3

Reproduction and the Drive for Survival

Introduction

This chapter is an introduction to cell structure and biological reproduction and the effects that these have on the survival of species according to the Darwinian model of evolution. The Darwinian model of evolution postulates that all living systems must compete for resources that are too limited to sustain all the organisms that are born. Those organisms possessing properties that are best suited to the environment can survive and may pass the favored properties to their offspring.

A system is said to be alive if it has certain properties. These life properties, e.g., metabolism, reproduction, and response to stimuli, interact with each other, and indeed, the interactions themselves must be part of the list of life properties.

Cells contain organelles, which are subcellular inclusions dedicated to performing specific tasks such as photosynthesis and protein synthesis. Membranes are organelles that are components of other organelles and are functional in their own right—they regulate material transport into and out of cells. Prokaryotic organisms (bacteria and blue-green algae) lack most organelles. Eukaryotic organisms (protozoa, fungi, plants, and animals) have cells with a wide range of organelles.

A cell's genetic information is contained along the length of certain organelles called chromosomes. In asexual reproduction, genetic material of one cell is exactly replicated and the identical copies are partitioned among two daughter cells. Thus the daughter cells end up with genetic information identical to that of the parent cell, a decided advantage if the environment is one in which the parent cell thrived. In multicellular organisms, certain genes may be "turned off" in mitosis; the result will be cells with different behaviors, which leads to the various tissues found in multicellular organisms. Genetic information is not lost in this way; it is merely inactivated, often reversibly. Mitosis also decreases the surface-to-volume ratio of cells, which allows the cell to take up food and release waste more easily.

Sexual reproduction, the combining of genetic information from two parents into one or more offspring, leads to variations among the offspring. This is achieved by the production of novel combinations of genetic information and by complex interactions between genetic materials affecting the same property. The result is the possibility

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for immense variation, which is one of the empirical observations at the heart of the Darwinian model.

Left unchecked, populations would grow exponentially, but factors in the environment always control the sizes of populations.

3.1 The Darwinian Model of Evolution

We introduce the Darwinian model of evolution, a model that ties all biology together. Finite resources of all kinds place limits on the reproduction and growth of organisms. All must compete for these resources and most will not get enough. Those that survive may pass their favorable properties to their offspring.

The diversity of organisms is represented by taxonomic categories.

A group of organisms is said to represent a *species* if there is real or potential exchange of genetic material among its members and they are reproductively isolated from all other such groups. Thus members of a single species are capable of interbreeding and producing fertile offspring. By inference, if individuals are very similar but reproductively isolated from one another, they are in different species. The definition above makes good sense in most cases: Horses and cows, different species, live in the same area but never mate; horses and donkeys, different species, may live in the same area and interbreed, but their offspring are sterile mules; lions and tigers, also different species, do not live in the same area, but have interbred in zoos to give sterile offspring. The definition also produces some odd results: St. Bernard dogs and chihuahuas would be in different species by the reproductive-isolation criterion, although both might be in the same species as, say, a fox terrier. English sparrows in the United States and in England would have to be put into different species, even though they are essentially identical. There are other, somewhat different definitions of species. For an in-depth discussion, see [5].

A group of species is a *genus* and a group of genera is a *family*. Higher levels are *orders*, *classes*, *phyla* (called *divisions* in plants), and *kingdoms*. To identify an organism, its generic and specific names are usually given in the following format: *Homo sapiens* (humans) or *Acer rubrum* (red maple trees).

Living systems operate under a set of powerful constraints.

1. *Available space is finite.* Some organisms can survive a few kilometers into the air or under water and others live a few meters under the ground, but that does not change the basic premise: Our planet is a sphere of fixed surface area and everything alive must share that area for all its needs, including nutrient procurement and waste disposal.
2. *The temperature range for life is very restricted.* Most living systems cannot function if their internal temperature is outside a range of about 0° to 50°C, the lower limitation being imposed by the destructive effect of ice crystals on

cell membranes, and the upper limit being imposed by heat inactivation of large molecules. Some organisms can extend this range a bit with special mechanisms, e.g., antifreeze-like substances in their bodies, but this temperature limitation is generally not too flexible.

3. *Energetic resources are limited.* The only energy sources originating on earth are geothermal, radioactive, and that which is available in some inorganic compounds. Some organisms, said to be *chemoautotrophic*, can use the latter compounds, but these organisms are exceptional. By far, the majority of the energy available for life comes from the sun. While the sun's energy is virtually inexhaustible, it tends not to accumulate in any long-term biological form on earth. This limitation lies in an empirical observation—the second law of thermodynamics—that energy becomes less useful as it undergoes transformation from one form to another. The transformations that solar energy undergoes are described by a food chain: the sun's energy is captured and used by photosynthetic plants, which are eaten by herbivores, which are eaten by carnivores, which die and are broken down by decomposing organisms. At each step, much of the useful energy is lost irreversibly to the immediate creation of disorder and/or to heat, which radiates away and creates disorder elsewhere. Thus the sun's radiant energy does not accumulate in living systems for longer than a single organism's lifetime, and must be constantly replenished. (See Yeargers [1] for further discussion.)

4. *Physical resources are finite.* Obviously, there is more mass to the inorganic world than to the organic one. The problem is that most of the earth's nonorganic mass is not available to the organisms that inhabit the earth's surface. For example, only tiny fractions of our planet's inventory of such critical materials as carbon, oxygen, and nitrogen are actually available to life. The rest is either underground or tied up in the form of compounds not chemically accessible to life.

The Darwinian model of evolution correlates biological diversity and the survival of species.

The four constraints listed above would not be so serious if living organisms were different from what they are. We might picture a world in which every organism was nonreproducing, had a constant size, and was immortal. Perhaps the organisms would be photosynthetic and would have unlimited supplies of oxygen, carbon dioxide, nitrogen, and other important inorganic substances. They would have infinite sinks for waste materials or would produce little waste in the first place.

The biological world just described is, of course, just the opposite of the real one, where there is rapid reproduction and a resultant competition for space and resources. Charles Darwin formulated a model to describe the nature and effect of this competition on living systems. This model may be presented as two empirical observations and two conclusions.

Observation 1. *More organisms are born than can survive to reproductive maturity.*

The high death toll among the young, from primitive plants to humans, is plain to see. There simply are not enough resources or space to go around, and the young are among the first to be affected.

Observation 2. *All organisms exhibit innate variability.*

While we are easily able to spot differences between humans or even other mammals, it is not easy for us to identify differences between members of a group of daffodils or coral snakes. The differences are there nonetheless, and if we observe the plants and snakes carefully, we will see that, because of the differences, some will thrive and others will not.

Conclusion 1. *The only organisms that will survive and reproduce are those whose individual innate variations make them well suited to the environment.*

Note the importance of context here: an organism suited to one environment may be totally unsuited to another. Note also the importance of reproduction; it is not enough to live—one must pass one's genes to subsequent generations. The ability to produce fertile offspring is called *fitness*. This combines the ability to attract a mate with the fertility of offspring. If Tarzan were sterile, he would have zero fitness in spite of mate attraction.

Conclusion 2. *Properties favored by selection can be passed on to offspring.*

Selection winnows out the unfit, i.e., those individuals whose innate properties make them less competitive in a given environmental context. The survivors can pass on favored characteristics to their progeny.

Reproductive isolation can generate new species.

Suppose that a population, or large, freely interbreeding group, of a species becomes divided in half, such that members of one half can no longer breed with the other half. Genetic mutations and selection in one half may be independent of that in the other half, leading to a divergence of properties between the two halves. After enough time passes, the two groups may accumulate enough differences to become different species, as defined in the previous section. This is the usual method for species creation (see also Section 15.1). An example is found at the Grand Canyon; the squirrels at the north and south rims of the canyon have evolved into different species by virtue of their geographical separation.

The idea of reproductive isolation may suggest geographical separation, but many other forms of separation will work as well. For example, one part of the population may mate at night and the other during the day, even if they occupy the same geographical area. As a second example, we return to dogs: St. Bernards and chihuahuas are reproductively isolated from each other.

3.2 Cells

A cell is not just a bag of sap. It is a mass of convoluted membranes that separate the inside of a cell from the outside world. These membranes also form internal structures that perform specialized tasks in support of the entire cell. Certain primitive cells, e.g., bacteria and some algae, have not developed most of these internal structures.

Organelles are cellular inclusions that perform particular tasks.

A cell is not a bag of homogeneous material. High-resolution electron microscopy shows that the interiors of cells contain numerous simple and complex structures, each functionally dedicated to one or more of the tasks that a cell needs carried out. The cell is thus analogous to a society, each different organelle contributing to the welfare of the whole. The sizes of organelles can range from about one-thousandth of a cell diameter to half a cell diameter, and the number of each kind can range from one to many thousands. The kinds of organelles that cells contain provide the basis for one of the most fundamental taxonomic dichotomies in biology: prokaryotes vs. eukaryotes.

Eukaryotes have many well-defined organelles and an extensive membrane system.

The group called the *eukaryotes*[1] include virtually all the kinds of organisms in our everyday world. Mammals, fish, worms, sponges, amoebas, trees, fungi, and most algae are in this group. As the name implies, they have obvious, membrane-limited nuclei. Among their many other organelles, all formed from membranes, one finds an *endoplasmic reticulum* for partitioning off internal compartments of the cell, *chloroplasts* for photosynthesis, *mitochondria* to get energy from food, *ribosomes* for protein synthesis, and an external membrane to regulate the movement of materials into and out of the cell.

Prokaryotic cells have a very limited set of organelles.

The organisms called the *prokaryotes*[2] include only two groups, the bacteria and the blue-green algae. They lack a matrix of internal membranes and most other organelles found in eukaryotes. They have genetic material in a more-or-less localized region, but it is not bounded by a membrane; thus prokaryotes lack true nuclei. Prokaryotes have *ribosomes* for protein synthesis, but they are much simpler than those of eukaryotes. The function of prokaryotic mitochondria—getting energy from foods—is performed in specialized regions of the plasma membrane, and the chlorophyll of photosynthetic prokaryotes is not confined to chloroplasts.

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[1] The word means “with true nuclei.”

[2] Prokaryotes lack true nuclei.

3.3 Replication of Living Systems

Living systems can be understood only in terms of the integration of elemental processes into a unified whole. It is the organic whole that defines life, not the components.

Asexual reproduction can replace those members of a species that die. The new organisms will be genetically identical to the parent organism. To the extent that the environment does not change, the newly generated organisms should be well suited to that environment.

Sexual reproduction results in offspring containing genetic material from two parents. It not only replaces organisms that die, but provides the new members with properties different from those of their parents. Thus Darwinian selection will maximize the chance that some of the new organisms will fit better into their environment than did their parents.

What do we mean by a "living system"?

To deal with this question we need to back up conceptually and ask how we know whether something is alive in the first place. This question causes at least mild embarrassment to every thinking biologist. All scientists know that the solution of any problem must begin with clear definitions of fundamental terms and yet a definition of "life" is as elusive as quicksilver.

If we start with the notion that a definition of a "living system" must come before anything else in biology, then that definition should use only nonbiological terms. However, one virtually always sees living systems defined by taking a group of things everyone has already agreed to be living things, and then listing properties they have in common. Examples of these life properties are organization, response to stimuli, metabolism, growth, evolution, and, of course, reproduction. A system is said to be alive if it has these properties (and/or others) because other systems that have these properties are, by consensus, alive. Thus living systems end up being defined in terms of living systems. This definition is a recursive one: The first case is simply given, and all subsequent cases are defined in terms of one or more preceding ones.

The list of life properties against which a putative living system would be compared is an interesting one because no one property is sufficient. For example, a building is organized, dynamite responds to stimuli, many metabolic reactions can be carried out in a test tube, salt crystals grow, mountain ranges evolve, and many chemical reactions are autocatalytic, spawning like reactions. Of course, we could always insist that the putative system should exhibit two or more of the properties, but clever people will find a nonliving exception.

In spite of these objections, definition by precedent, applied to living systems, has an appealing practicality and simplicity—most six-year-olds are quite expert at creating such definitions. At a more intellectual level, however, recursion always leaves us with the bothersome matter of the first case, which must be accepted as axiomatic—an idea foreign to biology—or accepted as a matter of faith, an idea that makes most scientists cringe.

One way out of this dilemma is to drop the pretense of objectivity. After all, almost everyone, scientist or lay person, will agree with each other that something is or isn't alive. One wag has said, "It's like my wife—I can't define her, but I always know her when I see her." There is, however, a more satisfying way to handle this problem, and that is to note the unity of the life properties list: The listed properties are related to each other. For instance, only a highly organized system could contain enough information to metabolize and therefore to respond to stimuli. A group of organisms evolves and/or grows when some of its members respond to stimuli in certain ways, leading some to thrive and some not. Reproduction, which requires metabolism and growth, can produce variation upon which selection acts. Selection, in turn, requires reproduction to replace those organisms that were weeded out by selection.

We see then that living systems perform numerous elemental processes, none of which is unique to living systems. *What is unique to living systems is the integration of all these processes into a unified, smoothly functioning whole.* Any attempt to limit our focus to one process in isolation will miss the point; for example, we must view reproduction as one part of a highly interacting system of processes. This does not preclude discussion of the individual processes—but it is their *mutual interactions* that characterize life. In Chapter 8, we will further discuss the importance of organization to biological systems by considering biomolecular structure.

Why do living systems reproduce?

To try to answer this question we must first lay some groundwork by stating something that is obvious: Every organism is capable of dying. If an organism were incapable of any kind of reproduction, it would surely die at some point and would not be here for us to observe.[3] Reproduction is therefore required as part of any lifestyle that includes the possibility of death, i.e., it includes all living things.

The cause of an organism's death may be built-in, i.e., its life span may be genetically preprogrammed. Alternatively, the organism may wear out, a notion called the "wear-and-tear" theory, suggesting that we collect chemical and physical injuries until something critical in us stops working. Finally, some other organism, ranging from a virus to a grizzly bear, may kill the organism in the course of disease or predation.

A number of reproductive modes have evolved since life began, but they may be collected into two broad categories—asexual and sexual. Asexual reproduction itself is associated with three phenomena: First, there is the matter of a cell's surface-to-volume ratio, which affects the cell's ability to take up food and to produce and release waste. Second, asexual reproduction allows the formation of daughter cells identical to the parent cell, thus providing for metabolic continuity under nonvarying environmental conditions. Third, asexual reproduction allows multicellular organisms to develop physiologically different tissues by allowing genetic information to be switched on and off. This provides for organ formation.

Sexual reproduction, on the other hand, rearranges genetic information by combining genetic contributions from two parents in novel ways; this provides a range

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[3] This reasoning is analogous to the "anthropic principle" of cosmology, in response to the question "Why does our universe exist?" The principle says that if any *other* kind of universe existed, we would not be here to observe it. (We do not wish to get too metaphysical here.)

of variations in offspring upon which selection can act. In Chapter 13, we will describe the details of asexual and sexual reproduction in cells. Here we will restrict our discussion to general principles.

Simple cell division changes the surface-to-volume ratio $\frac{S}{V}$ *of a cell.*

An interesting model connects asexual cell division to waste management. Consider a metabolizing spherical cell of radius R: The amount of waste the cell produces ought to be roughly proportional to the mass, and therefore to the volume, of the cell. The volume V of a sphere is proportional to R^3. On the other hand, the ability of the cell to get rid of waste ought to be proportional to the surface area of the cell, because waste remains in the cell until it crosses the outer cell membrane on the way out. The surface area S is proportional to R^2. As a result, the ratio $\frac{S}{V}$, a measure of the cell's ability to get rid of its waste to the cell's production of waste, is proportional to R^{-1}. For each kind of cell there must be some minimum value permitted for the ratio $\frac{S}{V} = \frac{1}{R}$, a value at which waste collects faster than the cell can get rid of it. This requires that the cell divide, thus decreasing R and increasing $\frac{S}{V}$. A similar model, describing the ability of a cell to take up and utilize food, should be obvious.

Asexual reproduction maintains the genetic material of a single parent in its offspring.

In general, asexual reproduction leads to offspring that are genetically identical to the parent cell. This will be especially useful if the environment is relatively constant; the offspring will thrive in the same environment in which the parent thrived.

Most eukaryotic cells replicate asexually by a process called *mitosis*.[4] In mitosis, a cell's genetic material is copied and each of two daughter cells gets one of the identical copies. At the same time, the cytoplasm and its organelles are divided equally among the daughter cells. Single-celled organisms, such as amoebas, divide asexually by mitosis, as do the individual cells of multicellular organisms like daisies and humans. The details of mitosis are spelled out in Chapter 13, where we also describe how the various cells of a multicellular organism get to be different, in spite of their generation by mitosis.

Entire multicellular organisms can reproduce asexually. A cut-up starfish can yield a complete starfish from each piece. Colonies of trees are generated by the spreading root system of a single tree. These and similar processes create offspring that are genetically identical to the parent.

The various tissues of multicellular organisms are created by turning genes on and off.

A human has dozens of physiologically and anatomically different kinds of cell types. Virtually all of them result from mitosis in a fertilized egg. Thus we might expect them all to be identical because they have the same genes.[5]

The differences between the cells is attributable to different active gene sets. The active genes in a liver cell are not the same ones active in a skin cell. Nevertheless,

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[4] Bacteria reproduce asexually by a somewhat different process, called binary fission. We will not go into it.

the liver cell and the skin cell contain the same genes, but each cell type has turned off those not appropriate to that cell's function.

Sexual reproduction provides for variation in offspring.

Sexual reproduction is characterized by offspring whose genetic material is contributed by two different parents. The interesting thing about the two contributions is that they do not simply add to one another. Rather, they combine in unexpected ways to yield offspring that are often quite different from either parent. Further, each offspring will generally be different from the other offspring. We have only to compare ourselves to our parents and siblings to verify this.

The variations induced by sexual reproduction maximize the chance that at least a few progeny will find a given environment to be hospitable. Of course, this also means that many will die, but in nature that is no problem because those that die will serve as food for some other organism. Note the lack of mercy here—many variants are tried by sexual reproduction and most die. The few survivors perpetuate the species.

Sexual reproduction is found in a very wide variety of organisms, ranging from humans to single-celled organisms such as amoebas and bacteria. In fact, organisms whose life cycles exclude sexual reproduction are so unusual that they are generally put into special taxonomic categories based solely on that fact. In simple organisms, sexual reproduction may not result in increased numbers, but the offspring will be different from the parent cells. Chapter 13 and references [2] and [3] contain detailed discussions of sexual reproduction and genetics.

3.4 Population Growth and Its Limitations

The size of a population, and its trend, has vital significance for that population, for interacting populations, and for the environment. It is believed that the Polynesian population of Easter Island grew too large to be supported by the island's resources, with disastrous consequences for most of the flora and fauna of the island. A large seagull population living near a puffin rookery spells high chick losses for the puffins. And in another example, at the height of a disease, the pathogen load on the victim can reach 10^9 *organisms per milliliter.*

We now combine the topics of the two previous sections of this chapter, namely, the increase in an organism's numbers and the struggle among them for survival. The result is that in a real situation, population growth is limited.

Unchecked growth of a population is exponential.

One of the observations of the Darwinian model of evolution is that more organisms

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[5] As always, there are notable exceptions. Mammalian red blood cells have nuclei when they are first formed, but lose them and spend most of their lives anucleate, therefore without genes.

are born than can possibly survive. (We use the word "born" here in a very broad sense to include all instances of sexual and asexual reproduction.) Let us suppose for a moment that some organism is capable of unchecked reproduction, doubling its numbers at each reproductive cycle. One would become two, then two would become four, four would become eight, etc. After N reproductive cycles, there would be 2^N organisms. If the organism's numbers increased M-fold at each reproductive cycle, there would be M^N organisms after N reproductive cycles. This kind of growth is exponential, and it can rapidly lead to huge numbers. Table 3.4.1 shows the numbers generated by an organism that doubles at each cycle.

Table 3.4.1.

***N*:**	0	1	2	10	25	40	72
Number of organisms:	1	2	4	1024	3.4×10^7	1.1×10^{12}	4.7×10^{21}

Many bacteria can double their numbers every 20 minutes. Each cell could therefore potentially generate 4.7×10^{21} cells per day. To put this number into perspective, a typical bacterium has a mass on the order of 10^{-12} grams, and a day of reproduction could then produce a mass of 4.7×10^9 grams of bacteria from each original cell. Assuming that the cells have the density of water, 1 gm/cm^3, 10^9 grams is the mass of a solid block of bacteria about 1.6 meters on a side. Obviously, no such thing actually happens.

Real life: Population growth meets environmental resistance.

Every population has births (in the broad sense described above) and it has deaths. The net growth in numbers is (births − deaths). The *per capita growth rate*, r, is defined by[6]

$$r = \frac{\text{birth rate} - \text{death rate}}{\text{population size}}.$$

The maximum value that r can have for an organism is $r_{\max}$, called the *biotic potential*. Estimates of $r_{\max}$ have been made by Brewer [4]. They range from about 0.03 per year for large mammals to about 10 per year for insects and about 10,000 per year for bacteria. These numbers are all positive, and we therefore expect organisms growing at their biotic potential to increase in numbers over time, not so dramatically as described by Table 3.4.1, but constantly increasing nevertheless.

We must remember that $r_{\max}$ is the rate of natural increase under optimal conditions, which seldom exist. Under suboptimal conditions, the birth rate will be low and the death rate high, and these conditions may even lead the value of r to be negative. In any case, the value of r will drop as inimical environmental factors make

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[6] The units of birth rate are (numbers of births per time) and those of death rate are (number of deaths per time). The units of population are (numbers of individuals) and r is in units of (time)$^{-1}$.

themselves felt. These factors are collectively called *environmental resistance*, and they are responsible for the fact that we are not waist-deep in bacteria or, for that matter, dogs or crabgrass.

From our discussion of evolution, we now understand that some organisms have a higher tolerance for environmental resistance than do others. Those with the highest tolerance will prosper at the expense of those with low tolerance. Our experience, however, is that every species is ultimately controlled at *some* level by environmental resistance.

3.5 The Exponential Model for Growth and Decay

Despite its simplicity, most populations do in fact increase exponentially at some time over their existence. There are two parameters governing the process, initial population size and the per capita growth rate. Both or either may be easily determined from experimental data by least squares.

If the growth rate parameter is negative, then the process is exponential decay. Although populations sometimes collapse catastrophically, they can also decline exponentially. Moreover, exponential decay pertains to other phenomena as well, such as radioactive decay. In conjunction with decay processes, it is customary to recast the growth rate as a half-life.

A constant per capita growth rate leads to exponential growth.

By a population we mean an interbreeding subpopulation of a species. Often this implies geographical localization, for example, the Easter Island community, or a bacterial colony within a petri dish. The first published model for predicting population size was by Thomas Malthus in 1798, who assumed that the growth rate of a population is proportional to their numbers y, that is,

$$\frac{dy}{dt} = ry, \tag{3.5.1}$$

where r is the constant of proportionality. By dividing (3.5.1) by y, we see that r is the per capita grow rate,

$$\frac{1}{y}\frac{dy}{dt} = r$$

with units of per time, e.g., per second. Hence Malthus's law assumes the per capita growth rate to be constant. For a no-growth, replacement-only colony, r will be zero.

Malthus's model is a vast oversimplification of survival and reproduction. Although population size can only be integer-valued in reality, by incorporating the derivative $\frac{dy}{dt}$, y is necessarily a continuous variable in this model; it can take on any nonnegative value. Further, the parameter r must be taken as an average value over all population members. Therefore, (3.5.1) is a continuum model and does not apply to extremely small populations. Nevertheless, it captures a germ of truth about population dynamics and is mathematically tractable. It is a significant first step from which better models emerge and to which other models are compared.

If these approximations are a concern, one can opt for a discrete model. The differential equation is replaced by a difference equation instead:

$$y_{t+1} - y_t = \rho y_t, \qquad t = 0, 1, 2, \ldots. \tag{3.5.2}$$

This model provides for increments to the population at the discrete times indicated in (3.5.2). The size of the population at time t is y_t. The relationship between the instantaneous growth rate r of the continuous model and that, ρ, of this one was worked out in Section 2.5; we repeat it here:

$$e^r = 1 + \rho. \tag{3.5.3}$$

In Table 3.5.1, we see that the two models agree closely for growth rates up to 6% or so.

Table 3.5.1. Discrete vs. continuous growth rates.

r	$1 + r$	e^r
0	1	1
0.01	1.01	1.010
0.02	1.02	1.020
0.03	1.03	1.030
0.04	1.04	1.041
0.05	1.05	1.051
0.06	1.06	1.062

From Section 2.5, the solution of the discrete model is given by

$$y_t = (1 + \rho)^t y_0,$$

where y_0 is the initial population size. For the solution of the continuous model, we must solve its differential equation.

Equation (3.5.1) can be solved by separating the y and t variables and integrating,

$$\frac{dy}{y} = r dt \quad \text{or} \quad \int \frac{dy}{y} = \int r dt.$$

These integrals evaluate to

$$\ln y = rt + c,$$

where c is the constant of integration. Exponentiate both sides to obtain

$$y = e^{rt+c}, \quad \text{or} \quad y = y_0 e^{rt}, \tag{3.5.4}$$

where $y_0 = e^c$. In this, the parameter y_0 is the value of y when $t = 0$; cf. Section 2.4.

Under Malthus's law (3.5.4), a population increases *exponentially*, ash shown by the solid curve in Figure 3.5.5. While exponential growth cannot continue indefinitely, it is observed for populations when resources are abundant and population density is low; compare the data designated by the circles in Figure 3.5.5. Under these conditions, populations approximate their biotic potential, $r_{\max}$; cf. Section 3.4.

The per capita growth rate parameter r is often given in terms of *doubling time*. Denote by T_2 the time when the population size reaches twice its initial value; from (3.5.4), we get

$$2y_0 = y_0 e^{rT_2}.$$

Divide out y_0 and solve for T_2 by first taking the logarithm of both sides,

$$\ln 2 = rT_2,$$

and then dividing by r; the doubling time works out to be

$$T_2 = \frac{\ln 2}{r} \approx \frac{0.7}{r}. \tag{3.5.5}$$

Thus the per capita growth rate and doubling time are inversely related, a higher per capita growth rate makes for a shorter doubling time and conversely. Rearranging (3.5.5) gives the per capita growth rate in terms of doubling time,

$$r = \frac{\ln 2}{T_2}. \tag{3.5.6}$$

Growth rate parameters are not always positive. In the presence of serious adversity, a population can die off exponentially. To make it explicit that the parameter is negative, the sign is usually written out,

$$y = y_0 e^{-\mu t}, \tag{3.5.7}$$

where $\mu > 0$. Such an exponential decay process is characterized by its *half-life* $T_{1/2}$, given by

$$\frac{1}{2} y_0 = y_0 e^{-\mu T_{1/2}},$$

or

$$T_{1/2} = \frac{\ln 2}{\mu} \approx \frac{0.7}{\mu}. \tag{3.5.8}$$

Exponential growth and decay apply to other natural phenomena as well as biological processes. One of these is radioactive decay, where emissions occur in proportion to the amount of radioactive material remaining. The activity of a material in this regard is measured in terms of half-life; for example, the half-life of ^{14}C is about 5700 years. Radioactive decay is the scientific basis behind various artifact dating methods using different isotopes. Figure 3.5.1 is a chart for carbon-14.

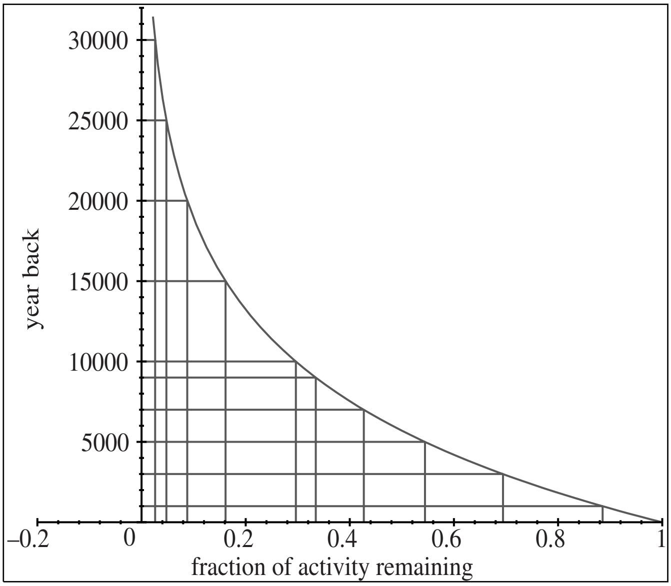


Fig. 3.5.1. Decay of carbon-14.

As observed above, Malthus's assumption of immediate reproduction embodied in (3.5.1) hardly seems accurate. Mammals, for instance, undergo a lengthy maturation period. Further, since no real population grows unboundedly, the assumption of constant per capita growth breaks down eventually for all organisms. Nevertheless, there is often a phase in the growth of populations, even populations of organisms with structured life cycles, during which exponential grow is in fact observed. This is referred to as the *exponential growth phase* of the population.

It is possible to mathematically account for a maturation period and hence more accurately model population growth. This is done by the incorporation of a *delay*, τ, between the time offspring are born and the time they reproduce. In differential equation form, we have

$$\left.\frac{dy}{dt}\right|_t = r \cdot y(t-\tau); \tag{3.5.9}$$

in words, the growth rate at the present time is proportional to the population size τ time units ago (births within the last τ period of time do not contribute offspring). Equation (3.5.9) is an example of a *delay differential equation*. An initial condition for the equation must prescribe $y(t)$ for $-\tau \le t \le 0$. As an illustration, let $r = 1$, $\tau = 1$, and $y(t) = e^{t/10}$ for $-1 \le t \le 0$ as an initial condition. Begin by setting $f_0(t)$ to this initial function and solving

$$\frac{dy}{dt} = f_0(t-1)$$

for y on the interval [0, 1], that is, for $0 \le t \le 1$. In this, solving means integrating, since the right-hand side is a given function of t. Define this solution to be $f_1(t)$ and repeat the procedure with it to get a solution on $[1, 2]$. Continue in this way, moving ahead by steps of length 1.

Code 3.5.1 is a computational procedure that produces the graph of a solution for (3.5.9).

Code 3.5.1.

Maple
```
> f0:=t–>exp(t/10);dsolve({diff(y(t),t)=f0(t-1),y(0)=f0(0)},y(t));
> f1:=unapply(rhs(%),t);dsolve({diff(y(t),t)=f1(t-1),y(1)=f1(1)},y(t));
> f2:=unapply(rhs(%),t);dsolve({diff(y(t),t)=f2(t-1),y(2)=f2(2)},y(t));
> f3:=unapply(rhs(%),t);
> plot({[t,f0(t),t=-1..0],[t,f1(t),t=0..1],[t,f2(t),t=1..2],[t,f3(t),t=2..3]},t=-1..3,y=-1..6,color=black);
```

Matlab
```
  % make an m-file, delayFcn0.m:
  %   function y=delayFcn0(t)
  %   y = exp(t/10);
> N=10; % # steps per unit interval
> delT=1/N; % so delta t=0.1
  % t is now linked to index i by t=-1+(i-1)*delT
  % set initial values via delay fcn f0
> for i=1:N+1
>    t=-1+(i-1)*delT; f(i)=delayFcn0(t);
> end
  % work from t=0 in steps of delT
  % ending time tfinal = 2, ending index is n
  % solve tfinal=-1+(n-1)*delT for n
> n=(2+1)*N+1;
> for i=N+1:n-1
>    t=-1+(i-1)*delT;
>    delY=f(i-N)*delT; % N back = delay of 1
>    f(i+1)=f(i)+delY; % Euler's method
> end
> t=-1:delT:2; plot(t,f);
```

Delay can also be incorporated into the discrete model in the same way. Equation (3.5.2) is modified to

$$y_{t+1} - y_t = \rho y_{t-\tau}, \quad t = 0, 1, 2, \ldots.$$

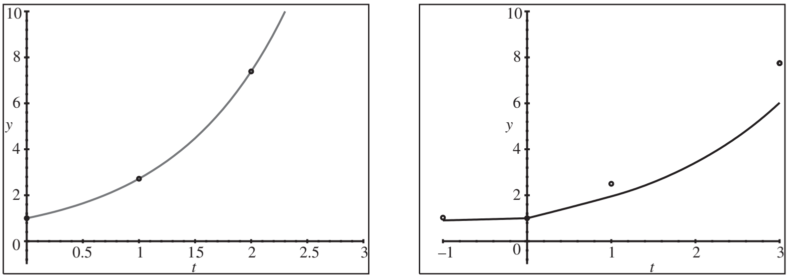
Just as for the continuous model, the values $y_{-\tau}, y_{-\tau+1}, \ldots, y_0$ must be prescribed.

A comparison of delay vs. no delay for both the continuous and discrete models is presented in Figure 3.5.2. Although the increase in population size is reduced under grow with delay, the population still follows an exponential-like growth law. The extent to which this is "exponential" is examined in the exercises.

Growth parameters can be determined from experimental data.

Exponential growth entails two parameters, initial population size y_0 and growth rate r. Given n experimental data values, $(t_1, y_1), (t_2, y_2), \ldots, (t_n, y_n)$, we would like to find the specific parameter values for the experiment. As discussed in Section 2.2, this is done by the method of least squares. We first put the equation into a form linear with respect to the parameters; take the logarithm of both sides of (3.5.4):

$$\ln y = \ln y_0 + rt. \tag{3.5.10}$$



(a) Growth with no delay.

(b) Growth with delay.

Fig. 3.5.2. The solid curves show the continuous model; circles show growth for the discrete model.

Now use equations (2.2.3) with ln y playing the role of y and t playing the role of x; in turn, the parameters are ln y_0 playing the role of b and r standing in for m. We get

$$\ln y_0 = \frac{\sum_{i=1}^{n} t_i^2 \sum_{i=1}^{n} \ln y_i - \sum_{i=1}^{n} t_i \sum_{i=1}^{n} t_i \ln y_i}{n \sum_{i=1}^{n} t_i^2 - \left(\sum_{i=1}^{n} t_i\right)^2}$$

and

$$r = \frac{n \sum_{i=1}^{n} t_i \ln y_i - \sum_{i=1}^{n} t_i \sum_{i=1}^{n} \ln y_i}{n \sum_{i=1}^{n} t_i^2 - \left(\sum_{i=1}^{n} t_i\right)^2}.$$

A slightly different problem presents itself when we are sure of the initial population size, y_0, and only want to determine r by fit. If there were no experimental error, only one data value (t_1, y_1), besides the starting one, would be needed for this; thus

$$y_1 = y_0 e^{rt_1},$$

so

$$r = \frac{\ln y_1 - \ln y_0}{t_1}.$$

Unfortunately, however, experimental error invariably affects data, and performing this calculation using two data values will likely result in two different (but close) values of r. Given n data values (beyond the starting one), $(t_1, y_1), (t_2, y_2), \ldots, (t_n, y_n)$, there will be n corresponding calculations of r. Which is the right one?

To solve this, we use a specialization of the least squares method. As above, we use the logarithm form of Malthus's equation, (3.5.10); squared error is then given by

$$E = \sum_{i=1}^{n} [\ln y_i - (\ln y_0 + rt_i)]^2. \tag{3.5.11}$$

As before, differentiate E with respect to r and set the derivative to zero:

$$2\sum_{i=1}^{n}[\ln y_i - (\ln y_0 + rt_i)](-t_i) = 0.$$

Now solve this for r and get

$$r = \frac{\sum_{i=1}^{n} t_i(\ln y_i - \ln y_0)}{\sum_{i=1}^{n} t_i^2}. \tag{3.5.12}$$

Alternatively, we can let the computer algebra system derive (3.5.12) as follows:

Suppose the starting value is known, $y(0) = A$, and we have data given symbolically as

$$\{[a[1], b[1]], [a[2], b[2]], [a[3], b[3]]\}.$$

We find the value of r given in (3.5.12) for this general problem in the following manner:

```
  Maple
> xval:=[seq(a[i],i=1..3)];
> yval:=[seq(b[i],i=1..3)];
> lny:=map(ln,yval);
> with(stats);
> fit[leastsquare[[x,y],y=r*x+ln(A),{r}]]([xval,lny]);
> coeff(rhs(%),x);
> combine(simplify(%));
```

```
  Matlab
  % least squares for r in y=A*exp(rt)
> A=2;
> t=[1 2 3]; % time data
> y=[3 5 9]; % corresponding y data
> lny=log(y)-log(A); % map to log and subtract bias
> M=t'; % set up independent variables M matrix
> r=M\(lny') % and solve
```

Example 3.5.1 (the U.S. census data). To illustrate these ideas, we determine the per capita growth rate for the U.S. over the years 1790–1990. In Table 3.5.2, we give the U.S. census for every 10 years, the period required by the U.S. Constitution.

Table 3.5.2. U.S. population census. (Source: *Statistical Abstracts of the United States*, 113th ed., Bureau of the Census, U.S. Department of Commerce, Washington, DC, 1993.)

1790	3929214	1860	31433321	1930	122775046
1800	5308483	1870	39818449	1940	131669275
1810	7239881	1880	50155783	1950	151325798
1820	9638453	1890	62947714	1960	179323175
1830	12866020	1900	75994575	1970	203302031
1840	17069453	1910	91972266	1980	226545805
1850	23191876	1920	105710620	1990	248709873

First, we plot the data to note that it does seem to grow exponentially. We read in population data as millions of people and plot the data in order to see that the population apparently is growing exponentially.

```
  MAPLE
> restart;
> tt:=[seq(1790+i*10,i=0..20)];
> pop:=[3.929214, 5.308483, 7.239881, 9.638453, 12.866020, 17.069453, 23.191876, 31.433321,
        39.818449, 50.155783, 62.947714, 75.994575, 91.972266, 105.710620, 122.775046,
        131.669275, 151.325798,179.323175, 203.302031, 226.545805, 248.709873];
> data:=[seq([tt[i],pop[i]],i=1..21)];
> plot(data,style=POINT,symbol=CROSS,tickmarks=[4,5]);
```

```
  MATLAB
> tt=[1790:10:1990];
> pop=[3.929214 5.308483 7.239881 9.638453 12.866020 17.069453 23.191876 31.433321 39.818449 …
       50.155783 62.947714 75.994575 91.972266 105.710620 122.775046 131.669275 151.325798 …
       179.323175 203.302031 226.545805 248.709873];
> plot(tt,pop,'o');
```

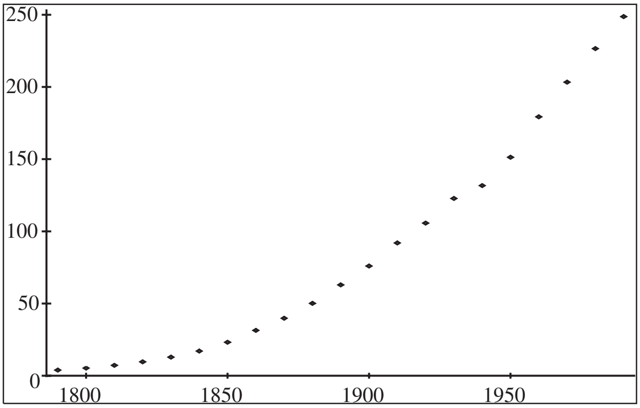


Fig. 3.5.3. Population data for the U.S.: years vs. millions of people.

In order to make the data manageable, we rescale the time data by taking 1790 as year zero. A plot of the rescaled data should look exactly the same:

```
  MAPLE
> tzeroed=seq[((i-1)*10,i=1..21)];
```

```
  MATLAB
> stt=0:10:200; % translated time
```

It appears that the growth of the U.S. population is exponential until about 1940. We will try to get an exponential fit between 1790 and 1930. We take the logarithm of the data. The plot of the logarithm of the data should be approximately a straight line (see Figure 3.5.4):

```
  MAPLE
> lnpop:=[seq(ln(pop[i]),i=1..21)];
> plot([seq([tzeroed[i],lnpop[i]],i=1..21)],style=POINT,symbol=CIRCLE);
```

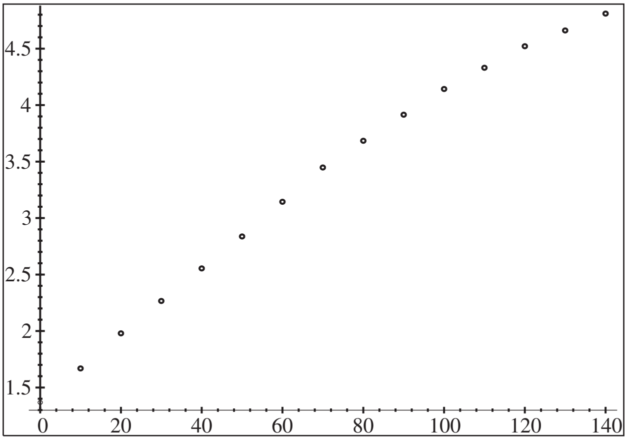


Fig. 3.5.4. Logarithm of population data.

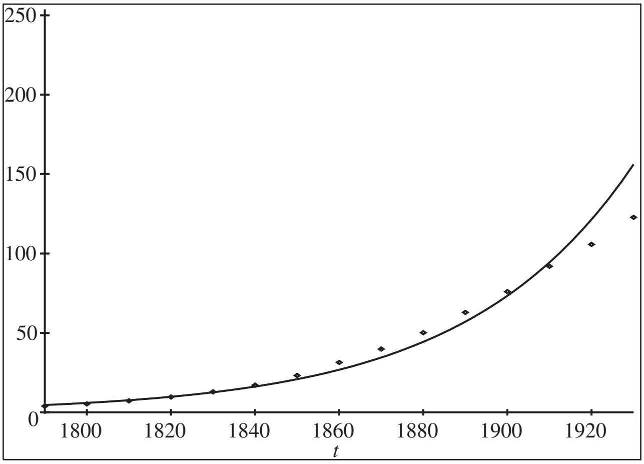


Fig. 3.5.5. Exponential growth data fit between 1790 and 1930.

```
  MATLAB
> lnPop=log(pop);
> plot(stt,lnPop,'o')
```

The exponential of this linear fit will approximate the data. (See Figure 3.5.5.) Recall that these techniques were used in Chapter 2.

```
  MAPLE
> with(stats):
> fit[leastsquare[[t,y],y=m*t+b]]([tzeroed,lnpop]);
> y:=unapply(rhs(%),t);
> J:=plot(exp(y(t-1790)),t=1790..1930,tickmarks=[4,5]):
> K:=plot(data,style=POINT,symbol=CROSS,tickmarks=[4,5]):
> plots[display]({J,K});
```

```
MATLAB
> MT=[stt; ones(1,21)];
> params=MT'\(lnPop')
> lnFit=params(2)+params(1)*stt
> plot(stt,exp(lnFit))
> hold on
> plot(stt,pop,'o')
```

To the degree that this graph fits the data, the U.S. population prior to 1930 was growing exponentially.

Exercises/Experiments

1. Repeat Example 3.5.1 with just 15 points of the U.S. population data instead of all of them. Which fit is better for the data up to 1930, the partial fit or the total fit? Using an *error* similar to the one in (2.2.1) give a quantitative response (i.e., compute the squared errors). (If this fit for the U.S. population data interests you, note that we will return to it again in the exercises for Section 4.3.)

2. We present below the expected number of deaths per 1000 people as a function of increasing age. Surprisingly, an exponential fit approximates this data well. Find an exponential fit for the data. The sequence `DR` is the death rate at the ages in the sequence `yrs`.

```
MAPLE
> yrs:=([9,19,29,39,49,59,69,79,89]);
> DR:=([.3,1.5, 1.9, 2.9, 6.5, 16.5, 37.0, 83.5, 181.9]);
> pts:=[seq([yrs[i],DR[i]],i=1..9)];
> plot(pts,style=POINT, symbol=CROSS);
> lnpts:=[seq([yrs[i],ln(DR[i]) ], i=1..9)];
> plot(lnpts,style=POINT,symbol=CIRCLE);
> with(stats): lnDR:=map(ln,DR);
> fit[leastsquare[[t,y],y=a*t+b]]([yrs,lnDR]);
> a:=op(1,op(1,rhs(%)));
> b:=op(2,rhs(%%));
> death:=t–>exp(a*t+b);
> J:=plot(pts,style=POINT, symbol=CROSS): K:=plot(death(t),t=0..90): plots[display]({J,K});
```

```
MATLAB
> yrs=[9,19,29,39,49,59,69,79,89];
> DR=[.3,1.5, 1.9, 2.9, 6.5, 16.5, 37, 83.5, 181.9];
> plot(yrs,DR); % so data exp. like
> lnDR= log(DR);
> MT=[yrs;ones(size(yrs))];
  % matrix of independent variable data
> params=MT'\lnDR';
> a=params(1); b=params(2);
> fit=exp(b)*exp(a*yrs);
> plot(yrs,DR,yrs,fit);
```

3. Using the least squares methods of this section, and by sampling nine data points on the interval [0, 3], determine whether the growth of the solution for the delay (3.5.12) depicted in Figure 3.5.2(b) is exponential.

4. In Section 2.2 we gave a cubic polynomial fit for the cumulative number of AIDS cases in the U.S. Find an exponential fit for those data. Determine which fit has the smaller error—the cubic polynomial fit or the exponential fit.

5. What would the U.S. population be today if the growth rate from 1790 were (a) 2% higher? (b) 5% higher? (c) 2% lower? (d) 5% lower?

Questions for Thought and Discussion

1. What is the surface-to-volume ($\frac{S}{V}$) ratio of a spherical cell with a radius of 2? What is the radius of a spherical cell with $\frac{S}{V} = 4$? A spherical cell with $\frac{S}{V} = 3$ divides exactly in two. What is the $\frac{S}{V}$ ratio of each of the daughter cells?

2. Name some factors that might prevent a population from reaching its biotic potential.

3. Variations induced by sexual reproduction generally lead to the early deaths of many, if not most, of the organisms. What could be advantageous about such a ruthless system?

References and Suggested Further Reading

[1] BIOPHYSICS OF LIVING SYSTEMS:
E. K. Yeargers, *Basic Biophysics for Biology*, CRC Press, Boca Raton, FL, 1992.

[2] CELL DIVISION AND REPRODUCTION:
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W. S. Beck, K. F. Liem, and G. G. Simpson, *Life: An Introduction to Biology*, 3rd ed., Harper–Collins, New York, 1991.

[4] POPULATION BIOLOGY:
R. Brewer, *The Science of Ecology*, 2nd ed., Saunders College Publishing, Fort Worth, TX, 1988.

[5] DEFINITION OF SPECIES:
C. Zimmer, What is a species?, *Sci. Amer.*, **298**-6 (2008), 72–79.