized as e (actually, 2.7183 is rounded off and thus is only approximate). It has the important mathematical property that its natural logarithm is equal to 1.0 or $\ln(e) = 1$.

So we can rewrite equation 4 as

$$N_t = e^{rt}, \quad (5)$$

which is the classical form of the exponential equation (where λ has been replaced with e^r). One more piece of mathematical manipulation is necessary to complete the toolbox necessary to model simple population growth. Another seemingly complicated but really rather simple relationship that is always learned (but frequently forgotten) in elementary calculus is that the rate of change of the log of any variable is equal to the derivative of that variable divided by the value of the variable. This rule is more compactly stated as

$$\frac{d(\ln N)}{dt} = \frac{dN}{Ndt}. \quad (6)$$

So take the natural logarithm of equation 5 as

$$\ln(Nt) = rt$$

and differentiate with respect to t to obtain

$$\frac{d(\ln N)}{dt} = r, \quad (7)$$

and we can then use equation 6 to substitute for the left-hand side of equation 7 to obtain

$$\frac{dN}{Ndt} = r.$$

After multiplying both sides by N , we obtain

$$\frac{dN}{dt} = rN. \quad (8)$$

Equations 5 and 8 are the basic equations that formally describe an exponential process. Equation 8 is the differentiated form of equation 5, and equation 5 is the integrated form of equation 8. They are thus basically the same equation (and indeed are quite equivalent to the discrete form—equation 3). Depending on the use to which they are to be put, any of the above forms may be used, and in the ecological literature one finds all of them. Their basic graphical form is illustrated in figure 1.1.

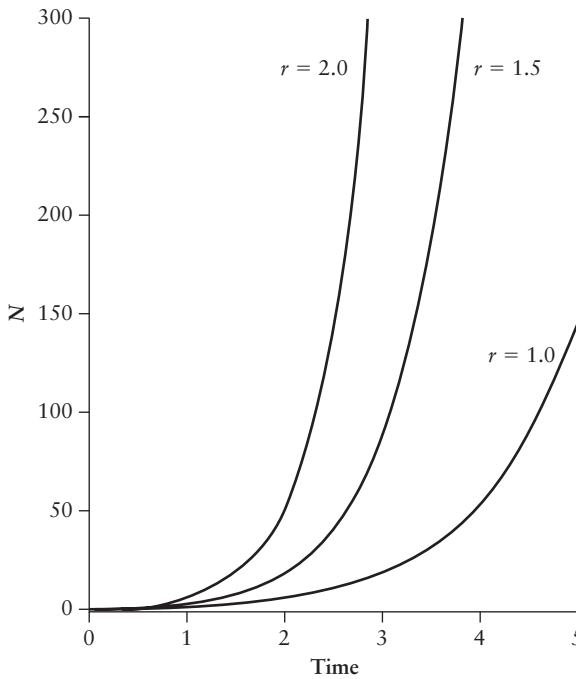


FIGURE 1.1. Graphs of equation 5.

EXERCISES

- 1.3 Derive an equation for doubling time in an exponentially growing population, and derive one for tripling time.
- 1.4 Plot the values computed in exercise 1.1 on a graph of N_{t+1} versus N_t , where N is the number of individuals and t is time. What is the shape of the plotted points? What would be the value of a regression coefficient through the points? How does that relate to the original values of λ ?
- 1.5 The human population in a small island nation is said to be doubling every 20 years. What would be the value of r (assuming an exponential model)?
- 1.6 Using the differential form (i.e., continuous time), suppose that $r = 0.5$. Compute N as a function of t , again beginning with a single individual. Do the same for $r = 1.5$ and for $r = 1.0$. Graph all three results, and think about the pattern.

In the examples of exponential growth introduced above, the parameter r was introduced as a birth process only. The tacit assumption was made that there were no deaths in the population. In fact, all natural populations face the reality of mortality, and the parameter of the exponential equation is really a combination of birth and death rates. More precisely, if b is the birth rate (number of births per individual per time unit) and d is the death rate (number of deaths per individual per time unit), the parameter of the exponential equation is

$$r = b - d, \quad (9)$$

where the parameter r is usually referred to as the intrinsic rate of natural increase.

One other simplification was incorporated into all of the above examples. We always presumed that the population in question was initiated with a single individual, which almost never happens in the real world. But the basic integrated form of the exponential equation is easily modified to relax this simplifying assumption. That is,

$$N_t = N_0 e^{rt}, \quad (10)$$

which is the most common form of writing the exponential equation. Thus there are effectively two parameters in the exponential equation, the initial number of individuals, N_0 , and the intrinsic rate of natural increase, r .

Putting the exponential equation to use requires estimation of these two parameters. Consider, for example, the data presented in table 1.1. Here we have a series of observations over a five-week period of the number of aphids on an average corn plant in an imaginary cornfield.

As a first approximate assumption, let us assume that this population originates from an initial cohort that arrived in the field on March 18 (one week prior to the initial sampling). We can apply equation 10 to these data most easily by taking logarithms of both sides, thus obtaining

$$\ln(Nt) = \ln(N_0) + rt, \quad (11)$$

TABLE 1.1. Number of Aphids Observed per Plant in a Milpa (Corn and Beans) in the Highlands of Guatemala (Morales, 1998)

Date	Number of aphids	$\ln(\text{Number of aphids})$
March 25	0.02	-3.91
April 1	0.50	-0.69
April 8	1.50	0.40
April 15	5.00	1.61
April 22	14.50	2.67

which gives us a linear equation relating the natural logarithm of the number of aphids to time (where we code March 18 as time = 0, March 25 as time = 1, April 1 as time = 2, etc.). In figure 1.2 is a graph of this equation along with the original data points, and in figure 1.3 is a graph of the original data along with the fitted curve on arithmetic axes.

From these data we have the estimate of 1.547 aphids per parent aphid per week added to the population (i.e., the intrinsic rate of natural increase, r , is 1.547, which is the slope of the line in figure 1.2). The intercept of the regression is -4.626, which indicates that the initial population was .0098 (i.e., the antilog of -4.626 is .0098), which is an average of about one aphid per 100 plants. Now, if we presume that once the plants become infected with more than 40 aphids per plant the farmer must take some action to try to control them, we can use this model to predict when, approximately, this time will arrive. The regression equation is

$$\ln(N \text{ of aphids}) = -4.626 + 1.547t,$$

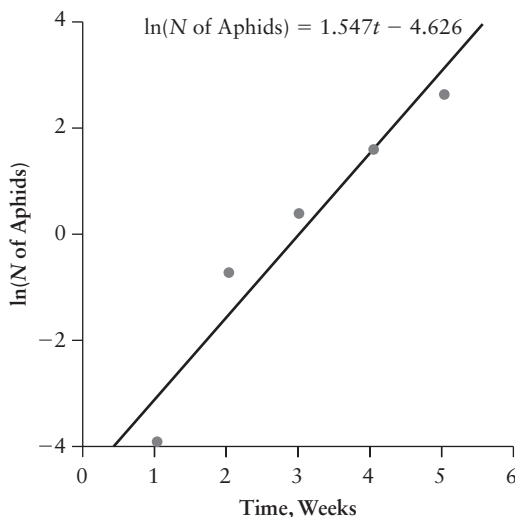


FIGURE 1.2. Plot of aphid data (from table 1.1).

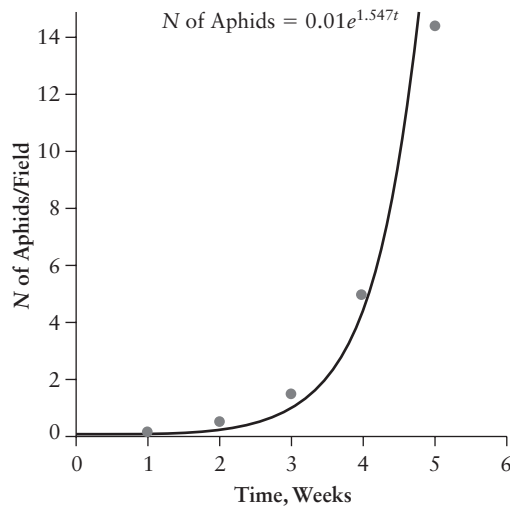


FIGURE 1.3. Aphid data from figure 1.2 plotted arithmetically.

which can be rearranged as

$$t = [\ln(N \text{ of aphids}) + 4.626] / 1.547.$$

The natural log of 40 is 3.69, so we have

$$t = (3.69 + 4.626) / 1.547 = 5.375.$$

Translating this number into the actual date (remember that April 22 was time = 5), we see that the critical number will arrive about April 24 (at 3:00 p.m. on April 24, theoretically).

In practice, calculations like these exclude many complicating factors, and we should never take too seriously exact predictions the model makes. On the other hand, April 24 really does represent the best prediction we have based on available data. It may not be a very good prediction, but it is the only one available. Furthermore, it may seem quite counterintuitive that, having taken five full weeks to arrive at only 14 aphids per plant, in only two more days the critical figure of 40 aphids per plant will be realized—such is the nature of exponential processes. A simple model like this could help the farmer plan pest control strategies.

EXERCISES

- 1.7 Plot the derivative (which you can approximate by subtracting the current N from its successive one and dividing by the change in time) as a function of N for the data calculated in exercise 1.6 (use a very small time interval, e.g., 0.01).
 - 1.8 From the data calculated in exercise 1.7, divide the estimated derivative by the average number of individuals during the time period, and plot them over time. What is the result, and what does it mean?
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Density Dependence

In the previous section we showed that any population reproducing at a constant per capita rate will grow according to the exponential law. Indeed, that is the very essence of the exponential law: each individual reproduces at a constant rate. However, the air we breathe and the water we drink are not completely packed with bacteria or fungi or insects, as they would be if populations grew exponentially forever. Something else must happen. That something else is sometimes referred to as intraspecific competition, which means that the performance of the individuals in the population depends on how many individuals are in it. More generally, it is referred to as density dependence. It is a complicated issue that has inspired much debate and acrimony in the past and still forms an important base for more modern developments in ecology.

The idea was originally associated with the human population, and was brought to public attention as early as the nineteenth century by Sir Thomas Malthus (1960 [1830]). It was formulated mathematically by Verhulst (1838) as the “true law of population” (Doubleday 1842); Verhulst’s version is better known today as the logistic equation (see below). Later, Pearl and Reed (1920), in attempting to project the human population size of the United States, independently derived the same equation. Associated with its mathematical formulation was a series of laboratory studies with microorganisms in the first part of the twentieth century. Most notable were those of Gause (1934), in which population growth was studied from the point of view of competition, both intra- and interspecific.

In the early part of the twentieth century a variety of terms were introduced, all of which essentially referred to the same phenomenon of approaching some sort of carrying capacity through a differential response of per capita population growth rate to different densities. Chapman (1928) formulated the idea in terms of “environmental resistance.” Howard and Fiske (1911) categorized mortality factors as either “catastrophic,” in which some proportion of the population died regardless of its density, or “facultative,” which caused an increasing proportion of the population to die with the increasing density of the population. In 1928 Thompson redefined *catastrophic* as “general” and “independent” of density and *facultative* as “individualized” and “dependent” on density, and later Smith (1935) proposed the density-dependent/density-independent gradient. Thus by the 1930s the dichotomy of density independence versus density dependence had taken firm root after having been sown not long after the turn of the century.

In the 1930s Nicholson (1933) and his colleague Bailey (Nicholson and Bailey 1935) formalized the concept of regulation through density-dependent factors and clearly associated the idea of intraspecific competition with density dependence. In Nicholson and Bailey’s conceptualization of density dependence, four points were proposed: (1) population regulation must be density dependent; (2) predators and parasites, as well as intraspecific competition, may function as density-dependent forces; (3) more than density dependence alone may function to determine actual population size; and (4) density dependence does not always function to regulate population density.

In contrast to the ideas of Nicholson and Bailey (and especially of their later followers) were the ideas of Andrewartha and Birch (1954). They held that the environment is not divisible into density-dependent versus density-independent forces and that, although resources might limit populations, they rarely do so because some aspect of the physical environment (usually collectively referred to as “the weather”) almost always imposes its effects. They furthermore noted that the mathematical models that presume equilibrium and persistence are not really necessary if there is indeed no “balance” in nature (density dependence strongly implying some sort of balance of nature). Most data sets failed to support the idea of density dependence, and the idea was viewed as possibly untestable. Rather, Andrewartha and Birch argued, the regulation of populations was frequently taken as an article of faith. The problem was this: how long could a population persist without regulation? The researchers’ recognition of the fact that local populations would frequently go extinct but would be refounded from other population centers anticipated ideas of metapopulations that would become popular some 20 years later.

Milne (1961) modified both versions of population regulation and noted that perfect density dependence, if it ever exists, does so only at very high densities. Rather, what most characterizes populations in nature is what might be referred to as imperfect density dependence, whereby predators and parasites plus density-independent effects usually hold populations below levels at which intraspecific competition can become important. More generally, Dempster (1983) suggested that density independence can be operative within limits, such that an upper ceiling will be imposed on the population and a lower limit will prevent the population from going extinct. Strong (1986) referred to such regulation within bounds rather than around a particular deterministic value as “density vagueness.” These variations are fundamentally in the density-dependence camp but with strong notions of nonlinearities and the importance of spatial distribution, topics discussed in later chapters.

In the end it would seem that the entire debate about density-dependent versus density-independent control of populations was focused on a false dichotomy. In a variety of guises (e.g., intermediate disturbance, metapopulations) modern ecology has come to acknowledge that both density-dependent and density-independent forces may function together to regulate populations in nature. But, more important, there is general agreement that the dynamic behavior of a population (its change in numbers over time) does not necessarily suggest any particular mechanism of regulation. Over the past two decades a large literature has developed that seeks to use advanced methods of analysis to determine whether density dependence operates (see, for example, Hastings et al. 1993), but that is beyond the intended scope of this text. Part of this later literature is associated with the possibility that many populations under density-dependent control actually may be chaotic (discussed more fully in chapter 4). Chaotic populations can easily be confused with random populations, and it has been noted that one way of resolving some of the earlier debates about the issue is to acknowledge that extreme density dependence

(which would promote chaos) could easily produce population behavior that looked quite density independent (i.e., chaotic) (Gukenheimer et al. 1977).

As one can see from the previous paragraphs, the literature on density dependence is enormous. Yet much of it can be divided conceptually into three categories. First, the effect of density on the growth rate of the population (be it through declining reproduction or increased mortality) is simply added to the exponential equation to form the famous logistic equation (as discussed below). Traditionally the logistic equation is expressed in continuous time as a differential equation, but recently there has been considerable interest in the special properties of the logistic idea expressed in discrete time, the logistic map. The logistic equation, in either its continuous or its discrete form, treats the population growth rate as a single constant, even though we understand that it actually represents birth rate minus death rate. Other approaches treat each of these rates separately.

Decomposing the population growth rate into its two components, the second category of literature focuses on the relationship between density and reproduction (i.e., on the fact that density modifies birth rate). We guess that the first acknowledgment of density dependence in nature was probably by the world's first farmers. When planting crops they soon realized that higher planting densities provide higher yields (which, in principle, are correlated with reproductive output), but only to a point. Once a high enough density is reached, further increases in density fail to provide further increases in yields. This general relationship is referred to as the yield–density relationship and is, in some respects, the most elementary form of density dependence. Originally developed mainly in the agronomy literature, the relationship between density and yield subsequently became an important theoretical baseline for general plant ecology. Yield was usually seen as a product of reproduction of plants such as corn and soybeans, and thus the subject of yield and density can be thought of more generally as the relationship between density and reproduction.

Finally, the third topic is the possibility that density affects survivorship rather than reproduction (i.e., that density modifies death rate). The main literature on this topic was originally conceived in the area of forestry, but it has since become generalized under the subject of self-thinning laws, which is used mainly in plant ecology but also in fisheries research. The yield–density relationship, discussed in the previous paragraph, involves examining yields of different populations that have been sown at different densities. It is a static approach in this sense. Once established through sowing, the population density remains constant and the variable of interest is the yield. An alternative approach is more dynamic and follows changes in both size (biomass) and density over time in the same population. This more dynamic approach considers mortality as well as growth, and in the context of forestry, where it was originally developed, mortality is known as thinning.

In the following three sections we follow this basic schema: (1) the logistic equation, (2) yield–density relations, and (3) self-thinning laws. But first we present some exercises to set the stage for the introduction of density dependence.

EXERCISES

- 1.9** The following are UN data on the global human population (in hundreds of thousands) from 1964 through 2007 (United Nations, Department of Economic and Social Affairs, 2011):

Year	Density	Year	Density
1964	3,278	1985	4,844
1965	3,347	1986	4,927
1966	3,417	1987	5,013
1967	3,486	1988	5,099
1968	3,558	1989	5,185
1969	3,632	1990	5,273
1970	3,708	1991	5,357
1971	3,785	1992	5,440
1972	3,861	1993	5,521
1973	3,936	1994	5,601
1974	4,011	1995	5,681
1975	4,084	1996	5,762
1976	4,156	1997	5,840
1977	4,226	1998	5,918
1978	4,298	1999	5,995
1979	4,372	2000	6,072
1980	4,447	2001	6,147
1981	4,522	2002	6,222
1982	4,601	2003	6,297
1983	4,682	2004	6,373
1984	4,762	2005	6,449

Estimate the intrinsic rate of increase (or decrease) for each successive year, and plot the estimated intrinsic rate versus the population density. Is it a flat, straight line, as would be expected if the population were growing exponentially? What kind of function would describe the data relatively well?

- 1.10** Graphically estimate the point at which the human population will stop growing (the number of individuals in the world at the point at which the present trend will reach zero. How would various sections of the data, if considered alone, change your conclusions? What if you had made your estimate in 1976 based on the most recent 10 years of data?
- 1.11** Using the UN data on the human population, insert the linear approximation of the intrinsic rate of natural increase as it relates to the population density, and graphically estimate the value of the intrinsic rate of increase (the limiting value as the density approaches zero).

- 1.12** Beginning with the exponential equation, assume that the rate of increase declines linearly with population density (i.e., substitute $a - bN$ for r). Show what substitutions you need to make to write the equation in its more biologically sensible form (i.e., with the intrinsic rate of natural increase and the carrying capacity evident). How do a and b of the linear approximation relate to the r and K of $\frac{dN}{dt} = rN\frac{K - N}{K}$?

The Logistic Equation

Density dependence is generally regarded as the major modifier of the exponential process in most populations. Consider, for example, the data shown in figure 1.4 (Vandermeer 1969). The protozoan *Paramecium bursaria* was grown in bacterial culture in a test tube, and the data shown are for the first 15 days of culture (the data are the number of cells per 0.5 ml). In figure 1.5 those numbers are shown as a graph of $\ln N$ versus time (recall how the intrinsic rate of natural increase was estimated in this way).

The relationship is approximately linear (see figure 1.5), and our conclusion would be that the population is growing according to an exponential law. If this equation were followed into the future, we would have a very large population of *Paramecium*. Indeed, considering the size of *P. bursaria*, about 3,000 individuals could fit into 0.5 ml if you stacked them as sardines. Thus the 3001st individual would cause all the animals to be squeezed to death, recalling the leitmotif with which this chapter began. We can compute exactly when this would happen from the equation of the line in figure 1.5, which is

$$\ln(N) = 1.239 + 0.227t.$$

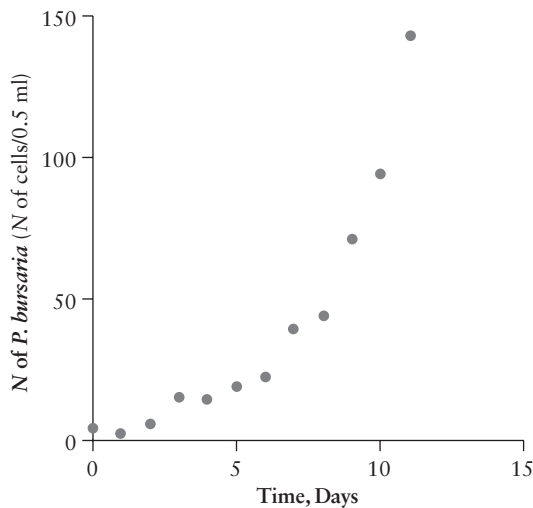


FIGURE 1.4. Growth of a culture of *Paramecium bursaria* in a test tube (Vandermeer 1969).

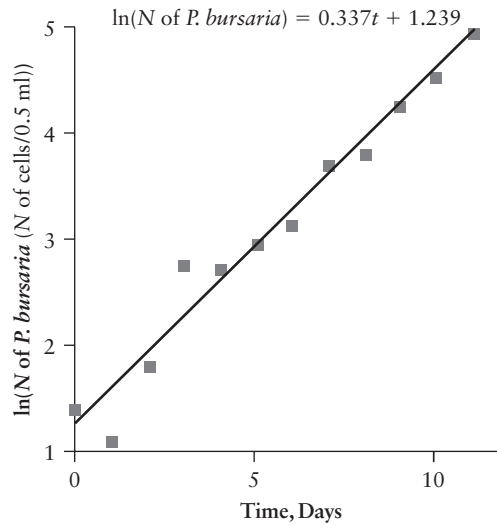


FIGURE 1.5. Logarithmic plot of the data from figure 1.4.

We substitute the critical value of 3,001 individuals to obtain

$$\ln(3,001) = 0.227 + .337t,$$

which can be arranged to read

$$t = \frac{[\ln(3,001) - 1.239]}{0.337} = 20.80.$$

Thus, on the basis of an 11-day experiment we can conclude that after about 21 days, the test tube will be jam-packed with *P. bursaria*, such that all the individuals will suddenly die when that 3,001st individual is produced. The actual data for the experiment carried out beyond the 24-day expected protozoan Armageddon are shown in figure 1.6.

These data suggest that something else happened. As the density of the *Paramecium* increased, the rate of increase declined, and eventually the number of *Paramecium* reached a relatively constant number. The theory of exponential growth must be modified to correspond to such real-world data.

Let us begin with the exponential equation but assume that the intrinsic rate of growth is directly proportional to how much resource is available in the environment. Thus we have

$$\frac{dN}{dt} = rN, \quad (12)$$

the classical exponential equation discussed earlier in this chapter. But here we presume that r is directly proportional to F (i.e., $r = bF$), where F is the amount of resources (F for food) in the system that is available to the population. Thus, equation 12 becomes

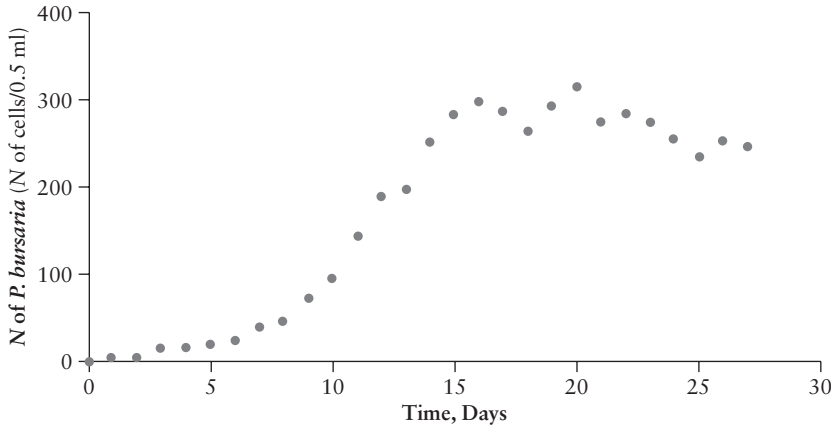


FIGURE 1.6. Long-term data for the same populations of *Paramecium bursaria* (data from time = 0 to time = 12 are the same as in figure 1.4).

$$\frac{dN}{dt} = bFN. \quad (13)$$

But now we assume that there is no inflow of resources into the system so that the total amount of resources is constant and is divided up into the part that is usable by the population and the part that has already been used. That is,

$$F_T = F + cN, \quad (14)$$

where F_T is the total amount of resources in the system and c is the amount of F held within each individual in the population. Equation 14 can be manipulated to read

$$F = F_T - cN. \quad (15)$$

Substituting equation 15 into equation 13, we have

$$\frac{dN}{dt} = b(F_T - cN)N, \quad (16)$$

whence we see that equation 16 is a quadratic equation. Finding the equilibrium points—that is, the points at which the population neither increases or decreases—is done by setting the derivative equal to zero, thus obtaining

$$0 = b(F_T - cN)N,$$

which has two solutions. The first solution is at $N = 0$, which simply says that the rate of change of the population is zero when there are no individuals in the population. The second solution is at F_T/c , which is the maximum value that N can have. This is the value of N for which $F = 0$ (when all the resources in the system are contained within the bodies of the individuals in the population). Because the limitations of the environment are more or less stipulated by the value of F_T and the maximum number of individuals that

the environment can contain is F_T/c , the value F_T/c is frequently referred to as the carrying capacity of the environment (the capacity of the environment to carry individuals). The traditional symbol to use for carrying capacity is K , so we write $K = F_T/c$. We also note that as the population approaches zero (as N becomes very small but not exactly at zero), the rate of increase of the original exponential equation will be bF_T (because the general equation is bF , and when N is near zero F is almost the same as F_T). After some manipulation of equation 16 we can write

$$\frac{dN}{dt} = bF_T N \left(\frac{\frac{F_T}{c} - N}{\frac{F_T}{c}} \right).$$

Now, substituting r for bF_T and K for F_T/c , we obtain

$$\frac{dN}{dt} = rN \frac{K - N}{K}, \quad (17)$$

which is the classic form of the “logistic equation.” Note the form of the equation. It has a very simple biological interpretation. The quantity $(K - N)/K$ is the fraction of the carrying capacity that has not yet been taken up by the individuals in the population. In shorthand we might refer to this quantity—the fraction of the carrying capacity or the fraction of total available resources—as the available resource space. Then the logistic equation is obtained by multiplying the original intrinsic rate of increase, r , by the available resource.

Returning to the earlier example of *Paramecium bursaria*, a glance at the data suggests that the carrying capacity is around 290 individuals (averaging all the points after the data have leveled off). The original estimate of r as 0.337 was probably too low (because the effects of density dependence were probably effective even during the time of the initial growth), so taking a slightly larger value, let $r = 0.5$. The logistic equation for these data then becomes

$$\frac{dN}{dt} = 0.5N \frac{290 - N}{290},$$

which is plotted in figure 1.7, along with the original data. This example represents a reasonably good fit to the logistic equation.

The existence of density dependence also calls into question the extrapolations that one is tempted to make from a process that seems inexorably exponential. The example earlier in this chapter of the aphids in the cornfield is a case in point. Concluding that the farmer had only two days before disaster struck may have been correct, but it also could have been grossly in error, depending on the strength of the density dependence. Indeed, with strong density dependence, the field’s carrying capacity for the herbivore could have been below the threshold at which the farmer needed to take action, in which case no action at all would have been necessary.

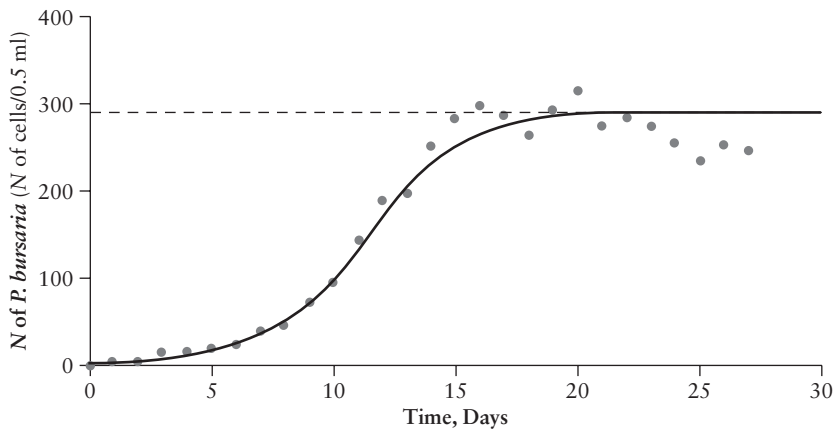


FIGURE 1.7. Fit of logistic equation to the *Paramecium bursaria* data from figure 1.6.

In some management applications, (e.g., fisheries) it is desirable to maximize the production of a population, which is to say, to maximize the rate of increase, not the actual population. The logistic equation can provide a useful guideline for such a goal because it is reasonably simple to calculate what population density will produce the maximum rate of population increase (see exercise 1.13). Thus, once the carrying capacity is known, the population density at which the rate of growth will be maximized is automatically known. In actual practice this so-called maximum sustained yield has some severe problems associated with it, largely stemming from the simplifying assumptions that go into its formulation (these issues are more fully discussed in chapter 4).

EXERCISE

- 1.13** Assuming that a population grows according to the logistic equation, what is the value of the population density that will give the maximum growth rate?

The Yield-Density Relationship

The process of intraspecific competition or, more generally, density dependence is certainly extremely common, if not ubiquitous, and thus legitimately calls for a theoretical framework, the most common and general of which is the logistic equation. However, for many applications it is not sufficient to consider only the population growth rate but rather is necessary to decompose that rate into its component parts, birth rate and death rate. In this section we consider the effect of density on birth rate. This theory was developed mainly from work on plants, especially in agroecosystems. Farmers need to know the relationship between planting density and the yield of a crop (which is frequently the seed output). This relationship is known as the

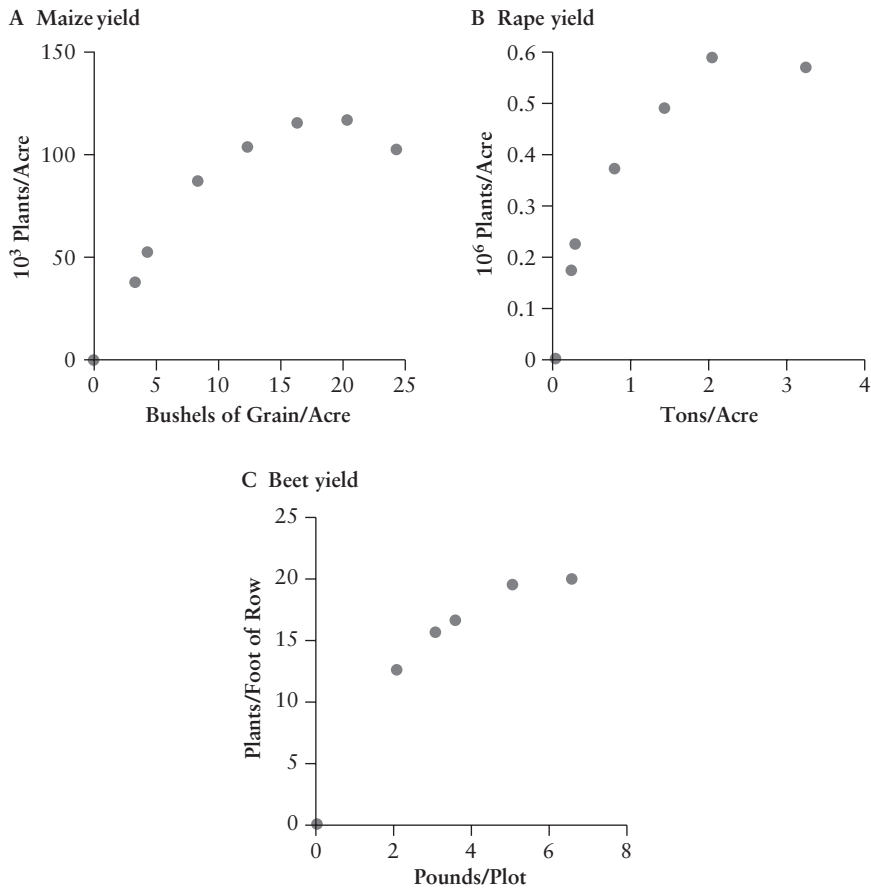


FIGURE 1.8. Exemplary yield versus density data for maize, rape, and beets (from Willey and Heath 1969).

yield–density relationship and is the basis of much agronomic planning as well as a springboard for much general plant ecology. For our purposes here, the yield–density relationship provides the most elementary form of the effect of intraspecific competition on reproduction and lays bare its essential elements. We thus give considerable space to the development of the principles of intraspecific competition as reflected in the yield–density relationship.

The formal elaboration of yield–density relationships probably first appeared in 1956 with the work of Shinozaki and Kira. These researchers noted, as had many before them, that plotting yield versus density for various plant species usually results in a characteristic form. Several examples are shown in figure 1.8.

Shinozaki and Kira suggested a simple hyperbolic form,

$$\frac{Nw_{\max}}{1 + aN},$$

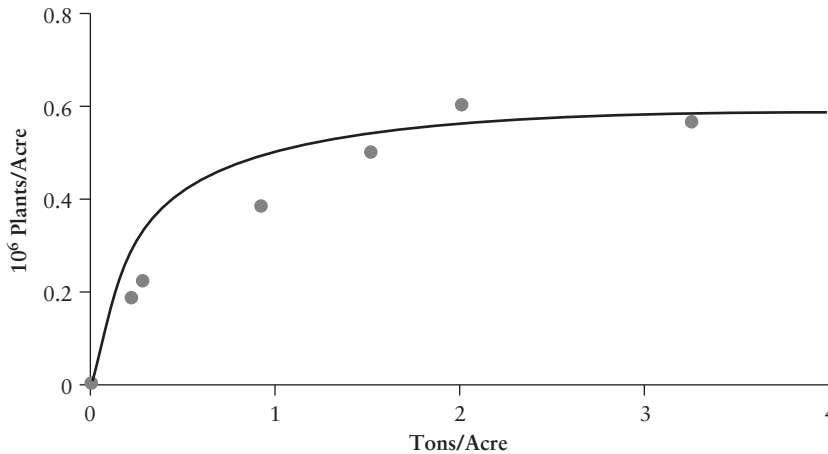


FIGURE 1.9. Equation of Shinozaki and Kira superimposed on the rape data from figure 1.8.

where N is population density, Y is yield, w_{\max} is the unencumbered (i.e., without competitive effects) yield of an individual plant, and a is an arbitrary constant. This equation asymptotes as N becomes very large and thus corresponds to another well-known empirical observation in plant ecology known as the law of constant final yield (which actually is not always true, as discussed below). In figure 1.9 Shinozaki and Kira's equation is shown in relation to the data for rape in figure 1.8.

This empirical curve fitting can be rationalized with some simple plant competition theory. We begin by considering what might happen with individual plants and later accumulate those plants into a population so as to examine the effect of density. Consider a single corn plant in a pot. When provided with all the necessary light, water, and nutrients, it will grow to some specified height with some specified biomass. If two corn plants are planted in a pot of the same size and provided with the same amount of light, water, and nutrients, each of the plants will attain a biomass smaller than that of the corn plant grown alone because the same amount of resources is being used by two individuals rather than one. If we symbolize the biomass a plant attains when growing alone as k , we can write the simple linear relationship

$$w_1 = k - \alpha w_2, \quad (18)$$

where w_1 refers to the biomass (weight) of the first plant, w_2 refers to the biomass of the second plant, and α is the proportionality constant that expresses the decrease in biomass of the first individual as a proportion of the biomass of the second individual. This makes the very reasonable assumption that larger plants have greater competitive effects so that competitive effects are directly proportional to their size. Rearranging equation 18, we see that

$$\alpha = (k - w_1)/w_2. \quad (19)$$

This same development could be applied to three plants growing in a single pot, in which case the equation describing the results would be

$$w_1 = k - \alpha_{12}w_2 - \alpha_{13}w_3, \quad (20)$$

where α_{12} is the effect of a unit of biomass of individual 2 on the biomass of individual 1 and α_{13} is the effect of a unit of biomass of individual 3 on the biomass of individual 1. The parameter α is frequently referred to as a competition coefficient because it represents the effect of one individual on another. The calculation of α from real data is quite easy when we have only two plants: grow a single plant in a pot, and measure its biomass after some specified time, giving the value of k ; then grow two plants in a pot, and measure their biomasses, giving the values of w_1 and w_2 ; then apply equation 18 to determine the value of α . The estimation of the competition coefficients when there are more than two individuals is somewhat more complicated but need not concern us at this point. For now it is important only to understand the logic of the thinking that went into the construction of equations 19 and 20. We now proceed to generalize equation 19.

Let us suppose that instead of planting just two or three individuals in a pot, we plant a large number of individuals. If the total number planted is n , we can expand equation 20 by simply adding more terms until we have added all n individuals to the calculation. That is, equation 20 for n individuals becomes

$$w_1 = k - \alpha_{12}w_2 - \alpha_{13}w_3 - \dots - \alpha_{1n}w_n$$

or, more compactly,

$$w_1 = k - \sum \alpha_{1j}w_j, \quad (21)$$

where the summation is taken from $j = 2$ to $j = n$. If all the individuals are exactly the same, it might be argued that all the α_{1j} values are equal. As a first approximation, this is probably a good assumption. However, there is a crucial way in which the competition coefficients differ from one another, as becomes evident below when we try to elaborate this same example from the level of a pot to the level of a field.

For now, assume (a bit unrealistically) that all individuals produce the same biomass and that the competition between any two pairs of individuals is identical from pair to pair (i.e., assume we can substitute the mean values for biomass and the competition coefficients). We can thus write

$$\bar{w} = k - N\bar{\alpha}\bar{w}, \quad (22)$$

where N is the population density, $\bar{\alpha}$ is the mean value of the competition coefficients, and \bar{w} is the mean biomass. Equation 22 can be rearranged as follows:

$$\bar{w}(1 + N\bar{\alpha}) = k,$$

and finally

$$\bar{w} = \frac{k}{(1 + N\bar{\alpha})}, \quad (23)$$

If \bar{w} is the biomass of an average individual in the population, the total population yield must be

$$Y = \bar{w}N.$$

Substituting from equation 23 for \bar{w} , we obtain

$$Y = \frac{Nk}{(1 + \alpha N)}, \quad (24)$$

which is identical to the empirical equation of Shinozaki and Kira. The advantage of equation 23 is that because of the derivation based on plant competition theory, the parameters in the equation have obvious meaning; k is the unencumbered yield of an average individual plant, and α is the mean competition coefficient between two individual plants.

An additional complication arises when we have data like the maize data in figure 1.8, where at high densities the yield actually falls. To accommodate data such as these Bleasdale and Nelder (1960) suggested modifying the basic Shinozaki and Kira equation with an exponent, citing either

$$Y = \frac{Nk}{(1 + \alpha N)^b} \quad (25)$$

or

$$Y = \frac{Nk}{(1 + \alpha N^b)} \quad (26)$$

as a reasonable approximation of data that are shaped parabolically. The constant b is, in the context of Bleasdale and Nelder's derivation, a fitted constant that they presume is related to an allometric effect (i.e., the harvested material is produced proportionally less at higher densities of the plant). Either equation reduces to Shinozaki and Kira's equation when $b = 1.0$. Bleasdale and Nelder chose the first of these two equations arbitrarily, and it has become something of a standard in plant ecology literature. It is worth noting that it is not only the allometric effect that can produce a yield–density curve that descends at high densities (see exercise 1.14).

The analyses in this section have been based on static descriptions of the consequences of different initial densities or reproductive yield within a single season. However, because reproductive yield in one year can be expressed as the number of offspring and therefore as the population size in the next time period (rather than biomass, as assumed so far), this formulation can be easily converted to a model of density-dependent population dynamics (Watkinson 1980), as shown in exercise 1.15 and discussed at the end of this chapter.

EXERCISES

- 1.14** The derivation of the Shinozaki and Kira equation presumed that competition remains constant among individuals. Yet basic plant ecology might suggest that as individual plants become closer to one another, their competitive effects will become more severe. Assume a declining relationship between competition and distance between individual plants, translate that assumption into a relationship between α and N , and substitute into the Shinozaki and Kira equation. What results?
- 1.15** In the Bleasdale and Nelder equation, the “yield” of the equation effectively represents the input into the next generation if, instead of total crop yield in terms of biomass, it is expressed as the number of offspring. Write an equation, using the basic Bleasdale and Nelder formulation, that relates the population density this year to that we expect next year, assuming 100% mortality (i.e., an annual species). If you plot the number this year on the x axis and the number next year on the y axis, what does the functional form look like for various values of the parameter b ?
-

Density Dependence and Mortality: Thinning Laws

In the above developments we assumed that density dependence acts in such a way that the growth of individuals is slowed by a larger population and that a decline in individual growth rate reflects a lower birth rate that eventually stabilizes the population at some particular number. In our explanation of the logistic equation, we made no explicit assumption about birth and/or mortality, and the derivation revolved around the intrinsic rate of natural increase, which includes both death and birth rates. However, implicitly in the section on the logistic equation and explicitly in the above section on the yield density–relationship, the assumption was that we were dealing exclusively or mainly with birth rate modifications rather than death rate modifications. There are times where the distinction can be crucially important. For example, the growth in total biomass of a plantation of trees is usually approximately logistic in form, but the same logistic equation could describe the pattern in either figure 1.10A or 1.10B. The difference between the two figures is not trivial from a forester’s point of view. In figure 1.10A there are large numbers of very small trees, none of which is harvestable, while in figure 1.10B there is a smaller number of larger trees. The point is that in figure 1.10A there has been a great deal of intraspecific competition, but it took the form of each individual growing more slowly and almost no mortality, while in figure 1.10B one of the main responses to intraspecific competition was for some individuals to die while others continued growing rapidly. The biomass of the forests in both figures is the same (that is the way the example was constructed), but one forest will be useful for harvest and the other not. Similar examples could be given for any organism with indeterminate growth. For example, many fish become stunted when in very dense populations and thus represent less of an attraction for sport fishers and can have significant consequences for commercial fisheries as well.

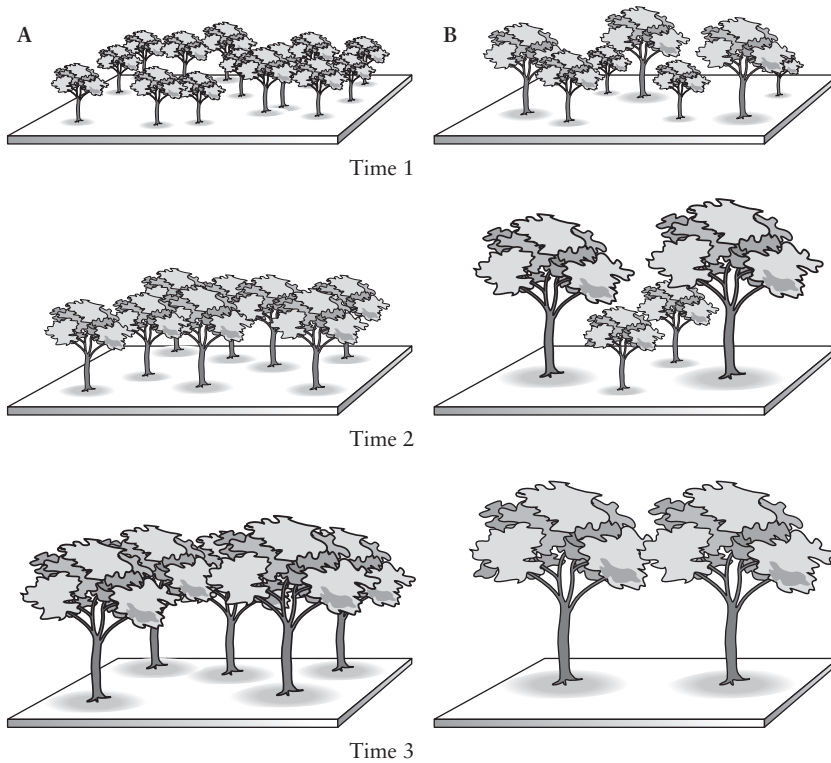


FIGURE 1.10. Diagrammatic representation of the process of thinning (see text).

Reflect for a moment on the pattern of growth and mortality in a densely planted tree plantation or in a natural forest when large numbers of seeds germinate more or less simultaneously. First, seedlings are established at a very high density. Walking through a beech-maple forest, for example, one is struck by the carpet of maple seedlings in almost every light gap one encounters. As the seedlings grow, the increase in biomass of each individual treelet is limited by intraspecific competition, as described above. But when populations are sufficiently dense, inevitably some individuals come to “dominate” (be larger) while others become “suppressed” (remain small due to competition from their neighbors). Eventually the suppressed individuals die, and we say that the population has been thinned. But then the trees keep on growing and the process repeats itself, with some suppressed and others dominating. In this way a population of plants that began at a very high density is thinned to the point that the adults are at some sort of carrying capacity. In some ways this process seems to be the reverse of what was described above in the development of the logistic equation. Here we begin with a number larger than K , and through the process of thinning the population is reduced to K , rather than beginning with a small population and increasing to the value of K . On the other hand, remember that biomass is increasing throughout the process.

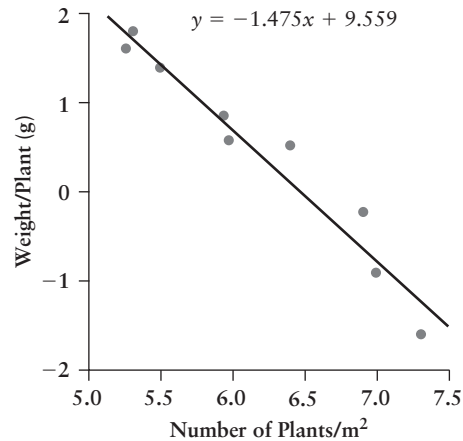


FIGURE 1.11. Typical relationship between log density of surviving plants and log dry weight. Example is of *Helianthus annuus* (Hiroi and Monsi 1966).

This phenomenon is most easily seen as a graph of the log of individual biomass versus the log of density at successive harvests of the same population over time, as shown with the data in figure 1.11 and more schematically in figure 1.12. Although plotting individual mass rather than total population yield, this seems similar to the analysis of density effects on birth rate in the previous section. But figure 1.11 is much more dynamic; we start with a single starting density and observe changes in biomass (or some related variable). If no mortality occurs, we expect a straight vertical line, that is, the per-plant biomass increases but the population density remains constant (see figure 1.12A). But if there is mortality, over time the curve will shift to the left, to lower densities, while at the same time the per-plant biomass will increase (see figure 1.12B). If, on the other hand we had begun with two different populations at slightly different densities we would see that both populations would increase in biomass. Further, assuming that densities were such that this initial increase in biomass happened without competition, both populations will grow in biomass by the same amount (see figure 1.12C). If we let both of these populations continue to grow, we can expect some thinning (mortality) to occur, especially in the more dense population (see figure 1.12D).

Here we can see both a plastic effect on growth and a mortality effect. The plastic effect is seen as a smaller biomass increase at larger densities, as shown in figure 1.12D. The mortality effect is seen as a decrease in density at higher densities, as shown in figure 1.12D. If we continue the pattern of development illustrated in figure 1.12 through time, we see that each population begins its process of thinning as it approaches a theoretical thinning line, as can be seen in the data shown in figure 1.13. Once mortality starts, the population tends to follow a straight line on a log-log scale. This kind of relationship has been shown many times—most often in herbaceous plants over time or in woody plants, comparing plantations at different densities.

This self-thinning law (*self-* because no forester or agronomist is there doing it) was first developed in plants, but many animals show a similar pattern. It is a very nice way of showing the growth and mortality effects of

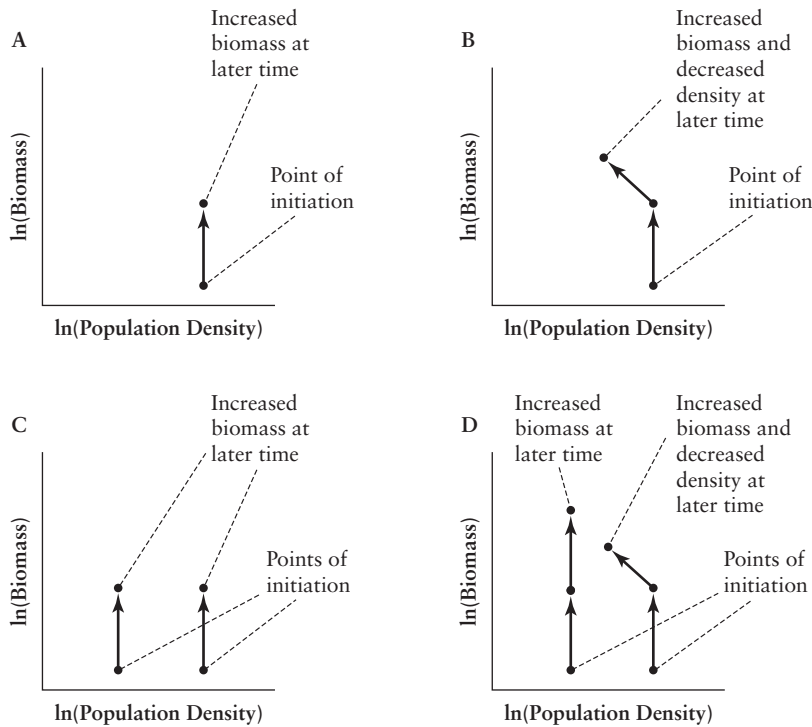


FIGURE 1.12. Expected pattern of growth and mortality as the thinning process and growth in biomass interact. $\ln(\text{biomass})$ refers to the natural logarithm of the biomass of an average individual in the population.

density in the same graph. But it also provides an elegant way of looking at density-dependent mortality that can be easily compared among species on very different time scales because time is not explicit. Furthermore, some time ago plant ecologists noticed that this process of self-thinning always seems to take on a particular pattern. When plotting the logarithm of the biomass of an average individual plant versus the population density at the time the biomass is measured, the points in a thinning population appeared linear; furthermore, the slope of the line always appeared to be nearly $-3/2$ (e.g., see figures 1.12 and 1.13), provided that the population was undergoing thinning. This phenomenon has come to be known as the three-halves thinning law.

Yoda and colleagues (1963) provided an elegant theory explaining the origin of the law. Suppose that each plant is a cube. If each side of the cube is x , the area of one of the cube's faces is x^2 and the volume of the cube is x^3 . Now imagine that the plantation is made up of a large number of these cubes and that they begin growing and thinning through intraspecific competition. The overall process is illustrated in figure 1.14. The area of the plantation is A . The population density is the total area divided by the surface area occupied by a single plant (that is, a single cube). Thus N , the population density, is equal to A/x^2 . Now presume that the biomass, w , of an individual plant is

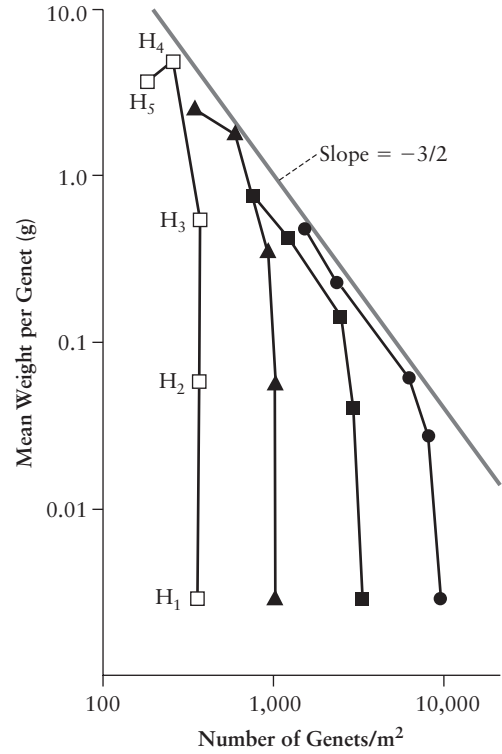


FIGURE 1.13. Relationship between the density of genets and the mean weight per genet in populations of *Lolium perenne*. H₁, H₂, and so on are successive harvests (Kays and Harper 1974).

approximately equal to the volume of the cube representing it, so that $w = x^3$. So we have the pair of equations

$$N = A/x^2$$

and

$$w = x^3.$$

Rearranging these equations, we write

$$x = A^{1/2}N^{-1/2}$$

and

$$x = w^{1/3}.$$

Because the left-hand side of both equations is equal to x , we can set the right-hand sides of both equal to each other, giving

$$A^{1/2}N^{-1/2} = w^{1/3},$$

which simplifies to

$$w = A^{3/2}N^{-3/2},$$

which can be put in the more standard form

$$\ln(w) = (3/2)\ln(A) - (3/2)\ln(N),$$

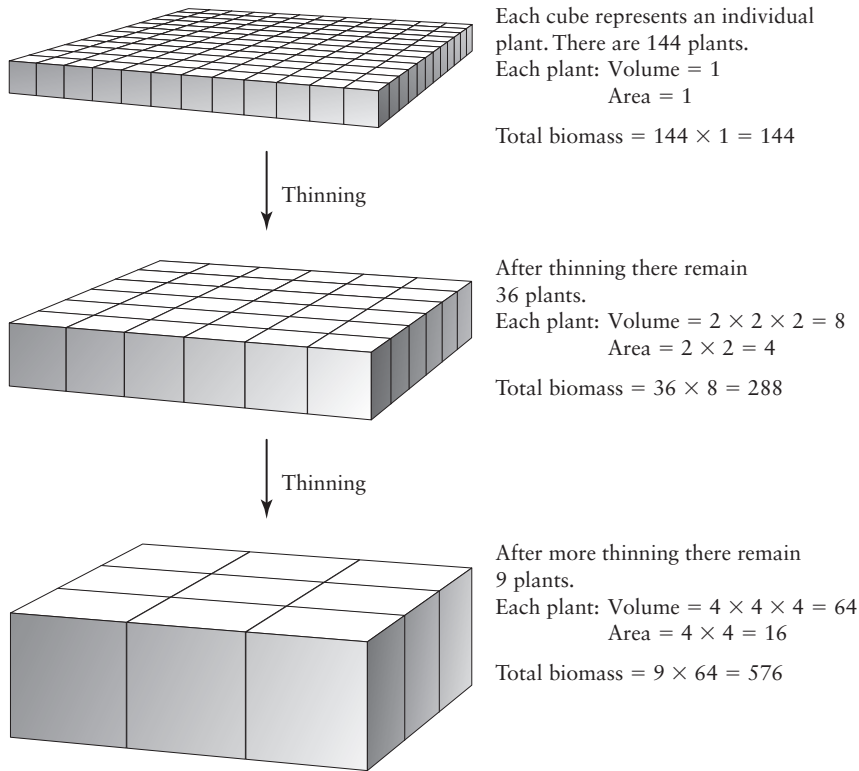


FIGURE 1.14. Yoda and colleagues' (1963) interpretation of the origin of the three-halves thinning law.

which represents a straight line with a slope of $-3/2$ on a graph of $\ln(w)$ versus $\ln(N)$.

Thus we see from simple geometric reasoning that it is not unusual to expect the three-halves thinning law. On the other hand, the basic empirical base of the “law” has been persistently questioned (e.g., Westoby 1984). In fact, when large numbers of data sets are examined, the slope has been shown to be closer to $-4/3$. And a prediction of $-3/2$ from geometric considerations is actually quite shaky—plants are not, after all, cubes.

Current thinking has largely moved away from purely geometric considerations. A quite different explanation and quantitative prediction of thinning relationships was provided by Enquist et al. (1998) based on fundamental metabolic scaling relationships for both plants and animals. The metabolic model is based on the observation that the resource use and metabolic rate of both plants and animals tend to increase with body size with a power of $-3/4$ (West et al. 1997). Assuming that plants grow until they are resource limited and that resources limit the total productivity (biomass \times density) of an area, this model predicts a thinning slope of $-4/3$, which is consistent with more recent and extensive data (Enquist et al. 1998).

Density Dependence in Discrete Time Models

Using much of the same qualitative reasoning as above, the process of density dependence can be formulated in discrete time rather than continuous time. Rather than asking how a population grows instantaneously, we can ask how many individuals will be in the population next year (or in other time unit) as a function of how many are here now. Recall equation 1.3, the exponential equation,

$$N_{t+1} = \lambda N_t,$$

which is a statement of population growth in discrete time. Now, rather than proceeding with a generalization about future numbers (which was the direction taken earlier), we remain in the realm of discrete time and ask what modifications might be necessary to make this equation density dependent. In other words, what do we come up with if we use the same rationale we used in developing the logistic equation but this time do it in discrete time?

It seems reasonable to suppose that the population will grow slowly if it is near its carrying capacity (K) and will grow more rapidly if it is far below its carrying capacity. This is the same as saying that λ varies with population density. If we simply allow λ to vary linearly with density (i.e., let $\lambda = r - bN_t$, precisely the same *conceptual* approach we took with the logistic equation), we write

$$\lambda = r - bN_t = \lambda \frac{K - N_t}{K},$$

where λ on the right-hand side takes on a different meaning (the maximum growth rate). This makes the original equation

$$N_{t+1} = \lambda N_t \frac{K - N_t}{K}.$$

We frequently define the variable N as a fraction of the carrying capacity, which is easily done by setting the carrying capacity equal to 1.0, a transformation that does not change the qualitative behavior of the equation and makes it easier to work with. Thus we have

$$N_{t+1} = \lambda N_t (1 - N_t). \quad (27)$$

This equation is usually referred to as the logistic map (*map* because it maps N_1 into N_2) or the logistic difference equation. It has some remarkable features that will be explored in more detail in chapter 4.

We add a short technical note here. The logistic map is *not* what you get when you integrate the logistic differential equation and then solve for N_{t+1} in terms of N_t , although the perceptive reader might be excused for thinking so because both equations are called logistic. The logistic map is derived directly from first principles (as above). Integrating the logistic differential equation gives a completely different time interval map.

It is worth noting that either of Bleasdale and Nelder's equations (equations 25 and 26) can be viewed as a form of a discrete map, much like the

logistic map, although with slightly different properties (recall exercise 1.15) (Watkinson 1980). If we think of yield as the number of organisms that will be found in the population in the next generation, this equation becomes equivalent to an iterative map (like the logistic map). In fact, the Bleasdale and Nelder formulation has been repeatedly invented in different contexts. For example, in fisheries biology both the Ricker (1954) map and the famous Beverton and Holt (1957) model have properties that are similar to the Bleasdale and Nelder formulation, as does the model proposed by Hassell (1975) in the context of a predator–prey model. Indeed, when $b = 1$, the Beverton and Holt model is identical to either of the forms of Bleasdale and Nelder, namely,

$$N_{t+1} = \frac{\lambda N_t}{(1 + \alpha N_t)}, \quad (28)$$

and the Hassell model is the same as the first form of the Bleasdale and Nelder model, namely,

$$N_{t+1} = \frac{\lambda N_t}{(1 + \alpha N_t)^b}. \quad (29)$$

The Ricker model has a similar overall form, although its formulation is exponential, namely,

$$N_{t+1} = N_t e^{r(1 - bN_t)}. \quad (30)$$

All have the property that when N_{t+1} is plotted against N_t a nonlinear form emerges with a quadratic-like hump, a fact that translates into some interesting and important dynamic generalizations that we discuss further in chapter 4.

EXERCISES

- 1.16** Using the exponential map and starting with 0.01 individuals, project the population 50 times with values of $\lambda = 1.0, 1.5, 2.0, 3.0$, and 3.5 . How does the time series change as a function of λ ?
 - 1.17** In exercise 1.4 successive values of population density were plotted against one another (i.e., N_{t+1} was plotted against N_t) for the exponential equation. Repeat that exercise for $\lambda = 1.5, 2.0, 3.0$, and 3.5 , and then modify the equation to be the logistic map (equation 27) and make the graphs again, for $\lambda = 1.5, 2.0, 3.0$, and 3.5 .
 - 1.18** Plot N_{t+1} against N_t for the Beverton and Holt model, the Hassell model, and the Ricker model (equations 28–30), and compare them. Let $\lambda = 1$, $\alpha = 1$, and $b = 2$. Once you get the three models on a spreadsheet, experiment with different values of b , λ , and α .
-