1

Density-independent growth

1 Introduction

What is a population?

The basic definition of ecology, the scientific study of the relationships between organisms and their environment, is rather vague and the word environment requires an explicit definition. An alternative definition of ecology, the scientific study of the distribution and abundance of organisms (Krebs 1994, Andrewartha 1961), is more germane to population ecology. In population ecology we want to know what factors most likely control the growth rates, abundances, and distributions of biological populations.

As used here, a population (synonymous with biological population) consists of a group of interbreeding organisms found in the same space or area (i.e. they are sympatric) at the same time. It is presumed that these individuals form a functional unit in that they interact with one another and there is interbreeding among the individuals of the population. A closed population is one in which we expect no immigration or emigration of individuals from outside of the population. In reality, unless we are considering a population on a remote island, a mountaintop, or an isolated cave, populations are not closed to immigration or emigration. And unless we have successfully marked all individuals in a population, we are usually unaware of which individuals might be recent immigrants. Turchin (2003) integrates these ideas in his definition of a population: "a group of individuals of the same species that live together in an area of sufficient size to permit normal dispersal and migration.behavior, and in which population changes are largely determined by birth and death processes."

A local population differs from a species or a **species population**, in that we are dealing with a group of individuals interacting in a particular time and space. White-tailed deer (*Odocoileus virginianus*) from northern Wisconsin and the Piedmont of Virginia, according to the biological species concept, are the same species as long as they produce viable offspring when they are interbred. But they would belong to different and distinct ecological populations. Actually, a population is often defined by the investigator(s) and may be somewhat arbitrary.

Fundamental principles and the use of mathematical models

What are the fundamental principles that dictate how populations grow? Population ecology is by necessity a quantitative discipline, and in order to answer questions about populations, mathematically oriented ecologists have derived a variety of predictive models. The first section of this book will examine growth models for populations of single species.

The diversity of life has led to a fantastic array of life histories. Just as the mass of a single bacterium is several orders of magnitude smaller than the mass of an elephant, population characteristics, such as generation time, also differ by several orders of magnitude.

Accordingly, no one model of population growth suits all organisms or all environments. This fact is both frustrating and stimulating. A search for a single set of models that applies to all life forms is pointless. On the other hand, the construction of quantitative models forces us to examine our assumptions about particular populations in an organized and explicit manner. Models, whether quantitative or qualitative, often produce unexpected results that may run counter to our intuitive sense of how things work. The work of Copernicus, Galileo, and others that culminated in the formal quantitative models of Newton showed that the solar system and the universe function in ways that were not at all intuitively obvious. A dissection of the life histories of both the emperor goose (*Chen canagica*) (Morris and Doak 2002) and the Amboseli baboon (*Papio cynocephalus*) (Alberts and Altmann 2003) populations, using a matrix population model, have shown us that adult survivorship has a greater impact on growth rates than either juvenile survivorship or fertility: a conclusion impossible to reach without the proper population model. As Atkins (1999) commented, "Quantitative reasoning (gives) spine to otherwise flabby concepts, enabling them to stand up to experimental verification." Models stimulate observations and experiments that allow us to learn more about our natural world.

A general rule of systems is that as one progresses from lower to higher levels of organization, properties are added that were not present at the lower levels. Thus an individual organism is not just a collection of physiological systems. Similarly, a population has properties not evident from the study of individuals. Populations have growth rates, age distributions, and spatial patterns. They also have allelic frequencies and other genetic properties. The first list of properties is within the province of **population ecology**; the latter is part of the discipline of **population genetics**. The two areas combined are known as **population biology**. Although this book deals only with population ecology, much of what I have written is based on the theory of evolution, which relies on principles of population genetics.

The models used here will be largely based on relatively straightforward algebra. However, matrix algebra and differential calculus will be introduced. For more sophisticated

mathematical treatments the reader should consult Roughgarden (1998), Case (2000), Vandermeer and Goldberg (2003), or Turchin (2003). I will emphasize the assumptions of the models and discuss them in qualitative terms. Proofs or derivations, where needed, have been minimized, but sample problems and graphs are used to illustrate the workings of the models.

A perfect model would be general, realistic, precise, and simple (Levins 1968). As discussed above, the diversity of life has ruled out the perfect model. In order to attempt generality and simplicity, precision and reality are often sacrificed. If students are able to understand how population models are built, they will then be able to evaluate their reality. It should become evident that most models, while lacking precision, do illuminate basic population trends.

The general laws of population ecology

Sutherland (1996) wrote that "population ecology suffers from having no overall a priori theory from which explanations and predictions can be devised." He continued that "behavioral ecology has such a theory – evolution by means of natural selection – which yields the prediction that individuals will maximize fitness." I take this to mean that the discipline loosely known as evolutionary ecology has an a priori theory. Population ecology, however, should be treated as an extension of evolutionary ecology. Therefore, we should ask ourselves under what circumstances might a characteristic such as the low fecundity of the wandering albatross (*Diomedea exulans*), or a phenomenon such as the population cycles known for snowshoe hares (*Lepus americanus*), have evolved.

By contrast to Sutherland, Turchin (2001, 2003) asserts that population ecology is a vigorous and predictive science and does have a set of foundational principles that are almost equivalent to the laws of Newton. He has listed these three fundamental concepts: (i) populations tend to grow exponentially, (ii) populations show self-limitation (or bounded fluctuations), and (iii) consumer–resource interactions tend to be oscillatory. In the first case, without density-dependent feedback from the environment, all populations show a nonlinear, exponential growth pattern. Turchin (2001) calls this "the exponential law," and sees a direct analogue to the law of inertia proposed by Newton. The exponential law provides a starting point for more complex mathematical descriptions of population dynamics. The second theorem or principle, self-limitation, is based on the idea that per capita population growth decreases with resource depletion. The usual form of this idea, the logistic equation, fails as a law because of its simplistic assumptions (see Chapter 2). Nevertheless, it remains useful as a starting point. Finally, the tendency of consumer–resource interactions (such as predator–prey) to produce oscillations is explored at length in later chapters.

1.2 Fundamentals of population growth

If we were trying to understand the growth rate and thus the potential rate of spread of an invasive species, or if we wanted to calculate the potential for long-term survival of the Florida panther (*Felis concolor coryi*) (Seal and Lacy 1989), what sort of information do we need? How do we gather it? What do we do with the data? What models are appropriate? Here we begin to address these questions.

As a first approximation, population growth is determined by a combination of four processes: **reproduction** (sexual or asexual), **mortality, immigration, and emigration.** The addition of new individuals through reproduction, termed **fertility** or **fecundity,** may be via sexual reproduction (i.e. live births, hatching of eggs, seed production) or through asexual reproduction (i.e. binary fission, budding, asexual spores, clonal spreading of higher plants). The distinction between fecundity and fertility is traditionally as follows.

1 **Fecundity** is the potential reproductive output under ideal circumstances. This limit is set by the genotype. That is, reproduction is limited by genetic potential, not by the environment.
2 **Fertility,** by contrast, is the actual reproductive performance under prevailing environmental conditions. The fertility rate, by definition, is less than the fecundity rate.

The distinction between these two terms is often not rigidly adhered to, but it is useful to keep it in mind.

Both fecundity and fertility are expressed as rates. That is, the mean number of offspring produced per individual (or per thousand individuals in human demography) in the population, per unit time. Often these values are also expressed for a given unit of area. For example, according to the Population Reference Bureau (Washington, DC), the fertility rate of the human population of the world declined from 28 per thousand in 1981, to 22 births per thousand in 2001. Meanwhile, the birth rate in North America moved slightly downward from 16 per thousand in 1981 to 14 per thousand in 2001 (Anonymous 1981–2004). In populations such as humans, however, which breed over a period of 30 years without respect to seasons, we need to know the fertility rate for each age category in order to accurately predict population growth. All references to human birth and death rates in this chapter are per year.

The second fundamental factor that affects population growth is **mortality.** Mortality must also be expressed as a rate. That is, the mean number of deaths per individual (or per thousand), per unit time, per unit area. As above, unless the population has a **stable age distribution** (meaning that **the proportion of the population in each age class remains constant over time**), in order to predict future population changes we would need to know the death rate for each age category. Again, using data from the Population Reference Bureau, the human death rate for the world in 2001 was 9 per thousand, a decrease from 11 per thousand in 1981. In North America, the comparable figures are 9 per thousand in 1981 and 9 per thousand in 2001 (Anonymous 1981–2004).

In populations with age distributions (age structures), growth is also affected by the actual number of individuals in the different age categories. We will explore the effects of age distributions in detail in Chapter 4. At present it is sufficient to note that basic data on the overall birth and death rates may not produce an accurate picture of population growth in the short term. For example, examine the population figures for Europe and Asia in 2001 (Table 1.1), again data from the Population Reference Bureau. Not only are the birth and death rates different, but also their age distributions are different. In Asia, 30 percent of the population is under 15 years of age, while in Europe the comparable figure is a mere 18 percent.

A measure of population growth is **the intrinsic rate of increase,** r. We will discuss r in more detail later. For now, we define r as the growth rate per individual (or **per capita**)

Table 1.1 Statistics for [...] from the Population Ref[...] rates are per thousand; [...]

Region	Population size (millions)	
Asia	3720	
Europe	727	

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Table 1.1 Statistics for human populations of Asia and Europe in 2001. All data are from the Population Reference Bureau (Anonymous 1981-2004). Birth and death rates are per thousand; r is per individual.

Region	Population size (millions)	Birth rate (per thousand)	Death rate (per thousand)	Rate of increase per individual (r)	Percent of population less than 15 years of age
Asia	3720	22	8	0.014	30%
Europe	727	10	11	−0.001	18%

per time unit (for example, per year) in a population, estimated as $b - d$, where b is the birth rate per individual per year, and d is the death rate per individual per year. The rate of growth per individual is:

$$r = b - d \qquad (1.1a)$$

If the birth and death rates are expressed per thousand, as in human demography, the growth rate is:

$$r = \frac{b - d}{1000} \qquad (1.1b)$$

From Table 1.1 we see that Asia had a positive growth rate, whereas Europe actually had a negative projected growth rate in 2001. If the intrinsic rate of increase of these two populations suddenly converged on the same value (a decrease in the Asian birth rate and an increase in Europe's fertility rate, combined with similar changes in the death rates), the population growth of Asia would still be greater than that of Europe for several decades, due to the higher abundance of reproductive individuals. Asia has a shorter generation time, which would affect population growth for a number of years. The estimated growth rate parameter, r (Eqn. 1.1), ignores the age distribution and generation time and actually assumes a stable age distribution (defined above). By **age distribution** we simply mean the **proportion** of the population in each age category, not the actual number per category.

Two other factors affect population growth: **immigration** and **emigration**.

1 The **immigration** rate is the number of individuals that join a population per time interval due to immigration. Ideally we should know the ages of individuals as they join the population.
2 The **emigration** rate is the number of individuals that leave the population per time interval. Again, it would be useful to know the age of the individuals that have left the population.

Unfortunately, gathering accurate information on immigration and emigration is extremely difficult in biological populations, and these factors are often ignored. When a population is termed **closed**, it is thought of as having negligible immigration and

emigration. In the last two decades, however, there has been a shift in emphasis from the study of single populations to "metapopulation" ecology. Since the concept of a metapopulation was developed by Levins (1969, 1970), major advances in both theory and field studies have taken place, particularly within the past 15 years (Hanski 1999). Levins originally defined a metapopulation as a "population of populations." In his view, local populations exist in a fragmented landscape of suitable and unsuitable habitats or "patches." Each local population is prone to extinction, but extinction may be balanced by immigration from other populations in the metapopulation landscape. The long-term survival of the metapopulation depends on the balance and interplay between extinction and immigration. Immigration and extinction are also key elements of the MacArthur and Wilson (1967) theory of island biogeography. However, MacArthur and Wilson were primarily concerned with the number of species in the community, while the metapopulation concept focuses on populations of single species. Another difference is that MacArthur and Wilson were concerned with the relationship between islands, where extinction could occur because of small population size or stochastic events, and a source of species (the mainland) in which extinction would not normally occur. By contrast, in a metapopulation, extinction may occur in any patch and colonization can occur from any one patch to another. The applications of metapopulation studies to conservation biology are obvious, and have resulted in an explosion of publications. We will explore metapopulation dynamics in Chapter 5. Suffice it to say that, after decades of being ignored, immigration, emigration, and local extinction are now the subject of many theoretical and field studies (Hanski 1999).

As already noted, a population is rooted in a time and a place. This means that population sizes or population growth rates are scaled for a particular time unit and for a specific spatial unit. When life histories of different organisms are compared (Chapter 6) it becomes obvious that generation times vary across several orders of magnitude. The space needed to sustain one population of elephants may support a metapopulation of butterflies or several separate populations of lichens. Therefore, we are forced to ask, what is the appropriate scale of an ecological investigation (Peterson and Parker 1998)? That is, over what time spans and/or over what spatial scales should ecological investigations be conducted? As we explore simple models of population growth we should be aware of their limitations, and the extent to which they are applicable to long periods of time and/or to large landscapes.

In summary, a population is affected by its rates of fertility, mortality, immigration, and emigration, by its recent history (through its age structure), and by its generation time, which is determined by its life history. Growth rate is also determined by the environment, and by how sensitive the population is to changes in the environment. By environment, we mean not only the physical environment, but also interactions of the population with other species in its habitat.

1.3 Types of models

In developing a model of a population we usually begin with the present population; that is, the population at time = 0, and project it t time units into the future. The populations at these times are expressed as N_0 and N_t, respectively. There are two types of population equations. Each has advantages and disadvantages.

In **difference equations**, populations are modeled using specific, finite, time units. The time units are usually realistic, in that populations are measured in the field once (or perhaps several times) per year, but not continuously. Difference equations are most often used to model populations that have "discrete," rather than continuous, growth (see below). A basic equation summarizing the ideas presented in the previous section might look like this:

$$N_{t+1} = N_t + (B - D) + (I - E) \tag{1.2a}$$

where
N_t = the population size at time, t
N_{t+1} = the population size one time unit later
B = the number of births and D = the number of deaths in the population during the time interval between t and $t + 1$
I = the number of immigrants and E = the number of emigrants during this same time interval

This equation can be rewritten as:

$$N_{t+1} = N_t + (B + I) - (D + E) \tag{1.2b}$$

In most population studies it is assumed that immigration and emigration rates are insignificant compared with birth and death rates (Turchin 2003, but see Hanski 1999). Equation 1.2b can be simplified, and the numbers of births and deaths are converted to per capita (per individual) rates, b and d, respectively. The difference between b and d becomes the single growth parameter, R, known as the **net growth rate per generation** or **net reproductive rate**. Alternatively, the difference between b and d also equals λ (lambda), the growth rate per time period, usually per year. λ can be calculated for all types of population models and is known as the **finite rate of increase**. The usual form for the difference equation (using R) is shown as:

$$N_{t+1} = N_t(b - d) = N_t R \tag{1.2c}$$

In **differential equations**, it is assumed that population growth is "continuous" and populations are being continuously monitored. Models based on differential equations have a long history in the biological literature, including the earliest models of competitive, predator–prey, and host–parasite relationships (Lotka 1925). A simple differential equation for population growth is:

$$\frac{dN}{dt} = rN \tag{1.3}$$

Here dN/dt measures the instantaneous growth of the population, N. On the left side of the equation, the symbol d is used to indicate change in N per change in the time interval, t. The intrinsic rate of increase, r (Eqn. 1.1a), measures the per capita birth rate minus the per capita death rate during these same small time intervals. In a sense, r measures the probability of a birth minus the probability of a death occurring in the population during a particular time interval.

1.4 Density-independent versus density-dependent growth

If a population invades a new environment with "unlimited" resources, no competitors, and no predators, fertility rates will be high (approximating fecundity rates) and death rates will be relatively low. Under these conditions, the population grows either "geometrically" or "exponentially" depending upon its life history. This is known as **density-independent growth**. This simply means that the growth-rate parameter of the population is not affected by its present population size. In both geometric and exponential models, the growth rate is determined by a fixed parameter (R, λ, or r) that is not modified by competition for resources. Population growth is often curtailed by the environment even if the population is undergoing density-independent growth. Major disturbances or catastrophes such as fire, wind storms, landslides, and floods significantly reduce certain populations and may even cause local extinctions. By contrast, in Chapter 2 we will examine models of **density-dependent growth**. In these models, it is assumed that the population encounters a limiting resource (food, water, nest sites, available nitrogen, space, etc.), which limits its growth. In these models the growth parameter is modified and the net growth rate eventually approaches zero at a carrying capacity. The realized growth rate is said to depend on the density of the population, hence the term **density-dependent growth**.

1.5 Discrete or "geometric" growth in populations with non-overlapping generations

The use of an appropriate model depends first on the life history of the organism. So you first need basic information on the life cycle of the species. In this first model of density-independent growth, the population has a life history with discrete, non-overlapping generations. That is, there are no adult survivors from one generation to the next. Examples include annual plants, annual insects, salmon, periodical cicadas, century plants, and certain species of bamboo. In most of these cases the organism passes through a dormant period as a spore, a seed, or an egg, and/or a juvenile stage such as a larva or pupa. Once the adults reproduce, they perish, and the future of the population is based on the dormant or juvenile stage of the organism. As noted above, when modeling such populations we usually collapse fertility and mortality into one constant, R, the **net replacement rate** or **net growth rate per generation** – or λ, the **finite rate of increase**, when measuring growth per specific time period. When we are discussing annual plants or insects, λ, the growth rate per year, and R, the growth rate per generation, are identical, since generation time equals one year. However, in some populations, such as the periodical cicada (*Magicicada septendecim*), generation time equals 13 or 17 years, and in these cases it is useful to make a distinction between the growth rate per generation and a finite rate of increase. That is, $R \neq \lambda$, when T, the generation time, $\neq 1$ year.

To find R we often count one life stage of the population in successive years. For gypsy moths (*Lymantria dispar*) we estimate R by counting egg masses in successive years (see Example 1.1). R is estimated from the ratio of egg masses at time $t + 1$ versus time t. For the periodical cicada (Example 1.2), however, we would have to wait 17 years between generations before we could estimate R. The overall model is based on finding successive estimates of the growth rate based on:

Example 1.1

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Answers

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Example 1.1

Gypsy moths (*Lymantria dispar*) are annual insects in which breeding takes place in early to mid summer. After the females lay their eggs, all adults die. The eggs hatch the following spring into larvae that feed on the leaves of tree species, especially species of oaks (*Quercus*). After a number of larval stages and a pupal stage, the adults emerge. After mating, females lay their eggs and die. Since generation time equals one year, Equations 1.4 or 1.5 may be used. In order to determine population growth in this species, we need to determine R. Assume that a local gypsy moth technician makes annual egg-mass counts in a local forest. She finds that in 2003 there are, on average, 4 gypsy moth egg masses per hectare and each mass contains an average of 40 eggs, for a total of 160 eggs per hectare. When she returns to the same forest in 2004, she finds 5 egg masses with an average of 40 eggs, or a total of 200 eggs per hectare. The local spraying program regulations state that spraying with Bt® (*Bacillus thuringiensis*) begins whenever egg masses reach 1000 per hectare. Assuming egg-mass density continues to increase at a constant rate, what is the predicted population for the year 2006? In what year would spraying be required?

Answers

In order to determine the net growth rate R, we find the ratio of $N_{t+1}/N_t =$ $200/160 = 1.25$. In the year 2006, three years have passed since the original survey in 2003. Using Equation 1.4:

$$N_{2006} = N_{2003}R^3 = (160)(1.25)^3 = 312.5$$

We therefore expect around 312 eggs per hectare in 2006.

We can now ask the question, if R continues at 1.25, in what year must spraying commence? Since we wish to solve for t, and time is an exponent in Equation 1.3, it is more convenient to use Equation 1.6:

$$\ln N_t = \ln(1000) = \ln(160) + \ln(1.25)(t)$$

$$6.91 = 5.08 + 0.223t$$

$$1.83/0.223 = t$$

$$t = 8.2 \text{ years}$$

Since the population only reproduces once a year, we cannot use a fraction of a year in the answer. Eight years after 2003, that is, in the year 2011, the number of egg masses is expected to be 954. By regulation, this does not trigger the spraying regime. One year later, however, the egg mass density would be 1192, and spraying would begin in 2012.

Example 1.2

The periodical cicada (*Magicicada septendecim*) has a most unusual life history (Borror *et al.* 1989). The juvenile stages spend 17 years underground feeding on plant roots. The population in a given area emerges synchronously from the ground as adults. After a great deal of racket, the males and females mate, and females lay their eggs in slits they have made in small branches of trees and shrubs in the forest. The adults then die, leaving the eggs as the next generation. The eggs hatch within a month. The nymphs drop to the forest floor and burrow underground, where they spend the next 17 years feeding and growing. The periodical cicada is obviously affected by disturbances within the forest habitat. Assume that in 1987 a survey found 500 adult female cicadas per hectare. The forest was selectively logged in the 1990s and a survey in 2004 found that the cicada population had dropped to 200 per hectare. More logging is planned during the next 20 years in this forest. Assume the population continues to decline at the same rate. If we define the minimum viable population for cicadas as 10 females per hectare, in what year is the population no longer viable? By minimum viable population we mean that the probability of extinction has become unacceptably high (Shaffer 1981, Miller and Lacy 2003). Random environmental perturbations or inability of males and females to find each other would likely cause this population to become extinct. See the section on population viability analysis in section 1.10 below.

Answer

First we must realize that only Equations 1.4 and 1.6, using net growth rate per generation, are applicable. But we also need to remember that generation time is 17 years. To find R, take the ratio of $200/500 = 0.40$. Since $R < 1$ we note that this population is decreasing. In order to find when the population is not viable, we solve Equation 1.6:

$$\ln 10 = \ln 500 + (\ln 0.40)t$$

$$2.3 = 6.2 + (-0.9)t$$

$$-3.9 = -0.9t$$

$$t = 4.3 \text{ generations}$$

Again, we cannot use fractions. After four generations, the population is projected to drop to between 12 and 13. After five generations, it declines to around 5 per hectare and is, by definition, no longer viable. Five generations, times 17 years per generation, equals 85 years. The population is not viable 85 years after the first survey in 1987. That is, in the year 2072. Evidently, however, action to conserve this forest cannot wait until 2072.

$$R_1 = N_1/N_0$$

$$R_2 = N_2/N_1$$

$$R_3 = N_3/N_2 \text{ etc.}$$

If we find that R remains more or less constant over time (that is, if these ratios of N_{t+1}/N_t remain constant), then we have:

$$N_1 = N_0R$$

$$N_2 = N_1R = (N_0R)R = N_0R^2$$

$$N_3 = N_2R = (N_0R^2)R = N_0R^3$$

and so on, leading to Equation 1.4:

$$N_t = N_0R^t \tag{1.4}$$

or

$$N_t = N_0\lambda^t \tag{1.5}$$

Note that the population grows whenever | R or $\lambda > 1$
the population is stationary (there is no growth) whenever | R or $\lambda = 1$
the population decreases whenever | R or $\lambda < 1$

The population grows according to the law of discrete or **geometric growth** (Fig. 1.1), when $R > 1$. Equations 1.4 and 1.5 can be rewritten using logarithms to make the growth curves linear. In Equations 1.6 and 1.7 we can use log to the base 10, or we can use natural logs (designated by ln) to the base e. Since other models use natural logs, we have used them in the equations below (and in the examples above).

$$\ln N_t = \ln N_0 + (\ln R)t \tag{1.6}$$

or

$$\ln N_t = \ln N_0 + (\ln \lambda)t \tag{1.7}$$

In each case $\ln N_0$ is the y-intercept and $\ln R$ or $\ln \lambda$ is the slope of a linear relationship between $\ln N$ and t (time), with time as the independent variable (x-axis). In Fig. 1.2, the value of $R = 1.2$ and the slope is therefore $\ln(1.2)$ or 0.18.

1.6 Exponential growth in populations with overlapping generations

In the previous section we dealt with a special kind of life history, one in which generations were distinct and non-overlapping. If the adults and juveniles are present
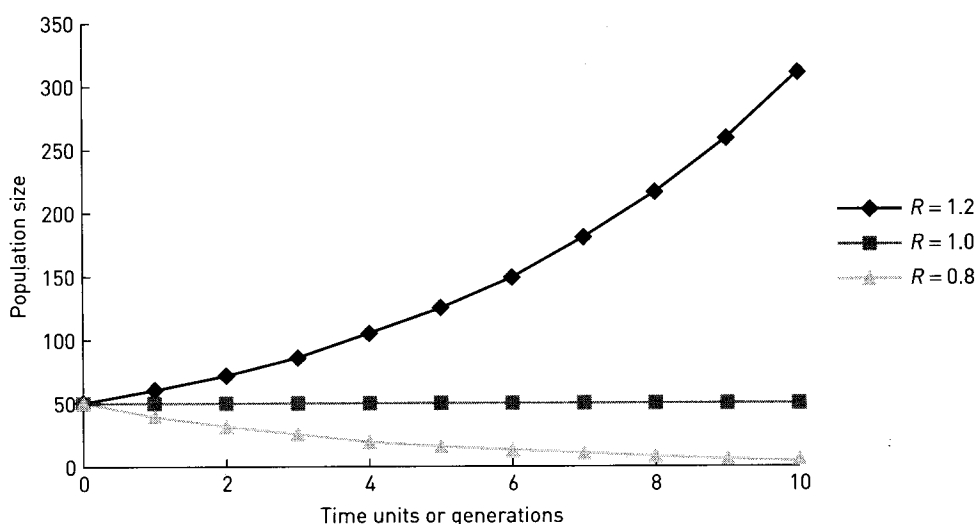
Figure 1.1 Discrete or "geometric" growth in a population with non-overlapping generations.
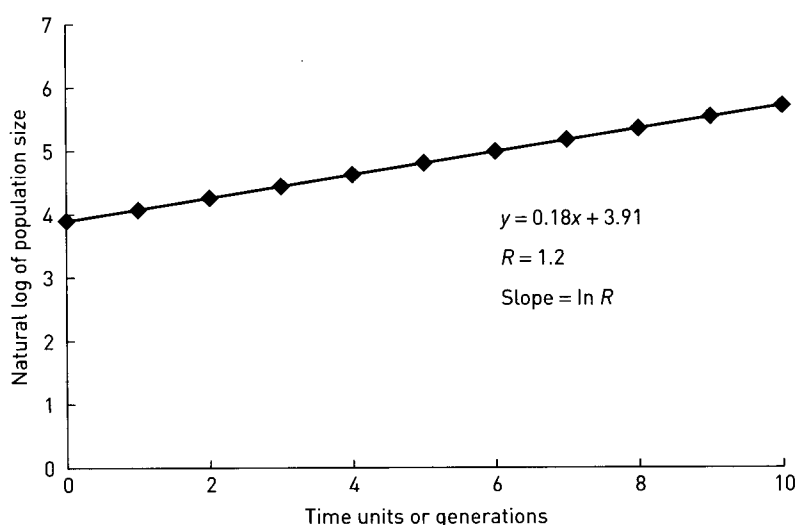

Figure 1.2 Natural log of growth in a population with discrete generations.

simultaneously and they interact with one another, our previous model is inappropriate. Instead we must use a model originally developed for a population capable of continuous growth, such as a *Paramecium* or a human population. That is, a population in which there is no distinct breeding season. Notwithstanding poetry about springtime and theories about phases of the moon, human babies are born throughout the year. In spite of the fact that this growth model is not strictly applicable for seasonal breeders such as deer, it is general enough that it is used whenever a population has a stable age distribution. (Recall that an age distribution refers to the proportions of the population belonging to different age classes, and that a stable age distribution is one in which these proportions remain

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$dN/dt = rN$, where r i

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The equation is ea

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which becomes: $\ln N$

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When r is positive, t

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We can make the

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Doubling time

A convenient statistic

graphy is the study

constant from year to year.) In order to have a stable age distribution, fertility and mortality rates must remain constant for an extended period of time. We can approximate human population growth rates using the model, but we should recall that because birth rates around the world increased following World War II and then decreased after 1960, few human populations are in a stable age distribution.

The basic form of this model is the differential equation shown earlier as Equation 1.3: $dN/dt = rN$, where r is the **intrinsic rate of increase** or the **instantaneous growth rate**.

r is calculated by finding the difference between the instantaneous per capita birth rate and the instantaneous per capita death rate. The parameter r can be compared to the interest rate in a bank account which is continuously compounded. Such a rate is the continuous growth rate per dollar in an interest-bearing account, while r is the continuous growth rate per individual in a population.

The equation is easily solved by taking the integral from 0 to t of both sides of the equation, as follows:

$$\int_{N(0)}^{N(t)} \frac{dN(t)}{N} = r \int_{0}^{t} dt$$

which becomes: $\ln N(t) - \ln N(0) = rt - r0 = rt$
After exponentiation of both sides of the equation, we have: $N(t)/N(0) = e^{rt}$

Rearranging, we get Equation 1.8. This solved form is the one usually used in making population projections to some arbitrary time t in the future.

$$N_t = N_0 e^{rt} \tag{1.8}$$

where e is the base of natural logs.

In the above equations, the population grows if	$r > 0$
the population is stationary if	$r = 0$
the population is negative if	$r < 0$

When r is positive, the growth is known as **exponential**; if r is negative the population is in exponential decline (Fig. 1.3).

We can make the equation linear by taking the natural logs of both sides of Equation 1.8, yielding:

$$\ln N_t = \ln N_0 + rt \tag{1.9}$$

When we graph $\ln N$ versus time, we again have a linear relationship, with $\ln N_0$ as the y-intercept and r as the slope of the line (Fig. 1.4).

Doubling time

A convenient statistic, often used by population ecologists and human demographers (demography is the study of population statistics), is doubling time. That is, how long will it
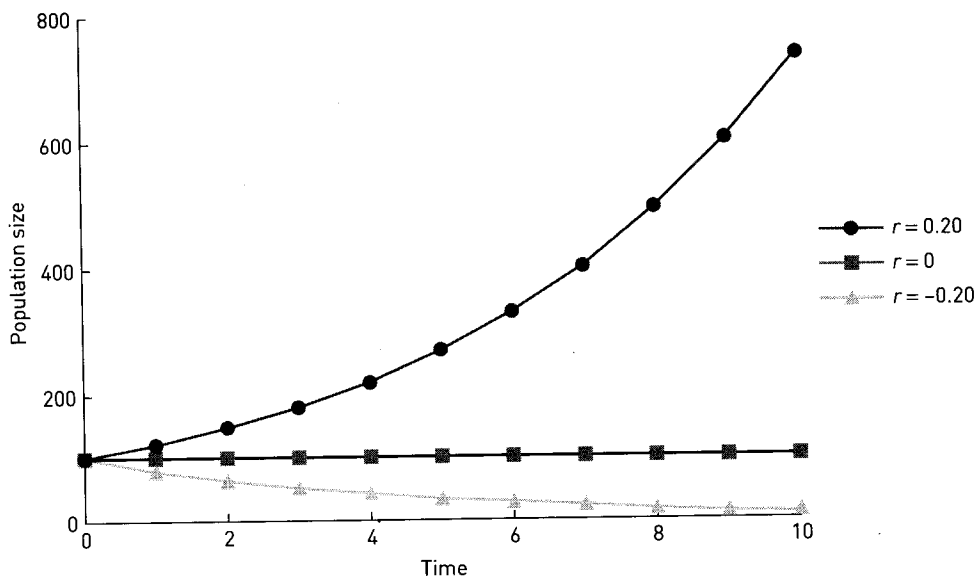
Figure 1.3 Exponential growth pattern in a population with overlapping generations and continuous breeding.
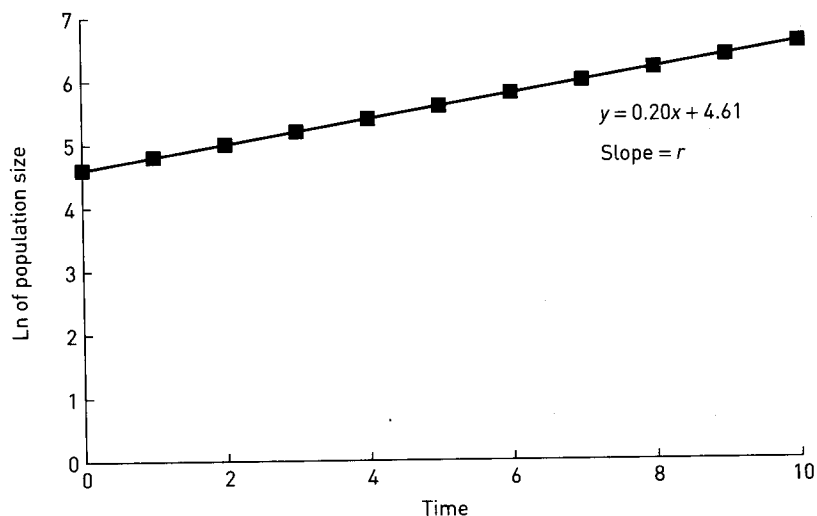

Figure 1.4 Natural log of growth in a population with overlapping generations and continuous breeding.

take a population to double from its present population size? Equation 1.8 can be rearranged to: $N_t/N_0 = e^{rt}$. We want to solve for the time at which the ratio $N_t/N_0 = 2$. So we have: $2 = e^{rt}$. Taking the natural log of both sides of the equation yields, $\ln 2 = rt$, where t is now doubling time. Since $\ln 2 = 0.693$, if we solve for t we end up with:

$$\text{Doubling time} = 0.693/r \tag{1.10}$$

Therefore if we know the intrinsic rate of increase we can easily find the projected doubling time of a population. Remember, however, that we are assuming that the population is not affected by its age distribution, and that r is a constant during this time period. That is, birth and death rates remain unchanged.

Doubling time probably has little meaning if r is very close to zero. Doubling time is undefined if $r = 0$. An r-value of 0.001, for example, would predict a doubling time of 693 time units; but it is extremely unlikely that r would remain a constant for such a long period of time. For a negative r-value ($d > b$), the result will be a negative number. The absolute value of this number is the time it will take the population to be reduced to half of its present size. Instead of "doubling time" the result is "halving time."

1.7 Exponential growth in an invasive species

During a hurricane in 1962, five captive mute swans (*Cygnus olor*) escaped into the Chesapeake Bay, in Maryland. Since they were pinioned and therefore flightless, their chance of survival during the winter was considered negligible and no attempt was made to capture them. One pair, however, successfully nested. By 1975 the descendents of this original pair numbered approximately 200, and by 1986 totaled 264. By 1999 the estimated population of mute swans in the Chesapeake Bay was 3955 (Anonymous 2003, Sladen 2003, Craig 2003). In 2001 the Maryland Department of Natural Resources, in an effort to control the swan population, began shaking (addling) mute swan eggs or covering them with corn oil to terminate embryo development. Mute swans were also removed from Federal National Wildlife Refuges. The result was a decline to 3624 in 2002 (Anonymous 2003). As shown in Fig. 1.5, prior to these control efforts, the population was growing exponentially with an intrinsic rate of increase of 0.17 and a doubling time of four years! (As an exercise, try using Equation 1.10 to verify the doubling time.)
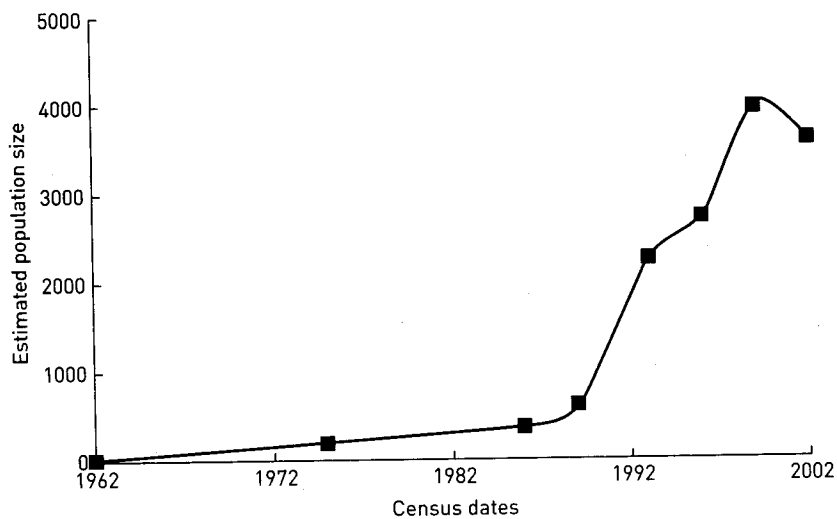
Figure 1.5 Mute swan (*Cygnus olor*) population in the Chesapeake Bay since 1962.

So what's the problem? Swans are considered graceful, even "majestic," and are thought of as harmless by their admirers. However, mute swans, in addition to being a non-native species, have become permanent residents. That is, they do not migrate as do other swan species. Recent data show that an average adult swan eats 3.6 kg of submerged aquatic vegetation (SAV) a day (Craig 2003). This is occurring at a time when biologists are struggling to re-establish SAV in the Bay. Is it necessary to control the mute swan population? If so, how?

The Fund for Animals took the US Fish and Wildlife Service to court to stop its plan to kill 525 swans in 2003 (Craig 2003). The debate evidently will continue for the indefinite future.

1.8 Applications to human populations

Few biological populations grow either geometrically or exponentially for long. As we will explore in the sections on intraspecific competition and logistic growth, as populations grow, resources become scarce. The resultant changes in birth and/or death rates slow growth. The human population of the world, however, has continued to grow since around 1650; it reached 6.0 billion by late 1999, and 6.3 billion by 2003 (Fig. 1.6a). Many scientists question how long this growth can be sustained. While most ecologists insist that human population growth must cease in the near future, some economists (Simon 1996) see no reason for limits to the human population. In the next section we will use data from the Population Reference Bureau (Anonymous 1981–2004) to illustrate how Equations 1.8 to 1.10 may be used in population projections.

Recall from Equation 1.9 that if we graph natural log of population growth versus time we can determine the intrinsic rate of increase by finding the slope of the graph. In Fig. 1.6b we have plotted the natural log of human population growth against time. The slope of this line, as determined by the statistical technique of linear regression and computed for us in an Excel™ spreadsheet, is 0.007. This is the best fit for the intrinsic rate of increase for the human population from 1650 to 2003.

If we examine Table 1.2, in which human populations in 2003 are broken down by continental regions, the strengths and weaknesses of this simple model become apparent. Most striking are the immense differences among populations. While the human population as a whole is growing twice as fast in 2003 as compared to the period of 1650 to the present (contemporary $r = 0.013$, historical $r = 0.007$), Europe has a negative r, while that of Africa is 0.024, almost twice the global growth rate. Secondly, over 60% of the human population resides in Asia.

Clearly, although human population growth is of global concern, it is a highly regional problem. From Table 1.2 you should be able to see that r is readily calculated as the difference between the birth and death rates. Secondly, you should try calculating projected doubling times based on Equation 1.10. You will find that the data published by the Population Reference Bureau differ slightly from your calculations. They are using more sophisticated models and are taking age distributions into account. Nevertheless, the differences in doubling times are remarkably minor. Finally, if you examine the last column you will also notice another great difference among these populations. The percentage of the population in the pre-reproductive years (15 years or younger) varies from 42% in Africa to a low of 17% in Europe.
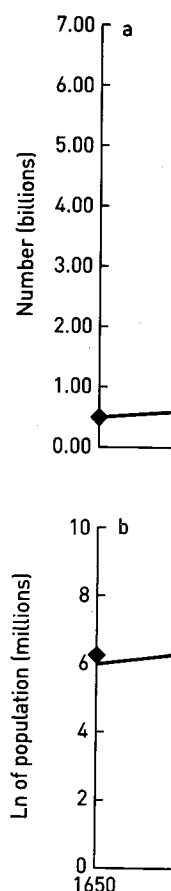

Figure 1.6 Human p[...] (b) natural log of pop[...]

In his book *The Sk[...]
about human populat[...]
states that rapid grow[...]
modern methods of s[...]
care, etc.) and that ev[...]
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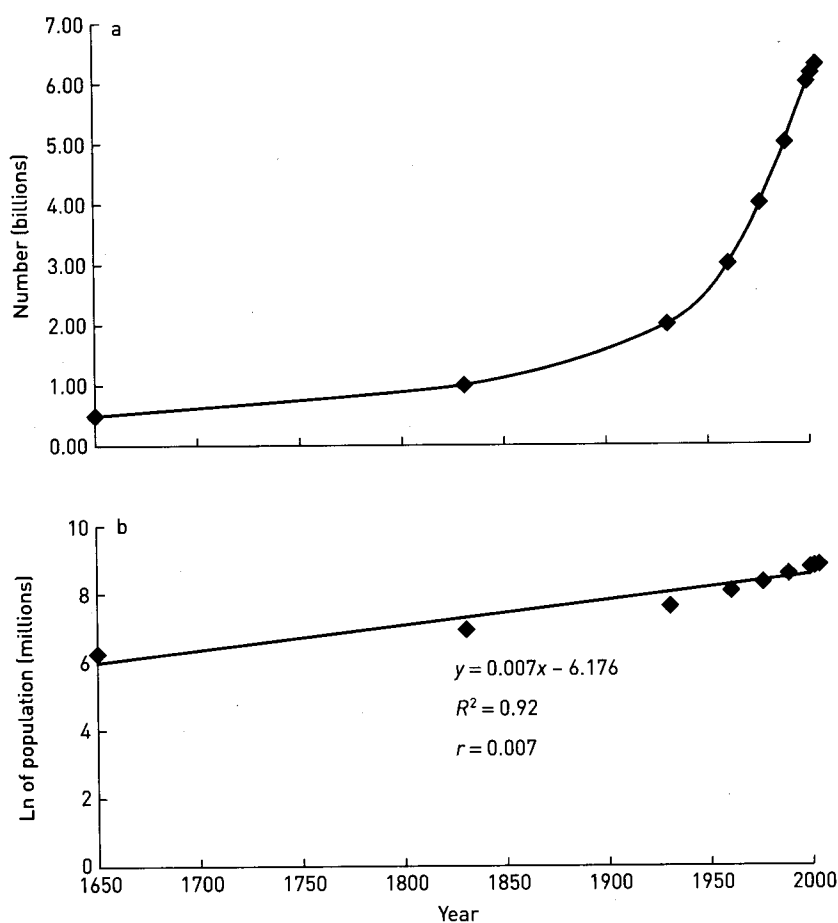Africa and Asia will no[...]

Figure 1.6 Human population growth since 1650: (a) world population, in billions; (b) natural log of population growth, in millions.

In his book *The Skeptical Environmentalist*, Bjorn Lomborg (2001) is rather sanguine about human population growth. He accepts the demographic transition model, which states that rapid growth has occurred because of a rapid drop in the death rate (due to modern methods of sanitation, improved food growth and distribution, better medical care, etc.) and that eventually, with improved standards of living and wealth, birth rates drop to match the low death rates. Indeed, in most European countries, human population growth has slowed, and even gone negative. In 2003, 20 countries out of 43 in Europe had a growth rate of zero or negative, including all 10 Eastern European countries. As noted above, the population growth rate (r-value) for Europe as a continent is negative. As for the future, Lomborg accepts a "medium variant forecast" from the UN. This prediction is zero population growth for the world by the year 2100. However, by then the world population is projected to be 11 billion. Consider that the world population was only one billion in 1850, two billion in 1950, and 6.3 billion in 2003. Lomborg is correct when he says that 60% of growth is from just 12 countries. Perhaps the world outside of Africa and Asia will not necessarily suffer a catastrophe from human population density,

Table 1.2 2003 human population data from the Population Reference Bureau (Anonymous 1981–2004).

Region	Population size (millions)	Birth rate (per thousand)	Death rate (per thousand)	Rate of increase per individual (r)	Doubling time (years)	Percent under 15 years
World	6314	22	9	0.013	53	30%
Africa	861	38	14	0.024	29	42%
North America*	323	14	8	0.005	139	21%
Latin America†	540	23	6	0.017	41	32%
Asia	3830	20	7	0.013	53	30%
Europe	727	10	12	−0.002	NA	17%
Oceania‡	32	18	7	0.011	63	25%

* North America = the United States and Canada.

† Latin America includes Central and South America and the Caribbean Islands.

‡ Oceania includes Australia, New Zealand and the South Pacific Islands.

Countries of the form : · USSR have been distributed between Asia and Europe.

but what will happen in China, India, Pakistan, Bangladesh, and Nigeria, for example, in the next 100 years? The 2003 data sheet from the Population Reference Bureau predicts that China's population will stabilize at about 1.4 billion (compared to its present estimated population of 1.289 billion) by 2050. By 2050, however, the PRB predicts a population for India of 1.6 billion (compared to present population of 1.069 billion). The question on the mind of the concerned biologist: Will there be any room for natural habitats on a planet with 11 billion or, worse yet, 15 billion people?

Examine Table 1.3, which describes overall human demographic trends since 1981. Lomborg (2001, p. 47) states that world population growth, in numbers per year, reached

Table 1.3 World human demographic trends since 1981. All data from the Population Reference Bureau (Anonymous 1981–2004).

Year	World population estimate (billions)	Birth rate per thousand	Death rate per thousand	r per individual	Projected growth in numbers per year (millions)	Actual average growth per year during specified time period (millions)
1981	4.492	28	11	0.017	77.0	
1985	4.845	27	11	0.016	78.1	1981–85: 88.3
1987	5.026	28	10	0.018	91.3	1985–87: 90.5
1989	5.234	28	10	0.018	95.1	1987–89: 104.0
1991	5.384	27	9	0.018	97.8	1989–91: 75.0
1995	5.702	24	9	0.015	86.2	1991–95: 79.5
2000	6.067	22	9	0.014	85.5	1995–2000: 73.0
2003	6.314	22	9	0.013	82.6	2000–03: 82.3

Table 1.4 Human
Population Refer

Year	Populat estima (billior
1981	0.25
1985	0.26
1987	0.27
1989	0.27
1991	0.28
1995	0.29
2000	0.31
2003	0.323

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Table 1.4 Human demographic trends in North America since 1981. Data from the Population Reference Bureau (Anonymous 1981–2004).

Year	Population estimate (billions)	Birth rate per thousand	Death rate per thousand	r per individual	Projected growth in numbers per year (millions)
1981	0.25	16	9	0.007	1.76
1985	0.26	15	8	0.007	1.83
1987	0.27	15	9	0.006	1.62
1989	0.27	16	9	0.007	1.90
1991	0.28	16	9	0.007	1.97
1995	0.29	15	9	0.006	1.75
2000	0.31	14	8	0.006	1.86
2003	0.323	14	8	0.005	1.62

a peak in 1990 at 87 million per year. Population Reference Bureau data agree on the time but not the number (over 100 million added in the period 1987–89). Absolute growth has averaged about 87 million per year in the latter part of the twentieth century, according to Population Reference Bureau data; Lomborg used the figure of 76 million, but this applies only to the 1990s. The 2003 Population Reference Bureau data sheet projects world population as 7.9 billion in 2025 and 9.2 billion in 2050. Lomborg's comparable numbers are "almost 8 billion" in 2025 and 9.3 billion in 2050.

Population growth in North America (Table 1.4) is rather variable, but reached a relative peak in 1991–92 when around two million people were added to the population per year. The data from 2003, however, reflect the fact that the 2000 census for the United States came in at almost seven million more than expected. Meanwhile, the US birth rate has fallen to 2.034 births per female (replacement rate is 2.10 births per female) (PRB, Anonymous 1981–2004).

Human population growth is greatest in Asia (Table 1.5). Peak absolute growth was in the period 1989–91, when around 58 million people were added per year. It declined unsteadily in the late twentieth century and is now about 50 million people per year. The r-value has declined steadily to 0.013 in 2003.

1.9 The finite rate of increase (λ) and the intrinsic rate of increase (r)

Both the intrinsic rate of increase (r) and the finite rate of increase (λ) are used commonly to track population growth and to compare growth rates among populations of the same species found in different environments, as well as among different species. Consequently it is important to understand the relationship between λ and r. As defined in Equation 1.5, λ is the growth rate per time period (usually per year) and is based on the ratio N_{t+1}/N_t. If the population lacks an age distribution or has a stable age distribution (SAD), the finite rate of increase, λ, is a constant. The population as a whole and each age class will grow as:

Table 1.5 Human demographic trends in Asia since 1981. Data from the Population Reference Bureau (Anonymous 1981–2004).

Year	Population estimate (billions)	Birth rate per thousand	Death rate per thousand	*r* per individual	Projected growth in numbers per year (millions)
1981	2.61	29	11	0.018	47.4
1985	2.83	28	10	0.018	51.4
1987	2.93	28	10	0.018	53.2
1989	3.06	28	9	0.019	58.7
1991	3.16	27	9	0.018	57.4
1995	3.38	24	8	0.016	54.5
2000	3.68	22	8	0.014	51.9
2003	3.83	20	7	0.013	50.1

$$\frac{N_{t+1}}{N_t} = \lambda \tag{1.11}$$

Rearranging Equation 1.8 and setting $t = 1$, we have: $N_{t+1}/N_t = e^{rt} = e^r$. Thus, when $t = 1$ and when there is a stable age distribution we have:

$$\lambda = e^r \tag{1.12}$$

and

$$r = \ln \lambda \tag{1.13}$$

1.10 Stochastic models of population growth and population viability analysis

All of the population models we have examined to this point are **deterministic models.** The models specify conditions leading to an exact outcome based on the parameters of the models. But natural systems are unlikely to be deterministic; rather they are more likely to be **stochastic.** In particular, small isolated populations are subject to stochastic processes because chance events can dominate their long-term dynamics. In stochastic models population parameters vary according to some kind of a frequency distribution. This distribution has a "central tendency" (a mean), but also has a range of variability around the mean. For example, in a deterministic model, if we know the present population size and the proper growth parameter, we forecast an exact expected population size for a specific time in the future. In a stochastic model, we would instead predict a range of possible population future sizes, with assigned probabilities.

Future population size in a small population is strongly influenced by **demographic stochasticity,** which is driven by variations in the fates of different individuals within a given year. For example, although the average female within a population may have 2.0

om the Population

Projected growth in numbers per year (millions)
47.4
51.4
53.2
58.7
57.4
54.5
51.9
50.1

(1.11)

e^r. Thus, when $t = 1$

(1.12)

(1.13)

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Example 1.3

A *Paramecium caudatum* population is cultured in the laboratory and sampled on a daily basis. Population sizes, based on 0.5 ml samples, are shown below. The population grows exponentially between days 0 and 3. Find the intrinsic rate of increase (r) for the population

Growth of a *Paramecium* population. Numbers are based on daily 0.5 ml samples.

Time in days	Number (N) per 0.5 ml	Natural log of N ln N	Per capita growth $\dfrac{N_{t+1} - N_t}{N_{t+1}}$
0	14	2.64	–
1	41	3.71	0.66
2	116	4.75	0.65
3	193	5.26	0.40
4	244	5.50	0.21
5	290	5.67	0.16
6	331	5.80	0.12
7	363	5.89	0.08

Answer

Since we want to know the value of the maximal rate of increase (the density-independent rate of increase), we examine growth only during the first three days (see Fig. 2.1 in the next chapter). From Equation 1.9 (ln $N = rt + $ ln N_0) we know that to find r we need only convert column 2 to natural logs (column 3). Then find the slope between days 0 and 3. To find the slope we can use the formula:

$$r = (y_2 - y_1)/(x_2 - x_1). \quad \text{Thus,}$$

$$r = (5.26 - 2.64)/(3 - 0), \quad \text{and}$$

$$r = 0.87$$

Using Excel™, a linear regression on the same data yields the value of r as 0.89.

Example 1.4

The birth rate for Latin America in 1978 was 33 per thousand, while the death rate was 10 per thousand. (a) What was the intrinsic rate of increase, assuming a stable age distribution? (b) If the population size was 344 million, what was the projected population in 1982? (c) Between 1982 and 1990 the population increased from 377 million to 415 million. What was the r during that time? (d) Given this r-value, what was the doubling time? (e) What is λ?

Answers

a Given $r = b - d$, we have $r = 33/1000 - 10/1000 = $ **0.023**

b From 1978 to 1982 is four years. Therefore:

$$N_4 = N_0 \times (e^{0.023 * 4}) = 344 \text{ million} \times (e^{0.092})$$

$$= 344 \text{ million} \times 1.096 = \textbf{377.15 million}$$

c From 1982 to 1990 is 8 years. Therefore: $415 \text{ million} = 377 \text{ million}(e^{8r})$

Simplifying: $415/377 = 1.10 = e^{8r}$

Taking natural logs: $\ln 1.10 = 8r$

Or, $0.096/8 = r = $ **0.012**

d Doubling time $= 0.693/r = 0.693/0.012 = $ **57.7 years**

e $\lambda = e^r = e^{0.012} = $ **1.012**

female offspring, some individuals may not reproduce at all, while others have a litter size of 4.0. Demographic stochasticity has effects not only on birth and death processes, but also on sex ratio. In the above example, some females may give birth only to males in a given year. Another important influence on population growth is **environmental stochasticity**, which is temporal variation in the population due to unexpected events, often tied to the physical environment, such as droughts, hail storms, fires, and landslides, but which may also include diseases. Environmental stochasticity can affect both large and small populations.

More realistic growth models, therefore, make forecasts based on probabilities, rather than predicting a single outcome. For example, weather forecasters no longer simply predict rain, but instead predict a certain probability of rain. Similarly, it would be prudent for population models to predict an expected population size, but allow for other population sizes to occur with particular probabilities. Again, this approach is especially important in small populations, and over short time intervals. If the population is large and the time frame is very long, the expected population sizes dictated by deterministic models become highly probable.

Stochastic models are the basis for the quantitative approach to conservation biology known as **population viability analysis** (PVA). Although it is beyond the scope of this book

to explore stochastic models and PVA in detail, there are excellent discussions of these models in Morris and Doak (2002) and Beissinger and McCullough (2002). For more information on stochastic models, see also Pielou (1977) and Nisbet and Gurney (1982).

PVA is so important because many wildlife populations that were once numerous, widespread, and occupied contiguous habitats are now small, restricted in distribution, and isolated from each other. The problem with small, isolated populations is that they are increasingly subject to stochastic processes and increasingly likely to go locally, if not globally, extinct. The purpose of population viability analysis is to predict the likely future status of a population or collection of populations (Morris and Doak 2002). PVA is a set of analytical and modeling approaches for assessing the future course and risk of extinction of a population (Beissinger and McCullough 2002). PVA examines how (i) genetic, demographic, and environmental stochasticity, (ii) catastrophes and "bonanzas," and (iii) spatial variation affect the future of the population.

Demographic and environmental stochasticity were defined above. Small populations are also affected by genetic processes such as (i) genetic drift resulting in the loss of genetic diversity in the population, (ii) inbreeding depression, and (iii) monopolization by a small number of males in a polygynous mating system. The biggest concern is the rate of loss of heterozygosity and its effects on the future fertility and mortality rates of the population.

PVA also attempts to anticipate how rare events which result in extremely low survival and/or reproduction (catastrophes) or their opposite (bonanzas) might affect the future course of a population. Catastrophes can be local or regional events of low probability with significant density-independent effects. For example, one of two remaining whooping crane (*Grus americana*) populations in the United States was decimated by a hurricane in 1940 and this population went extinct soon thereafter. The only remaining population of the black-footed ferret (*Mustela nigripes*), at Shirley Basin in Wyoming, was being decimated by an outbreak of distemper, while the prairie dogs (*Cynomys ludovicianus*), its prey species, were suffering from the plague. In 1986, conservation biologists, fearing extinction unless action was taken, captured the last remaining 18 ferrets to start a captive breeding program. The captive population grew rapidly, and by 1992 biologists determined the captive population was large enough to sustain a reintroduction program. Currently black-footed ferrets have been reintroduced into six areas in their historic range.

Finally, variation in fertility and mortality can also be spatial. That is, if a population is subdivided into different locations, vital statistics can vary depending on the location of the subpopulation. Again, we cannot explore these topics in detail here. But the following paragraphs explore the consequences of demographic stochasticity for density-independent growth.

In a simple stochastic approach we specify probabilities for births and/or deaths rather than using an exact population average. For example, suppose the arithmetic average litter size of a small mammal population is 1.167 females per female per year, but the actual number of females produced per year varies from zero to two (for simplicity, we follow the traditional practice of only counting females). We then must determine the probability that a given female produces zero, one, or two female offspring. For a given number of females at time = zero, we can then make predictions as to the likelihood of various numbers of offspring in the next year.

In the following simple example, assume that adults die after reproduction, but all individuals in a given litter survive. However, litter sizes (B_i) vary from 0 to 2 with the probabilities shown in Table 1.6. The value of λ is based on the arithmetic average of the litter

Table 1.6 Probability that an individual female will have 0, 1, or 2 female offspring, and the expected net reproduction.

Probability, p_i, of having a given litter size, B_i	Litter size (B_i) = the number of female offspring per year	Expected net reproduction = p_iB_i
0.167	0	0
0.500	1	0.500
0.333	2	0.667
		$\lambda = 1.167$

sizes $= \sum p_iB_i$. The expected finite rate of increase for the population as a whole is therefore the sum of the last column ($\lambda = 1.167$).

For N females, there are, therefore, finite probabilities that the next generation will produce anywhere between 0 and $2N$ female offspring in the next generation. The probability that a population of N females goes extinct in the next year, for example, is $(0.167)^N$. For a population of six females the probability that the population will go extinct in the next year is $(0.167)^6 = 2.17 \times 10^{-5}$. For a population of one female, the probability equals 0.167. Similarly, the probability that the population will double in one year is $(0.333)^N$. A radical population shift such as extinction or doubling in one year is likely only in very small populations.

In Fig. 1.7 the probabilities from Table 1.6 are applied to a population of three females at time $= 0$. One time unit later ($t = 1$), the population size has a possible range of values from 0 to 6. The most likely outcome is $\lambda N = 1.17 \times 3$, or 3.51. In reality there cannot exist fractions of individuals, so the population, one time unit later, is equally likely to remain at three or grow to four females.
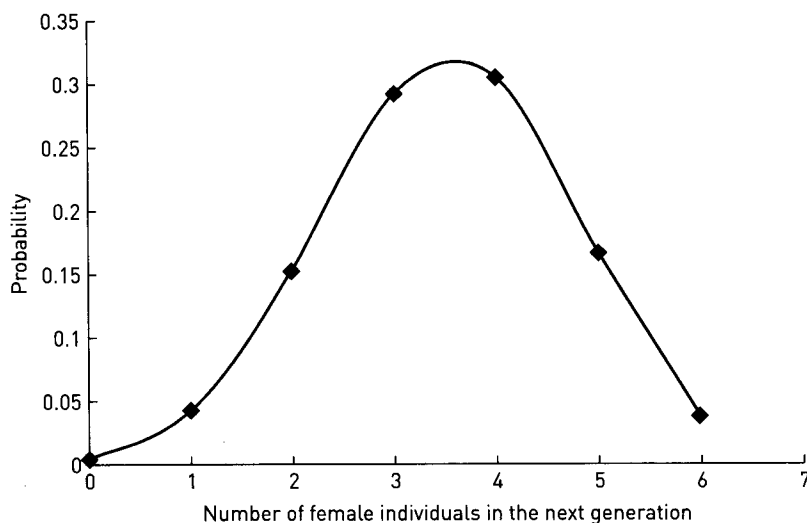

Figure 1.7 Stochastic growth in a population of three females, based on the parameters of Table 1.6.

As noted by Pielou (1977) and others, the probability that a population will go extinct can be estimated by Equation 1.14:

$$P_{0,t} = \left(\frac{d}{b}\right)^{N_0} \tag{1.14}$$

where
$P_{0,t}$ = the probability of extinction at time t
d = per capita death rate and b = per capita birth rate

For any finite population there is a probability of one that the population will go extinct, given enough time, unless the birth rate is higher than the death rate ($b > d$, $\lambda > 0$). Even then, there is a finite non-zero probability of extinction in any generation. Again, this chance of extinction is heavily influenced by the size of the population, with the smallest populations the most likely to go extinct.

As pointed out by Morris and Doak (2002), adding variability to population statistics does not simply mean that population growth is more variable; it means that populations do worse than they would without variation. The use of an arithmetic mean, as in the example above, overestimates growth most of the time. As Morris and Doak (2003, p. 25) state, "using simple arithmetic averages to characterize the population growth rate in a variable environment is not just a simplification, it is actually wrong."

When variation is added the most likely result is that the population will grow according to the geometric mean, rather than the arithmetic mean. The geometric mean of a set of numbers is always less than or equal to the arithmetic mean, and the difference between the two increases as the variability in the data increases.

For example, assume that a population with an initial population size of 50 grows for 100 time periods ($t = 100$), with an arithmetic mean value for λ of 1.05. With no variation, using Equation 1.5, we get the predicted population size of:

$$N_{100} = N_0 \lambda^{100} = 50(1.05^{100}) = 6575.$$

Now assume that we allow λ to vary between 0.90 and 1.20, with equal probabilities ($p_i = 0.50$ for each). We have:

$$N_{100} = 50(0.90^{50})(1.20^{50}) = 50(0.005)(9100) = 2345$$

This is the most likely outcome and is based on the geometric, rather than the arithmetic, mean. As shown in Table 1.7, the arithmetic mean $= \sum_{i=1}^{n} p_i \lambda_i$ where p_i = probability of a given λ_i. In the above case, $p_1 = 0.50$ for λ_1 ($= 0.90$), and $p_2 = 0.50$ for λ_2 ($= 1.20$).

Therefore the arithmetic mean $= (0.50 \times 0.90) + (0.50 \times 1.20) = 1.050$

However, the geometric mean $= \prod_{i=1}^{n} \lambda_i^{p_i} = 0.90^{0.5} \times 1.20^{0.5} = 0.949 \times 1.095 = 1.039$

As stated above, the geometric mean is always less than or equal to the arithmetic mean, and in this case the geometric mean of 1.039 is less than the arithmetic mean of 1.050. If

Table 1.7 Calculating the arithmetic versus the geometric mean for population projections.

Probability, p_i	λ_i	$p_i \lambda_i$	$\lambda_i^{p_i}$
0.25	0.60	0.15	0.880
0.25	0.80	0.20	0.946
0.50	1.40	0.70	1.183
		Arithmetic mean	Geometric mean
		$= \sum_{i=1}^{n} p_i \lambda_i$	$= \prod_{i=1}^{n} \lambda_i^{p_i}$
		$= 1.050$	$= 0.985$

we use the geometric mean instead of the arithmetic mean in Equation 1.8, we have the most likely outcome when λ varies between 0.90 and 1.20 with equal probabilities:

$$N_{100} = (50)(1.039^{100}) = 2345$$

which is the same result we found above, but is much less than the projected population of 6575 using the arithmetic mean.

Let us try another example. Assume that $\lambda = 0.60$ 25% of the time, $\lambda = 0.80$ 25% of the time, and $\lambda = 1.40$ 50% of the time (Table 1.7). The arithmetic mean is, again, 1.05. Based on the arithmetic mean, we expect the population to grow since $\lambda > 1.00$. However, the geometric mean is less than one, and the most likely result is that this population will decline.

The geometric mean, however, provides us only with the "most likely" outcome when population parameters vary. In fact, if the population parameters are allowed to vary randomly, many different outcomes are possible. For example, in Fig. 1.8 we see the results
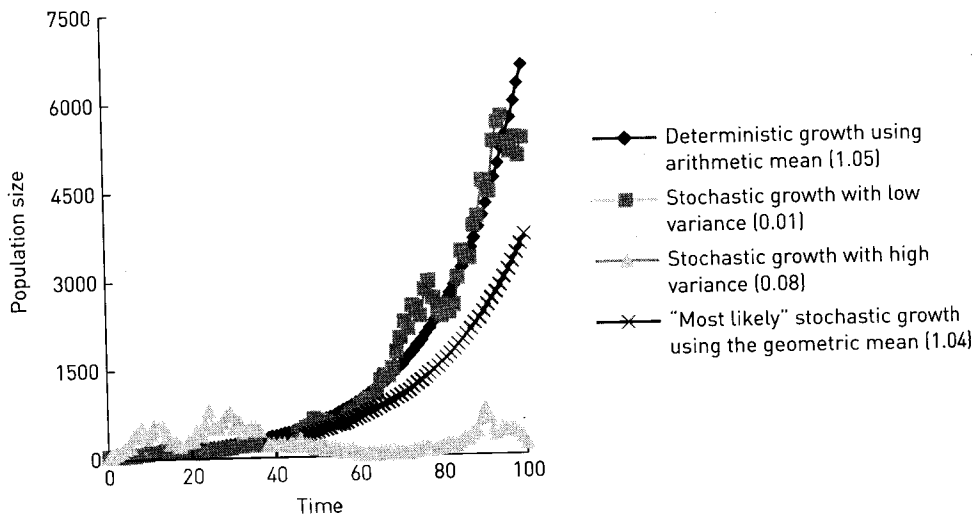

Figure 1.8 Deterministic versus stochastic growth with high and low variance. Initial population size = 50; $\lambda = 1.05$, except where noted.

population
$\lambda_i^{p_i}$
0.880
0.946
1.183
Geometric mean
$= \prod_{i=1}^{n} \lambda_i^{p_i}$
$= 0.985$

n 1.8, we have the
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$= 0.80$ 25% of the
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istic growth using
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(0.01)

c growth with high
(0.08)

ely" stochastic growth
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low variance.

Table 1.8 Results of 20 simulations of population growth for a deterministic model versus two stochastic models, one with low and one with high variability. In all cases the initial population size was 50 individuals, the arithmetic mean finite rate of increase (λ) was 1.05, and the simulation was run for 100 time units. In the low-variability simulations, λ was allowed to vary between 0.90 and 1.20 ($\bar{x} = 1.05 \pm 0.1$); in the high-variability simulation, λ was allowed to vary between 0.55 and 1.55 ($\bar{x} = 1.05 \pm 0.3$). In the stochastic simulations, growth rates were randomly generated using the Excel™ RAND functions. Note that the deterministic result is greater than the stochastic result/low variability in 15 of 20 simulations and greater than the stochastic result/high variability in 19 of 20 simulations.

Simulation number	Deterministic result	Stochastic result (low variability)	Stochastic result (high variability)
1	6575	3729	5772
2	6575	4156	28
3	6575	5972	1004
4	6575	3631	13
5	6575	5516	291
6	6575	5700	13
7	6575	2363	201
8	6575	3796	1
9	6575	5821	246
10	6575	2845	44
11	6575	7107	5244
12	6575	2113	3169
13	6575	19,561	106
14	6575	3910	640
15	6575	2509	122
16	6575	13,731	8
17	6575	3706	1917
18	6575	6304	53
19	6575	15,570	4
20	6575	12,972	8450
Average for the 20 simulations	6575.0	6550.6	1366.3

of one simulation. A comparison of growth using the arithmetic and geometric means yields the expected results. Stochastic growth with low variability (variance around the mean is 0.01), shows growth, but with obvious variation. The end result of growth with high variation (variance of 0.08 around the mean) is a population of only 178 individuals (N_0 was 50) after 100 time units.

Although this result is "typical" there are many other possible outcomes. Table 1.8 presents the results of 20 different simulations of population growth for a deterministic and two stochastic models (low versus high variability). The basic result is that the deterministic model, using the arithmetic mean for λ of 1.05, produced a larger final population

size than did the stochastic/low-variability model in 15 of the 20 simulations. The final population size for the deterministic model was greater than that of the stochastic/high-variability model in 19 of 20 simulations. The low-variability result is larger than the high-variability result in 18 of 20 simulations.

In summary, a stochastic model generates a frequency distribution of probabilities that particular population numbers will appear in the next generation. There will always be a finite probability that the population will go extinct, but the most likely outcome (i.e., the highest probability) will be that $N_{t+1} = N_t\lambda$, using the geometric mean for λ.

1.11 Conclusions

In this chapter we have explored models illustrating the Turchin (2001) first law of population ecology. That is, biological populations tend to grow exponentially. Populations with discrete or continuous generations, as well as populations with age structures, all obey the exponential law. As will be detailed in Chapter 4, populations with age structures must first achieve a stable age distribution before growing according to the exponential law. The exponential law even applies to populations undergoing demographic stochasticity as described in section 1.10 above (Turchin 2001). And we do not have to assume a constant environment. If the environment varies such that per capita birth and death have a stationary probability distribution, we still obtain exponential growth or decline in the population (Maynard Smith 1974).

Accordingly, if the environment does not affect the population in a systematic manner, all types of biological populations show exponential growth. Traditionally, ecologists have treated populations with discrete generations differently from those with overlapping generations. Difference equations such as 1.4 and 1.5 have been used in the first case. By contrast differential equations (1.3) and their solved forms (1.8) have been employed to describe populations with overlapping generations. In both cases we use the finite rate of increase, λ, or the intrinsic rate of increase, r, as a common currency for comparing population growth potentials.

However, populations do not grow forever. Eventually individuals begin to run out of space, food, water, or other resources and/or become increasingly subject to predation or disease. This is where the second principle, that of self-limitation, comes into play. In the next chapter we will examine this principle, and the models, traditionally known as density-dependent models, that attempt to implement it.

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2.1 Introduction

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