

— LARRY L. ROCKWOOD —

INTRODUCTION TO POPULATION ECOLOGY

2ND EDITION



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Introduction to Population Ecology

Introduction to Population Ecology

Second Edition

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WILEY Blackwell

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Preface

The problem with a textbook, especially in a fast moving science such as population ecology, is that the moment it is published, it is out of date. Given the delays between actually writing a book and its appearance in print, most of the writing for my 2006 first edition was done in 2003–2005. Therefore, the first objective in producing this second edition was to bring it up to date as much as possible. Obviously, this did not mean throwing the first edition into the dustbin and writing everything new from scratch. In many cases it meant finding new examples that illustrate what are still valid ideas or theories. In other cases it meant casting doubt on old favorites such as the theory of r- and K-selection (called by at least one author a “zombie” theory).

In Chapter 1, for example, I have brought the data on human populations as up to date as possible, recognizing that the number of humans in the world has moved from 6.3 billion in my first edition to over 7.1 billion as of 2014. The example of the exponential growth of the gray wolf population in Wisconsin was not available previously. Information on a renewed interest in the Allee effect is new in Chapter 2.

The chapters on population regulation (Chapter 3) and life tables (Chapter 4) use a variety of new and better examples compared to those in the first edition.

Chapter 5, which deals with metapopulations and the MacArthur and Wilson equilibrium theory, benefit from a great deal of new information published in the last few years, much of it reviewed extensively in Losos and Ricklefs (2010).

A great deal has been written recently relevant to life history theory including the metabolic theory of ecology and its spawn (Sibly et al. 2012). At the same time, Dobson and Oli (2007), and Dobson (2007, 2012) have produced a series of papers proposing to replace the theory of r- and K-selection with a theory centered around mass, “life style” and phylogeny. I have attempted to at least introduce the reader to the idea that it may be time to realize the limits of r- and K-selection, if not retire the theory altogether.

In the chapter on competition (Chapter 7), my major contribution is to introduce the reader to the poetic niche theory written by Dr. Seuss (Geisel 1955). A critical evaluation of the Tilman (1982) resource-ratio theory and an example of character displacement among Darwin’s finches (Grant and Grant 2006) are other highlights.

The chapter on mutualism (Chapter 8) features an update on the classic Janzen (1966) paper on the Central American ant-acacia mutualism as well as a new long section on the recent brilliant work on ants and acacias in Africa (Palmer et al. 2010). These studies confirm a major point of the chapter, which is, that without constant co-evolution, mutualistic relationships can easily move toward parasitism by one of the partners. Also new in this chapter is a section on geographic variation in coevolution of mutualism (Rickson 1977), which leads into the similar idea of geographic defenses in host-parasite interaction described in Chapter 9 (Foitzik et al. 2003).

The chapter on predator-prey relationships (Chapter 10) brings the reader new information on examples that are engrained in the literature as classics, yet are now being questioned. These include doubts about the hypothesized trophic cascade in Yellowstone after wolf introduction (Middleton 2014) and the apparent failure of the wolf population to either thrive or control the moose population on Isle Royale in Michigan (Mlot 2013). Meanwhile Chapter 11 brings us new information on the potential responses of plants to defoliation.

The last chapter, contributed by my colleague Jon Witt, is entirely new and presents a discussion of multiple trophic level models in much more detail than in the previous edition. Topics examined include trophic cascades, intraguild predation, cannibalism and meso-predator release.

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About the companion website

This book is accompanied by a companion website:

www.wiley.com/go/rockwood/populationecology

The website includes:

- Pdfs of all figures from the book for downloading
- Powerpoints of all tables from the book for downloading

Part 1

Single species populations

Why population ecology? What distinguishes the study of populations from the study of landscapes and ecosystems? The answers lie in scale, focus, and traditions. In population ecology the scale is a group or groups of taxonomically or functionally related organisms. The emphasis is on fundamental properties of these populations: growth, survivorship and reproduction. The tradition is based on the interplay of theory, laboratory testing and, ultimately, field work. The competition and predator–prey equations of Lotka (1925) and Volterra (1926; 1931) stimulated the laboratory work of Gause (1932; 1934); Park (1948; 1954), Huffaker (1958) and others. But Elton (1924), Errington (1946); Lack (1954); Connell (1961a; 1961b); Paine (1966); Krebs et al. (1995) and many others have brought population ecology into the field, where its theoretical underpinnings are constantly tested. In the age of personal laptop computers and the Internet, data can now be analyzed, sent around the world, and experiments redesigned without ever leaving the field site. Increasingly sophisticated experimental design and statistical rigor constantly challenge new generations of scientists. Indeed much of the training of modern ecologists is in methodology.

Yet why do we become ecologists in the first place? Is it because of our love of computer programs and statistics? For most of us, that would be, “No.” More likely it is because of a love of the organisms that we find in natural (“wild”) places. We love the sounds, the smells, the feel, the being in nature. Perhaps it is also because of our love of the idea of nature and of places not yet under the total domination of man. Nothing quite matches a day (or night) in the field for an ecologist, and we are usually eager to communicate these experiences to other people. Contrast an ecologist to a typical urban dweller like Woody Allen. In one of his movies Woody complains that he hates spending nights in the country because of the “constant noise of the crickets.” Undergraduate students at George Mason University often approach the first field trip of the semester with fear and trepidation. Yet, such individuals have little fear of automobile traffic and find traffic noises normal and even soothing. Obviously an ecologist has a different orientation to the world.

Population ecology is, in a primitive sense, an organized way of communicating our ideas about nature to others. Population ecology, with its emphasis on groups of individuals and their survival and reproduction, their relationships with their competitors and their predators, is rooted in both field work and in natural history. As such it appeals to us at a very fundamental level. Instead of (or perhaps in addition to) swapping tales around the campfire at night, we communicate by publishing in journals or books.

Furthermore, without the basic data from population studies, most landscape and ecosystem studies would either be impossible to carry out, or would lack fundamental

meaning. The advantage of ecosystem studies is the comprehensiveness of the approach. However, the disadvantage is the complexity of interactions among species and our lack of understanding of community organization. Everyone can agree, I believe, that we need a better understanding of interspecific interactions, and this is the role of population ecology. To develop laws of ecosystem functioning, we need to comprehend how individual populations behave. From there we can develop an understanding of interactions among populations. Therefore it seems to me that studies at the landscape and ecosystem level must be informed by data first gathered by population ecologists.

But this all sounds rather grand and theoretical. In the real world, knowledge of population ecology is absolutely necessary for conservation biologists, wildlife managers, and resource biologists. They are often faced with problems of preserving biodiversity or a wild living resource without adequate information. How can they best decide whether to limit or even shut down a fishery and for how long? Is it necessary or wise to allow wolf hunting in Alaska in order to increase the caribou herd? How do we control deer populations or is it foolish to attempt to control them in urban environments such as Rock Creek Park in Washington, D.C.? Has the introduction of wolves into Yellowstone actually decreased the elk herds? What are causes of reptile and amphibian declines throughout much of the world? What accounts for the proliferation of Lyme Disease in North America? Although an ecosystem approach may be helpful and necessary to answer many of these questions, basic population data are also necessary. Beyond this we must understand how populations with different life histories grow and/or are limited. We need a fundamental understand of the roles of competitors, parasites and predators and their potential effects on a given population.

When Audubon was in the state of Kentucky in 1813, he witnessed the passing of a great flock of passenger pigeons (*Ectopistes migratoris*). This flock blackened the sky for more than 3 days as they passed overhead. Later Audubon estimated their numbers at between 1.1 and 25 billion birds (Souder 2004). Yet the last passenger pigeon was shot in the wild in 1900, and the last individual in captivity died in 1914. How can a population decline to extinction so swiftly, even if one acknowledges the role of hunting and habitat destruction?

Red grouse go through population cycles every 4–5 years. The numbers oscillate over three orders of magnitude (Hudson et al. 1998), and these oscillations are synchronized over large geographical areas (Cattadori et al. 2005). Yet the population recovers regularly. On the other hand, when tawny owls (*Strix aluco*) were studied in Oxford, the number of mating pairs remained steady, at 17–30 pairs, even though their major rodent prey species oscillated from 10–150 per acre (Southern 1970). What are the differences between red grouse and tawny owls: reproductive parameters, developmental time, or survivorship? Or is it the fact that red grouse are primarily herbivores and owls primarily predators? Are there differences in their competitors, parasites, or predators? These are questions that only knowledge of population ecology allows us to answer.

When the moose population crashed in Isle Royale in Lake Superior, Michigan, in the late 1990s, was the cause wolf predation? Or was it parasites or over-browsing of the vegetation? By 2013 the wolf population was in decline and moose population was increasing, but fitting this interaction to a simple predator–prey model has proven problematic (Mlot 2013). Wildlife scientists have complained for many years that white-tailed deer are over-browsing their habitats and causing changes in the

vegetation. If so, why don't these deer populations crash? Is the recent movement of coyotes into the eastern United States and puma into the mid-western United States the result of these large white-tailed deer populations? If not, what explains these dispersals from the "wild west" to the more urbanized areas of the United States, east of the Mississippi River (Bozarth et al. 2011)? One goal of this book is to give you the background and weapons that will allow you to address these questions.

In the twentieth century, the principles of population ecology, as we understood them, were applied to agriculture, forestry, wildlife management, fisheries, and conservation biology. Exploitation of populations in the name of "maximum sustainable yield" was based on the flawed logistic equation and/or inadequate data. Before the days of environmental impact statements, however, politicians and engineers largely ignored advice based on ecological science. While this situation has changed, ecologists, in order to remain credible, must work to develop better theoretical approaches. Applied ecologists must be able to recognize which of several possible theoretical approaches to use for the population or community of concern. The purpose of this book is to help guide undergraduates, graduate students, future wildlife refuge managers, EPA officials, or other applied ecologists through the workings of basic population principles and theory so that they make wise decisions in the future.

In part one of this book we will establish the fundamentals of population growth for single species populations. After determining these basic properties, we will examine how intraspecific competition affects population characteristics. We will also consider the evolution of different types of life histories and discuss whether a biological population is naturally "regulated."

Once we have an understanding of how single populations grow and sustain themselves in particular environments, we can begin to examine how interactions with populations of other species affect their life histories. In part two we will progress to an examination of interspecific interactions such as competition, predation, parasitism, and mutualism. Finally, as we move through these interactions, we can evaluate their relative importance in population growth and regulation.

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1 Density independent growth

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1.1 Introduction

1.1.1 *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. 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.”

However, as discussed by Waples and Gaggiotti (2006) the term population has a myriad of definitions depending on whether the context is ecological, evolutionary, or statistical. They list six different definitions within the ecological context, but I remain satisfied that they all converge on either the first definition I presented above and/or the Turchin (2003) definition.

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 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. In actuality, a population is often defined by the investigator(s) and may be somewhat arbitrary.

1.1.2 *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 (Morris and Doak 2002) and the Amboseli baboon (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.” Or as May (2010, p. 8) put it, “Mathematics is ultimately no more ... or less than a way of thinking clearly.” Thus, 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.

1.1.3 *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, or a phenomenon such as the population cycles known for snowshoe hares, 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.

It should be noted that Turchin stimulated a number of rebuttals to his proposal of three fundamental “laws” of population ecology (Berryman 2003; O’Hara 2005; Owen-Smith 2005). My particular favorite is O’Hara’s “The anarchist’s guide to ecological theory. Or, we don’t need no stinkin’ laws.” He states that “law” is much too strong a word, although he is willing to accept the term, “principle.” He asserts that, “calling them laws is to give them an epistemological status that they do not deserve ... the laws are not strict enough to judge if a species has broken a law” (O’Hara 2005, p. 393).

Nevertheless, I find these ideas useful as a set of null hypothesis with which to begin our study of population ecology.

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 (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, and seed production) or through asexual reproduction (i.e., binary fission, budding, asexual spores, and 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 and is based on the interaction of the genotype with the biological and physical environment.

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, the fertility rate of the human population of the world declined from 28 per thousand in 1981, to 20 births per thousand in 2012. Meanwhile, the birth rate in North America moved slightly downward from 16 per thousand in 1981 to 13 per thousand in 2013 (Anonymous 2012). 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.

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 2012 was 8 per thousand, a decrease from 11 per thousand in 1981. In North America, the comparable figures are: 9 per thousand in 1981 and 8 per thousand in 2012 (Anonymous 2012).

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

Table 1.1 Statistics for human populations of Asia and Europe in 2012.

Region	Population size (millions)	Birth rate (per thousand)	Death rate (per thousand)	Rate of increase per individual (r)	Percent of the population less than 15 years of age
Asia	4,260	18	7	0.011	25
Europe	740	11	11	0.000	16

Birth and death rates are per thousand; r is per individual.

Source: Anonymous 2012. Data from the Population Reference Bureau.

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 2012 (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. The percentage of the population under 15 years of age in Asia is 25, while that of Europe is a mere 16.

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) 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:

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

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

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

From Table 1.1 we see that Asia had a positive growth rate, whereas Europe actually had a projected growth rate of zero in 2012. 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 also has a shorter generation time, which would affect population growth for a number of years. The estimated growth rate parameter, r (equation 1.1b), 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.

- 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.
- The emigration rate is the number of individuals that leave the population per time interval, and how old they are when they leave.

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 20 years (Hanski 1999). Levins (1969) 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 or 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 applicability 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; i.e., the population at time = 0, and project it t time units into the future. This is 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:

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

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 $t - t + 1$;

I = the number of immigrants and E = the number of emigrants during this same time interval.

This equation can be rewritten as:

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

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 the net reproductive rate. Alternatively, the difference between b and d also equals λ , the growth rate per time period, usually per year. The 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 as shown in equation 1.2c.

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

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:

$$\frac{dN}{dt} = rN \quad (1.3)$$

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 (equation 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 “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), which 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. 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 an environmental limit termed 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. Therefore 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, an egg, or as 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. Alternatively, we use the finite rate of increase, λ , 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, generation time equals 13 or 17 years, and in these cases it is useful to make a distinction between the growth rate per generation as opposed to a finite rate of increase. That is, $R = \lambda$, when T , the generation time, equals 1 year.

To find R we often count one life stage of the population in successive years. For gypsy moths (Lepidoptera: *Lymantria dispar* L.) we estimate R by counting egg masses in successive years (See example 1, below). R is estimated from the ratio of egg masses at time $t + 1$ versus time t . For the periodical cicada, (Homoptera: *Magicicada septendecim* L.), 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:

$$R_1 = N_1/N_0$$

$$R_2 = N_2/N_1$$

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

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

$$\begin{aligned} N_1 &= N_0R \\ N_2 &= N_1R = (N_0R)R = N_0R^2 \\ N_3 &= N_2R = (N_0R^2)R = N_0R^3 \end{aligned}$$

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 (Figure 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 will use them in the equations below.

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

or

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

Fig. 1.1 Discrete or “geometric” growth in a population with non-overlapping generations.

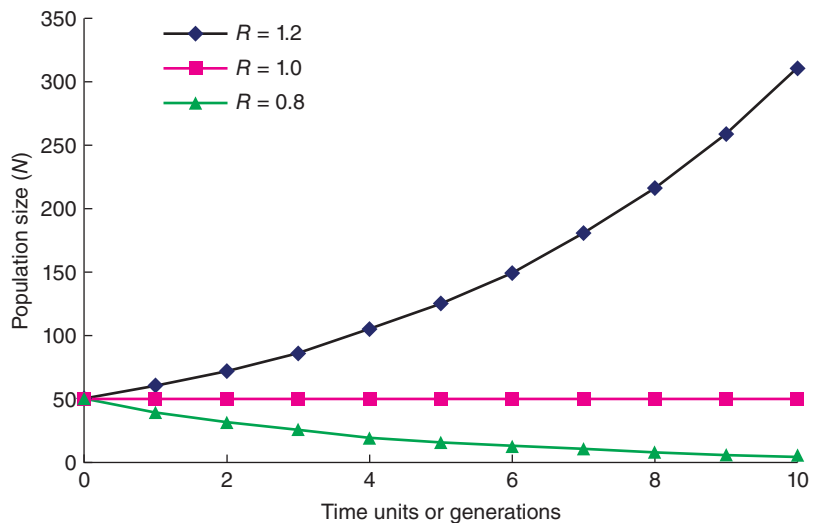
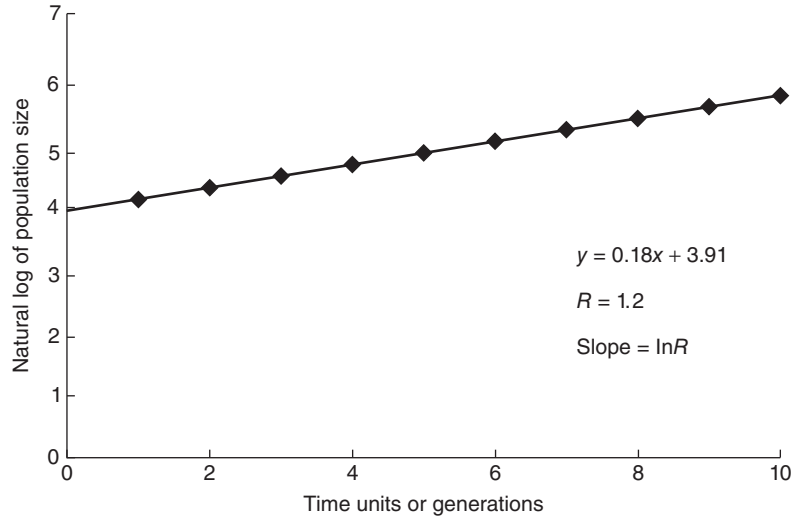


Fig. 1.2 Natural log of growth in a population with discrete generations.



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 Figure 1.2, the value of $R = 1.2$ and the slope is therefore $\ln(1.2)$ or 0.18.

Example 1.1 Gypsy moths (*Lymantria dispar* L.) 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, as noted above. 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 2013 there are, on average, four 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 2014, she finds five 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[®] 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 2016? In what year would spraying be required?

Answer:

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 2016, 3 years have passed since the original survey in 2013. Using equation 1.4:

$$N_{2016} = N_{2013}R^3 = (160)(1.25)^3 = 312.5$$

We therefore expect around 312 eggs per hectare in 2016.