

6

Life I: Evolution— Origin of Complex Organisms

Conceptual Outline

■ **6.1** ■ We are interested in developing an understanding of organisms in their environments. The primary focus is on the evolutionary dynamics of populations of complex organisms, rather than on how they act collectively.

■ **6.2** ■ Evolution is a general approach to the formation of complex organisms through incremental change. The phenomenology of life is rich and motivates the discussion of evolution. Conceptual models of incremental evolutionary processes include monotonic evolution on a fitness incline, divergence of traits and extinction.

■ **6.3** ■ In theories of evolution, fitness is the only property of the organism which determines the evolutionary dynamics. The fitness can be described as a function of the genome, but it is more directly related to the phenome. Variations in the fitness as a function of changes in either phenome or genome may sometimes be large and may sometimes be insignificant. Conventional evolutionary theory is, however, based upon gradual changes in fitness.

■ **6.4** ■ A model of organisms evolving by diffusing on a fitness landscape is equivalent to particles moving on an energy surface. In the context of this model, many aspects of evolution can be discussed. However, it is far from trivial to account in a robust way even for basic phenomena such as the existence of groups of organisms with well-separated traits.

■ **6.5** ■ The use of dynamical equations that model reproduction, competition for resources, and predation can model a variety of dynamic phenomena in populations. They illustrate how various organism properties contribute to fitness. Moreover, the dynamics of such models is fundamentally different from that of the models discussed in Section 6.4. However, like the models in Section 6.4, these models cannot account for the existence of groups of organisms with well-separated traits. To overcome this problem requires introducing a variety of resources, with their own dynamics.

■ **6.6** ■ Returning to the consideration of collective behavior of components, we find that sexual reproduction takes advantage of composite patterns to form high-fitness organisms. A mean field approach that neglects correlations in the genome

does not apply when organism types diverge due to correlations imposed by selection and reproduction. Moreover, a discussion of altruism and aggression in evolution is relevant to understanding the existence of organisms formed out of components, or social groups of organisms, that exhibit collective behaviors.

6.7 Various systems, including the immune system and artificial computer software, can be used as laboratories for developing an understanding of evolution.

6.1 Living Organisms and Environments

The study of living organisms, their behavior and evolution, using mathematical tools, is one of the rapidly developing areas in the study of complex systems. In this chapter we discuss the collective evolutionary dynamics of living organisms. There is an essential difference between this endeavor and the study of neural networks (Chapters 2 and 3) or protein folding (Chapters 4 and 5). In discussing spatial substructure and temporal relaxation in these systems, we were able to construct models from the interactions of simple elements. Even though these elements were drastic simplifications of neurons or amino acids, meaningful questions were addressed. They were meaningful because our focus was on the complex collective behavior. When we discuss life in general, we are not interested in the collective behavior of the organisms, but in the behavior of complex individual organisms in interaction with their environment. It is still possible to consider the emergent collective behavior of many individuals; however, it is not clear that this behavior is complex. In contrast, the individual behavior is often complex.

The contrast can be illustrated by two examples. The first example is related to the concept of subdivision discussed in Chapter 2. Collections of animals or plants do not generally satisfy the conditions that were considered necessary for a complex organism. Flocks of animals or collections of plants can be diminished in size without essentially affecting their collective behavior. Indeed “diminished in size” would not be the natural phrase in the previous sentence. We would say instead “diminished in number.” While there are collective effects, they are not sufficient to satisfy our criteria for a complex organism. The second example is related to the development of life over time, analogous to our discussion in Chapter 4 of protein folding. The development of life is generally described as evolution. Evolution is the development of capabilities of the individual organism—specifically, an increase in its complexity. While there is also a development of species and ecosystems, evolution is not considered primarily the development of a collective behavior of many organisms. We will discuss this more fully later in this chapter. Our primary focus, however, is to explore the consequences of the shift in emphasis from the collective system to the individual.

As a result of the shift in emphasis, in discussing models of life we cannot use a two-state variable to represent the elements of our system. And yet, in the construction of models, the use of simple elements cannot be avoided. In order to design models of complex organisms, they must themselves be composed out

of suitably designed simple elements that capture as much of the complexity of their behavior as we are interested in.

As we consider the construction of models of life, it must be understood that any model of life includes a model of the environment. Behaviors of individual organisms are generally measured in response to external stimuli. The relationship between the capabilities of the individual and the demands of the environment plays an important role in the description of the organism. The environment also plays a central role in the dynamics of evolutionary change. As we discuss both here and in Chapter 8, the complexity of an organism and the complexity of its environment are often closely related. Moreover, while the behavior of individual organisms is central to the discussion of life, much of the interest in describing life is in the interaction of an organism with other organisms. This interaction may take the form of competition, cooperation, reproduction, communication, exploitation, consumption, etc.

Since our objective is to model aspects of the evolutionary dynamics of populations, we can adopt quite abstract models of organism behavior that do not relate directly to their biology. Nevertheless, these models provide insight into population dynamics and interactions. The models describe an organism and its behavior as a coordinate in an abstract configuration space. In general, we are not concerned with the mapping of this coordinate to specific behavioral attributes. Any concrete computational model of behavior must be represented by a set of parameters that we consider to be our abstract configuration space. In this way we ensure that our discussion is relevant to behavioral models of organisms. The generality of the representation we use for organisms may be argued on the basis of universality of computation and information theories described in Sections 1.8 and 1.9. However, any choice of representation emphasizes particular aspects of a complex system. There is no claim that these models address all of the questions of interest in discussions of life.

There are important connections between this chapter and Chapter 7. In both chapters we are considering processes associated with heritable organism traits. The heritable physiological and behavioral traits are called the “phenome.” These traits also exist in an encoded form called the “genome,” which is commonly associated with DNA, though some other heritable molecular and cellular structures should be included. In this chapter, we are concerned with the joint evolution of the phenome and genome, which are linked together. In Chapter 7 we are concerned with the process of expression of the genome—the process of development which connects the genome with the phenome. This connection is essential to our understanding of evolution. Moreover, the same central question is present in both: How are complex systems formed? In this chapter we discuss concepts relevant to self-organization. In Chapter 7 we discuss concepts relevant to organization by design. Also significant is the connection between the processes that we consider. In both cases it will turn out that we are considering pattern formation. In this chapter we consider patterns of organisms in the space of possible organisms. In Chapter 7 we consider pattern formation in cell populations and physiology.

This chapter is divided into five major sections. In Section 6.2 we review briefly the phenomenology of life that motivates evolutionary theory. Section 6.3 sets a gen-

eral tone for discussions of evolution by considering the representation space in which organisms evolve, and the concept of fitness which is central to the theory of evolution. Section 6.4 presents, mostly through conceptual discussion, a Monte Carlo random-walk model of evolution. Fundamental limitations of this model motivate the introduction in Section 6.5 of a collection of models of evolution by reproduction and selection. These models also turn out to have fundamental limitations that become apparent through simulation and analysis. While the models of Sections 6.4 and 6.5 have difficulties, they provide various insights into evolution. Moreover, through recognizing the difficulties, we are forced to develop a better concept of the aspects of organism-environment and organism-organism interactions that must be incorporated in more complete models of evolution. Finally, in Section 6.6 we return to discuss the relationship between components and collective behavior. We discuss sexual reproduction and social behaviors (altruism and aggression) to make connections between the behavior of genes (genome components), molecules, cells, organisms and populations of organisms.

6.2 Evolution Theory and Phenomenology

6.2.1 The theory of evolution

For modern biologists, evolution evokes the rich phenomenology of life on earth. Evolution is considered to be a universal process (dynamics) that gives rise to the nonuniversal (diverse) phenomenology of life. The nature of evolution from a biologist's perspective has also been modified over the years. In particular, the relationship of evolution to organism complexity has been bypassed almost entirely in recent years. This arises in part from the recognition that the process of evolutionary change need not give rise to more complex organisms. However, for our purposes it is essential that evolution is a process that *can* give rise to more complex organisms, whether or not it does so under particular circumstances. Thus we focus on the concepts that have been developed in biology to understand the change in organisms as a part of a theory of evolution that not only pertains to the phenomena of life but also indicates quite generally how complex systems can arise.

In this context, the objective of the theory of evolution is to explain the existence of complex life on earth. The need for an explanation arises because it is assumed that the earth began in a state devoid of life. Since living organisms today are complex, they are highly improbable combinations of the building blocks of nature—atoms. An explanation of their existence is necessary. Traditionally, the scope of evolution is divided into two parts. This separation is in recognition of the essential role played by organism self-replication (reproduction). The first part is the formation of relatively simple self-replicating organisms from molecules. The second part is the formation of complex organisms from simple organisms. While our discussion will focus on the latter, the dividing line is not fundamental. Conditions exist in which various molecules can replicate, and thus a theory of evolution can apply to molecules and the formation of cells as complex molecular structures, as well as to organisms. Our discussion of this point will be delayed to the end of the chapter in Question 6.6.6.

Evolutionary theory was introduced as an alternative to two older theories. The first of these is the theory of creation by a prior being capable of creating life. This theory is manifest in some form in most mythologies and religions. Typically this model assumes that life was created at a particular time in a form similar to that we see today. The creation model is difficult to accept because it assumes an external agent that has not been observed. It also gives no explanation for the phenomenology that exists in life discussed below. The second theory is that of spontaneous generation. This theory assumes that life can form spontaneously under certain conditions that arise naturally. In an experimental context it was discussed as a reason for the formation of maggots in rotting meat, until it was shown that without parent organisms that could lay eggs this would not happen. The difficulty with the model of spontaneous generation is precisely our original problem, that the spontaneous formation of a complex system is highly improbable.

Evolutionary theory provides an alternative to these models by proposing that incremental changes over many generations of organisms led to increasing complexity. Spontaneous changes by themselves are assumed to be random, but organism selection through interaction with the environment can lead to a process that systematically increases the complexity of the organisms. The selection process is the driving force in evolution that replaces the physical force in systems governed by classical mechanics. A relevant image is that of biased random walk or biased diffusion similar to that discussed in Section 1.4. In evolution, the biased diffusion occurs in the space of possible organisms. Selection is a consequence of differences in fitness, which plays the role of the energy. Fitter organisms survive at the expense of less fit organisms. We say that the organisms compete for survival, though the intentionality in the term “compete” may be an unnecessary anthropomorphism. The concept of incremental changes leaves many details of the theory unspecified. The importance of the theory is that it provides a framework in which we can understand the appearance of complex systems through a dynamic pathway. The incremental changes are understood to be encoded largely in the genome, which transfers information from generation to generation.

Evolutionary theory is powerful because it describes a large variety of phenomena in life. Darwin’s articulation of the theory of evolution preceded the discovery of DNA and its role in preserving traits from generation to generation, and many other relevant discoveries that have given a firm basis for the concept of incremental changes, which is necessary for evolutionary theory to hold. Nevertheless, as a theory of the origin and phenomena of complex life on earth, there are missing pieces, because it is not easy to verify whether processes articulated conceptually, but not reproduced experimentally are sufficient to explain the phenomena of life on earth. For some there is a belief that evolutionary theory requires only verification; others suggest that major new concepts are likely to be discovered that will modify qualitatively our global understanding of evolution. There are also key unanswered questions related to the incremental concept of change.

There is a connection to be made between the study of evolution and the problem of protein folding considered in Chapters 4 and 5. Both deal with dynamics of or-

ganization. Chapters 4 and 5 assumed that a unique folded structure had to be reached by a process that selected one out of many possible structures. We can articulate the problem of the formation of life in a similar manner. The problem is the formation of a biological organism from atoms. The developmental process from, e.g., a fertilized egg, can be included as part of this process. Like the protein-folding problem, an attempt to search all possible arrangements of atoms is impossible on any reasonable time scale (e.g., the lifetime of the earth). Even the formation of a single protein out of its atomic components is a much more difficult problem than folding the same protein. Much more difficult still is the formation of long DNA chains found in living organisms. The protein is an engineered system with a specified amino acid sequence. We assumed that it was designed to lead to a special conformation, and discussed the properties of the energy that were necessary in order to enable this to occur. For the formation of life on earth, there is no readily apparent analog to the initial amino acid sequence that served as a template for the formation of life. Thus we have a much more difficult problem with fewer tools. The opportunity present is that, unlike protein folding, we are not required to succeed every time. A process can be designed where many attempts are made. A successful attempt may be reproduced and can be the starting point for successive developments.

While the process of incremental change is conceptually powerful, we will encounter fundamental difficulties in our attempt to understand the overall process of the development of life. Perhaps one of the key issues that underlies these difficulties is that the theory of evolution assumes that the emergence of complex organisms is reducible to understanding incremental changes. We have found in previous chapters that a system composed out of many components cannot be understood in a reductionist manner as trivially related to the behavior of components. Instead, it is necessary to understand their interactions and how these interactions result in collective behavior. Similarly, the process from atoms to organisms cannot be understood as a direct result of a few elementary incremental evolutionary processes. This becomes apparent in this chapter as we attempt to construct a global representation of fitness that can account for evolution by an incremental model.

6.2.2 *Fitness—what is being optimized?*

We should pause and consider the fundamental justification for use of a fitness property in the dynamics of organisms. Our study of thermodynamics specified that the state of a system is determined by maximizing the entropy of an isolated system or minimizing the free energy at a particular temperature. What gives us the freedom to postulate an alternate dynamical process—a process in which organisms increase their fitness rather than decrease their free energy? The key point is that the earth is not in equilibrium. It receives energy from the sun and emits lower energy photons to black space. This energy flow implies that the second law of thermodynamics does not apply, and it enables the existence of nonequilibrium structures that themselves consume energy and emit waste heat. Without the energy flow, this would be impossible. Having said that such structures are possible does not necessarily mean that they must occur in the form of living organisms. However, as an underlying concept, the idea

that this nonequilibrium circumstance can lead to nonequilibrium entities then enables us to ask constructively what entities or organisms will be in existence. The answer provided implicitly by evolutionary theory is that in some sense the organisms that exist are those that optimize some function of the energy flow. Ultimately this is the nature of fitness.

To reach the fitness of organisms, the discussion also requires an additional step that would relate the overall process of energy flow not to the whole system, but rather to individual organisms. The overall nonequilibrium conditions create local nonequilibrium conditions in which organisms exist. The availability of energy in various derivative forms different from that provided by the sun, as well as the availability of heat sinks of other derivative forms, enables the local process of a living organism to proceed. Within this local circumstance, the organisms that exist are the result of some dynamic process that need not optimize the free energy, but may optimize some function of the energy flow. When we can interpret each organism as optimizing the cost function separately, the resulting cost function is the fitness. The process of optimization causes incremental changes to appear in the system. The assumption of independent optimization by particular organisms bears resemblance to parallel processing in the protein-folding problem, where components of the system act, in part, independently.

6.2.3 Phenomenology of life

The phenomenology of life is rich and diverse. There is a lot of specific information that is known, and general observations that can be made. The general observations should be addressed by a complete theory of evolutionary dynamics. In each of the following paragraphs, we summarize some of the general observations to motivate aspects of our discussion of evolution.

Existence of life—Aside from the observation that without life we wouldn't be here to talk about it, the existence of life tells us that in principle it is possible to have life. What it doesn't tell us is whether it is a highly improbable or a probable occurrence, and whether there are other forms we have not encountered.

Existence of variety of life—Not only do we find that life exists, we also find that various forms of life exist. The variety is remarkable: animals and plants, living beings that can exist in various environments, animals that can swim, walk and fly. Conventional life-forms range in size from single-celled organisms to whales. We can also say that life exists in many different degrees of complexity. This indicates that not only can life exist, but that there are many varied forms it can take.

Existence of distinct traits—Organisms living today are grouped together in various ways. Certain animals are similar and others are quite different. There is no continuum of organism traits at the present time. Instead there are groupings of organisms that are more similar and less similar to other organisms. For example, there is no continuum of organisms between a giraffe and a spider or a giraffe and a grass plant. There are many different forms of variation that appear to exist, and others that do not. One might wonder, for example, why domestic dogs come in a wide range of sizes, while domestic cats do not.

Existence of shared traits—Various quite different organisms share similar traits. For example, bony fishes, sharks and dolphins share a superficial body form. Butterflies, birds and bats share certain attributes of wing structure. Organisms share similar numbers and roles of appendages. Mice and men share common organs, tissues and chemical processes.

Existence of fossils—Fossils illustrate various changes in traits of organisms over geologic times. Specifically:

- a. *Changing of traits*—Many existing organism traits did not exist in previous times. The rate of change is not uniform over history. Slow changes occur at some times, and rapid changes at others.
- b. *Extinction*—One example of dramatic change is extinction. Large dinosaurs are the most prominent example of disappearance of a set of complex organisms. Other organisms also have disappeared at particular times.
- c. *Persistence of species*—While some organisms have disappeared, others have persisted over long times. Single-celled organisms similar to those existing today are found in fossils at the beginning of recorded life 3×10^9 years ago. Among the longest continuously existing animals are cockroaches, horseshoe crabs and certain sharks.
- d. *Systematic changes (evolutionary progress)*—Among the changes that are shown by fossils are examples of incremental monotonic changes from an initial form to another form. A classic example is the horse for which a sequence of progressively larger fossils was found.

Trait persistence from generation to generation by reproduction—Organisms that reproduce (asexually or sexually) pass traits from generation to generation. Dogs don't give birth to plants. More specific traits ranging from size to color are correlated from generation to generation, though a detailed description of inheritance must include mixing in sexual reproduction and various statistical correlations rather than deterministic relationships.

Death—All organisms appear to die. Death is due to various circumstances including accidents, disease, hunger and predation. Barring other causes, for some organisms there appears to be a "natural life span" following which death occurs by senescence, i.e., "old age."

Migrations and domains—Organisms may migrate from place to place on the earth. Generally a species exists within a certain domain. Other places it is not found.

Trait change by human (artificial) selection—When human beings select members of a domesticated species to reproduce, this can cause progressive changes in organism traits. Eventually, different varieties can be formed. Various properties can be modified, such as size, disease resistance, or quantity of a product (milk, eggs, meat, grain, etc.). This is apparent in both plants and animals that have been domesticated over many years.

Apparent competition for resources—Studies of organisms suggest that they compete for resources such as food, territory and mating rights.

Apparent interdependence and reliance—Organisms are also interdependent. There are parasitic relationships, symbiotic relationships between species and social behaviors within a single species.

Food web—There is a food web that corresponds to organisms consuming other organisms as food. There is specialization in this food web. There are herbivores and carnivores as well as omnivores. Other aspects of specialization in the consumption of resources are also apparent. Different herbivores consume different plants, or different parts of the same plant. Different carnivores consume different animals.

Reproduction—All organisms reproduce. There exists asexual and sexual reproduction among all major groups of living organisms. Sexual reproduction appears to become more prevalent among more complex organisms.

Relevance of organism size—Among organisms with larger body sizes there are characteristically fewer individuals, fewer progeny and also fewer species.

Role of DNA—Many traits have been traced to DNA sequence. Various genetic associations of traits and generational transfer of traits as well as the direct manipulation of DNA have established DNA as a source of information that determines hereditary physiological traits of plants and animals.

6.2.4 Life and reproduction

The existence of life relies upon a diversity of molecules and molecular types. Polymers, discussed in Chapters 4 and 5, formed of several types of units are essential. Proteins appear to serve primarily as enzymes. DNA and RNA, formed from chains of nucleotides (bases), appear to serve primarily as repositories of information. This information is represented by the particular sequence which is composed of four distinct molecular units. For DNA the units are adenine, cytosine, thymine and guanine. For RNA the thymine is replaced by uracil and all have a systematic modification that changes deoxyribose to ribose forms. DNA and RNA could also be used as catalysts, but this does not appear to be their primary function in cells. Polysaccharides and lipids are polymers that serve both structural functions, and for storage of energy.

A number of polymers are involved in the formation of two-dimensional membranes that are self-organizing molecular assemblies. A membrane is formed when certain polymers having both hydrophobic and hydrophilic ends are present. Under a certain range of conditions, the polymers form a planar double layer consisting of internal hydrophobic ends that avoid water, and external hydrophilic ends that seek water. Once a membrane is formed, other molecules can be added to modify its behavior. The formation of a membrane is, more than the existence of complex molecules, the boundary of living and nonliving. It bridges from molecular systems to organisms because it establishes a distinction between the interior and exterior of a system. Ultimately a membrane enables the interior environment to be controlled so that, in turn, a variety of molecular processes can be controlled.

The hierarchy of living organisms is now understood to be classified into largely single-cell prokaryotes and largely multicell eukaryotes. By number, most of the organisms on earth are in the category of prokaryotes. Prokaryotes, which include bacteria, are simpler and, according to fossil records, arose earlier (3×10^9 years ago) than

eukaryotes (1.5×10^9 years ago). Prokaryotic cells consist of a cellular membrane with molecules or molecular aggregates inside. In contrast, eukaryotic cells have additional internal levels of structure in the form of membrane-bound organelles. These can include a nucleus, mitochondria, chloroplasts, endoplasmic reticulum, Golgi apparatus and food vacuoles. Eukaryotic cells are typically at least 10 times larger than prokaryote cells. Prokaryotes can form colonies but never achieve the highest levels of organization seen in eukaryotes. Eukaryotic cells can be either single-celled organisms or part of multicellular organisms including plants and animals.

Prokaryotic cells reproduce by replication. The DNA in a prokaryotic cell replicates as materials are available. It consists of a single DNA double helix. In the bacterium *E. coli* it is 2×10^6 bases long. Eukaryotic cells undergo a more complex process of reproduction. Individual cells reproduce by mitosis, which involves DNA duplication and then separation in an organized fashion to ensure proper grouping of multiple DNA strands, each of which is called a chromosome.

Multicellular organisms frequently reproduce by sexual reproduction, which involves two processes. The first is the formation of gametes consisting of cells that contain half of the full set of chromosomes. This occurs by a process of cell division called meiosis, during which a mixing (recombination) of the parent chromosomes occurs. The second is a developmental process that occurs once two gametes from different organisms are combined. This developmental process creates a new multicellular organism by cell division, growth, differentiation, locomotion and changes in shape and function of cells. The developmental process is the topic of Chapter 7.

Cell replication involves both molecular replication and cell growth. DNA can be replicated because the nucleotides preferentially bind in specific pairs: adenine with thymine, cytosine with guanine. This enables a complementary chain to be readily formed with the help of additional molecular machinery—a polymerase. The reaction of replication can be performed in a test tube. The test-tube version is called the polymerase chain reaction, and it is the basis of modern methods for determining the sequence of DNA nucleotides and other uses of DNA. What does it mean to replicate the molecule? Since this is the most basic biological replication process, it is helpful to ask exactly what is being replicated. The atoms are not replicated, thus it is better to think about DNA replication as a replication of the information in the sequence of the polymer. More generally, polymers can grow by selective addition of monomers facilitated by catalysts. Cell growth occurs by selective addition of molecules to the cell. This generally requires consumption of energy in order to execute the selection against the influence of entropy.

Replication is central to the process of evolution, which involves changes in the organism type over many generations. Incremental changes occur through processes that we generically call mutation. The simplest of these is the change of a single base—a transcription error. There are other processes that change the genome from generation to generation. The main process is that involved in sexual reproduction. In this process, the DNA of male and female parent are mixed, typically by taking half of the chromosomes from each. In order for this to make sense, there must be some way to ensure that all essential functions of the cell and multicellular organism will be repre-

sented in the final combination. This is accomplished by the presence of two (or more) homologous chromosomes in each organism that would perform similar function but are different. When the chromosomes are separated into zygotes, which have only half of the chromosomes, the process of meiosis is designed to ensure that one of each of the homologues ends up in each of the zygotes. The mating of zygotes then gives a new DNA sequence formed out of the DNA of the parents. In human beings there are 23 homologous pairs of chromosomes. With such a process, the number of distinct individuals would be the product of the number of distinct homologue chromosomes. During meiosis, however, there is also a process that encourages crossover between the homologue chromosomes. Segments of DNA are transferred between them. The locations of the DNA segments can also be rearranged. This results in a much larger set of possible variations in the DNA of offspring. The basic functional parts of chromosomes are called genes. In the simplest picture, a single gene contains the code for a single protein. Finally, other processes, such as extra chromosome duplication, can change the number of chromosomes in the cell. Note that genetic mixing by sexual reproduction is quite analogous to the formation of composite states discussed in Section 2.4 and similarly assumes partial independence of component function.

In our discussion of evolution, we will assume the existence of a basic cell with DNA and replication machinery. Processes that led to such a system would involve molecular evolution that can be discussed in a similar framework. The difficulty in discussing molecular evolution is that organisms that involve other types of polymers might be possible and we have no grasp of the space of possibilities. Even restricting the organisms to those primarily encoded by DNA and ancillary molecules, we know little about the enormous space of possibilities. Our discussion of proteins at the beginning of Chapter 4 counted the large number of conformations for a protein. The number of possible DNA sequences which are no longer than human DNA is $4^{10^{10}}$. Our interest is in this space of possibilities. We note that the number of possibilities in *Star Trek's* domain—"Space, the final frontier"—pale in comparison to the space of possibilities that is being explored by nature through the process of evolution, in which exploration human beings participate.

6.2.5 Qualitative incremental dynamics of evolution

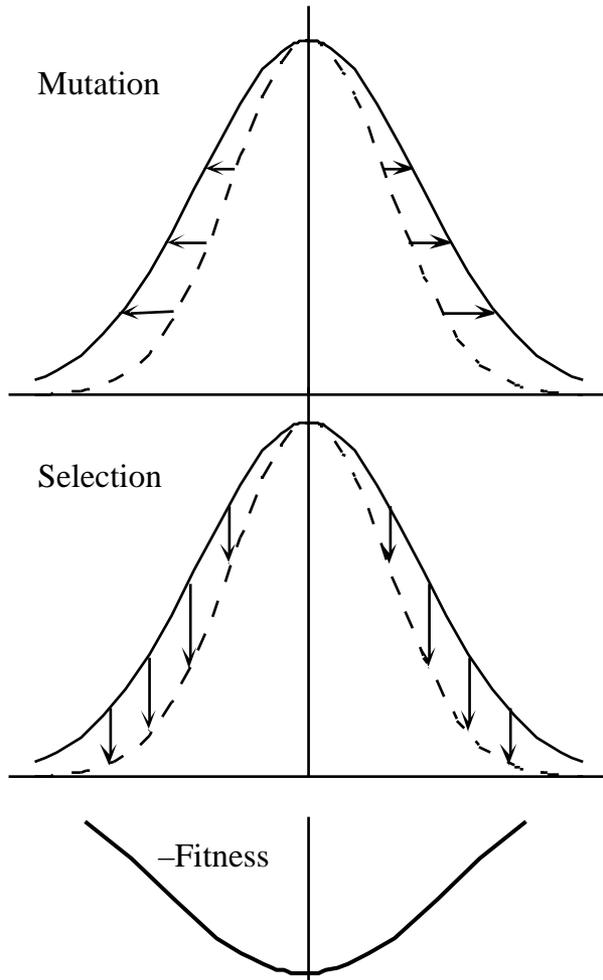
The theory of evolution is based upon two processes, mutation and selection, that are assumed to give rise to incremental changes in organisms. We discuss here qualitatively the processes and the types of incremental changes, and then we address their properties more systematically through mathematical models that turn out to be more subtle than the qualitative picture would suggest. The approach we take here illustrates the dangers of qualitative models, how more quantitative models can be constructed, and some of the problems, as well as the benefits, of doing so.

Mutation, as previously mentioned, is used as a generic term for heritable variation in an organism largely through changes in the genome. Specific processes that result in changes in organisms from generation to generation include point mutations, rearrangement, mixing by sexual reproduction and gene duplication. Mutation increases the variety of organisms, thus enabling selection to effect a change in the overall population of organisms.

Selection in a qualitative sense is differential reproduction. Organisms reproduce. The type of organism that is more likely to be around in the future is one that has more offspring. The ability to have offspring requires survival and reproduction. This can be prevented by various problems—nonviability, nonfertility, lack of food, death by predators, death by disease, lack of a mate—leading to death without offspring. Fitness is, by definition, the quality that is selected for.

Equilibrium—To illustrate conceptually the processes of selection and mutation it is helpful to consider first a condition in which there is no net change in the population of organisms from generation to generation. We will often call this an equilibrium, but it is actually a steady-state condition, because resources are consumed. We imagine a population of organisms (Fig. 6.2.1) that has a distribution of some property and whose population is described by a Gaussian distribution. Without considering many implicit assumptions in this picture, we suggest that mutation is a process

Figure 6.2.1 Conceptual illustration of an equilibrium that results from mutation and selection. The top figure shows the increase in diversity of a population of organisms as a result of mutation. The middle figure shows the decrease in diversity due to the action of selection. When these processes are balanced, there is no net change. The relative normalization of the curves is chosen only for convenience. The horizontal axis is some heritable property of the organisms. The bottom figure illustrates the variation of the fitness with this heritable property. In order to retain consistency with dissipative physical systems that move to lower energy, we plot the negative of the fitness. By this convention, equilibrium occurs in a valley. ■



that would, by itself, increase the width of the distribution, while selection decreases the width, thus leading to equilibrium.

Evolution—The central process of evolutionary change is the displacement of a population along some coordinate. Qualitatively this is illustrated in Fig. 6.2.2, where motion on a slanted fitness surface as a function of some property is assumed to give rise to population evolution. This motion results from a combination of mutation and selection, where the mutation increases the width of the distribution, and selec-

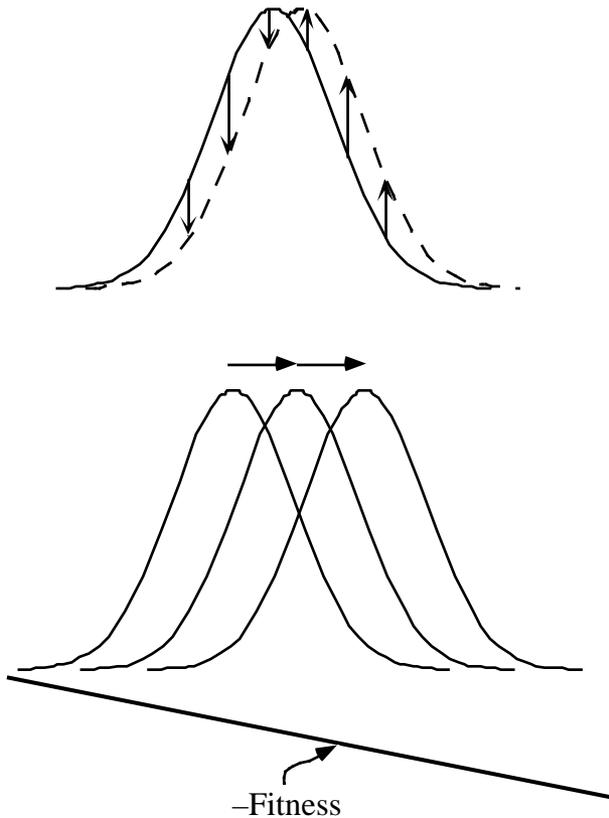


Figure 6.2.2 Conceptual illustration of a process of incremental evolution by biased selection. In the top figure, nonuniform selection is shown acting on a population of organisms. Selection occurs by preferential death of organisms and/or by preferential reproduction of organisms. In the figure, only the effect of both is shown. This results in a net movement of the population. The bottom figure illustrates progress down a fitness slope. Only one of the subtleties that arise in this illustration is that we did not appear to need mutation. Mutation is necessary because the population is discrete rather than continuous and therefore does not have an arbitrarily long tail. At every step, mutation must create the forward tail of the distribution, which is then increased by reproduction. ■

tion causes the preferential selection of the more fit organisms. We say that selection is a force driving the evolutionary process.

Trait divergence and speciation—In order to account for the existence of a variety of organism types, it is necessary to have a possibility of splitting a single population into two populations with distinct traits. For this to occur it is assumed that under some circumstances there is a process of divergence of the organism traits. The beginning of this process is called disruptive selection. This is illustrated in Fig. 6.2.3. The opposite process of true convergence of two populations is not often considered, for reasons discussed below. The formation of groups of organisms with distinct traits may also lead to the formation of distinct species—organisms that cannot interbreed.

Extinction—Finally, organism types can disappear through extinction (Fig. 6.2.4). It is also possible for an organism type to increase dramatically in population over a short period of time. Of the four processes illustrated in Figs. 6.2.1–6.2.4 this process is the one that most clearly suggests that what is shown is only part of the picture, since extinction is a strictly time-dependent phenomenon. This implies that something external to the organism—its environment—is changing. We note that the nonreversibility of evolution is manifest in extinction, since the reverse process is spontaneous generation.

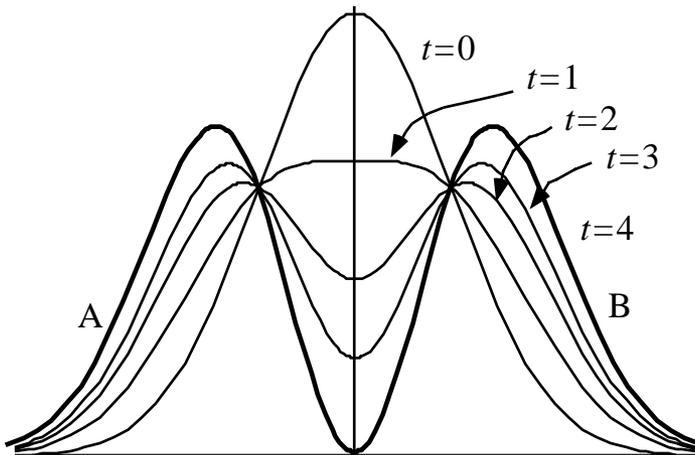
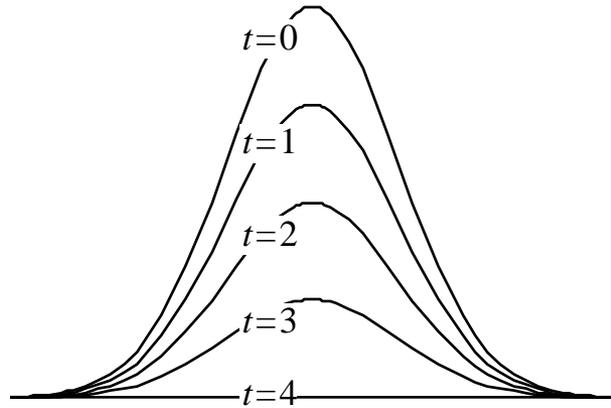


Figure 6.2.3 Conceptual illustration of a process that may result in trait divergence — the formation of two populations with distinct traits starting from one population. Beginning from a population that is located at a particular value of a heritable trait, the population separates into two parts by disruptive selection that broadens the distribution and then forms two peaks that separate over time. In order for this to occur, the fitness in the center must be smaller than at the sides of the distribution. A question that immediately arises is, Why did the initial single population peak form? Resolution requires some additional features that must be included in a model but are not contained in this picture. ■

Figure 6.2.4 Conceptual illustration of extinction where a population of organisms disappears for reasons that are not apparent from this picture. Influences of the environment are responsible but their nature is not specified. ■



6.3 Genome, Phenome and Fitness

6.3.1 *Complex to simple: a single behavioral parameter*

The theory of biological evolution is predicated on the assumption of a measure of fitness and its relationship to survival, reproduction and competition for resources with other organisms. Fitness is considered to be a single valued function of the parameters, s , describing the organism. Depending on one's viewpoint, the parameters describing the organism may refer to the genetic code or to physiology and behavior. It may be easiest to imagine the organism described by the genome as an explicit list containing the sequence of DNA base pairs. For example $s = (ATCGAAGCT...A)$. The genome should also be understood to include a description of other parameters such as molecules used in transcription and inherited cellular materials. Alternatively, we can consider s as a representation of the phenome: physical and behavioral characteristics such as height, weight, speed, instinctive behavior patterns, disease resistance, etc. These attributes appear more closely related to capabilities of the organism. The genomic space is related to the phenomic space through development. The converse relationship, where behavior and physiological traits affect the genome, is a consequence of evolution. Our primary objective here is not to relate the genome to the phenome, but rather to discuss the generational dynamics of s as a representation of the processes of evolution. When we want to emphasize the distinction between phenome and genome, we will use w for the former and s for the latter.

The fundamental assumption of evolutionary theory is that the fitness can in principle be expressed as a unique function of the organism. More specifically, we have a real number $K(s)$, which is the fitness. It will turn out that the models that we will develop to describe evolution will have quite distinct roles for the fitness. These models are a random walk model and a collection of differential reproduction models. Before we discuss these models, we will describe in Sections 6.3.2 and 6.3.3 the basic properties of the genomic and phenomic space and the sources of fitness.

6.3.2 Genome and phenome

Before we consider various models for fitness and evolution, we must first clarify the nature of the variable s . The space of possibilities of s can always be enumerated discretely as a set, but this is not necessarily helpful. The space of s generally indicates the connectivity of the space—what values are able to make transitions to what values. A transition is a change in s from generation to generation. The spatial structure of values of s thus represents our expectations of changes that are likely (states that are close together in the space) and changes that are less likely in a single step but might occur through a number of steps (states that are far apart in the space). We illustrate using a few relevant examples.

The first case is a binary variable $s = \pm 1$, similar but not necessarily with the same dynamics as the two-state system of Section 1.4. This model could be a simplified single base—considered as two possibilities rather than four. In sexual reproduction, a binary variable can represent a gene with two possibilities (alleles) in a population. The alleles might correspond to particular traits—for example, brown or blue eyes among humans. We are concerned with the time dependence of the relative proportion of the two traits. A standard picture of evolution would indicate the growth and eventual dominance of one trait over the other. We can expand the two-state system to a larger set of discrete possibilities. As long as there are only a few, a discussion of the dynamics is similar to that for the two-state system.

The second case is a one-dimensional continuum. For our purposes, the continuum and a set of discrete possibilities associated with the integers is the same. How does such a model relate to the genomic or the phenomic space? The phenome appears to have continuum parameters such as the height or weight of an organism. For animal breeding, we might consider chickens with a larger egg, cows with more milk, or faster horses. A conventional picture of evolution would include the classic example of incremental growth in size of the horse over time. How does this relate to the genome? The natural continuum parameter of the genome is its length. We could consider the possibility that the height of the organism is related to genome length—the addition of bases in a particular part of the sequence increases the height. It would be more reasonable, however, to assume that a number of discrete modifications of the genome lead to a larger animal. How can discrete modifications lead to a continuum? If we assume that each modification is independent and their effects are additive, then the height, w , is determined by an expression of the form:

$$w = w_0 + \sum_i s_i \delta w_i \quad (6.3.1)$$

where w_0 is a constant added for convenience. We assume a representation $s = \{s_i\}$, where s_i is either ± 1 . δw_i is a number that determines the effect of s_i on w . A very rough but useful first approximation is to consider each s_i to correspond to a single gene or even base. It is important to recognize that this expression has implications for the natural distribution of heights, which is different from the distribution expected in a continuum. If we assume that all possible genomes are equally represented in a

population (selection does not apply) then there is a natural distribution of heights. This would correspond to setting the values of s_i at random.

The simplest case to consider is when all δw_i have the same value, $\delta w_i = \delta w$. Then a random distribution of s_i implies that the heights have a Gaussian distribution with a width given by $\delta w \sqrt{N}$, where N is the number of independent terms. This is unlike a usual continuum, where a random distribution would correspond to equal probability of all heights. This also implies that there are bounds to the values of possible heights, $\pm N\delta w$, though the bounds are much wider than the distribution. There is another way that this model is relevant to any discussion of evolution. When we apply a selective force to such a continuum parameter, it gives rise to a bias in the probabilities of values of the s_i . However, the phase space of possible genetic representations decreases with increasing deviation of the height from the unbiased average.

The distribution of values of δw_i for a more realistic model should be considered carefully. A single value might be replaced by a power-law distribution, or a distribution which implies that particular mutations have a large effect and others have a small effect. For example, eye color, while dominated by the blue/brown dichotomy, also has more subtle distinctions. Moreover, the additive representation might be replaced by a contingent representation where one mutation can occur only after another has happened. Complicated distributions of traits among organisms that are not subject to selection reflect features of the underlying genomic representation. As usual, in modeling such distributions it is reasonable to build a preliminary discussion upon simple models which illustrate features of more complete models.

The existence of an underlying genomic representation also has direct impact on the dynamics of the continuum model. There is no reason to believe that the probability of a mutation to the right is the same as to the left. These probabilities will vary at different location in the continuum. The simplest example is an organism that starts with a genome of the form $(-1, -1, -1, -1, \dots, -1)$ and we study evolution of an ensemble of these organisms where the only trait we measure is the total number of 1s, which is the relevant phenomic property. Then the genome mutates at random in every generation. Initially, every mutation changes one of the digits to a 1. This would look like a constant drift in the value of the phenome. Then as time goes on there are fewer -1 s, and the mutations may change either -1 s to 1s or 1s to -1 s. Without any selection bias it will eventually set the digits equally on average to 1s and -1 s with a distribution that extends from $N/2 - \sqrt{N}$ to $N/2 + \sqrt{N}$. This distribution is not changed by mutation. We will discuss the effect of a bias due to fitness selection in the following sections.

There are many other possible spaces to consider in addition to a binary and a continuum space. We can consider various d -dimensional continuum spaces and combinations of continuum and discrete spaces. We could also consider a set of N binary variables, an Ising-like model, representing the various bases or alleles of genes.

The final case we consider is a more direct representation of the genome as a space of strings, $s = (s_1 s_2 s_3 \dots s_l \dots)$ where all characters s_i for $i > l$ are zero, and l is the genome length. The s_i might be taken to be bases or genes with a prespecified alphabet of possibilities. One kind of transition in this space alters the characters but does

not change the string length. For example, point mutations change the value of a single character. Another kind of transition changes the length of the genome—for example, adding or deleting a single base at the end, or inserting or deleting a base somewhere in the middle. If we limit ourselves to considering only these transitions, we can consider the process of genome extension as distinct from the process of changing the genome for a specific length. The rate of point mutation need not be the same as the rate of mutations that change the genome length. Later, we will discuss the implications of this model for the problem of generating organisms of higher complexity.

In considering the space of possible organisms, it is essential to consider the independence or dependence of parameters. Only when parameters are independent is it possible to consider a phenomic trait or a particular gene as the subject of evolutionary study. Similar to the discussions in Chapters 2 and 4, there are likely to be parameters that are partially independent. For example, the structure of the digestive system is largely independent of the mating behavior or the absolute size of the organism. Because of the independence of certain physiologic or behavioral parameters, we can consider evolutionary change in the different parameters separately. Even when they are coupled, partial independence implies that there are organisms that share one trait but vary in another. This variation can allow for evolutionary selection in one and not in another. When chickens are bred for increased size, this can be done largely independent of the color of the chicken. The independence of phenomic traits should, however, be carefully considered in the context of the underlying genomic representation. The essential point is illustrated by considering the representation described in Eq. (6.3.1) and allowing for two different traits w, v to rely upon the same representation:

$$w = w_0 + \sum_i s_i \delta w_i \quad (6.3.2)$$

$$v = v_0 + \sum_i s_i \delta v_i$$

As long as we are considering values of w and v that can be represented by a large number of possible genomes, then w and v may act independently. However, when one of the phenome parameters is pushed by selection to an extreme limit, then the space of available genomes becomes reduced and the possible values for the other phenome parameter also becomes reduced. For example, if all (or nearly all) s_i in Eq. (6.3.2) are selected to have the same sign as δw_i to achieve the maximal value of w then we are restricted to a particular value (or limited set of values) of v which is (are) unlikely to be optimal. Systematically, we can say that a high selection pressure increases the coupling between various phenomic parameters. Moreover, this shows that it is progressively difficult to optimize multiple phenomic parameters at the same time. This is important when we consider several different traits that superficially are independent, such as chicken size, the number of eggs laid per day, and the resistance to a particular disease. Starting from an unbiased distribution, by selection we may be able to change them independently. Once they are strongly selected they often become coupled to each other.

The idea of trait independence, and direct coupling of a single trait to a single gene, has attained a popular following that is reflected in the searches for individual genes responsible for a variety of human physiological and behavioral traits. It is not unreasonable to suggest that this view arises largely out of our ignorance of the complex interplay of genome and phenome.

In a more global context, the coupling of attributes is a motivation for diversity of life even if the possible organisms are continuous. We can consider different organisms that optimize particular capabilities and not others: sensory acuity or large size or quickness. Each of these can provide an opportunity for fitness improvement, but eventually to the exclusion of improvements in other properties. This suggests that different organisms could survive by optimizing different traits. However, in order for this to be the case, there must be a nonlinear relationship between fitness and the phenomic properties. A linear optimization would still mean that a particular combination of characteristics wins over the others, and diversity would not result.

6.3.3 *Fitness sources*

The variation of fitness as a result of mutation may range from large to insignificant. A large variation in fitness may result in offspring that aren't viable—that are unable to survive or reproduce. An insignificant variation in fitness means that the difference doesn't affect selection; such mutations are called neutral. In a historical controversy it has been debated whether neutral mutations dominate the space of possible mutations. The controversy is relevant, because if neutral mutations dominate, then random changes (diffusion) of the genome, rather than selection, would cause evolutionary changes. Conventional evolution by selection occurs when changes in fitness are significant but gradual, so that populations change over many generations. On the other hand, the proportion and spatial distribution of nonviable organisms may result in boundaries to the course of evolution that are likewise important to understand. In this section we discuss some of the possible reasons for large variations in fitness, or a lack of variation in fitness, that can give insight into these issues. Remarks in later sections will clarify the neutralist/selectionist controversy.

Fitness may be considered as a function of the genome or phenome space. The function $K(s)$ has different properties depending on what s represents. Contributions to fitness variation are considered for each case in the following paragraphs.

We begin with the contributions to the fitness for the genomic space. We focus on complex multicellular organisms and their viability. A specific genome may not be viable because it does not provide for its own reproduction, or for effective expression of its information. The genome contains markers that indicate where to begin and where to end transcription so that proteins are formed. Eliminating or adding such markers may be readily understood to cause nonviability of the genome. Moreover, the genome acts as a set of instructions that lead to development of a multicellular organism. It may fail due to inconsistent instructions. It may also describe a nonviable organism where necessary physiological functions do not exist, or where organs or systems are improperly connected or sited. We might also distinguish between organisms that are viable under some circumstances, but not the circumstances that prevail. For example, a fish born on land. We could introduce the concept of a domain

of viability as the set of conditions under which a particular organism is viable. Evidence for a large number of nonviable genomes exists. It is believed that approximately one-third of successful impregnations in human beings result in early (first trimester) miscarriages that are often unnoticed. A significant proportion of these are believed to be due to nonviability of the genome. It should be understood that this occurs even though the possible genomes are very selectively chosen due to their origination from functional genomes of the parents with limited types of variation. This also suggests that developmental viability is a major constraint on fitness. Finally, some organisms are not fertile even when properly developed, with the classic example being the mule.

In contrast to the reasons for nonviability, there are also reasons that mutations are neutral. A significant amount of DNA in cells does not appear to code for proteins and, at least to a first approximation, does not directly affect the system function. Discussions of the role of this “junk DNA” have yet to resolve whether it has a functional role, such as in the structure of the DNA molecule or as latent coding DNA, or if it has no functional role at all. At the present time it is reasonable to assume that a significant fraction of changes in this part of the DNA are neutral with respect to selection. We can also discuss changes in the coding parts of the DNA. Changing a single base that codes for a particular protein may not change the amino acid that it codes for. This is because the mapping of DNA to amino acids is not one-to-one. Even if a base change does change the amino acid, changing one amino acid generally does not affect the structure of a protein or its enzymatic activity. Even when a protein is changed so that its activity is compromised, the change may be compensated by other cellular or physiological mechanisms. This suggests that many changes in the genome do not affect the phenome and thus do not affect the fitness in a conventional way.

When we consider the fitness as a function of the phenome, we would consider as coordinates various properties of an organism such as height, weight, bone structure or speed of locomotion. However, a central problem with this description is that it is not clear whether it is possible to create an organism with a particular set of physiological properties from a genomic description. We can describe various organisms in terms of their traits, but they may be impossible to create. We could protect ourselves from this problem by considering only organisms that are known to exist and comparing their fitness. However, this simplification does not allow us to address basic questions that we want to understand regarding the reasons for the existence of organisms in the form and with the evolutionary history that is found. Moreover, from a practical point of view it is important to understand what are the factors that prevent horses from running faster, chickens from laying more eggs or cows from giving more milk. Thus nonviability has meaning in this context as nonfeasibility. Feasibility can be divided into several categories according to which constraint prevents the formation of the organism—physical or representational. We also can discuss generally the effect of population interactions.

Physical constraints—In the context of particular external circumstances, physical law places various constraints on possible organisms. There are requirements on strength of bone in order to support an organism in a certain gravity. There are also constraints on senses—ears and eyes are limited in their sensitivity by quantum me-

chanics. External conditions such as temperature, air pressure and composition impose additional constraints. For example, the visibility in air is limited to a window of frequencies that are relied upon by the eye. The composition of the atmosphere places constraints on the organisms that can exist in it. The terrain places constraints on the nature of locomotion and the limbs that may be useful for it. The ocean and its composition imposes quite different constraints. The cycle of day and night results in other constraints. The qualitative differences between organisms in the water and on the land, or even between fresh and salt water and between different land climates, and specifically the lack of viability of one organism in another environment, suggests the importance of physical constraints on fitness.

Representation constraints—Even if certain traits are possible within physical law they might not be possible when we consider their implementation using DNA encoding. The process of developmental biology does not allow all systems to be formed. For example, automobiles are possible, but it appears likely that developmental biology cannot create a car directly using DNA encoding (indirectly, of course, it has). There may also be limitations in the structures that can be formed because of the use of particular chemical processes. This is not due to physical law but rather to the mechanisms of coding. A milder form of the encoding constraints exists in the form of coupled traits. Thus certain physiological/behavioral traits may be coupled to others due to their representation in the genome. Such constraints are difficult to consider without understanding the processes involved in developmental biology. They will become somewhat clearer as we discuss these processes in Chapter 7.

Population interactions—Population interactions might be thought to be significant only after issues of viability cease. This is not entirely true because, for example, parenting can enable organisms to be viable when they would not otherwise be. There are various interactions between different organisms that are important for fitness. There are interactions between organisms that are distant from each other in the genomic space. Examples include: interactions between plants and animals, interactions between bacteria and multicellular organisms and interactions between parasites and their hosts. There are also interactions between organisms that are proximate to each other in the genomic or phenomic space. They can include competition for the same resource, cooperation in group protection, reproductive interactions and parental attention.

Is the variation in fitness dominated by interactions between organisms or by inherent (physical or genomic) limitations? This question is superficial in that it is quite clear that both contribute in essential ways to the determination of fitness. Moreover, physical considerations, such as the composition of the atmosphere, due in part to the balance of plants and animals, may also reflect indirect interactions between organisms. Interactions and their effect on fitness are also related to physical considerations. Nevertheless, the issue of the relative importance of interactions and physical causes of fitness is important because it is relevant to questions that are at the heart of evolutionary theory. For example, it is relevant to the importance of randomness and historical accident in determining the course of evolution.

It is tempting to consider all variation in phenomic traits as significantly affecting fitness so that there are no neutral variations. The more practical aspect of this approach is to understand the existing variation of phenomic properties of a particular population of organisms. The central issue becomes whether the variation in phenome represents a diversity that is being acted upon by selection and therefore certain traits will eventually be forced to disappear in favor of others, or whether the variation is neutral with respect to selection and will persist. This limits the scope of the question from the space of all possibilities to the space of extant organisms. Even in this context, the controversy between neutralists and selectionists is not easy to resolve. The issue is still more complicated since populations of organisms may not act solely to select individual properties but also properties of the whole population. In this case variation may reflect the effects of selection. This will be discussed in Section 6.6.2.

From the discussion in this section, we see that there are a wide variety of contributions to the fitness of an organism. These factors change in time due to various events that range from change of weather to fluctuations in populations of other organisms. Since we are describing the evolution of organisms due to a fitness that itself depends on the existence of organisms, we are describing a self-consistent process. Such self-consistency was discussed in Section 1.6 in the simpler context of the Ising model for magnets. In essence, the concept of fitness itself represents a mean field approach. The assumption is that at any time, an average over influences that affect fitness is a meaningful concept, and that evolution takes place in the context of this average fitness. This is one of the central assumptions in evolutionary theory, not just in the models we will be discussing. Whenever the fitness is discussed as a fixed external parameter independent of the changes in the population, this simplification is being made. Corrections to the mean field approximation can be included in various ways; however, it is not clear how well it serves as a first approximation.

Question 6.3.1 If large regions of the space represent nonviable organisms, this might prevent evolution from one part of the space to another. The relevant question is the degree of isolation of regions of the space, like valleys in a mountain range. What phenomenological evidence suggests that the phenomic space is connected?

Solution 6.3.1 One observation that suggests that the space is connected is the existence of various widely different classes of animals such as land animals, winged animals, and water animals. The existence of flying insects, flying birds and flying mammals also suggests that there are multiple pathways between widely separated parts of phenomic space, as does the existence of different kinds of swimming animals. It is difficult, however, to rule out the possibility that other classes of organisms do not occur because evolution is unable to reach them. ■

6.4 Exploration, Optimization and Population Interactions

6.4.1 Exploration and optimization on a fitness landscape

At the root of evolutionary theory is the concept of optimization. It is not to be assumed that the optimum has been, or ever will be, reached. However, incremental evolutionary processes increase the fitness. Thus, it makes sense that a first mathematical model of evolution relies upon our understanding of the dynamics of optimization. Optimization problems can generally be written as a moving point on a landscape representing the cost function. The prototype optimization problem is the motion of a particle on an energy landscape where dissipation of kinetic energy causes it to move to lower potential energy. A nonzero temperature causes the particle to bounce around, enabling movement up in potential energy, but the tendency is to settle in lower regions. This system was introduced in Section 1.4 for simple energy landscapes and discussed in Section 1.7 in the context of Monte Carlo computer simulations. It was also the basis of our discussion of the relaxation of proteins to their folded conformation. For evolution, we modify this picture by allowing the existence of more than one organism performing the optimization at the same time. Interactions between the organisms change the nature of the optimization. We first introduce and motivate a conventional optimization picture, and later discuss how the interactions affect it.

A central difficulty in constructing mathematical theories of evolution is the necessity of describing reproductive proliferation of a single organism, a variable population size and population interactions. On the other hand, survival pressure is based on the concept of a population of limited size. In a simplified form, one organism replaces another due to limited resources. It is not unreasonable to model this first by using the dynamics $s(t)$ of an organism that reproduces and dies immediately after giving birth to a single mutated offspring. Thus, as a basis for our discussion we can consider a single mutating organism in a fixed size population—an ensemble. This is a Monte Carlo random walk model (Section 1.7.2).

In the Monte Carlo random walk model we begin with a population of N non-interacting organisms identified by their locations $\{s^j\}$ on the fitness landscape. The organisms are called walkers. In each time interval, every walker attempts to take a step. Steps correspond to changes in the value of s^j . The step of an organism is selected at random from all changes in s that are allowed by organism mutation. The probability of a mutation is represented by a matrix $\lambda(s | s')$ which gives the probability of a mutation from s' to s in a particular step. The move is accepted or rejected according to the fitness $K(s)$. A convenient, but by no means unique, way to do this uses the Metropolis form, which says that if the new fitness is higher, the step is taken. If the new fitness is lower, then the step may still be taken but with a reduced probability given by the ratio of fitnesses: $K(s)/K(s')$. The lower the fitness is at s , the smaller is the chance the step will be taken. When the step is not taken, the walker stays in its original location. We can think about this process in terms of the competition for survival. Starting with an organism at s' , we perform a mutation to s . We think about

this as the momentary existence of two organisms at s and at s' . Then we perform selection. Either the new or the old organism survives and the other one disappears. In the Metropolis form there is an asymmetry between the selection of the old and new organisms. If the mutation leads to an organism that is more fit, the new organism always survives. If the mutation leads to an organism that is less fit, then there is still a probability that the new organism will survive. This probability is given by the fitness ratio. We could also choose a selection rule that treats the new and old organisms the same. This would not change the overall evolutionary behavior in this model.

Quite generally, the stochastic dynamics of an ensemble with walkers that do not interact can be written as a Markov chain (Section 1.2). The ensemble is represented by the probability $P(s; t)$ of finding a particular organism s at time t . This probability changes with time due to mutation, reproduction and death. The probabilities of organisms at one time determine the probability of organisms after an interval of time by a linear matrix equation (Eq. (1.2.5)) which we rewrite here:

$$P_s(s'; t) = \sum_s P_s(s | s') P_s(s'; t - 1) \tag{6.4.1}$$

The matrix $P_s(s | s')$ is the probability an organism at s' will go to s in the next step. It is specified by the matrix $\lambda(s | s')$ and the fitness $K(s)$. The precise expression for $P_s(s | s')$ is not essential for our discussion, but for the Metropolis form it is given by Eq. (1.7.19) as:

$$\begin{aligned} P_s(s | s') &= \lambda(s | s') \frac{K(s)}{K(s')} < 1 & s = s' \\ P_s(s | s') &= \lambda(s | s') K(s) / K(s') & K(s) / K(s') < 1 & s \neq s' \\ P_s(s | s') &= 1 - \sum_{s'} P_s(s' | s) \end{aligned} \tag{6.4.2}$$

It is important to note that Eq. (6.4.1) is linear in the organism population. It applies when there are no explicit interactions between organisms. Because the equations are linear, we can consider evolution by starting from a population located at a single point, and apply superposition to obtain the evolutionary behavior of any initial set of organisms.

There is also one more point that we must consider—the granularity of the ensemble. Eq. (6.4.1) uses continuous values of the probability $P(s; t)$. We should not use a continuum model to describe populations, because a subunit population makes no sense biologically. The Monte Carlo random walk has granularity built in. However, as long as the model is linear this granularity is not essential. When we consider interactions between organisms that make the model nonlinear, we can do so in the context of the random walk model.

Since we are discussing the properties of a system for which we do not actually know the landscape, we should review what we know about the general properties of Markov chains that are true for any landscape. We know that after enough time has passed, a Markov chain in a connected finite space will reach equilibrium. This is true about the model populations independent of whether the parameters of the model are derived by assuming nonequilibrium organisms and nonequilibrium processes of

birth, consumption and death. The extensibility of the genomic space suggests it may not be finite. However, any limit on the ultimate length of the genome implies that over long enough time the system must reach equilibrium. The time to reach equilibrium may be much longer than any reasonable amount of time (e.g., the lifetime of the universe) but our discussion does not depend upon this, since in this chapter (contrast Chapter 4) we are concerned about the dynamics of the ensemble, not the time scale to reach equilibrium.

The overall behavior of the Markov chain is that of a relaxation process of $P(s; t)$ to the target (equilibrium) probability distribution $P(s)$ which we recognize as the fitness $P(s) = K(s)$. This follows from our use of the fitness to determine the probabilities of taking a step in the random walk. We may choose to represent the fitness as:

$$K(s) = P(s) = e^{-E(s)/kT} \quad (6.4.3)$$

where $E(s)$ is determined as a function of the fitness using

$$E(s) = -kT \log(K(s)) \quad (6.4.4)$$

We call $E(s)$ the energy since it plays a similar role to the energy in particle motion on an energy landscape. However, the energy as it is defined here is not the actual energy or energy consumption of the system—it is only a way of writing the fitness. High energy implies low fitness, and low energy implies high fitness. The energy landscape is the landscape for motion of particles representing the genome of organisms. In principle, the parameter kT plays no essential role and could be set to 1. If the temperature kT is kept as a tunable parameter, it is an overall scale factor that changes how flat the fitness landscape is. This reflects the influence of chance in the selection process. For low kT the chance of a higher-energy organism surviving is insignificant. For higher kT higher-energy organisms are more likely to survive.

The identification of the fitness with the target probability distribution of the organisms enables us to think about the evolutionary process directly. The concept of selection appears in the target population distribution, since the higher the fitness, the greater the target population of the organism. Even though the target distribution $K(s)$ is not the same as the distribution at a particular time $P(s; t)$, under some circumstances the relative populations between organisms given by $K(s)$ may be the same as in $P(s; t)$. We will discuss the conditions under which this is true below.

There is one aspect of this model that may already be troubling. If the fitness is directly related to the current population of organisms, this would strongly favor microbes over insects and insects over human beings. The difficulty here is not superficial and is important for the understanding of evolutionary theory.

Our objective will be to discuss generally the consequences of the random walk model. In particular, we will focus on building an understanding of the relationship between general biological phenomena and the motion of populations on the fitness landscape. We will also consider the effect of the environment through the shape of the landscape and the implications of interaction between organisms. Eventually we will find this model to be quite limited and will discuss ways that it must be improved to account for the phenomena we hope to describe.

Quite generally, the dynamics of a Monte Carlo random walk on a landscape is an exploration of the space with longer times spent in regions of lower energy. As we discussed in Section 6.3.2, the nature of the space of possibilities s can be used to describe the possible mutations. The coordinates of organisms that can mutate to each other are close in space, and those that require several steps are further apart. Once we have determined the nature of the space, we must provide values for the fitness. Then we can tentatively apply our intuition to the dynamics of a population that appears to diffuse in the space.

6.4.2 *Shape of the landscape*

In a theory of evolution based upon fitness, there is only one mathematical entity—the fitness. Thus we must satisfy ourselves that using only the fitness landscape we can account for all of the phenomena of life. If we knew the landscape, we could analyze it to arrive at these conclusions. Alternatively, we may analyze the requirements that the landscape must have in order to satisfy these properties. At this time, the latter phenomenological approach is appealing, since we have yet to develop a systematic approach to obtaining the actual landscape. A systematic determination of the landscape would require us not only to know the fitness of specific organisms, but also their genome or phenome in order to map the fitness space. It would be necessary to know this both for organisms that are found on earth and organisms that might be created by genomes that do not exist. Using the phenomenological approach, we can relate general properties of the landscape to the phenomena of life. Various experiments have more specific bearing on the nature of the landscape.

When we consider mathematical models for the landscape of the fitness there are several generic possibilities:

Flat—The landscape may be essentially flat, corresponding to the neutralist perspective.

Smooth—When there are variations it might be smooth, so that fitness varies continuously with changes in the organism. It suggests that there are only a few widely separated minima.

Rugged/random—A rugged landscape implies that the fitness of one organism is uncorrelated with the fitness nearby. The fitness might be selected at random from a distribution.

Locally correlated—If there is local correlation then the fitness is correlated within a limited distance, and becomes random for larger distances.

Locally rugged with long-range correlations—If the landscape is random over short distances, it may still be smooth if we average the values of fitness over neighboring sites, or look at the minimum of the values of fitness over neighboring sites and consider the longer-range variation.

Complex—A truly complex landscape implies that there exists structure on every scale. There might be power-law correlations between different locations as a function of distance. Different regions may be smooth or rough. This allows for many different kinds of evolutionary behavior. In this case we should not infer from one or two phenomenological examples what the general behavior is like. However,

the existence of various possibilities does not necessarily mean they are relevant to the global behavior of evolution.

6.4.3 Evolution—local landscape dynamics

We start by considering incremental pictures of the dynamics of a population of organisms analogous to Section 6.2.5. These should be related to smooth fitness surfaces for continuum s . The first picture of equilibrium as a balance between mutation and selection (Fig. 6.2.1) can be readily understood as the behavior of a population in a valley. The equilibrium distribution $P(s) = K(s) = e^{-E(s)/kT}$ is realized with the energy a parabola $E(s) \propto (s - s_0)^2$ to first order in arbitrarily many (continuous) dimensions. This picture works. In the dynamics of Monte Carlo walkers, mutation increases the diversity of the population, while selection reduces it.

We run into some trouble with the second picture (Fig. 6.2.2), of population motion on a linear slope. In the model that we are considering the population does diffuse down the slope, but the distribution broadens (Fig. 6.4.1). What happens when we add more dimensions? When the landscape is smooth, there is only one direction in which the fitness is increasing (the steepest descent direction of the energy $K - E$), and all orthogonal directions have no change in fitness. This is a property of a

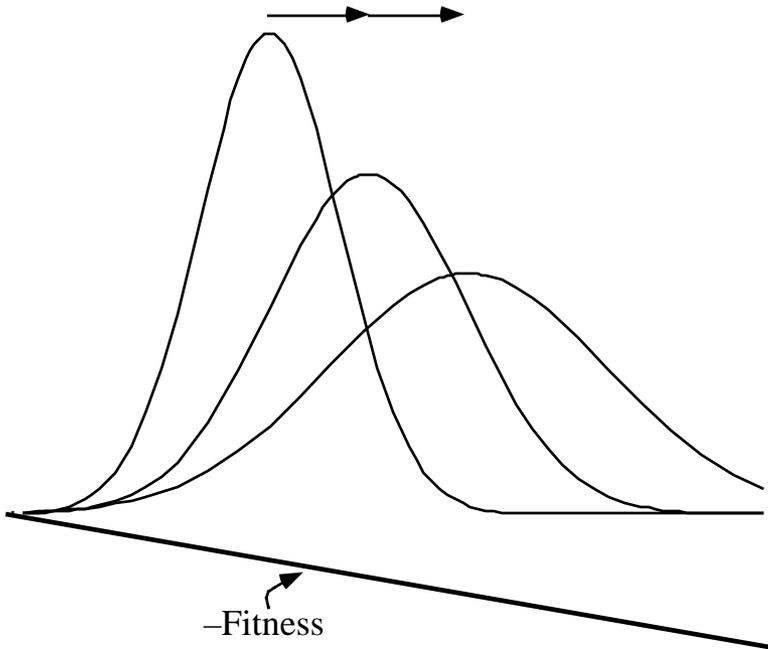


Figure 6.4.1 Schematic illustration of evolution on a linear fitness slope in the Monte Carlo random-walk model. Equivalent to the problem of diffusion, the model always results in a spreading of the population unless it is confined in a well. Thus the population spreads as it translates in average location. This is unlike the conceptual illustration of Fig. 6.2.2, and is unlike the models that will be described in Section 6.5. ■

smooth function, and does not require any special conditions. This should be recalled in the context of the selectionist/neutralist controversy. To first order (i.e., valid for incremental evolution) only one out of many dimensions of variation of the mean of a population of organisms can be affected by selective pressure. In the other dimensions the population will spread out until it reaches second-order changes in the fitness.

In general, the landscape model readily accounts for the spreading of a population throughout space. We might argue that this is a favorable outcome for the explanation of the diversity of life. However, there is greater difficulty in accounting for confinement of the population. Confinement is evident when a population of organisms has a limited range of traits. It can be confined in a valley; however, a population evolving as a whole cannot be in a valley. In order to confine an evolving population, it is necessary to assume that the evolution is in one dimension only and that other dimensions are confined as in a channel. Even in this case, from Fig. 6.4.1 we see that spreading occurs in the direction of evolution.

Trait divergence requires the confinement of population traits, since two populations of organisms must be separated from each other. To understand the formation of two groups of organisms with distinct traits, as illustrated in Fig. 6.4.2 we would consider a spreading population encountering a ridge that will separate the population at later times. As long as the landscape is smooth, the population will be continuous. Only when there arise barriers will the population separate into different parts. While there is need for a cause for the separation, there is no need for a cause for the broadening of the distribution.

Another way to understand the existence of groups of organisms with distinct traits is through local minima in the landscape. A rough or correlated landscape has multiple minima and barriers over which walkers must cross to reach them. Starting at a point within a particular valley, the population spreads and becomes a Gaussian distribution at the minimum. Over time, the population will escape from the valley to find other valleys. For two valleys this is just the two-state model of Section 1.4. The population evolves by changing the relative probability of the two states until an equilibrium is established between them. There is a characteristic time for this equilibration. As shown in Fig. 6.4.3, this can serve as a model for trait divergence or extinction.

When there are many valleys, we can characterize the population at any time by a quasi-equilibrium that applies to the region of space which has been reached by the population. In this region of space the relative population of different organisms is given by their relative fitness. Thus, in this region the population approximates the expression

$$P(s; t) = \frac{K(s)}{K(s)} = \frac{e^{-E(s)/kT}}{e^{-E(s)/kT}} \tag{6.4.5}$$

where the values of s in the sums are also limited to the region of space that the population has reached. It is important to note that a feature of this model is that the population of organisms in a well does not evolve together. Instead, individual organisms explore space and accumulate at valleys that are then identified as groups of organisms with similar traits. Since there is no interaction between the organisms, there is no reason for them to evolve together. This is related to the problem of con-

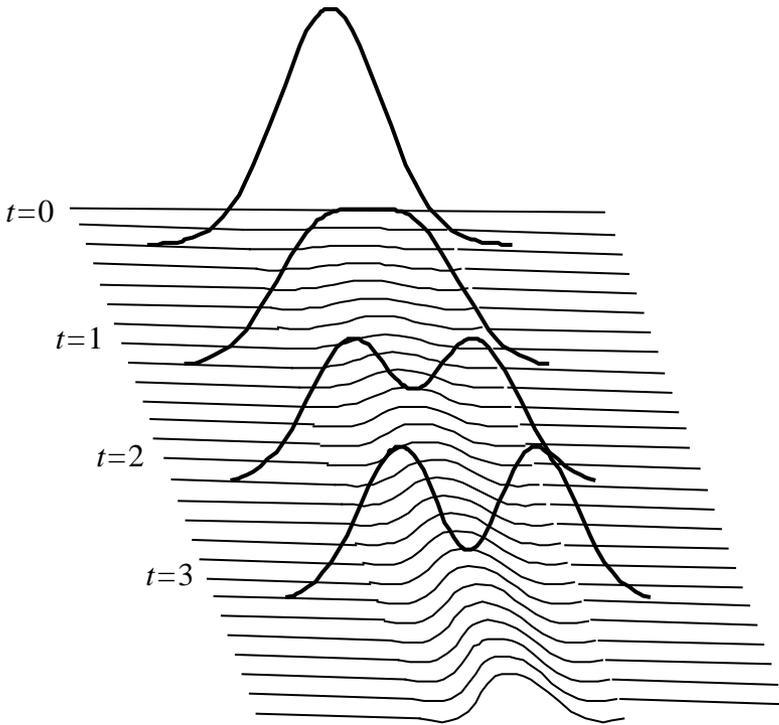


Figure 6.4.2 Schematic illustration of trait divergence in the Monte Carlo random-walk model. The process requires at least two dimensions in which fitness is varying. In the first direction, a linear fitness slope causes the population to translate over time. This dimension is indicated in the figure by successive closely spaced curves displaced towards the bottom right of the page. The second dimension is shown by the curves themselves. As the population evolves down the slope, it encounters a fitness ridge in the second dimension which causes the population to split into two parts. ■

finement. The problem related to confinement is most apparent when we consider whether the population maintains a structure of separated groups of organisms or continues to disperse until each organism is isolated.

On a rough landscape in a one-dimensional space, the population of walkers is confined to a limited region of space, because barriers prevent it from expanding to fill the space. However, in higher dimensions the population can generally escape around barriers to explore ever larger regions of space and therefore also find progressively lower minima if they exist. We note that in order to account for the phenomena of life, the landscape must be constructed in such a way that groups of organisms continue to exist: there isn't complete accumulation in one valley, and at the same time there isn't complete dispersal.

We can see that describing a landscape that enables the creation of distinct organism types without causing complete dispersal is difficult in this model. The need for this kind of balance is not healthy in a generic model, because it compels us to pro-

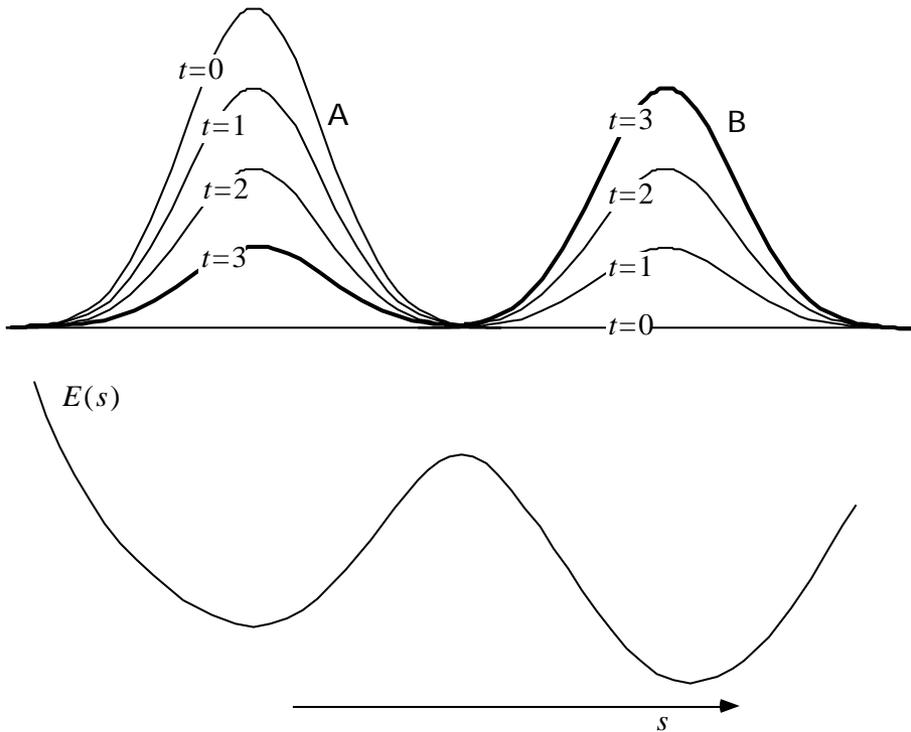


Figure 6.4.3 Evolution of population on a landscape with two wells, similar to the time evolution of the two-state system in Section 1.4. Starting from a population in one of the two wells, the population in the other well grows until equilibrium is reached. This can be a model for trait divergence if organisms of both types continue to exist in equilibrium, or if multiple wells are being filled and emptied, as in a washboard energy with progressively lower wells. It is also a model for extinction, when a well becomes completely depopulated. Note that for trait divergence we could also start from a population in the lower well and create a smaller population of new organisms by occupying the upper well till it reaches equilibrium. ■

vide some reason that the landscape is so constructed. No reason is readily apparent. We will try to solve this problem with interactions between organisms in Section 6.4.5, but we will be only partially successful.

In the random-walk model there is a natural way to discuss the effect of the mapping of genome to phenome. The genomic representation can be accounted for by writing an effective phenome fitness in terms of the genome fitness as:

$$K(w) = \sum_s \delta_{w(s),s} K(s) \tag{6.4.6}$$

which says that the fitness of the phenome coordinate is the sum over the fitness of the respective genomes that give rise to this phenome. This makes sense, because the phenome target population is the sum over the respective genome target populations

for all genomes that give rise to this phenome. Eq. (6.4.6) is the same as treating the fitness using a free energy for the phenome coordinate.

$$K(w) = \sum_s \delta_{w(s),s} e^{-E(s)/kT} = e^{-F(w)/kT} \quad (6.4.7)$$

The free energy, defined as in Eq. (1.4.27),

$$F(w) = -kT \ln \left(\sum_s \delta_{w(s),s} e^{-E(s)/kT} \right) \quad (6.4.8)$$

plays the same role for the phenome as the energy did for the genome. It contains the effects of the different number of possibilities of the genome for each value of the phenome.

The free energy can also be written in terms of an entropy with the usual relationship between energy, entropy and free energy. Assuming the fitness is only a function of the phenome w means that the energy $E(s)$ can be written as $E(w)$ and can be removed from the sum in Eq. (6.4.7) to obtain:

$$F(w) = E(w) - kT \ln \left(\sum_s \delta_{w(s),s} \right) = E(w) - TS(w) \quad (6.4.9)$$

The sum in the logarithm is the distribution of possible values of $w(s)$.

For the phenome representation of Eq. (6.3.1) with $\delta w_i = \delta w$, the use of a phenome fitness takes into account the larger number of possibilities of the distribution being near w_0 . For random s_i (no selection), $w(s)$ is a random walk in the variables s_i . Thus the distribution is a Gaussian (Eq. (1.2.39)) and the free energy is a quadratic in w (constant terms due to the normalization of the Gaussian can be neglected):

$$F(w) = E(w) + (kT/2N\delta w^2)(w - w_0)^2 \quad (6.4.10)$$

Thus the maximum of the phenome fitness is at w_0 . A similar calculation was done at the beginning of Chapter 5.

The use of a phenome fitness enables us to perform the Monte Carlo walk in the phenomic space without considering the genomic space. In general we have to be concerned about the possible transitions in w as a result of mutations in s . For this simple case where $\delta w_i = \delta w$, mutations can change w by only ± 1 . As discussed in Section 6.3.2, when there is no fitness bias in the underlying genome representation, $E(w) = 0$, there is still a fitness bias in the phenome representation $F(w) \neq 0$. Changes in w are linear in time if we start sufficiently far away from w_0 . Every step toward w_0 is accepted and every step away is rejected. Near w_0 steps are random. Eventually the population reaches equilibrium in the Gaussian distribution.

To consider a fitness bias and selection that would lead to a phenome that has, for example, taller horses, we would write the free energy as:

$$F(w) = -\alpha w + (kT/2N\delta w^2)(w - w_0)^2 \quad (6.4.11)$$

where the linear energy $E(w) = -\alpha w$ is the phenome fitness bias. The new equilibrium value of the phenome is obtained by minimizing the free energy and is given by

$$w_0 = w_0 + \alpha N \delta w^2 / kT \tag{6.4.12}$$

The equilibrium distribution $e^{-F(w)/kT}$ is a Gaussian of the same width as before. Because it is displaced from the center of the genomic space, there are fewer distinct genomes that comprise the population. This reduction can be estimated by the number of genomes at the peak location w_0 which is reduced from the number at w_0 by a factor:

$$\frac{\delta_{w_0,s}}{\delta_{w_0,s}} = e^{(S(w_0) - S(w_0)) / k} = e^{-(kT / 2N\delta w^2)(w_0 - w_0)^2} = e^{-\alpha^2 N \delta w^2 / kT} \tag{6.4.13}$$

This illustrates the effect of selection which, by definition, decreases the number of possible organisms in the population.

Question 6.4.1 Consider a genome that consists of the values of all $\delta w_i = \delta w$ except for one mutation s_0 which has the value of $\delta w_0 = N \delta w$. Start from an equilibrium distribution without selection. Discuss strategies for artificially selecting organisms for obtaining large w .

Solution 6.4.1 The initial distribution of w consists of two Gaussian peaks located at $w_0 \pm \delta w_0$. It is clear that the organisms that are optimal all have $s_0 = 1$. The key point in performing selection, however, is realizing that in addition to the gross effect of the single mutation, the best organisms also have many small effects due to $s_i = 1$ for $i \neq 0$ that accumulate to reach the optimal w . To achieve a population of such organisms, the best approach is not to select the upper peak of the equilibrium distribution but rather the upper tails of both peaks. The upper tail of the lower peak is only one mutation away from the upper tail of the upper peak. In contrast, organisms in the lower tail of the upper peak are many mutations away from the upper tail of the upper peak.

Consider the problem of developing a selection strategy for a more complex distribution of δw_i . Also, does the answer change for sexual reproduction? ■

6.4.4 Complexity increase

The increase of complexity of organisms is tied to the increasing length of the genomic representation. For now we can consider this as an intuitive relationship which will be clarified somewhat during the discussion. A more careful formulation of the relationship of genome length and complexity is deferred to Chapter 8.

A simple model of the process of genome extension can be constructed out of the genome-space model consisting of strings of characters where point mutations, insertions and deletions are allowed. There is a difficulty with this model that will become apparent in a moment. Consider first a model where the fitness is the same for all possible genomes. We are interested in the time dependence of genome length $l(s)$ of the population when we start from a population of organisms with a short genome,

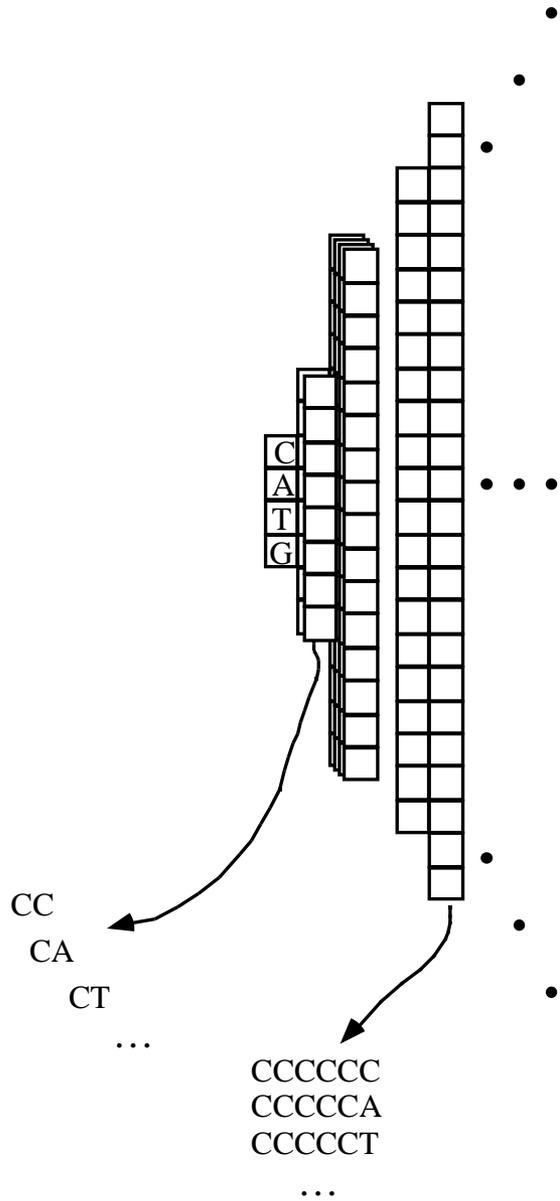
which we might for simplicity take to be length zero. As a result of mutation, the population will spread out in genomic space. It will radiate outward from short genomes to longer ones. Without any fitness bias, there is equal probability of reaching any of the genomes of a particular length. We can treat the genome probability as a function of the length $P(l)$. Over time the characteristic length of the genome increases. However, it does not behave like a usual random walk in one dimension. One reason for this is that the genome lengths must be nonnegative, so steps to negative lengths are rejected. More significantly, since we have an expanding number of possibilities for longer-length genomes (Fig. 6.4.4), each step of an organism in length has a larger probability of increasing than decreasing its length. The number of ways to increase the genome is $q(l+1)$ (if we assume there are $l+1$ places to insert q possible bases) and only l possible deletions to decrease it. This leads to a bias toward longer sequences.

The bias corresponds to an entropy (and free energy) difference between strings of length l and $l+1$. The number of possible organisms of length l is q^l . The effective entropy of strings of length l is $S(l)/k = l \ln(q)$. The free energy difference between strings of length l and $l+1$ is $-kT \ln(q)$. Thus, without any underlying fitness bias, the increasing number of possibilities (phase space) for longer genomes creates a bias in the diffusion. The bias would result in an average genome length that grows linearly with time. Does this mean that it is easy to create more complex organisms? The increasing number of organisms that are more complex appears to cause a bias in favor of their creation. There is a basic problem with this argument, however, because we have ignored the entropy loss associated with adding a base to the genome from the fluid that surrounds it. Under normal circumstances we would assume that bases in free solution have a higher entropy than bases in a long chain. Adding a nucleotide to the end of a chain decreases the overall physical entropy even though it increases the entropy in the genomic space. This would cause a counterbias against the creation of longer genomes. A more complete analysis would include the energy and entropy in the free energy difference for adding the base to the chain. An even more complete analysis would also include the nonequilibrium conditions of chemical energy sources in the cell that drive such processes as DNA replication. The main lesson to be learned is that a simulation of the genomic space cannot ignore the physical free energy, because this neglect can give rise to an unphysical bias to the formation of longer chains.

We still have to address the question of the bias from a different point of view. Is it sufficient to argue that for a particular set of conditions the genome may be driven to longer lengths to explain evolution? Should we argue that the conditions in the cell may be such as to form longer genomes, and that this is responsible for the increasing complexity of organisms? To answer this question we must consider again, and more carefully, the complexity of organisms. If there is a bias to the addition of more bases, does this really create more complex organisms? No. It is only when the longer DNA is used for some purpose that the organism is more complex.

The problem is that if all possible genomes are created, then the description of the population is simple. It is the selection of organisms by some criteria that makes them complex (Question 6.4.2). This arrives at the crux of the evolution of complexity. It is the selection of an organism from a large number of possibilities that makes

Figure 6.4.4 Illustration of the expanding space of genome possibilities that starts from a single base on the left. Lengthening the genome by a single base moves one step to the right and multiplies the number of possibilities by four. The space is only schematically indicated after three bases. Many different steps are possible between genome lengths if we allow deletion or insertion of bases. If we only consider the space available, starting from an organism of a particular length genome, and without any selection, the genome will lengthen by diffusion because of the much larger number of longer genomes. This, however, does not take into account the actual free energy for adding a base. ■



it complex. In the theory of evolution, the selection criterion is fitness. The assumption is that longer genomes are systematically able to represent fitter organisms. Since there are many more possible organisms of longer genome length, this enables selection of more specific traits that correspond to higher fitness. It is presumed that the highest fitness of a particular length genome

$$K(l) = \max_{l(s)=l} K(s) \tag{6.4.14}$$

is a monotonically increasing function of the genome length.

We can see the advantage of lengthening the genome if we look at our phenotype/genome relationship in Eq. (6.3.1). This relationship describes a phenomic trait in terms of the available genomic parameters. As long as the optimal trait exists within this representation, there is no problem. However, if it does not, the addition of extra parameters in the form of possible genome coordinates increases the possible options for a particular trait or for combinations of traits. This increase in the phase space of possibilities is exactly the motivation for increase in genome and organism complexity.

Our discussion of selection and organism complexity is also relevant to the neutralist/selectionist controversy. If neutral mutations dominate the space of possible organisms, then we are left with the circumstance of a large number of possible organisms with selection not playing a significant role in evolution. This is unsatisfactory as an explanation of the evolution of complex organisms that, without selection, have no mechanism by which to arise. Thus, even if neutral mutations account for many of those that are possible, it is the mutations that do affect fitness that account for the part of evolutionary changes that we are most interested in.

Question 6.4.2 We noted that selection is what causes an organism to be complex. What is wrong with the following statement: “If you create all organisms of length 10^{10} base pairs, you will also create human beings, and therefore you will have created complex organisms”?

Solution 6.4.2 A part of the problem with this statement is the number of organisms that would have to be created, which is $4^{10^{10}}$. However, this is not yet a complete answer. Another problem with the argument is that in order to see that you have also created human beings, you must have some way of pointing them out among the large (huge) number of other organisms. It is pointing them out which is equivalent to selection. Otherwise we can only see a typical organism out of this set, which would not be a complex organism. ■

Question 6.4.3 (for further thought) If there are a larger variety of complex organisms, then why are there fewer distinct types of complex organisms than simple organisms currently on earth?

6.4.5 Interactions

In this section we consider interactions between organisms—reproduction, consumption, predation, symbiosis, parasitism—which affect fitness. To understand the effects of interactions in the random-walk model we treat fitness as a property of the entire population of organisms rather than of a particular organism. We write the fitness as $K(\{N(s)\})$, where $N(s)$ is the number of organisms of genome s . Using this fitness of the whole population, we can still treat evolution as an optimization of fitness. We can also define the fitness of a particular organism as the difference in the

fitness of the total collection of organisms minus the fitness when the organism is not present:

$$K(s) = K(\{N(s) + \delta_{s,s}\}) - K(\{N(s)\}) \tag{6.4.15}$$

We can see that our original fitness landscape already included interactions. However, they were included only in a time-independent average (mean field) way. To get back to our original picture, we would write the mean field landscape of a single organism in terms of the fitness of the population as

$$K(s) = K(\{N_0(s) + \delta_{s,s}\}) - K(\{N_0(s)\}) \tag{6.4.16}$$

for a reference population $\{N_0(s)\}$. This assumes that variations that occur in the populations of organisms do not significantly affect the fitness of a particular organism. This tends to be valid when the population of organisms is large and unchanging. For smaller populations that change on the time scale relevant to the evolutionary dynamics (this would seem to be a tautology), we must include the interactions explicitly. This means that the existence of a particular organism affects the fitness of other organisms. From Eq. (6.4.15), the fitness landscape changes with time along with the changes in populations.

It is important to recognize, however, that as soon as we assume a fitness which is only a function of the population, $K(\{N(s)\})$, we also have a symmetry of interaction. When an organism at s lowers (raises) the fitness of an organism at s' , then an organism at s' lowers (raises) the fitness of an organism at s . This symmetry is shown in Question 6.4.4. If we want to model asymmetric interactions, then we must use entirely different models discussed in Section 6.5. Within the Monte Carlo random-walk model there are thus only two types of interactions, interactions between organisms that raise their fitness and interactions that decrease their fitness.

Question 6.4.4 Prove that “When an organism at s lowers (raises) the fitness of an organism at s' , then an organism at s' lowers (raises) the fitness of an organism at s .” This assertion is true whenever we have a model that assigns a unique fitness to the collection of organisms $K(\{N(s)\})$, where $N(s)$ is the number of organisms with genome s .

Solution 6.4.4 The only difficulty is translating the English into an equation. The statement is an answer to the question, How does adding an organism to s affect the fitness of an organism at s' ? Start from a set of organisms $\{N(s)\}$. The change in fitness due to adding an organism at s before adding an organism at s' is:

$$K(\{N(s) + \delta_{s,s}\}) - K(\{N(s)\}) \tag{6.4.17}$$

After adding an organism at s' it is:

$$K(\{N(s) + \delta_{s,s} + \delta_{s',s'}\}) - K(\{N(s) + \delta_{s,s}\}) \tag{6.4.18}$$

The difference between these two is:

$$\begin{aligned} & (K(\{N(s) + \delta_{s,s} + \delta_{s,s}\}) - K(\{N(s) + \delta_{s,s}\})) - (K(\{N(s) + \delta_{s,s}\}) - K(\{N(s)\})) \\ & = K(\{N(s) + \delta_{s,s} + \delta_{s,s}\}) + K(\{N(s)\}) - K(\{N(s) + \delta_{s,s}\}) - K(\{N(s) + \delta_{s,s}\}) \end{aligned} \quad (6.4.19)$$

which is symmetric in s and s' , so the assertion is proven. ■

A convenient way to think about the interactions is that adding an organism at one place in the phase space (genome or phenome) changes the landscape for other organisms by raising or lowering their fitness. A uniform raising or lowering of the landscape does not affect anything; only the differential effect on the fitness matters. The simplest interactions are those that raise the fitness of all nearby organisms, or those that lower the fitness of all nearby organisms. The effect is assumed to decrease with distance. When the fitness of organisms is raised (the energy is lowered), a depression (energy well) is created around the organism that causes other organisms to be drawn toward it—an attraction between organisms. If the fitness is lowered, other organisms tend to move away—a repulsion between organisms.

When there is an attraction, the energy well may cause a self-consistent trapping, effectively binding the organisms in a group. This trapping causes the organisms to move together on the landscape rather than as individual organisms. This is the effect we need in order to account for the confinement of populations discussed in Section 6.4.3.

For evolution down an incline, Fig. 6.4.2, the spreading of the organisms would be limited. For more than one dimension, the mutual attraction automatically creates a channel. Then the co-moving organisms would appear to be analogous to our understanding of evolutionary change in Fig. 6.2.2. There still is a difficulty with this picture because the local interactions become less relevant as the dimension of space increases. In particular, in four or more dimensions, short-range interactions are irrelevant. Intuitively, this is because in a large dimensional space there are too few encounters between organisms for their interactions to matter. Alternatively, the reason is that the mean field theory becomes exact in four or more dimensions. Thus in the apparent high number of dimensions of the phenomic or genomic space, the attractions should be irrelevant. There are two possible flaws in this argument. The first is that the number of relevant dimensions in distinguishing between organisms may not be as large as the number of apparent dimensions. The second is that the way we are modeling interactions is inadequate. The latter would again force us into a different class of models.

Even if attractions help with confinement, they do not as readily help with trait divergence (Fig. 6.2.3). The picture of a ridge, Fig. 6.4.3, would be difficult to justify except as a low-probability occurrence. On a smooth landscape, the likelihood that a self-attracting population is precisely at a location where a ridge occurs (as opposed to on one side or the other) is small. Speciation would be more readily understood as a process where a self-attracting population splits by chance into two populations by random processes. The most likely scenario is when a small population separates itself from the whole. This is just the escape of one (or a few) organisms from the energy well created by the large population. If several individual organisms escape, they

may encounter each other and aggregate to form a co-moving group. Once again, however, this scenario requires a delicate balance between the tendencies of organisms to disaggregate and aggregate, which cannot be expected to apply generically.

Before leaving the topic of attraction, we consider, for future reference, the rate of change of a self-attracting population in two cases. When the collection of organisms moves together, random motion on a flat landscape is slower than the motion of an individual organism. In Chapter 5 the same problem was discussed for a polymer. The diffusion constant was shown to decrease with the number of monomers as $D \propto 1/N$ and the distance traveled as $r_{cm} \propto N^{-1/2}$. On an incline, the speed of travel of the self-attracting population would be the same as for a single organism, because on average each organism of the group feels the effect of the bias.

Thus far we have discussed attraction. An organism that repels other organisms would move on the landscape in isolation. If, because of a valley, the organisms accumulate, they would tend to escape more readily and rapidly from it than without the repulsion.

Thus far we have discussed the effects of either attraction or repulsion separately. In order to understand how attraction and repulsion affect evolutionary behavior, we must recognize that the attraction and repulsion are properties of each place in the space, not of the walkers themselves. The primary effect of the interactions is to cause organisms to bunch in regions of space where they are attracting each other. Regions where they repel would tend to be empty—all other things being equal. Since the properties of attraction and repulsion vary from place to place in the space, an evolving population may encounter both aggregation and dispersal. We might consider creating a model using this variation to account for trait divergence and other properties of evolution. It is important, however, to recognize that this kind of model is a significant departure from the model that tries to explain evolution from a single fitness function of individual organisms.

Finally, we discuss long-range interactions. Long-range interactions between organisms can cause circumstances where the fitness valley in which one type of organism exists depends on the existence of another organism at some other location in the space. This is most simply illustrated by the dependence of animals on plants in general, or by specific relationships between predator and prey. Note that these relationships are largely untreated in this model of an energy landscape (for example, they are not symmetric). However, in general we can recognize that relationships of mutual dependence exist. Changes that occur in one organism thus result in changes in the fitness landscape of other organisms and thus changes in the other organisms as well. This leads us to a recent innovation in evolutionary theory—the concept of avalanches in evolutionary change. Over time, a system of dependencies is developed which can be disrupted when one organism undergoes a change in population that is sufficiently severe, whether due to evolutionary change or external influence, such as environmental change. The change causes a cascade of changes in other organisms. Depending on the nature of the mutual dependencies, the cascade of changes can be large or small. The modeling of such phenomena is outside of the fitness landscape model because it is dependent on interactions that are only being added as secondary

effects to the fitness landscape. A model that has been used to think about such processes is a sandpile model. In this model, grains of sand fall at random onto a surface. They cause piles to grow which are formed out of grains supporting themselves on other grains. The addition of a single grain can destabilize a pile and cause an avalanche that can move many grains of sand. The sandpile model has a power-law distribution of avalanche sizes. This model has been used as an analog of what may happen in mutually interacting networks of organisms.

There is now substantial evidence that evolutionary change has undergone periods of rapid change in many organisms (e.g., the Precambrian explosion) after long periods of slow change. Known as the model of punctuated equilibria, it may be possible to describe this by a model of avalanches. The idea of a mutually consistent network of dependencies is also a model for the sudden extinction of large dinosaurs after their extended existence. The fitness of individual organisms was high due to mutual interactions. However, when a sufficient disturbance occurred (possibly due to impact of a comet) then the self-consistent network of dependencies was disrupted. Once this occurred, other organisms that were less fit under the original circumstance (not just for climactic reasons) were able to increase and dominate the population of organisms.

We will return to consider interactions between organisms in Section 6.5 in the context of a different class of models. We will also discuss the impact of interactions such as altruism and aggression and the formation of collective behaviors in Section 6.6.

6.4.6 Evolution—global landscape dynamics

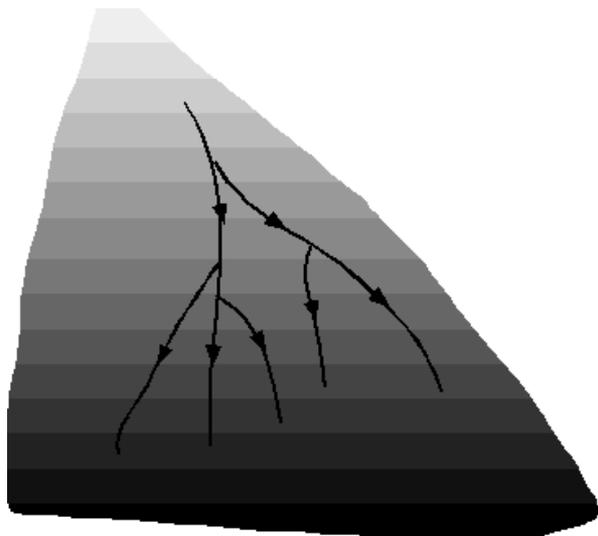
There are conceptual problems in understanding a global fitness landscape that includes microorganisms and man. After several billion years of evolution, we might expect that the relative populations of microorganisms, insects and man would reflect evolutionary progress and fitness. On one hand, the fossil record suggests that evolution proceeded from microorganisms through insects to mammals. On the other hand, the numbers appear to have remained in favor of the smaller and simpler organisms that arose earlier in evolution.

If the fitness is directly related to the number of organisms according to Eq. (6.4.3) where $P(s) = K(s)$, then fitness would strongly favor microbes over insects and insects over human beings. There is, however, an alternative definition that is equally valid. We could set the fitness to be the mass times the organism population, $P(s)M(s) = K(s)$. $K(s)$ would still be the limiting distribution of the ensemble which represents mass rather than organisms. A Monte Carlo walker would represent a unit of organism mass. This definition gives a much higher relative fitness for large organisms. We do not want to argue which definition is correct, but to understand why there is an ambiguity. The key point is that the use of an ensemble is predicated on the existence of a conserved total number of elements in the ensemble. The total number of organisms is not conserved. Neither is the total mass of the organisms, though this might seem to be a better approximation. Since such quantities are not conserved, we do not have a well-defined ensemble. This is only one of the problems that give rise to

a difficulty in defining the relative fitness of widely different organisms. With this in mind, we discuss three scenarios for the global behavior of evolution on the fitness landscape. The first is evolution downhill, the second is evolution uphill, and the third is an alternative that relies upon a changing landscape.

One traditional view of evolution is most easily considered as starting from the pinnacle (or somewhere on the side) of a long hill (Fig. 6.4.5). The motion of the population consists of a descent downward. Grooves in the hill and self-attraction are essential to account for trait divergence causing a separation into droplets. Unlike flowing water on a hill that typically converges upon a single channel, the flow is an outward branching that results in a treelike structure of different subpopulations with distinct traits. The branching is an assumption about the dynamics; it is more reasonable for a large-dimensional landscape than the usual two-dimensional one. Of course, we must also explain why there isn't a complete dispersal into very few organisms per subpopulation. Starting from this picture, however, another key question would be, Why do there persist primitive organisms such as single-celled organisms or insects that were formed earlier and thus higher on the hill? One possible answer is that these organisms continued to evolve and increased their fitness without dramatically changing form. The problem with this picture is that improving fitness would seem to require manifest changes in phenotype that are not evident. A second possible answer is that nonconservation of organisms enables the microorganisms to continue to regenerate even though they are high on the hill. However, the ability to regenerate populations alters radically the assumptions of selection according to the fitness landscape. Any such new model requires its own analysis. Thus, while the picture of evolution downhill is consistent with the view that fitness propels forward the process of evolution, it is difficult to reconcile this with the population ratios that

Figure 6.4.5 A first model of the global fitness landscape considers all of evolution to occur on a single long fitness slope upon which the evolution of organisms consists of progress to increasing fitness, like the flow of water downhill in energy, but with the added assumption of outward branching. ■



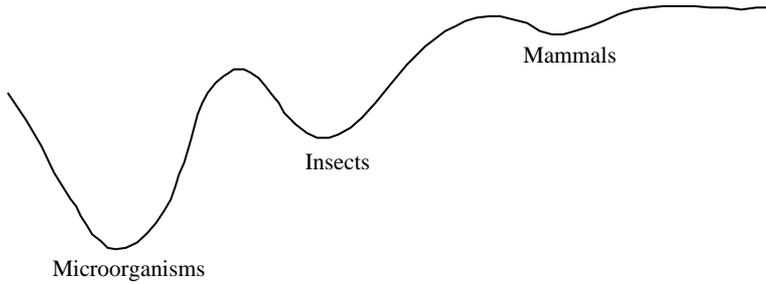


Figure 6.4.6 A second model of the global fitness landscape assumes that organisms are found today in rough proportion to their fitness, and therefore that the fitness landscape consists of energy valleys that are lowest for microorganisms, higher for insects and higher still for mammals. ■

continue to retain most of life as microorganisms, virtually independent of the existence of the higher forms of life.

An alternative view would adopt the existing population ratios as a model for the probability function $P(s)$ and use this probability function to define fitness (Fig. 6.4.6). In this model evolution started with microorganisms that are low-energy, high-fitness organisms. What is the driving force for the existence of higher forms of life? The answer is that random mutations provide a possibility of moving upward. The landscape of mountains and valleys is then responsible for the observed pattern of organism traits and species. The smaller numbers of complex organisms that occurred later in evolution reflect their lower fitness. A low fitness does not preclude their existence, because there are only a few of them compared to the high-fitness microorganisms. The fossil record is explained by the motion of populations upward to overcome an obstacle, and downward into the subsequent valley. Thus far the model seems to account for observations, but this quickly breaks down with further thought. Extinctions are a problem. They might be explained by temporary occupation of local minima that are higher in energy than minima currently occupied. However, extinctions would not be permanent, since such valleys are likely to be repopulated later. A more serious problem is that organisms would be expected to regularly evolve from valley to valley, both forward and backward in evolutionary order. This conclusion follows, because once a time scale of moving from one valley to another is reached, migration between them continues to occur. It is possible that existing experiments missed such processes, but it would require a dramatic revision of prevailing thought. Another controversial conclusion that follows from this model is that organism populations are close to equilibrium. Even though randomness through mutation plays the essential role of causing evolutionary change, because populations are close to equilibrium, they must be independent of history. However, the main problem with this model is that it does not agree with the overall size of the phase space of organisms. If we are close to equilibrium, then essentially all possible organisms would be

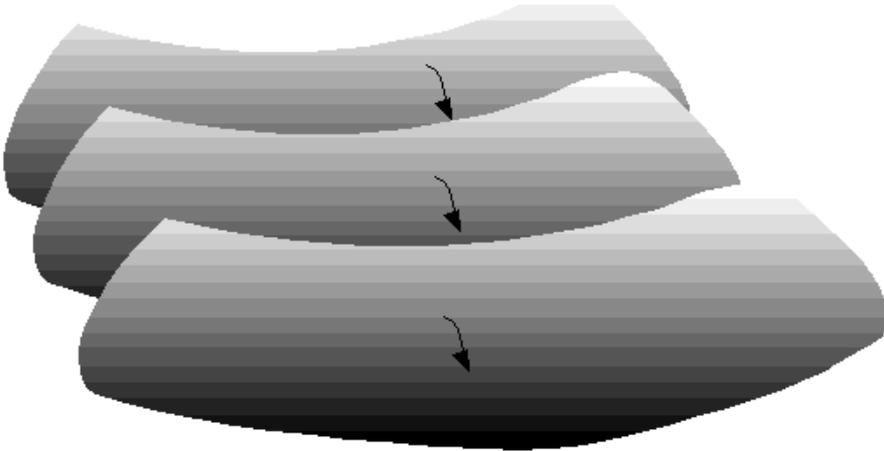


Figure 6.4.7 A third model of the global fitness landscape is a dynamic landscape that consists of expanding waves upon which organisms always evolve toward decreasing energy, like surfers on ocean waves. ■

represented in existing organisms. Since the genomic space is so large, we would have to assume that almost none of the genomic space is viable, but that organisms evolved anyway. This is not reasonable.

There is a third alternative for the fitness landscape that is consistent with the existence of a diversity of organism types at different stages of evolutionary progress but maintains the evolutionary pressure of fitness. This approach emphasizes that the long-range structure of the landscape must include the long-range interactions between organism types discussed in the previous section. For simplicity we can set the inherent fitness to be the same everywhere. The existence of a long-range interaction implies that a particular organism type promotes the existence of another organism type that may be far away on the landscape. For example, the fitness of a sheep would not be high without plants. A picture that takes advantage of this property of the landscape considers evolution as a process of surfing on self-consistent expanding waves where the large populations of simpler organisms are responsible for the fitness waves on which higher organisms evolve (Fig. 6.4.7). This picture is consistent with a local evolutionary pressure of fitness, and the persistence of primitive organisms. A specific mathematical model that is related to this picture will be introduced at the end of Chapter 7, because it is in the class of models of pattern formation in developmental biology. In Section 6.5.4 we also address related issues.

6.4.7 Randomness and determinism

Many of the questions often articulated about evolution, such as

- How does the formation of life depend on the conditions?

- What is the likelihood of the formation of life and how likely is life to be found elsewhere?
- How sensitive is the present form of life to chance, and how determined is it?
- Is the form of life on earth unique or are there viable alternatives?

have to do with randomness and determinism. One of the difficulties, however, is understanding what we mean by these terms. The statement that existing forms of life were determined “by chance events” and therefore were not predetermined is not a sufficiently clear statement since there are multiple issues that must be resolved. First, it must be recalled (Section 1.1) that chaotic behavior is deterministic. The reason for chaotic behavior is that the system is sensitive to initial conditions—small differences become amplified over time. Second, a stochastic system (Section 1.2) is a system where external influences affect the system behavior and are presumed random. Finally, in the study of thermodynamic systems (Section 1.3) randomness played a crucial role in the dynamics, but the equilibrium state of a system is completely and uniquely determined and is stable and insensitive to initial conditions.

Our objective here is to clarify rather than answer the fundamental questions. We separate the discussion into two issues. The first issue is whether life that exists on earth is representative of what would arise from any evolutionary process under a wide range of initial and intermediate conditions. If it is representative, then life is essentially determined in the same sense that equilibrium states are determined. On the other hand, if life is not a typical outcome of evolutionary processes, then the second issue is to determine which influences were important in determining the existing form of life. Are these the effect of microscopic thermal vibrations or macroscopic influences? Do the macroscopic or microscopic effects trace themselves to the initial conditions or to persistent external influences such as solar radiation?

We have noted several times that stochastic iterative dynamics of an ensemble should lead to equilibrium. The equilibrium state is not affected by the specific and possibly random path it took to get there. Thus, the existence of randomness in the dynamics does not necessarily mean that the outcome is not determined. Thermodynamics uses an ensemble in the same way that we are thinking about the collection of organisms on earth. There is, however, a basic assumption in thermodynamics which need not be true about the collection of organisms. An ensemble is an arbitrarily large collection of systems. The sense in which it must be arbitrarily large is that the number of systems is larger than the number of system states. Even if this is not satisfied, at least a significant fraction of distinct high-likelihood possibilities must be represented. The reason that an ensemble is not affected by randomness is that whenever one of the systems takes a step, another takes a step in the opposite direction.

Let us consider the organisms on earth as a limited set of examples of possible organisms. We know that the genomic space is very large and therefore we could easily argue that even with all of the organisms on earth, there is unlikely to be a representative sampling of genomic space. However, we may not care about sampling the genome space, but rather the phenome space. It is harder to tell if we have represen-

tatives of all viable phenomes. To take this discussion further, we should include the interactions between organisms. A self-attracting population that forms a species which moves together on the fitness landscape becomes correlated, and therefore a single system rather than a collection of systems. This both reduces the number of independent samples present on earth and increases the time scale over which random changes occur. More generally we know that any interaction that causes interdependence of organisms reduces the effective number of independent systems present on earth. However, we may still focus on the set of organisms and try to determine if they are representative.

Can we arrive at any conclusions from the general phenomenology of life? On one hand the existence of a wide variety of organisms suggests that many are possible; on the other hand this wide variety might be sampling all possibilities. The persistence of certain organisms since early in evolution suggests that the correlation time for organisms is very long, and therefore that independent samples of all possibilities may not have been realized. On the other hand, their persistence suggests that there may not be many other alternatives. A better source of evidence is the artificial breeding of organisms. By demonstrating the existence of many varieties of organisms that differ from those found in nature, we can conclude that the naturally occurring organisms are not representative of the possibilities. The large dinosaurs also provide an important piece of evidence through their persistence and complete disappearance. The more different they are from current living organisms and the longer their persistence on earth, the better is the argument that there are many possible living organisms and the present samples of life on earth are only a few nonrepresentative examples.

Our discussion indicates that the ratio between the number of organisms to the space of possible organisms is important in determining whether the existing population is representative. This suggests that microorganisms might be effectively in equilibrium even if multicellular organisms are not. Thus we might not want to ask whether equilibrium applies, but rather at what level of organism complexity it applies. If it turns out that the simplest prokaryotes are not fully represented, then we may conclude that this is also true about more complex organisms (Question 6.4.5).

Let us now assume, reasonably, that the existing organisms on earth are not representative of all possible living organisms. Then it becomes relevant to discuss the nature of the pathways of evolution, and the role of initial conditions or external perturbations. Either becomes important when there are multiple options at a particular moment for incremental evolutionary changes, of which only one can be chosen. The question becomes how the path is chosen, and our interpretation of randomness or determinism in this context. Of course it is not enough that different pathways exist; they must also not converge at later times. The evolutionary path taken by an organism, or a collection of self-attracting organisms, must be distinct at all later times from other possible paths in order for the choice to be important. The expanding phase space for ever more complex organisms is the best argument in favor of a lack of converging pathways. A model (or phenomenology) that shows that over time organisms are always exploring new regions of space would be relevant.

The main point to understand in this discussion is the relevance of selection. The whole idea of selection is that there are multiple possibilities of which only a few are selected. This is also the nature of what we mean by a complex organism—that it is differentiated from other possible organisms by many details that must be selected. Thus we must further ask whether the pathway taken in evolution is selected by fitness or whether other effects are significant. If fitness is the primary selective force, then we are attributing the selection to macroscopic environmental effects external to an organism and not to microscopic or macroscopic randomness. Another possibility is that, of the possible mutations that might occur, only a small subset do occur. In this case selection due to fitness can only apply to the possibilities that occurred, and microscopic randomness is relevant. Moreover, if the survival of a particular organism is not determined by fitness but only statistically related to fitness through random occurrences, then macroscopic randomness plays a role. Here again we must be careful to recognize that if fitness selection eventually forces the organisms to reach a particular place in genome space, then all prior divergences in paths due to randomness are irrelevant.

Question 6.4.5 Discuss evidence that microorganisms involved in diseases are not in equilibrium.

Solution 6.4.5 Equilibrium implies that all possible microorganisms exist. If this were true, the eradication of disease (by natural or artificial methods) and the appearance of new diseases would both be impossible. Since both appear to be possible, it seems reasonable to assume that microorganisms are far from equilibrium. ■

6.4.8 *Space and time*

Thus far our fitness landscape has been discussed as a function of genome or phenotype. We must also include the dimensions of space in our considerations. Assuming a well-defined fitness landscape as a function of the phenotype or genome also assumes that spatial variation in the landscape is smooth or that its effect can be averaged over. Rapid spatial variations are likely to have a significant impact on the model properties. However, even relatively smooth variations in space and time have important effects. The main effect of a spatial dimension is the existence of populations of organisms that exist simultaneously in time and can evolve in part independently. This would be a valid statement even if the fitness landscape is the same in different locations. However, the situation is more interesting because the fitness landscape is different in different locations. Including ocean and land environments, different climates as well as the existence of distinct combinations of organisms causes the fitness landscape to vary greatly on earth. All organisms survive only in a limited range of conditions, and have restricted spatial regions in which they are found on earth. The dynamics of the entire system become more interesting when we consider coupling the different environments through migrations. Migrations enable organisms evolving in one location to encounter alternate environments. An important realization is that this gives rise to an additional type of selection—selection

tion by the organism of its environment. Thus, organisms are not necessarily subject to a unique fitness criteria. By migrating they may be able to select an environment to which they are well suited.

Time-dependent variations in the fitness can also cause a variety of effects. An example is the mass extinction attributed to a comet that changed climactic conditions on earth and led to the demise of large dinosaurs. A more current example might be a forest fire. In either case it is easy to understand how such events might be disastrous for evolution if they happen too often or too severely. However, the comet may have been responsible for a large step forward in evolution by enabling other animals (mammals) to emerge. As discussed earlier, the disruption of an existing network of organisms may enable other organisms to arise and cause rapid evolutionary changes. The smaller example of a local forest fire is now understood to provide opportunities for the survival of organisms that would not have a chance in well-developed forests. One way to think about this is through the fitness landscape, where valleys are formed by interactions that cause self-trapping of the population. When the existing organisms are reduced in number, these valleys may also not be as deep. This enables more rapid movement of organisms on the landscape.

When large variations in the fitness landscape occur frequently, there are other effects that may occur, including the development of organisms that are better suited to these variations either through self-imposed genetic diversity (requiring collective behaviors discussed in Section 6.5) or adaptability.

Question 6.4.6 Why can't we just think about the dimensions of space as additional dimensions for the fitness landscape?

Solution 6.4.6 The nature of steps in the spatial dimension is radically different from the nature of steps in the genome dimension. Nevertheless, within the context of the model of Monte Carlo steps on a fitness landscape, we can consider the different types of steps in the same way. The only place we run into trouble is when the steps in space are directed rather than random. Specifically, when an organism can identify which direction it should move in, then there is a violation of the assumptions of the model. ■

Question 6.4.7 Discuss the relevance of spatial dimension to the problem of walkers exploring the space of possible organisms.

Solution 6.4.7 The fitness landscape may involve obstacles that consist of regions that are not viable under particular environmental circumstances. Thus we can expect that the connectivity of the phenomic or genomic space is very poor if we consider only one particular environment. The existence of a spatial dimension with different environments enables organisms to move around obstacles in the genomic space because there are more possible ways to have organisms in a variety of environments. For example, it is not clear that whales could develop from fish directly. However, according to the current view, by a process of moving from water to land and back to water it became possible for whales to appear. ■

Question 6.4.8 Discuss, from the point of view of a fitness landscape, the process of organisms crossing a mountain range to an isolated valley.

Solution 6.4.8 This scenario contains a number of important elements. First it is assumed that a population of organisms evolved in one region of the land but was not found across a particular mountain range. The mountain range is a barrier in both physical and fitness space because it is assumed that the organisms do not live easily on the mountain. By crossing the mountain, a group of organisms becomes independent of the original set of organisms of which it was a part. They participate in the evolutionary process in the isolated valley. The distinct evolutionary pressures or random influences that affect this small population also change its position in genomic space. Some time later the organisms may recross the barrier, but the two populations that evolved separately are now at different positions in genome space. This is significant, because we expect that an attractive interaction between organisms of similar type prevents the separate evolution of subpopulations. Thus, physical separation is an additional mechanism for the formation of distinct organism types. ■

6.4.9 Adaptive organisms

An adaptive organism responds to its environment in a manner that adjusts behavior to improve fitness. We could more generally state that an adaptive organism has a phenome that depends on its environment. However, this does not affect the fundamental relationships of genome or phenome and fitness. Specifically, given a genome of an adaptive organism, the fitness is still as well defined a quantity as it is without the adaptation. However, by making additional assumptions, we can try to understand the effect of adaptation.

One perspective is that there is no special ability that adaptation provides over nonadaptive organisms. However, an adaptive organism can approximate the behavior of more than one nonadaptive organism. It cannot do so exactly, because adaptation carries its own cost. However, it can do so well enough to reach close to their fitness. This is an advantage when the fitness landscape is spatially or temporally varying, because the adaptive organism can survive in varied conditions. We might write that:

$$K(s, e) = \min_s K(s, e) + \epsilon \quad (6.4.20)$$

where s represents an adaptive organisms and s varies over a set of nonadaptive organisms. We have written the fitness as a function of the environment e explicitly. ϵ represents the inherent cost to fitness of adaptation, because the optimal behavior is not automatically realized for a particular environment.

A consequence of this view is that the fitness landscape due to changes in genome (that do not affect the adaptive ability) for adaptive organisms tends to be flatter than for nonadaptive organisms. As the genome of an adaptive organism changes, if the domain of s in Eq. (6.4.20) does not change, then neither will its fitness. Even if the

domain of s in Eq. (6.4.20) changes, the variation in the fitness will be more gradual than for a nonadaptive organism. The organism, in effect, reduces barriers to evolution by using adaptation to move around them. This picture, however, also implies that the ultimate benefit of adaptation becomes small for a relatively static fitness landscape, since it is advantageous for adaptation to disappear in favor of the genetically determined optimal behavior pattern.

A different perspective suggests that it may be possible that adaptation can enable certain phenomes to exist that cannot be described directly by the genome-to-phenome developmental relationship. Thus, for example, certain behavioral patterns may not be possible to specify genetically and can only arise through adaptation. In this case, adaptation becomes an extension of the physiological developmental process in creating the resulting phenome.

6.4.10 Limitations of the fitness landscape

We have discussed many limitations of the fitness landscape in previous sections and have introduced some ways to work around them. Here, however, we recall the most basic ways in which the fitness-landscape model breaks down, to motivate a different approach taken in the following section. Ultimately, the main problem in the fitness-landscape model is the use of a conserved population that forces a particular treatment of reproduction and death. Let us think what this means in terms of the model behavior. When an organism reproduces or dies, it causes a change in the local population of organisms at a particular genome or phenome. The random-walk model treats this by assuming that reproduction of a single offspring and death, either of the offspring or the parent, are directly linked. If we do not do this, but still require the conservation of population, then the birth of one organism is tied to the death of another organism. However, the death and birth may be at very different locations in the genomic space. Thus we are forced to consider various nonlocal moves. Including nonlocal moves is not, however, sufficient, because a Monte Carlo move is possible or impossible independent of the population itself. The birth of one organism and the death of another forces a particular nonlocal move that would not be possible without the existence of the parent organism. Specifically, we can imagine an organism that gives birth to many offspring as a process of ingathering of organisms from various other regions of space. This type of nonlocal move is not readily treated in Monte Carlo and another approach is necessary.

One illustration of how reproduction can affect the behavior of evolution on a fitness landscape is a hybrid picture in which we think about organisms evolving on a landscape but with reproduction and a nonconserved population. By processes of mutation, an organism might overcome a fitness barrier and end up in a fitness well. There is no need for other organisms to follow over the barrier, since the organism can reproduce, increasing the population in the well that is reached. Even if we include sexual reproduction, there is only need for a reproducing population to cross the barrier. The decoupling of the population in one well from the population in another well is a problem for the model we have been discussing. To enable us to think about this picture, we must develop different tools. We might note, however, that this image

suggests additional problems for a single global fitness function tied to the independence of growth and death of different populations.

Consistent with this discussion, we recognize that the Markov chain, even in its most general form, does not allow the transition rate from one location in space to another to depend on the population. This is because the description is limited to that of an ensemble of independently evolving systems treated statistically. To progress, we must write a time dependence of the organism population $N(s; t)$, as given by a non-linear dependence on its population and other populations $\{N(s; t)\}$. We therefore abandon the Markov chain formalism in favor of a more explicit discussion of reproduction, death and selection and the interaction of organisms.

Finally, by abandoning the Markov chain formalism we can also eliminate the use of a target limiting distribution for the dynamics. This inherently prevented us from considering many possible dynamical behaviors of population evolution. For example, fluctuations in populations driven by predator-prey relationships. The lack of such dynamics is related to the impossibility of including asymmetric interactions between organisms that increase the fitness of one and decrease the fitness of the other. It should be noted that this is a limitation that is often assumed in evolutionary theory even without the assumption of a Markov chain or limiting distribution, because fluctuating populations would be represented by fluctuations in the fitness function with time.

Our efforts to understand the random-walk model were not in vain. It is a difficult and valuable accomplishment to demonstrate that an entire class of models is not adequate, and to understand in what way it is not adequate. Moreover, we have discussed many important issues and gained insights that will also show us limitations in the seemingly better models that we will proceed to investigate.

6.5 Reproduction and Selection by Resources and Predators

The objective of this section is to present and discuss several mathematical models for the process of incremental evolutionary change in a population of reproducing organisms. We will see that there are subtleties that arise in such models that may initially be counterintuitive, and this will lead to a better understanding of evolution. In these models we often assume two or more types of reproducing organisms and follow their relative populations as a function of time. Our attention will be focused on understanding what parameters control selection—the survival of one type of organism at the expense of the other. One common model for evolution relates fitness directly to reproductive rates. Organisms with more offspring are more likely to survive and therefore more fit than organisms with fewer offspring. We will see by analyzing a few more detailed models that this is too simplified and incomplete a picture.

The models we will use directly describe the behavior of a population of organisms $N(s; t)$ in terms of an iterative map:

$$N(s; t + 1) = f_s(\{N(s; t)\}; t) \quad (6.5.1)$$

or in terms of a differential equation:

$$\frac{dN(s;t)}{dt} = f_s(\{N(s;t)\};t) \tag{6.5.2}$$

In either iterative map or differential equation forms, the models of the last section would account for any case where the function f_s is linear and population conserving. We will rapidly depart from this in our efforts to describe reproduction, death, resources and predators.

6.5.1 Reproduction, resources and selection

We start with a simple model for population growth. An organism that reproduces at a rate of $\lambda > 1$ offspring per individual per generation has a population growth that is exponential. Using an iterative equation (Section 1.1) this is written as:

$$N(t) = \lambda N(t - 1) \tag{6.5.3}$$

In the simplest interpretation, this represents synchronous generations with death following reproduction, but the behavior is more general. We can also write a differential equation that represents similar growth:

$$\frac{dN(t)}{dt} = \lambda N(t) \tag{6.5.4}$$

where $\lambda > 0$. If we have two organisms whose populations grow exponentially, the faster growing population will eventually dominate the slower one. However, both organisms continue to exist.

We obtain a standard model for fitness and selection by taking two equations of the form Eq.(6.5.3) for two populations $N_1(t)$ and $N_2(t)$ with λ_1 and λ_2 respectively, and normalize the population at every step so that the total number of organisms remains fixed at N_0 . We have that

$$\begin{aligned} N_1(t) &= \frac{\lambda_1 N_1(t-1)}{\lambda_1 N_1(t-1) + \lambda_2 N_2(t-1)} N_0 \\ N_2(t) &= \frac{\lambda_2 N_2(t-1)}{\lambda_1 N_1(t-1) + \lambda_2 N_2(t-1)} N_0 \end{aligned} \tag{6.5.5}$$

Because we did not change the relative dynamics of the two populations, and only the total population is affected by the normalization, we know that the faster-growing population will dominate the slower-growing one. If we call λ_i the fitness of the i th organism we see that according to this model the organism populations grow at a rate that is determined by the ratio of their fitness to the average fitness of the population. This model is similar in form, but not behavior, to the two-state system of Section 1.4, which is a prototype for the model of evolution discussed in Section 6.4. Question 6.5.1 addresses the similarities and differences of this population model and the two-state system.

Question 6.5.1 We can choose to write Eq. (6.5.5) in terms of the probability of having each organism type by writing $P_1(t) = N_1(t)/N_0$ and similarly for $P_2(t)$. Compare the qualitative behavior of Eq. (6.5.5) with the behavior of the two-state system that also describes the dynamics of two probabilities.

Solution 6.5.1 The most dramatic difference between the behaviors of the two models is that the two-state system, at any particular energy difference and temperature, equilibrates at a particular ratio of the two different populations. In Eq. (6.5.5), unless the fitnesses are exactly equal, the lower fitness population will eventually disappear no matter what the relative fitnesses are. The relative fitness only controls the rate of disappearance. ■

The model for selection in Eq. (6.5.5) is useful in that it provides an alternative dynamics to the two-state model. However, we would like to develop an understanding of the process by which population size is limited. The model of Eq. (6.5.5) does not represent population limits directly. Instead it simply normalizes the population size. In order to have a better model for the interaction between organisms that gives rise to selection, we should directly limit the number of organisms and then see how one organism grows at the expense of the other. A standard way to limit the population growth is to use a differential equation of the form:

$$\frac{dN(t)}{dt} = \lambda N(t) (1 - N(t)/N_0) \quad (6.5.6)$$

This equation appears similar to the quadratic iterative map discussed in Section 1.1, but this differential equation is not the same (Question 6.5.3) and it has a relatively simple behavior. Eq. (6.5.6) can be solved analytically or integrated numerically to obtain the behavior shown in Fig. 6.5.1 (Question 6.5.2). Starting from a small population, the population grows exponentially, then saturates at the value N_0 . The qualitative behavior can be understood directly from Eq. (6.5.6) because the factor $(1 - N(t)/N_0)$ reduces the growth rate to zero as $N(t)$ approaches N_0 .

Question 6.5.2 In this section we use both iterative maps and differential equation models when convenient. It is simplest to integrate the differential equations by converting them to an iterative map, as long as it is well behaved, by the straightforward method of converting an equation of the form

$$\frac{dN(t)}{dt} = f(N(t)) \quad (6.5.7)$$

to

$$N(t) = N(t - dt) + f(N(t - dt))dt \quad (6.5.8)$$

and reducing dt until the results are insensitive to it.

Try this for Eq. (6.5.6) and plot the results.

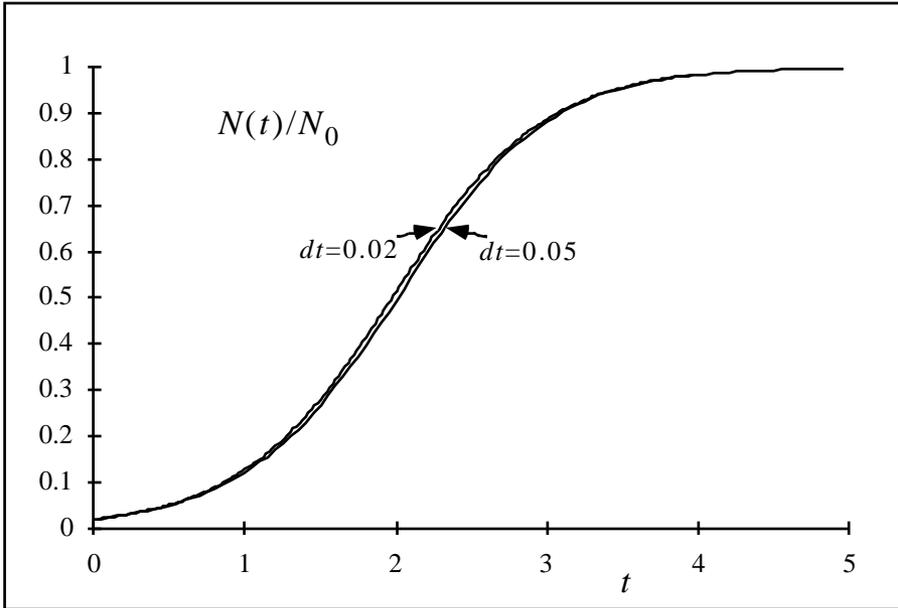


Figure 6.5.1 Solution of the logistic equation (Eq. 6.5.6) with $\lambda = 2$ using an iterative map to perform the integration. When starting from low values, the population increases and saturates at the value N_0 . The two curves are for different time increments in the integration (see Question 6.5.2). ■

Solution 6.5.2 See Fig. 6.5.1. ■

Question 6.5.3 Show analytically that Eq. (6.5.6), unlike the quadratic iterative map, should not have chaotic behavior.

Solution 6.5.3 The iterative map corresponds to the equation:

$$\begin{aligned}
 N(t+1) &= N(t) + \lambda N(t)(1 - N(t)/N_0)dt \\
 &= (1 + \lambda dt)N(t) - (\lambda dt/N_0)N(t)^2 \quad (6.5.9) \\
 &= (1 + \lambda dt)N(t)(1 - cN(t))
 \end{aligned}$$

where

$$c = \frac{\lambda dt}{N_0(1 + \lambda dt)} \quad (6.5.10)$$

Defining $s(t) = cN(t)$ we have the same quadratic map as in Section 1.1:

$$s(t+1) = (1 + \lambda dt)s(t)(1 - s(t)) \quad (6.5.11)$$

where the coefficient can be made incrementally greater than one, which is in the stable regime. ■

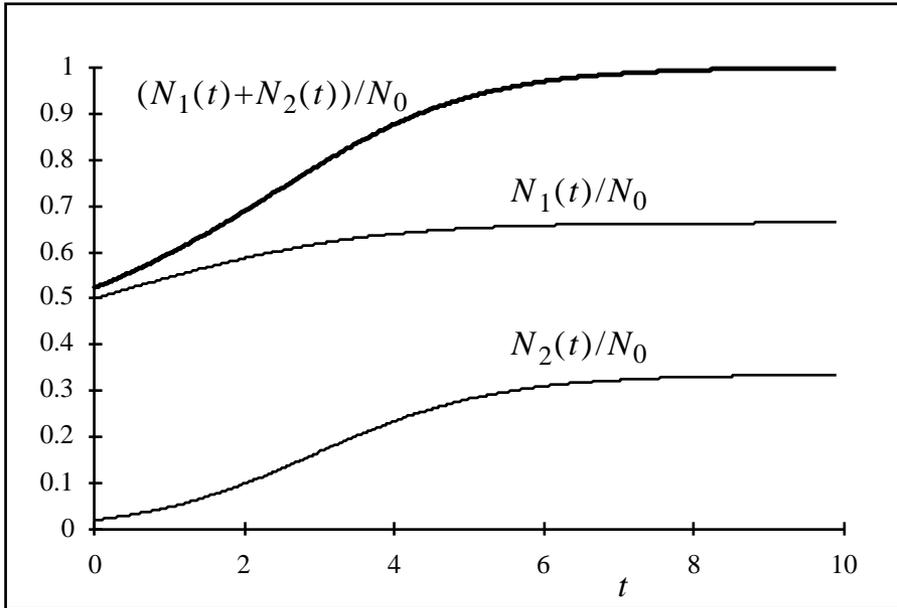


Figure 6.5.2 A model of competition based on Eq. (6.5.6) where two types of organisms are limited to have a total population less than N_0 . The first organism has a reproduction rate $\lambda_1 = 0.2$ and the second $\lambda_2 = 10\lambda_1$. The initial conditions are set so that the first organism with $N_1 = 0.5N_0$ dominates the second $N_2 = 0.02N_0$. The concept of evolution by selection suggests that the second organism should grow in number and eventually dominate the first organism. However, the figure shows that both populations grow so that the first organism continues to dominate the second. ■

In order to consider selection between two organisms, we use two equations that describe the growth of each of the populations with the same form as Eq.(6.5.6) but with different growth-rate parameters λ_1 and λ_2 :

$$\begin{aligned} \frac{dN_1(t)}{dt} &= \lambda_1 N_1(t) \left(1 - \frac{N_1(t) + N_2(t)}{N_0} \right) \\ \frac{dN_2(t)}{dt} &= \lambda_2 N_2(t) \left(1 - \frac{N_1(t) + N_2(t)}{N_0} \right) \end{aligned} \quad (6.5.12)$$

To couple the equations, we have assumed that the limitation on the number of organisms applies to both of them together. In solving these equations, our intuitive assumption is that one type of organism will dominate over the other and grow to have most of the population regardless of the initial starting point. However, when we look more closely we see that this cannot be true.

We notice first that if at any time the total population $N_1(t) + N_2(t)$ is N_0 , then regardless of the mix of organisms, the number of organisms of each type does not change, because the expression in parenthesis is zero. So we consider instead starting the organisms with a total population below N_0 . In this case both populations are monotonically increasing as long as the total population is smaller than N_0 . This means that whatever our initial conditions are, the lower growth-rate type of organism will never have fewer than its starting number. This is illustrated in Fig. 6.5.2, where the population of the lower growth-rate type of organism starts at $0.5 N_0$ and the population of the higher growth-rate type of organism starts at $0.02 N_0$. We see that it is not possible for the organisms with the higher growth rate to overcome the organisms with the lower growth rate. This does not correspond to our intuition about selection. According to this equation, an organism type that exists cannot be superseded by a newcomer even if the newcomer is reproducing more rapidly.

To try and overcome this problem we might consider the possibility of adding noise that would cause the total population sometimes to be greater than N_0 and sometimes to be less than it. This would cause the populations of the organisms alternately to grow and shrink. Then we might expect to see the higher growth-rate type of organism dominate. In a numerical integration this would look like:

$$\begin{aligned}
 N_1(t) &= \lambda_1 N_1(t - dt) \left[1 - \frac{N_1(t - dt) + N_2(t - dt)}{N_0} \right] dt + N_1(t - dt) + \delta \cdot (\Xi(t) - 0.5) \\
 N_2(t) &= \lambda_2 N_2(t - dt) \left[1 - \frac{N_1(t - dt) + N_2(t - dt)}{N_0} \right] dt + N_2(t - dt) + \delta \cdot (\Xi(t) - 0.5)
 \end{aligned}
 \tag{6.5.13}$$

where $\Xi(t)$ is a random number in the range 0 to 1 and δ controls the impact of the noise. If we simulate this problem many times, we will find that the faster growing population does not usually dominate. If δ is large enough, there are large fluctuations, and one or the other population might become extinct, but it is the population that starts out with the greater number that survives on average. The reason for this is that Eq. (6.5.12) assumes that the factors λ_1 and λ_2 control the population increase when the total population is less than N_0 , and they also control the population decline when the total population is greater than N_0 . Thus the faster-growing population is also the faster-declining population when there are too many organisms, and this prevents it from dominating the slower-growing one.

We are now faced with an interesting situation where we have several options. The model as we have constructed it has a built-in assumption about the relationship between the population growth and the population decline of an organism. We could argue that this relationship might not be correct, and introduce a model where there are two parameters; one describing the population growth and one describing the population decline. While this can work, we should learn something more significant: that the rate of population growth in a circumstance of plenty is not the factor that controls the fitness of the organism from an evolutionary perspective. The necessity

of introducing an additional parameter demonstrates this. If we introduce another parameter, then an interplay between the two different parameters controls the fitness. Thus, according to our analysis, the reproduction rate by itself does not determine the fitness.

Rather than pursuing a model with a new parameter for population decline, we can consider instead whether there is a different model that better captures what we have in mind when we consider selection. The real difficulty with the model in Eq.(6.5.12),and Eq.(6.5.6) upon which it is based, is the way the limitation on population is implemented.

A more natural model for selection represents organisms in competition for a resource. Instead of limiting the population directly, the population is limited by the resource necessary for reproduction. This resource could be food—e.g., grass that regrows to a limited height after being grazed—or space—e.g., nesting sites that are limited in number but are available again after offspring are grown. We will call this model the renewable-resource model. The amount of resource is measured in elementary units, each of which is sufficient to enable an organism to reproduce. We let $r(t)$ be the amount of resource available at time t . This amount is determined by resource renewal as well as by the amount that is consumed by organisms. If there are no organisms, the amount of resource reaches a maximum value r_0 . The resource that is available at time t is assumed to be given on average by:

$$r(t) = r_0 - N(t-1)P(t-1) \quad (6.5.14)$$

where the available resource has been reduced by the product of the number of organisms at the previous time $N(t-1)$, times the probability that any one of them will consume the resource $P(t-1)$.

Each type of organism is assigned an effectiveness κ , which is the probability that the organism can consume the resource if there is only one available. The probability that it consumes the resource when there are $r(t)$ available is:

$$P(t) = (1 - (1 - \kappa)^{r(t)}) \quad 1 - e^{-\kappa r(t)} \quad (6.5.15)$$

The latter expression is valid when $r(t)$ is large and κ is small. It is not a very limiting assumption, though we will not need to use it. Finally, the number of organisms at time t is given by:

$$N(t) = \lambda N(t-1)P(t-1) \quad (6.5.16)$$

which means that each organism that consumes a resource produces λ progeny for the next generation, and then dies. The model described by the three Eqs. (6.5.14)–(6.5.16) is an iterative map that can be used to represent competition for a resource. For a single type of organism, the population grows like the solution of Eq. (6.5.6). This is shown in Fig 6.5.3. The organism grows until it reaches an equilibrium. However, when we have two organisms, the behavior is quite different from what we found before. Question 6.5.4 describes the construction of equations that generalize this model for two organisms. The results of a simulation show that if we have one organism at equilibrium and add a single organism of a type that has a

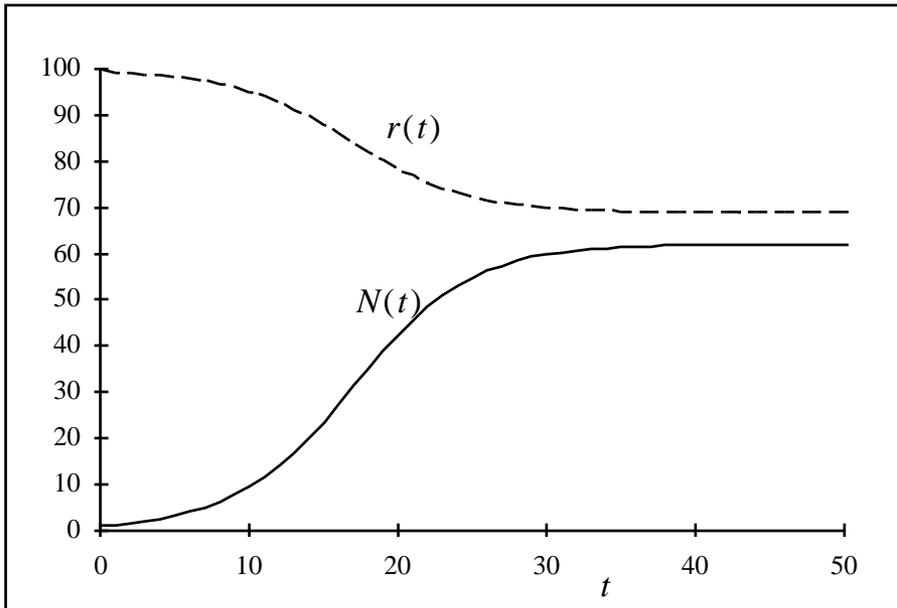


Figure 6.5.3 Renewable-resource model of population growth described by Eqs. (6.5.14)–(6.5.16). The organism population, $N(t)$, grows and saturates in a similar manner to Fig. 6.5.1. The limitation in population growth arises, however, from a reduction in the amount of resources, $r(t)$, consumed by the organism. The parameters used for this simulation are $r_0 = 100$, $\lambda = 2$, and $\kappa = 0.01$, and the initial population is $N(0) = 1$. An incremental version of the model discussed in Question 6.5.5 gives similar results. For other values of the parameters, e.g. higher values of λ , the incremental model is necessary due to chaotic behavior in the original equations. ■

slightly higher effectiveness κ , or a slightly higher reproduction rate λ , then the new organism will grow and the original organism will become extinct (Fig. 6.5.4).

Question 6.5.4 Write the equations for two types of organisms and simulate their behavior for various initial conditions and parameter values.

Solution 6.5.4 Instead of Eq. (6.5.14) the resource left is:

$$r(t) = r_0 - N_1(t-1)P_1(t-1) - N_2(t-1)P_2(t-1) \quad (6.5.17)$$

The other two equations are the same as before for each of the organisms:

$$\begin{aligned} P_1(t) &= (1 - (1 - \kappa_1)^{r(t)}) \\ P_2(t) &= (1 - (1 - \kappa_2)^{r(t)}) \\ N_1(t) &= \lambda_1 N_1(t-1)P_1(t-1) \\ N_2(t) &= \lambda_2 N_2(t-1)P_2(t-1) \end{aligned} \quad (6.5.18)$$

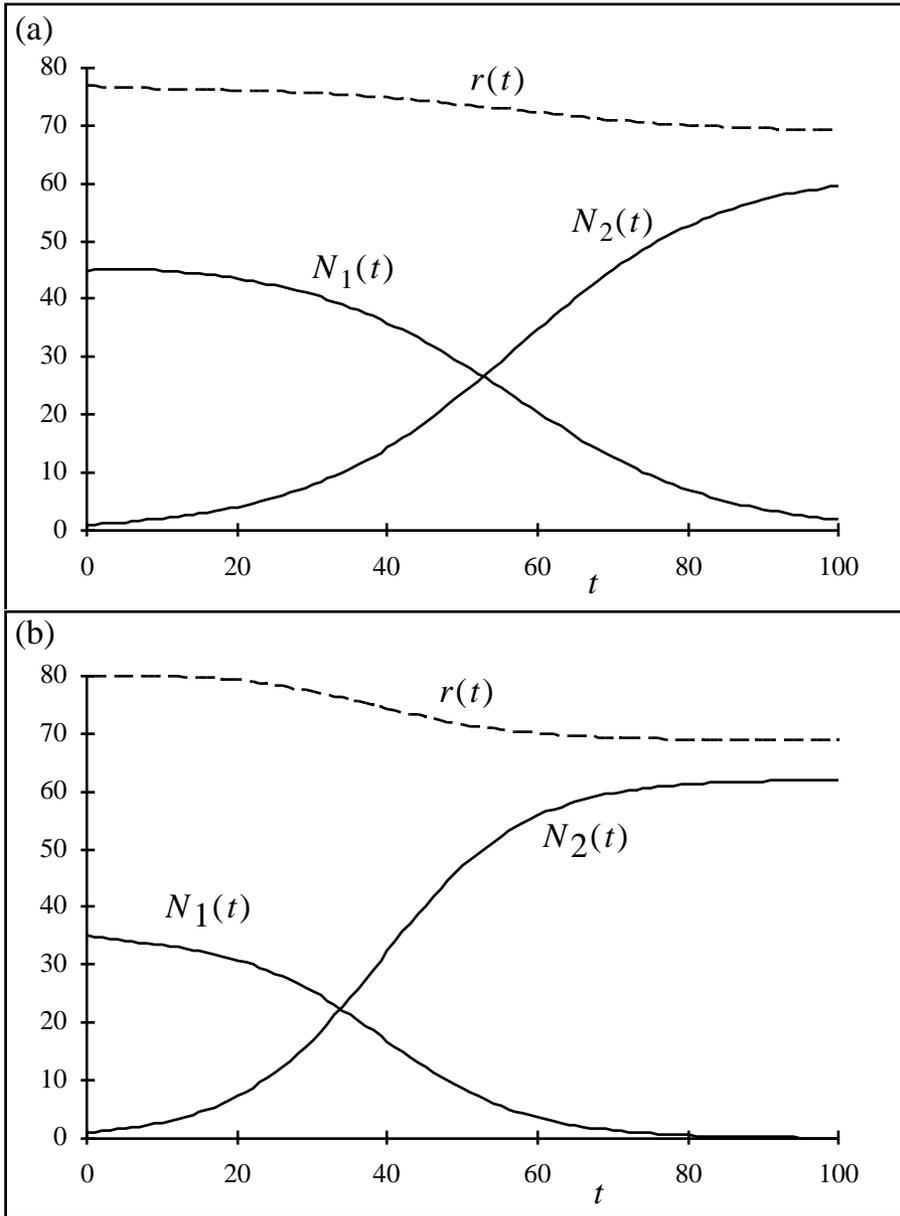


Figure 6.5.4 Renewable-resource model of competition between two organisms showing how the second organism population grows and dominates the first organism. The two figures illustrate different reasons for selection of the second organism over the first. In both cases the second organism has the same parameter values as in Fig. 6.5.3 ($\lambda = 2$, $\kappa = 0.01$). For (a) the first organism has a lower consumption effectiveness, $\kappa = 0.009$. For (b) the first organism has a lower number of offspring per resource consumption $\lambda = 1.8$. The initial conditions are close to, but not equal to, the steady-state value for the first organism. The initial population of the second organism is $N_2(0) = 1$. The baseline resource is set to $r_0 = 100$. ■

See Fig. 6.5.4 for two simulations for organisms with different values of the parameters. ■

Question 6.5.5 Eqs. (6.5.14)–(6.5.16) together constitute an iterative map with a tendency to chaotic behavior. The reason for this is that the whole population is being updated at once. We can, however, use a model where both population growth and consumption of the resource occur incrementally. Set up an incremental analog of the iterative map. Hint: The difficulty is in determining how the resource should behave.

Solution 6.5.5 One way to do this is to assume a continuously growing resource that grows in proportion to the amount that is missing:

$$r(t) = r(t - dt) + (r_0 - r(t - dt))dt - N(t - dt)P(t - dt)dt \quad (6.5.19)$$

Eq. (6.5.15) requires no modification and Eq. (6.5.16) becomes:

$$N(t) = N(t - dt) + (\lambda P(t - dt) - 1)N(t - dt)dt \quad (6.5.20) \blacksquare$$

We see from Fig. 6.5.4 that this model displays an intuitive behavior of selection of one organism over another. The reason for this behavior can be found by considering the nature of the population control exercised by a resource. For a single organism, the equilibrium population is reached when there is no change in the value of $N(t)$. We can solve the equations in this case directly. Using Eq. (6.5.16) we find that $N(t) = N(t - 1)$ implies:

$$1 = \lambda P(r) \quad (6.5.21)$$

and from Eq. (6.5.15) that:

$$1/\lambda = (1 - (1 - \kappa)^{r(r)}) \quad (6.5.22)$$

We can solve this for the amount of resource that is available in equilibrium as:

$$r(r) = \frac{\log(1 - 1/\lambda)}{\log(1 - \kappa)} \frac{1}{\lambda \kappa} \quad (6.5.23)$$

The latter expression applies when λ is large and κ is small. The meaning of $r(r)$ is that when this amount of resource is available, the population is self-sustaining. This implies that the probability of consumption is enough to generate the same number of organisms in the next generation. We can also conclude that if the amount of resource is less than $r(r)$ the population of the organism will fall; if the amount of resource is greater than $r(r)$ the population of the organism will grow. The product of the effectiveness of the organism and the reproduction rate sets this equilibrium value of the resource, and the resource controls the population.

Consider what happens when we have two organisms that are competing for the resource. The relevant parameter of each one is their respective $r(r)$. This reflects the efficiency of utilization of the resource. The more efficient the organism is, the smaller is $r(r)$. The population of the organism that has a higher efficiency will grow at the equilibrium concentration of resource of the organism that is less efficient, while the

population of the organism that is less efficient will shrink at the equilibrium concentration of resource of the organism that is more efficient. Thus the less-efficient organism must disappear while the more efficient one must increase in number and dominate the population. Thus, in this model fitness is given by the efficiency of resource utilization:

$$K = 1/r(\kappa) - \lambda\kappa \tag{6.5.24}$$

To see how the fitness is distinct from the population of the organism in equilibrium, we can write down the equilibrium population of each type of organism by itself. This is given by:

$$N(\kappa) = \lambda(r_0 - r(\kappa)) \tag{6.5.25}$$

This means, reasonably, that the population is the reproduction rate times the amount of resource that is consumed. We can think about the case where the efficiency of organisms is high so that the residual resource $r(\kappa)$ is much smaller than r_0 . Then the population of a type of organism is directly proportional to its reproduction rate λ . However, this is not the same as the fitness in Eq. (6.5.24). Thus we have found that starting from a first organism type with an equilibrium population $N_1(\kappa_1)$ we can introduce a second organism type that grows and dominates the first organism type because it has a higher fitness $K_2 > K_1$. But even after the first organism is entirely eliminated, and the second organism has reached its equilibrium population $N_2(\kappa_2)$, we find that $N_2(\kappa_2) < N_1(\kappa_1)$. Specifically, when $\kappa_2 > \kappa_1$ then the fitness can increase, even though the total number of organisms decreases because $\lambda_2 < \lambda_1$.

6.5.2 Predators and selection

The discussion of the previous section leads us to consider what happens when one evolving organism serves as a resource for another organism. A first model that considers a reproducing organism as a resource is the Lotka-Volterra predator-prey model. This model is a pair of coupled differential equations that describes the exponential growth of a population of prey whose population is limited only by its consumption by a predator. The predator population is limited by the availability of prey, without which it declines. For convenience we write the prey population as $a(t) = N_a(t)$ and the predator population as $b(t) = N_b(t)$. The equations are:

$$\frac{da}{dt} = \lambda_a a - \gamma ab \tag{6.5.26}$$

$$\frac{db}{dt} = -\mu b + \lambda_b \gamma ab$$

The parameters are the reproduction rate of the prey λ_a , the probability that predators meeting prey consume them γ , the rate of death of predators in absence of prey μ , and the number of offspring produced by predators after consumption of prey λ_b . Solutions of these equations display oscillations as shown in Fig. 6.5.5. These oscillations result from the interplay between the effects of growth of the two organisms.

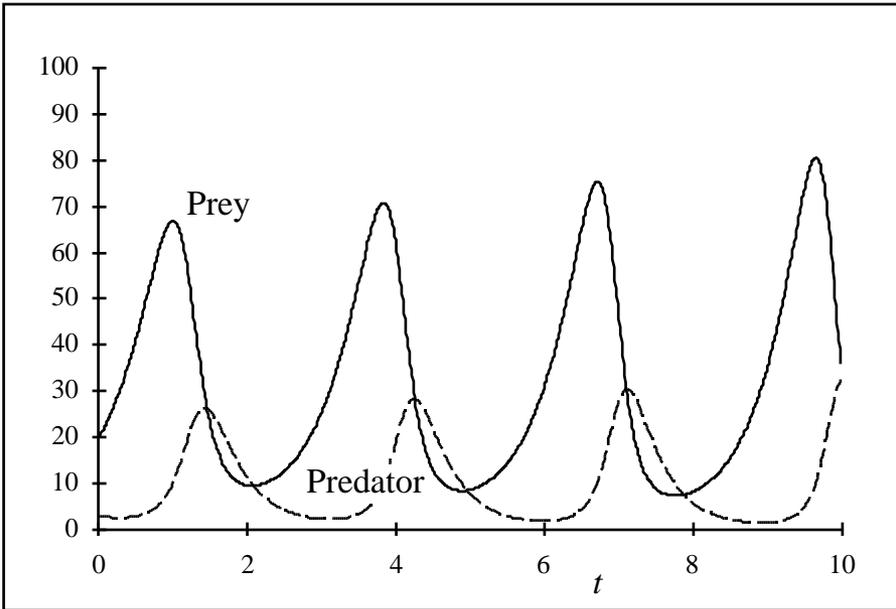


Figure 6.5.5 Simulation of the predator-prey model described by Eq. (6.5.26). The predator and prey populations undergo periodic oscillations as discussed in the text. The parameters are $\lambda_a = 2$, $\gamma = 0.2$, $\mu = 3$, $\lambda_b = 0.5$ and the initial conditions are $a(0) = 20$ prey, and $b(0) = 3$ predators. It is important to recognize that the progressive increase in the height of the peaks is an artifact due to the numerical integration of these equations using Eq. (6.5.8) and a time increment of $dt = 0.01$. A solution using smaller values of time increment would be more closely periodic. An analytic solution of the equations is exactly periodic. This is an illustration of the inherent sensitivity of the predator-prey model to perturbations. ■

When the prey increases in population, the predator population increases so much that it decreases the prey population, which then results in a decrease in predator population. We can add a second type of prey to this model and see how the fitness selection of the two types of prey would work:

$$\begin{aligned} \frac{da_1}{dt} &= \lambda_1 a_1 - \gamma_1 a_1 b \\ \frac{da_2}{dt} &= \lambda_2 a_2 - \gamma_2 a_2 b \\ \frac{db}{dt} &= -\mu b + \lambda_b (\gamma_1 a_1 + \gamma_2 a_2) b \end{aligned} \tag{6.5.27}$$

The result is simulated in Fig. 6.5.6 for several variations in parameters. We see that the prey which has either a higher reproduction rate (larger λ) or a better avoidance

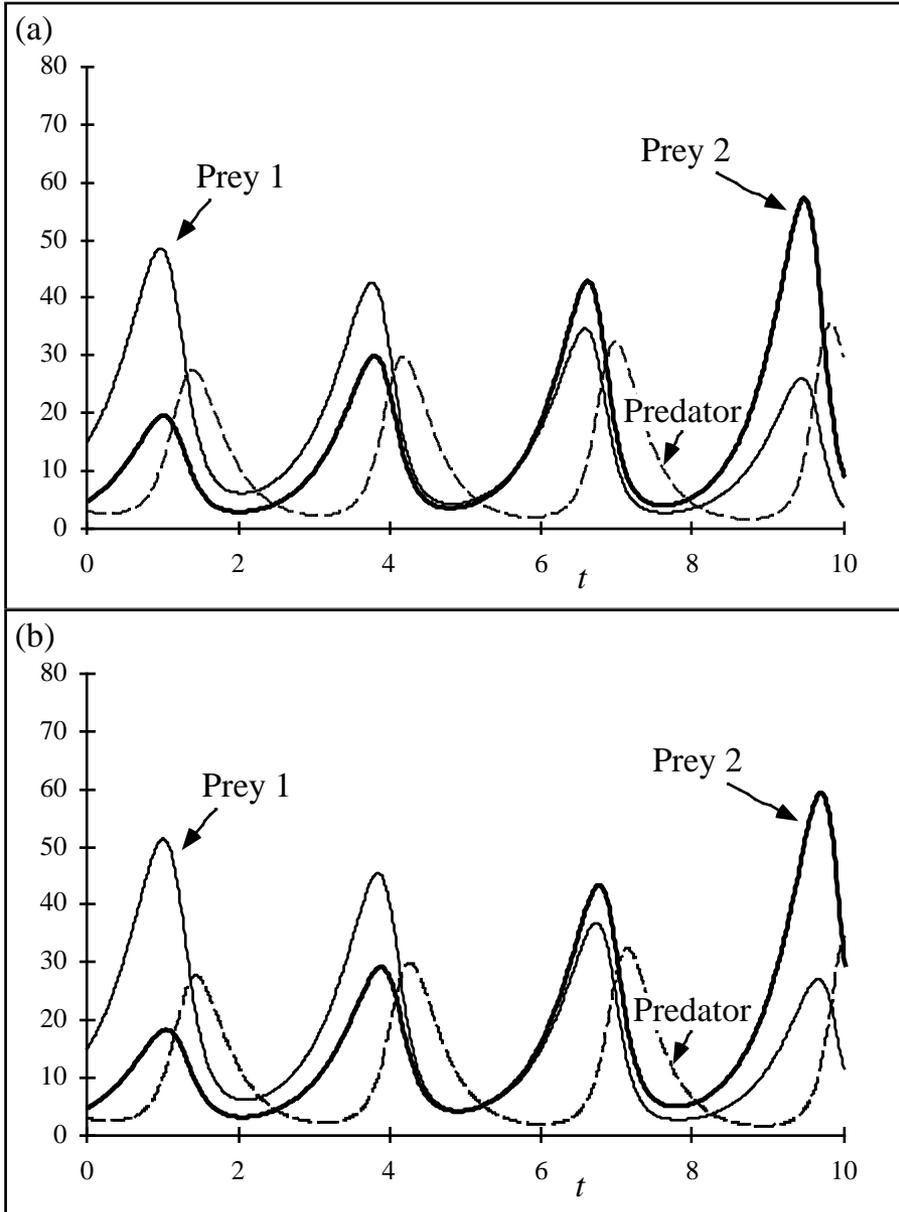


Figure 6.5.6 Predator-prey model of competition between two types of prey, showing how the second type of prey population grows and dominates the first type of prey. The two figures illustrate different reasons for selection of the second type of prey over the first. In both cases the first type of prey has the same parameter values as in Fig. 6.5.5 ($\lambda_a = 2$, $\gamma = 0.2$). For (a) the second type of prey has a higher reproduction rate, $\lambda_a = 2.2$. For (b) the second type of prey has a lower probability of being eaten $\gamma = 0.18$. The initial population of the first and second type of prey are 15 and 5 respectively. ■

of being eaten (lower γ) will survive and therefore is the fitter organism. It is a combination of these two traits that is the important criteria for fitness. Question 6.5.6 describes a method for obtaining the longer time dynamics of the evolutionary process from these equations. It is significant that in this model, as in the renewable-resource model, it is not just the population growth by itself that is important.

Question 6.5.6 When there are two or more different types of prey whose parameters (λ, γ) differ by a small amount, they together undergo oscillations in population. As this occurs, one of them increases in population at the expense of the others. This longer-time evolutionary dynamics can be separated from the short-time oscillations. Write a differential equation for the longer-time dynamics of the ratio of the populations of two types of prey with incrementally different parameters. Determine the unique parameter that controls the fitness.

Solution 6.5.6 We write the density of the second prey in Eq. (6.5.27) as

$$a_2(t) = \psi(t)a_1(t) \tag{6.5.28}$$

so that $\psi(t)$ is the population ratio. Inserting in Eq. (6.5.27) we obtain:

$$\psi \frac{da_1}{dt} + a_1 \frac{d\psi}{dt} = \lambda_2 a_1 \psi - \gamma_2 a_1 \psi b \tag{6.5.29}$$

Substituting the first prey equation from Eq. (6.5.27) we have:

$$\psi (\lambda_1 a_1 - \gamma_1 a_1 b) + a_1 \frac{d\psi}{dt} = \lambda_2 a_1 \psi - \gamma_2 a_1 \psi b \tag{6.5.30}$$

or:

$$\frac{d\psi}{dt} = \lambda \psi - \gamma b \psi \tag{6.5.31}$$

where $\lambda = \lambda_2 - \lambda_1$ and $\gamma = \gamma_2 - \gamma_1$. This equation has the same form as the differential equations describing the prey population. However, since the parameters λ and γ are small, we know that the change in ψ is small, and so we can average the coefficient of ψ on the right over the time that b is fluctuating. This shows that the population ratio changes at a rate controlled by:

$$\lambda - \gamma < b > \tag{6.5.32}$$

which means, quite intuitively, that the fitness is controlled by the difference in the reproduction rate minus the average probability that an organism will be eaten over time. ■

We can consider a similar question to that asked about the renewable-resource model. If a particular prey is replaced by a fitter organism, would the eventual total population of the prey be larger after the change? The result of Question 6.5.6 contained in Eq. (6.5.32) might be wrongly interpreted to mean that with a higher

reproduction rate and/or a lower consumption rate, the population of the prey would necessarily increase. However, this is not the case. The average population of the prey is not determined solely by the parameters; it is very sensitive to the initial conditions—how many predator and prey are present at a particular time. Since there is no unique stable equilibrium toward which the equations lead, we cannot define the average prey population directly. We can, however, make some relevant remarks.

For the one steady-state solution of Eq. (6.5.26) obtained by setting the time derivative to zero,

$$\begin{aligned} a &= \mu/\gamma\lambda_b \\ b &= \lambda_a/\gamma \end{aligned} \tag{6.5.33}$$

there is an increase in the value of a with lower consumption rate γ , but there appears to be no effect of its own reproduction rate λ_a . The reason is that the predator population is affected by the rate of increase of the prey population which then affects the prey population. Moreover, for a particular set of initial conditions, it is possible to show (by simulations or by solving the differential equations) that the average prey population does not increase with its reproduction rate.

The predator-prey model with evolving prey can be readily expanded to consider what happens when both the predator and the prey can evolve. This process of evolution of coupled organisms is called coevolution. Its study is a step toward developing an understanding of the network of interdependence discussed in Section 6.4.5. An essential parameter in the fitness of both the prey and the predator is the ability of the predator to eat the prey. Changes in one organism are echoed by changes in the fitness criteria for the other organism, which in turn drive its selection.

The results we have found from the models in this and the previous section contribute to our understanding of fitness and evolution on a more global scale. An important conclusion was the decoupling of fitness from the equilibrium or average number of organisms. As discussed in Section 6.4.6, a relationship between fitness and population, e.g., $P(s) = K(s)$, is in conflict with the idea that selection resulted in evolution to larger, more complex organisms. We know that the number of small, relatively simple organisms greatly exceeds the number of complex organisms. This might suggest that the fitness of the smaller organisms is greater. However, the results that we have found indicate that fitness is not directly related to the number of organisms. In these models, parameters such as the efficiency of resource utilization as well as reproduction rate control the fitness rather than the equilibrium number of organisms. We are still left with the problem of understanding why the presumably less fit small organisms continue to exist in the presence of the more fit complex organisms. This will be addressed in Section 6.5.4.

6.5.3 Mutation

In the discussion of selection in the previous sections, we assumed the existence of two types of organisms and investigated the consequences. In this section we consider the process by which changes in organisms occur through mutation. Our objective is

to consider implications of the existence of many possible mutations that can occur in an organism. In the context of a simple evolutionary model, we would categorize the effect of these mutations in terms of their effect on fitness. Some mutations improve the fitness, others decrease it. In general, it is also important to allow mutations that do not change the fitness. Moreover, once a mutation has occurred, the organism has changed and the effect of subsequent mutations is contingent on the mutation that has already occurred. We will start, however, by considering only mutations that increase or decrease the fitness by a fixed amount. Of particular significance is the fundamental assumption that mutations occur at random. Mutations occur with a probability that is not affected by the contribution of the mutation to the fitness. This does not mean, however, that mutations that improve fitness are equally likely to those that decrease it.

We simplify the problem by considering what happens if there is a fixed proportion $1/\Lambda$ of mutations that increase fitness for any organism. Moreover, all mutations change the fitness by the same amount up or down. With these assumptions there is no significant difference between two organisms that have distinct genomes or phenomes but the same fitness. Organisms that have the same fitness will coexist and their population will grow or decline together. We can consider together the class of organisms of the same fitness—a fitness class. Our concern is to understand how the population in a fitness class changes with time through the effect of mutation and selection. We have chosen to write $1/\Lambda$ for the proportion of fitness-improving mutations because, due to prior fitness selection, it is less likely to have a mutation that increases fitness to one that decreases it. Thus we expect and assume that Λ is significantly greater than one.

For definiteness we consider an organism that reproduces while consuming a renewable resource as given by Eqs. (6.5.14)–(6.5.16) or, better, their incremental analog (Question 6.5.5). We introduce a certain rate μ at which mutations can occur that change the fitness class of offspring. Each fitness class is identified by its limiting resource r_i (). For simplicity we will consider only variations in the resource utilization effectiveness κ which will be taken to have the value:

$$\kappa_i = g^{i-1} \kappa_1 \tag{6.5.34}$$

where i is the fitness class and g is the ratio of the value of κ_i from one class to the next, assumed to follow a geometric sequence. This is a convenient choice because we will find that the ratio of κ_i determines the relative growth of the population of a fitness class.

The simulation must be performed in such a way that a fractional organism is not allowed to reproduce or mutate. The use of a differential equation can cause problems when care is not taken with this granularity. A set of incremental equations that do account for the granularity are developed in Question 6.5.7.

Question 6.5.7 Write a set of incremental equations based on those in Question 6.5.4 that account for granularity and allow for mutation between a set of fitness classes.

Solution 6.5.7 Two of the relevant equations are:

$$r(t) = r(t - \delta t) + (r_0 - r(t - \delta t))\delta t - N_i(t - \delta t)P_i(t - \delta t)\delta t \quad (6.5.35)$$

$$P_i(t) = (1 - (1 - \kappa_j)^{r(t)}) \quad (6.5.36)$$

A subtlety in setting up the equation for the number of organisms in a class is realizing that mutation into a class should be treated probabilistically. Specifically, at any step there is a certain probability of mutation. When a mutation occurs, one organism moves from one class to another. If we naively try to make the continuum equations deterministic, we would introduce a fractional transfer of organisms. This can be treated by accumulating fractional organisms inside a class but not using them for reproduction or mutation. When the fraction of an organism reaches a whole organism, then we do use it. This corresponds, on average, to the moment at which one organism in a stochastic process would have reached there.

The number of offspring that would arise in a single generation of the organism in class i is given by:

$$O_i(t) = \lambda_i P_i(t) N_i(t) \quad (6.5.37)$$

where x indicates the integer part of x . Some of these offspring will mutate to another class—specifically, μO_i will. To write an incremental model we assume that only a fraction dt of the organisms reproduce at once and we have:

$$\begin{aligned} N_i(t) = & N_i(t - dt) + (O_i(t - dt) - N_i(t - dt))dt \\ & + \mu \frac{1}{\Lambda + 1} O_{i-1}(t - dt) + \frac{\Lambda}{\Lambda + 1} O_{i+1}(t - dt) - O_i(t - dt) dt \end{aligned} \quad (6.5.38)$$

The subtraction of $N_i(t - dt)$ in the first line corresponds to the assumption that the parent dies when the offspring are born. The second line describes the effect of mutation, where a fraction μ of the offspring of class i mutate and leave the fitness class. Of these $\mu/(\Lambda + 1)$ go to the next higher fitness class and $\mu\Lambda/(\Lambda + 1)$ go to the next lower one. The equation is written in terms of the changes in the i th fitness class due to mutations from the $i + 1$ and $i - 1$ classes. We can see that this part of the equation corresponds to a biased diffusion of population in fitness classes. ■

A simulation of the model of mutation is shown in Fig. 6.5.7. As mutations occur, the fitness class of the organisms increase. We might imagine this process as accounting for some of the historical fossil record where over many years an organism changes monotonically from one form to another. However, since there is no specific trait or traits assumed to be associated with the mutations, this is also a general description of evolutionary progress.

There are several interesting features of this model that we can understand by considering the effect of various parameters. First we should recognize that there is a finite range of possible fitness classes. This range is set by the total amount of the re-

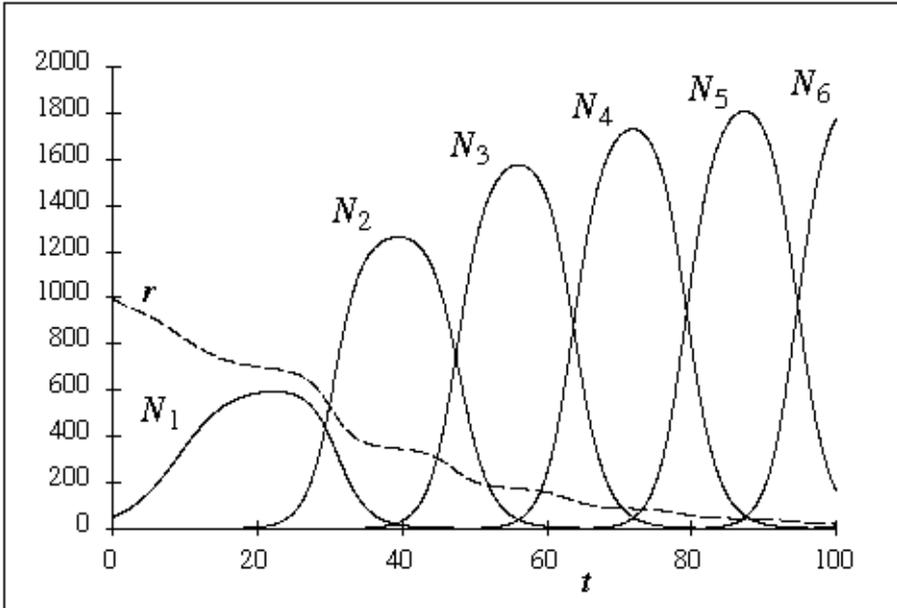


Figure 6.5.7 Model of evolutionary progress by mutation and selection based upon the renewable-resource model. Mutation enables organisms to move from one fitness class to another. The improved resource utilization by the higher fitness classes causes their population to increase and dominate the lower fitness classes, as the amount of resource available, r , declines due to its utilization. In this simulation the base resource is $r_0 = 10^3$, all fitness classes have $\lambda = 2$ offspring per unit of consumed resource, the first fitness class has a resource utilization effectiveness $\kappa_1 = 10^{-3}$, the resource utilization effectiveness of each successive fitness class is multiplied by $g = 2$, the ratio of fitness improving mutations to fitness reducing mutations is $1/\Lambda = 1/4$, and the mutation rate is $\mu = 10^{-3}$. The first fitness class starts with 50 organisms and all others start with none. The time increment for integration is $dt = 0.05$. ■

source r_0 . The smallest value of κ which makes sense is $\kappa_{\min} = 1/(r_0\lambda)$. A smaller value results in an organism that is not viable with this amount of resource. Recognizing that there is a lower bound to the viability of an organism is important. It is related to the problem of creating the first viable organism. On the other end of the scale there is also a maximum fitness that arises when there is only one unit of resource left. This gives $\kappa_{\max} = 1/\lambda$. It is impossible for an organism to improve further because there is no resource to be consumed. Thus, a finite amount of resource leads to a bound on how much improvement in fitness is possible.

We can gain additional insight into the behavior of this model by determining the rate of evolutionary progress—the time for fitness class $i - 1$ to be replaced by fitness class i . There are two parts to this process the first is the time τ_1 till a first organism appears in class i and the second is the time τ_2 till its population becomes dominant. We can make a complete analysis when τ_1 is longer than τ_2 . In this case

equilibrium is reached in class $i - 1$ and it dominates the population of organisms before mutation creates organisms in class i .

To study the condition of equilibrium, we use Eq. (6.5.38) to describe the time dependence of class $i - 1$ by shifting i to $i - 1$ everywhere. We can then impose the equilibrium condition, $N_{i-1}(t) = N_{i-1}(t - 1)$. The resulting equation simplifies because when class $i - 1$ is dominant the population of other classes is negligible; also, we don't need to take the integer part of $N_{i-1}(t)$. We find:

$$N_{i-1}(t) = (1 - \mu)O_{i-1}(t) \tag{6.5.39}$$

which says that the offspring that do not mutate replace their parents. From Eq. (6.5.37) we have:

$$1 = (1 - \mu)\lambda_{i-1}P_{i-1}(t) \tag{6.5.40}$$

From the resource equation Eq. (6.5.35), with $r(t) = r(t - 1)$, we can obtain a value for $N_{i-1}(t)$:

$$N_{i-1}(t) = (r_0 - r(t))/P_{i-1}(t) = (1 - \mu)\lambda_{i-1}(r_0 - r(t)) / (1 - \mu)\lambda_{i-1}r_0 \tag{6.5.41}$$

The latter approximation holds unless the organism is just marginally viable.

The time τ_1 to create a first organism in class i is determined by Eq. (6.5.38) with all of the terms equal to zero ($N_i(t) = 0$) except for the contribution by mutation from class $i - 1$:

$$N_i(t) - N_i(t - 1) = \frac{\mu}{\Lambda + 1}O_{i-1}(t - dt)dt = \frac{\mu\lambda_{i-1}r_0}{\Lambda + 1}dt \tag{6.5.42}$$

This equation is linear, so the time to reach a single organism τ_1 is:

$$\tau_1 = (\Lambda + 1) / \mu\lambda_{i-1}r_0 \tag{6.5.43}$$

This expression says that the time to obtain a single organism in class i is proportional to the difficulty in finding a fitness-improving mutation, and inversely related to the number of mutated offspring per generation produced by fitness class $i - 1$.

Once class i has an organism, we can neglect mutation from class $i - 1$, because $N_i(t)$ grows by reproduction. Moreover, now that class i has more than one organism, it is not essential to take the integer part of $N_i(t)$. $N_i(t)$ grows according to (Eq. 6.5.38):

$$N_i(t) - N_i(t - dt) = ((1 - \mu)\lambda_i P_i(t) - 1)N_i(t - dt)dt \tag{6.5.44}$$

To solve this we recognize that the amount of resource available during the growth of $N_i(t)$ is determined by the equilibrium resource of the fitness class $i - 1$. It is essentially independent of time, and therefore so is $P_i(t)$. From Eq. (6.5.36) the equilibrium resource of fitness class $i - 1$ is:

$$r(t) = \frac{\ln(1 - 1/(1 - \mu)\lambda_{i-1})}{\ln(1 - \kappa_{i-1})} = \frac{1}{(1 - \mu)\lambda_{i-1}\kappa_{i-1}} \tag{6.5.45}$$

Then we have:

$$(1 - \mu)\lambda_i P_i(t) = (1 - \mu)\lambda_i (1 - (1 - \kappa_i)^{r(t)}) = (1 - \mu)\lambda_i \kappa_i r(t) = \frac{\lambda_i \kappa_i}{\lambda_{i-1} \kappa_{i-1}} = g \tag{6.5.46}$$

where we have used approximations to simplify the form of the result. Using this in Eq. (6.5.44) we have exponential population growth in class i :

$$N_i(t) = e^{t/(g-1)} \tag{6.5.47}$$

τ_2 is the time for the population of class i to grow from a single organism to the equilibrium population of class $i - 1$. This is given by:

$$N_{i-1}(t) = e^{\tau_2/(g-1)} \tag{6.5.48}$$

or:

$$\tau_2 = \ln(N_{i-1})/\ln(g - 1) = \ln((1 - \mu)\lambda_{i-1}r_0)/\ln(g - 1) \tag{6.5.49}$$

We conclude that the total time for a change of fitness class is given by (setting $\lambda_i = \lambda$):

$$\tau = \tau_1 + \tau_2 = (\Lambda + 1)/r_0\lambda\mu + \ln((1 - \mu)\lambda r_0)/\ln(g - 1) \tag{6.5.50}$$

This is the evolution time between fitness classes. It becomes invalid when the second term becomes large enough compared to the first that significant growth of class i occurs before the growth of the class $i - 1$ is completed.

We can develop an understanding of Eq. (6.5.50) by realizing that the first term is large compared to the second term when the mutation rate μ is small or the probability of finding a fitness-improving mutation is small (Λ is large). In this case, the organisms evolve in distinct stages where a fitness class replaces the one immediately preceding it. If Λ is not too large and the mutation rate becomes high enough (it cannot be greater than one), τ_1 may become shorter than τ_2 . In this case there are several overlapping classes that exist at the same time, and Eq. (6.5.50) is no longer valid. Fig. 6.5.8 illustrates the latter case, where at any time there is a heterogeneous population of organisms undergoing selection.

The model of mutation and selection appears in its overall behavior to be similar to the Monte Carlo random-walk model of downhill diffusion that was discussed in Section 6.4. However, there are a number of differences between these two models. The most important difference is the role of the rarity of fitness-improving mutations (phase space). In the Monte Carlo model we can analyze its role through the properties of equilibrium. In equilibrium the number of organisms that mutate from class $i - 1$ to class i is the same as from class i to class $i - 1$. The relative number of organisms in equilibrium in the different classes is set by this condition. We can calculate the number of mutating organisms in the random-walk model using the parameters of the mutation and selection model. In each time step, a walker chooses one of the possible mutations. The proportion of these that improve the fitness is $1/(\Lambda + 1)$, while the proportion that decrease it is $\Lambda/(\Lambda + 1)$. All of the mutations that improve the fitness are accepted, but only $K(i - 1)/K(i) = 1/g$ of those that decrease the fitness are accepted. This means that in equilibrium the proportion of the population in class $i - 1$ and class i is given by:

$$N_i/N_{i-1} = g/\Lambda \tag{6.5.51}$$

This means that the population of the lower fitness class will be larger if the number of fitness-improving mutations is sufficiently small. If we think about dynamics,

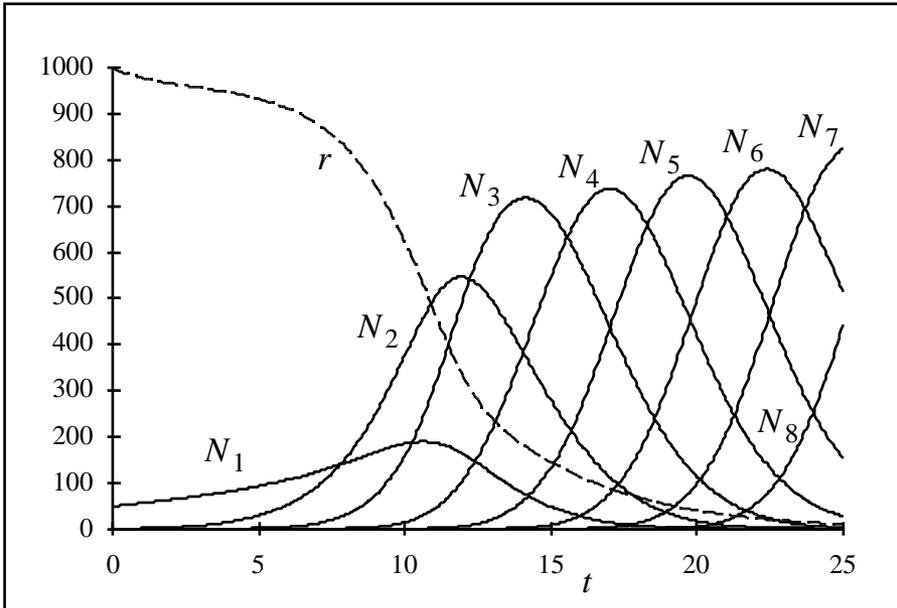


Figure 6.5.8 Simulations similar to those shown in Fig. 6.5.7. The only difference is that a higher mutation rate $\mu = 10^{-1}$ was used. The fitness classes overlap because each one does not reach a steady state population before the next one arises. ■

under these circumstances the evolution will progress uphill rather than downhill. The reason for this is that the balance between entropy and energy is being won by the entropy of the much greater number of lower-fitness organisms.

This conclusion is not true for the reproduction and selection model. The time that it takes to improve the fitness Eq. (6.5.50) increases with increasing Λ . However, for any value of Λ the fitness increases. This is an important result for our understanding of evolution. It means that selection with reproduction is more powerful than entropy. Our understanding becomes more complete if we recognize that the advance in fitness does stop when the resource is scarce—when the fitness reaches κ_{\max} so that the amount of resource is a single unit. Thus it is the nonequilibrium driving force of resource consumption that plays a different and more powerful role than a difference in energy or entropy.

A related difference between the two models arises when we consider the possibility that an individual organism will move counter to evolutionary progress—downward in fitness or upward in energy. In a reproduction and selection model, the possibility of movement to a significantly lower fitness class is vanishingly small. This is because steps downward in fitness become progressively more and more difficult. A step downward consists of two parts, a mutation downward and a successful reproduction in the lower fitness class. The first part does not depend on which fitness class

we start from. However, the second decreases for lower-fitness classes because the reproduction rate is controlled by the available resource which is controlled by the dominant fitness class. In contrast, Monte Carlo steps upward in energy have the same probability no matter what the starting energy is. If we think about the fitness landscape as formed of valleys and ridges, this difference in model behavior is directly relevant to the possibility of climbing over ridges to find other valleys. In the Monte Carlo model, it may be possible. In the reproduction and selection model, it is very unlikely. This is also related to the observation that in the Monte Carlo model the population tends to spread out on an incline. In the reproduction and selection model this is not the case.

Finally, there is also a difference in the effect of the absolute population size in the two models. In a simple Monte Carlo model where each walker moves independent of the others, the population size does not enter in any way. When there is self-attraction of the organisms (Section 6.4.5), it plays a role in random movement on a flat landscape—the motion is faster for smaller populations. However, population size does not play a role in the rate of evolution on an incline. On the other hand, in the reproduction and selection model, the probability of finding a rare mutation per generation increases with population size. Thus the rate of evolution increases almost linearly with population size when the probability of finding the right mutation is small. We can also think about the reproduction and selection model as a kind of fitness optimization algorithm. The linear increase in rate of evolution with population size implies that it works as an efficient parallel algorithm where each processor (organism) contributes to the optimization.

Qualitatively our conclusions from this section are that the process of reproduction and selection is effective at finding rare fitness-improving mutations and therefore is effective at forcing evolutionary progress against the influence of entropy. This is precisely what is needed to generate complex organisms. However, we also find that reproduction and selection tend to drastically confine the exploration of possible organisms to a steepest descent in the fitness landscape. Thus, evolutionary progress should become stuck in the first fitness valley that is encountered, and organism change will no longer be possible. This problem leads to even more dramatic consequences when we consider it in the context of trait divergence in the next section.

6.5.4 Trait divergence, extinction and the tree of life

The incremental process of evolution by mutation and selection described in the previous section must be accompanied by a discussion of trait divergence in order to account for the phenomenology of life. As discussed before and illustrated in Fig. 6.5.9, it is assumed that all organisms, ranging from single-celled organisms to plants and animals, originated from the same microorganisms early in evolutionary history. This requires a process of divergent evolution. At various moments in time, originally similar organisms evolved in different ways to create (at least) two types of organisms from the original one. The evidence in support of this picture includes the similarity of various organisms in their various levels of structure (chemical, cellular, physiological) and the experience of breeding where distinct varieties can be generated. The

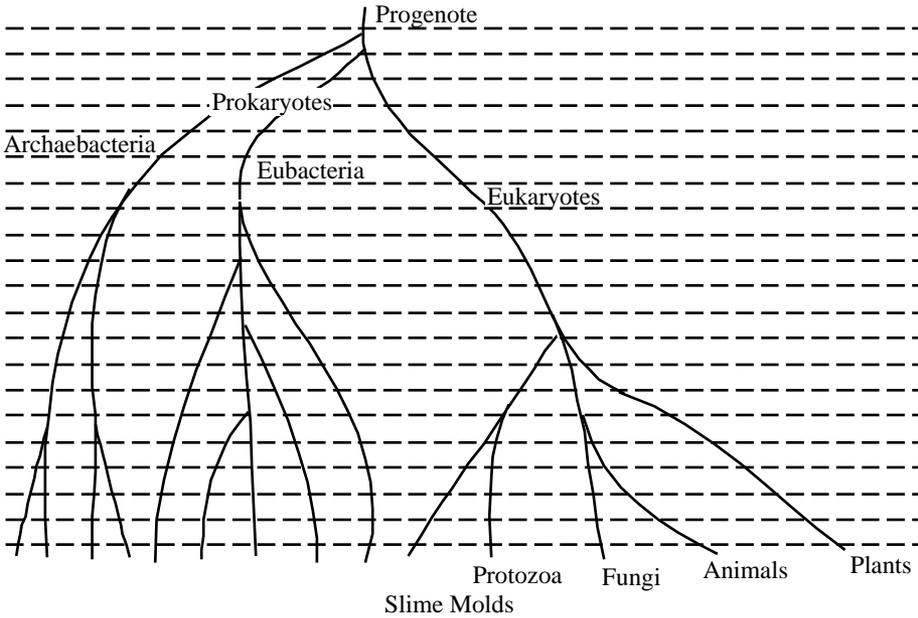


Figure 6.5.9 Schematic illustration of the tree of life formed by evolution and trait divergence, resulting in all of the diversity of life, and originating in one type of single-celled organism. As discussed in the text, a model of reproduction and selection that requires competition based on fitness between all organisms would not be able to account for trait divergence, because at every time all of the species must have essentially the same fitness. This would require all to evolve in precise lockstep. In order to account for trait divergence, selection must be understood to apply separately to organisms that consume distinct resources—identified both by resource type and geographical location. ■

relative proximity of organisms on the tree of life has been studied by assuming that the number of differences in the genome reflects their distance on the evolutionary tree. In Section 6.4.6 we discussed several global models, flow downhill, uphill motion and expanding waves, which might be considered in the context of Monte Carlo models for speciation. What can we say about the reproduction-and-selection models discussed in this section?

Remarkably, we can point out that any of the reproduction-and-selection models discussed in this section are inconsistent with trait divergence. For definiteness, consider the reproduction-and-selection model based upon resource utilization in Section 6.5.3. We can introduce branching channels for organisms in a pattern consistent with that shown in Fig. 6.5.9. Progress along any channel is directly mapped onto mutations that increase fitness. Thus we identify a particular fitness class with the horizontal lines in Fig. 6.5.9. Starting from an organism at the beginning of the tree, the organism evolves downward to the first branching. Then some organisms

move to one channel and some to the other. The problem with this model arises in the interplay between organisms evolving in the two channels. Assume that organisms in one channel, even by chance, progress to a higher class slightly before they do so in the second channel. Then the organisms in the second channel will be rapidly suppressed by selection. This suppression is an accelerating process, because once there are fewer organisms, they have less chance to reach the subsequent fitness class. Thus, unless we could demonstrate a reason for all organisms to evolve in lockstep, there is no possibility that the reproduction-and-selection model will allow the coexistence of distinct types of organisms. This is the literal conclusion of “survival of the fittest”—only one type of organism can exist. This conclusion applies not only to the renewable-resource model but also to the simplest reproduction-and-selection model in Eq. (6.5.5), and to the predator-prey model for the evolution of prey (or predators) in Section 6.5.2.

Question 6.5.8 Contrast the formation of diverse organism traits in the Monte Carlo model with its absence in the reproduction-and-selection models. What is the key difference?

Solution 6.5.8 The key difference is the scope of selection. In the Monte Carlo model, selection only occurs between an organism and its one mutated offspring. In the reproduction-and-selection model, selection occurs between all organisms at the same time. In the first case, we can have different traits for every walker. In the second, essentially only one organism type is possible. ■

Question 6.5.9 Consider neutral mutations in the model of the last section. These mutations consist of additional genome or phenome dimensions in which the organisms can change without affecting their fitness. How does the population evolve in these dimensions? For simplicity, consider the case where Λ is large.

Solution 6.5.9 The trick is to recognize that evolution in the direction of increasing fitness affects the population movement in the neutral dimensions as well. Thus we cannot describe the evolution of the population as a diffusion in the neutral dimensions.

The case where Λ is large means that fitness-improving mutations are rare. As a result there is essentially only one organism that mutates to a higher fitness class. This organism reproduces to form the entire population at the next fitness class. Thus the population of every fitness class begins from a unique genome. During the proliferation of the organisms in this class, they diffuse in the neutral dimensions to form a more diverse population. Then a mutation takes one organism to the next fitness class, and the process of spreading starts over. Thus, the width of the distribution in the neutral dimensions is limited to be the width of a random walk that occurs in the time to reach the next fitness class; i.e., it is proportional to $\sqrt{\tau}$. In our model where Λ does not change, the width of the distribution also does not

change as the organisms evolve. This is consistent with the observation that this model precludes the coexistence of distinct organism types.

However, there is a change over time in the average location of the population in the neutral dimensions. At the time a fitness-improving mutation occurs, the population consists of a distribution of width $\bar{\tau}$. From this distribution, one organism mutates to the higher fitness class. Thus in the next class the average location of the population in the neutral dimensions will be different from that in the previous class by a distance proportional to $\bar{\tau}$. We see that the population as a whole undergoes a random walk in the neutral dimensions. The typical distance traveled in the random walk is proportional to $\bar{\tau}n = \bar{t}$, where n is the total change in fitness class. This means that the typical distance traveled in the neutral dimensions is independent of τ . ■

Where have we neglected an essential element in our models that would enable evolutionary coexistence of organism types? By considering natural phenomena, we recognize that the main problem in this picture is that all organisms do not compete directly for the same resource. Instead, there are many different resources that organisms are consuming. The primary resource is the energy that is arriving from the sun and radiated as heat into space. This resource is converted by interaction with the physical world, as well as with the biological organisms that exist, to other forms. The utilization of this resource by one organism type (e.g., plants) leads to another resource type (oxygen, sugar) that can be used by other organisms. The interplay of this process with physical climate and geologic conditions also leads to variations in the form the resource takes and conditions under which it can be utilized. In addition to their distinct forms, resources may also be distinct through spatial physical isolation—the separation of two different areas by physical obstacles that prevent easy migration from one to the other. This variation and isolation of resources leads to distinct channels of evolution related to their utilization.

We conclude that it is the existence of different resources that enables distinct organism types. Thus, to simulate the formation of different types in a model similar to that in Section 6.5.3, we must modify it to allow for the existence of distinct resources, say r_1 and r_2 . These may represent different sides of the same mountain range, different types of grass, or grass and leaves or even sunlight and plants. To allow the formation of different types of organisms, mutation (or migration) must then allow creation of organisms that pursue these distinct resources. Construction of a model of this kind is not difficult. We assume a number of organism types indexed by i that consume the two resources with efficiencies κ_{i1} and κ_{i2} . Trait divergence would occur when organisms consume the resources in a manner that would systematically cause one type of evolving organism to consume one resource, while the other consumes the other resource. In the simpler model of Eq. (6.5.5) the same effect would be modeled by introducing more than one fitness parameter per organism. We will not expend effort to build and simulate such models here. In Chapter 7, models will arise naturally that contain the essential features discussed here.

Question 6.5.10 Let us try one more time to create a global fitness model using an equation similar to Eq. (6.5.4) to define what we mean by fitness in the most direct and natural way. The fitness K is the rate of increase in the population of the organism defined as:

$$\frac{dN}{dt} = KN \quad (6.5.52)$$

In what way might this be a useful definition? In what way is it not?

Solution 6.5.10 The concept of a fitness assumes that it can be expressed in terms of the organism properties—in particular, as a function of the genome s . To the extent that we can obtain $K(s)$ independent of the evolutionary dynamics we wish to describe, it is useful. If we use the definition in Eq. (6.5.52) in the context of the model of Section 6.5.3, we see that for any fitness class, $K(s)$ starts out greater than one, passes through unity when it is populated and becomes smaller than unity as it disappears. This shows that the fitness defined in this natural way is a strong function of time through changes in the environment, which also consists of other organisms.

Using Eq. (6.5.52) as a model for global evolution, we imagine a fitness landscape $-K(s)$ (the negative sign is for consistency of up and down with the energy model). Organisms do not diffuse downward on the landscape; instead the landscape itself moves upward. This is not an essential difference. What is different is that all the organisms at any time are points located on a band near unit fitness. Organisms increasing in number have slightly higher fitnesses (are lower on the landscape) and those decreasing have slightly lower fitnesses. This picture would be appealing and simple if the landscape were rigid. It would then correspond to all organisms evolving uniformly in lockstep. However, if we consider an organism that persists for long times and organisms that undergo dramatic evolutionary changes during the same time, we see that the landscape itself is changing shape (morphing). Regions of the landscape where organisms are evolving move quickly, while other regions remain fixed in place. This illustrates how the existence of multiple resources manifests itself in this model. ■

The necessity of considering multiple resources in the study of multiple organism types is an indication that an essential problem in studying evolution is understanding the dynamics of the resources and their categorizations and distinctions. Since most of the time, aside from sunlight and space, the resources that are consumed are themselves organisms or related to the existence of organisms, this creates an interdependence between the evolution of one organism and the evolution of others. For our limited purposes here, we need only recognize that without a model for the dynamics of the resources, a dynamics of organism types cannot be understood. Within such a model, formation of distinct organism types can be readily understood.

Another process that may be understood within this picture is extinction. There are various times in evolutionary history where organism types that existed become

extinct. We can understand this by assuming that after multiple organism types are created, there is parallel evolution of organisms that are consuming different resources. Some time later, one organism type may have a mutation that enables it to better consume a resource that the second organism type depends upon. This leads to extinction of the second organism type.

A process that is rarely considered is true convergent evolution: two organisms evolve by mutation and become the same organism. This is the opposite of divergent evolution. There are several reasons why it is not likely. The first is the large space of possible organisms. Moving around in this space, two evolutionary tracks are unlikely to encounter each other. Another reason that this is not likely can be seen from the multiple-resource model. As two organisms become similar they become competitors for the same resource. However, as this occurs they are still different enough so that one should have a lower fitness than the other and will become extinct.

In order to understand the role of different resources in causing multiple organism types, it is helpful to consider the notion of organism complexity, which will be developed further in Chapter 8. We can think about a particular environment and resource as establishing a particular demand on organisms. As discussed above, associated with an amount of resource is a minimum fitness that corresponds to the first viable organism that can survive by utilizing it. This also means that there is a minimal complexity for viable organisms. This is the minimum complexity of organisms that have sufficient fitness to survive in the environment by consuming this resource. For example, it appears that there are photosynthetic organisms that can exist in the ocean which are simpler than photosynthetic life on land. We might imagine a map of the minimal complexity of viable organisms at every location on the two-dimensional surface of the earth, for each of multiple resources present there. We can view the process of evolutionary progress as the creation of new organisms that are complex enough to exist in a certain environment and consume a particular resource. Progress enables organisms to spread from one environment to another. One example is the often discussed emergence of life from ocean to land. Once life exists that consumes a particular resource in a particular place, evolution continues until it reaches the maximal fitness for the resource. This maximal fitness is the lowest fitness that enables organisms to consume all of the resource. It also corresponds to a maximum complexity that would be reached by evolution in this environment. This picture may be described as the evolution of organisms to fill ecological niches that exist due to the presence of resources. We can intuitively understand that in order for an organism to be able to consume more than one type of resource it must be more complex than an organism that consumes only one type of resource. Qualitatively, this explains why evolution created progressively more complex organisms but did not systematically eliminate the previous organisms. Organisms that existed and filled ecological niches remain. This also includes the prokaryote single-celled organisms that may have initiated the process of organism evolution.

This description of evolution enables us to compare and contrast human beings with the most closely related species—the apes. Apes occupy small ecological niches and consume limited resources. In contrast, human beings utilize a significant frac-

tion of many different resources in many distinct environments. This suggests that apes evolved in order to be able to utilize resources that can only be consumed by such highly complex organisms. Human beings break this pattern by being sufficiently complex to meet the challenges of consuming a large variety of resources. Within this context, we can understand the potential and actual extinction of various organisms as a result of the actions of mankind in consuming resources. Human consumption of plants and animals is in part a predator-prey situation where overconsumption can lead to decline of the predator (human beings) as well as the prey. On the other hand, the direct competition for resources (prey or space) causes extinction or danger of extinction to many animals and plants. This is consistent with considering human beings as part of the evolutionary process where the increased fitness of human beings through their ability to consume resources is an advantage over animals and plants and may cause extinction of the latter. Of course, an explanation for extinction does not mean that it is in the best interest of human beings. However, we see that the widespread ability to cause extinction for many different organisms signals a qualitative change in what is more typical of evolution. Organisms typically evolve and are complex enough to occupy only specific ecological niches.

The discussion of multiple resources allowed us to introduce spatial variation in resources and thus in fitness. It is also relevant to discuss temporal variation in resources. We consider the possibility of a fluctuating base line resource $r_0(t)$ for the renewable-resource model. This can be seen to cause a variation in the selection pressure. Without any variation, the selection pressure is great due to consumption of the available resource by the fittest organisms present. If, however, the resource suddenly becomes more plentiful, then the amount of resource $r(t)$ is more than the equilibrium value $r_i(\)$ for organisms in lower fitness classes. The organisms in these classes then increase in numbers. It is less significant that the fittest organisms multiply faster. The increase in population of lower-fitness organisms allows, in principle, for the possibility of escape from valleys in the fitness landscape. This solves a major problem of describing evolutionary progress in the reproduction-and-selection model. An illustrative example is the effect of forest fires. Originally thought to be solely harmful, the occasional loss of old trees is now understood to have many benefits. We discussed the effects of forest fires in the context of interdependent networks of organisms in Section 6.4.5. Here, the effect of such catastrophes is direct. We can recognize that a fire enables a larger variety of plant life and other organisms to grow in the plentiful resource (sunlight) whose consumption is not dominated by a particular type of optimal-fitness tree. This increase in diversity of organisms participates in the process of evolution through creation of variety that can then be the subject of selection as the forest matures.

One final temporal consideration is important when we consider the competition that causes extinctions. If we consider competition between two species, we see that the organism type that evolves faster has an advantage when competition for the same resource occurs. Thus, fitness of a species can depend not only on the fitness of a particular organism but also of the rate of organism evolution. This can be directly affected by the lifetime of a generation that sets the time scale for the models of

evolutionary progress. We see that selection may cause organisms to have short life spans—a possible reason for senescence. Even more significantly, considering these effects causes us to look beyond the individual to the effects of selection on species, since the rate of evolutionary progress is not part of the fitness of a particular organism. This will be the topic of the following section.

6.6 Collective Evolution: Genes, Organisms and Populations

Our objective in this section is to reconsider the properties of components in complex systems and their relevance to evolution. Sexual reproduction involves an entire species in an evolutionary process rather than each individual organism. Interestingly, it is possible to take another approach in which sexual reproduction decouples the evolution to a process that pertains to individual genes that are parts of the organism. We will discuss this approach in Section 6.6.1, developing an understanding of when (and in what sense) it is valid and when it is invalid, since we are interested in the nature of interdependence of components of complex systems. In Section 6.6.2 we will approach more generally the problem of understanding why systems built out of components are formed in evolution. Why don't the components just fend for themselves? This question is related to philosophical questions about selfish and altruistic individuals in a society, and conceptual problems of understanding the appearance of altruism in evolution. By addressing these questions, we will gain an intuitive understanding of the process of formation of collectives in evolution.

6.6.1 Genetic mixing in sexual reproduction

One of the interesting phenomena of biology is the existence of sexual reproduction in all but relatively simple organisms. Sexual reproduction mixes hereditary traits. This mixing poses serious philosophical problems for the understanding of evolution. Simply stated, the problem is that in sexual reproduction the organism that is selected for is not the same as its offspring. How is this consistent with the concept of selection as a mechanism of evolution?

One of the approaches that has been taken to deal with this issue is the gene-centered view of evolution. In this view there are assumed to be indivisible elementary units of the genome (often thought of as individual genes) that are preserved from generation to generation. Different versions of the gene (alleles) compete and mutate rather than the organism as a whole. Thus the genes are the subject of evolution. We will show below that this view is precisely equivalent to a mean field approach (Section 1.6) where correlations between the different genes are ignored. Each gene evolves in an effective environment formed within the organism and its environment. This effective environment is an average environment (mean field) within a sexually reproducing population (species). By showing that the gene-centered view of evolution is a mean field approach, we can recognize why it is useful and we can also recognize when it is invalid—when correlations between genes are significant.

Correlations between genes arise when the presence of one allele in one place in the genome affects the probability of another allele appearing in another place in the genome. One of the confusing points about the gene-centered theory is that there are two stages in which correlations must be considered: selection and sexual reproduction (gene mixing). Correlations occur in selection when the probability of survival favors certain combinations of alleles, rather than being determined by a product of terms given by each allele separately. Correlations occur in reproduction when parents are more likely to mate if they have certain combinations of alleles. If correlations only occur in selection and not in reproduction, the mean field approach continues to be at least partially valid. However, if there are correlations in both selection and sexual reproduction, then the mean field approach and the gene-centered view becomes completely invalid. It is sufficient for there to be very weak correlations in sexual reproduction for the breakdown to occur. This turns out to be particularly relevant to trait divergence of populations.

In order to understand the gene-centered view we will study a simple model of the process of sexual reproduction that explicitly eliminates correlations in reproduction. Two specific examples will be worked out in some detail. Then we will discuss a more complete theory showing that the simple theory is a mean field approach. Later we will present reasons for the existence of sexual reproduction. It is helpful to recall that during sexual reproduction an offspring obtains half of the chromosomes of nuclear DNA from each parent. The chromosomes are paired in function—homologous pairs. Each homologue chromosome of the offspring is formed in a parent by a process (crossover during meiosis) that combines segments of DNA from both of the parents' homologues.

A first model of sexual reproduction begins by assuming that recombination of the genome components during sexual reproduction results in a complete mixing of the possible alleles, not just in the organism itself but rather throughout the species—the group of organisms that is mating and reproducing. Thus the offspring represent all possible combinations of the genomes from reproducing organisms. From the point of view of a particular allele at a particular gene, the complete mixing means that at all other genes, alleles will be present in the same proportion that they appear in the population—there are no allele correlations after reproduction.

In the simple model, selection operates on the entire genome of the organism. Thus, after selection there may be correlations in the allele populations. It is assumed that the reproducing organisms are the ones that have successfully survived the process of selection. If we would further simplify this model by assuming that each gene controls a particular phenomic trait for which selection occurs independent of other genes, then each gene would evolve independently; a selected gene reproduces itself and its presence within an organism is irrelevant. The existence of a gene as part of an organism means, however, that selection occurs on the genome, not on individual genes, and allele correlations after selection will occur. This means that fitness depends not on individual genes but rather on gene combinations. As the proportion of one allele in the population changes due to evolution, the fitness of another allele at a

different gene will be affected. However, due to the assumption of complete mixing in sexual reproduction, only the average effect (mean field) of one gene on another is relevant. We could consider the organism to be part of the changing environment in which the gene evolves. The following two examples will help us examine this more carefully.

The first example we discuss is the special case of interdependence of two homologue genes. This is special because the same alleles are found in both genes. We allow there to be only two different alleles. The evolutionary dynamics describes the proportion of genes with each allele in the population. The proportion of the alleles is given by $P_1(t)$ and $P_{-1}(t) = 1 - P_1(t)$. An individual organism has two homologue genes and may be either homozygous with both of the same kind or heterozygous with one of each. Using our assumption of random mixing during reproduction, offspring represent the ensemble of possible combinations of the alleles; the specific composition of the parent generation cannot matter to the composition of the offspring. Thus the offspring organisms are in proportions:

$$\begin{aligned}
 P_{1,1}(t) &= P_1(t-1)^2 \\
 P_{1,-1}(t) &= 2P_1(t-1)(1 - P_1(t-1)) \\
 P_{-1,-1}(t) &= (1 - P_1(t-1))^2
 \end{aligned}
 \tag{6.6.1}$$

where $P_{i,j}$ is the proportion of an organism with i and j alleles. If there is no selection bias, these organisms will reproduce to form the subsequent generation. We confirm that the proportion of alleles is unchanged from generation to generation (Hardy-Weinberg theorem). The proportion of one allele is given by

$$P_1(t) = \frac{1}{2} \left(2P_{1,1}(t) + P_{1,-1}(t) \right)
 \tag{6.6.2}$$

where the prefactor of 1/2 comes from normalization of the probability because there are two alleles per organism. From Eq. (6.6.1) this is:

$$\begin{aligned}
 P_1(t) &= \frac{1}{2} \left(2P_1(t-1)^2 + 2P_1(t-1)(1 - P_1(t-1)) \right) \\
 &= P_1(t-1)
 \end{aligned}
 \tag{6.6.3}$$

To introduce selection we assume that it acts on the organisms, and assign a fitness to each of the organisms, not each of the alleles. We use the simplest selection model of Eq. (6.5.5) where number of offspring λ determines fitness. The parameters are indexed by the two alleles λ_{11} , $\lambda_{1,-1}$, and $\lambda_{-1,-1}$. We have a two-step dynamics consisting of reproduction and selection. In generation t the population proportions after selection (indicated by primes) are:

$$\begin{aligned}
 P_{i,j}(t) &= \frac{\lambda_{i,j}}{\langle \lambda \rangle} P_{i,j}(t) \\
 \langle \lambda(t) \rangle &= \lambda_{i,j} P_{i,j}(t) = \lambda_{1,1} P_1(t)^2 + 2\lambda_{1,-1} P_1(t)(1 - P_1(t)) + \lambda_{-1,-1} (1 - P_1(t))^2
 \end{aligned}
 \tag{6.6.4}$$

The reproduction step that determines $P_1(t)$ is given by Eq. (6.6.2) with primed probabilities:

$$\begin{aligned}
 P_1(t) &= \frac{1}{2} \left(2P_{1,1}(t-1) + P_{1,-1}(t-1) \right) \\
 &= \frac{1}{\langle \lambda(t-1) \rangle} \left(\lambda_{1,1} P_1(t-1)^2 + \lambda_{1,-1} P_1(t-1)(1 - P_1(t-1)) \right)
 \end{aligned}
 \tag{6.6.5}$$

We can find the steady state where $P_1(t) = P_1(t-1) = P_1$. Multiplying Eq. (6.6.5) by $\langle \lambda \rangle$ gives the equation:

$$\lambda_{1,1} P_1^3 + 2\lambda_{1,-1} P_1^2(1 - P_1) + \lambda_{-1,-1} P_1(1 - P_1)^2 = \lambda_{1,1} P_1^2 + \lambda_{1,-1} P_1(1 - P_1)
 \tag{6.6.6}$$

We have two trivial solutions $P_1 = 0, 1$. Dividing this equation by $P_1(1 - P_1)$ —the easiest way is to combine together the first term on both sides—enables us to obtain the third root, which is given by:

$$2\lambda_{1,-1} P_1 + \lambda_{-1,-1}(1 - P_1) = \lambda_{1,1} P_1 + \lambda_{1,-1}
 \tag{6.6.7}$$

or:

$$P_1 = \frac{\lambda_{1,-1} - \lambda_{-1,-1}}{2\lambda_{1,-1} - \lambda_{-1,-1} - \lambda_{1,1}}
 \tag{6.6.8}$$

The two trivial solutions occur when either $\lambda_{1,1}$ or $\lambda_{-1,-1}$ is the highest fitness. In this case we can say that one of the alleles is more fit than the other. If $\lambda_{1,-1}$ is the highest fitness, then the third solution that corresponds to a mixed population results. This is the circumstance where an organism with one allele of one type and one allele of the other type is most fit. A well-known example is the sickle-cell allele which, when combined with a normal allele, has higher fitness in the presence of malaria. To see how this mixed solution functions, we can assume that the fitness for homozygous organisms is zero, so that none of them reproduce. Then we have $\lambda_{1,1} = \lambda_{-1,-1} = 0$. From Eq. (6.6.8) $P_1 = 1/2$. Even though the organisms that are homozygous do not reproduce, they still exist in every generation and comprise half of the population at birth. Thus, selection in favor of heterozygotes creates a mixed population.

In a sense, this is a straightforward example of the creation of correlations between alleles that might be expected to violate a mean field theory. Selection imposes a correlation by requiring the existence of different alleles at the two genes. However, if we only consider the composition of offspring, then the alleles become uncorrelated due to sexual mixing. The dependence of one allele on the other allele for survival is obscured by the averaging due to reproductive mixing. In Question 6.6.1 the replacement of the fitness of an organism with an effective fitness of an allele is discussed. Note also, that the way the model is formulated so that the population is always normalized, obscures the need to overcome selection by having greater numbers of offspring.

This example can be generalized. We could consider two genes with two alleles each, where the only reproducing organism has a combination of all different alleles. Each of the alleles on each gene would be present half of the time and the reproducing organism occurs only one-quarter of the time. Three-quarters of the organisms

do not reproduce. We can see that survival would become poor for organisms if there is such severe selection for particular combinations of genes. Since there are estimated to be of order 10^5 genes in mammals, this is an unlikely scenario. Specifically, if many individual genes strongly affect selection, then the number of organisms surviving to reproduce becomes very small. This problem will become more significant when we consider correlations between nonhomologue genes.

As a second example, we consider a case of selection in favor of a particular combination of alleles on nonhomologue genes. Specifically, when allele A_1 appears in one gene, allele B_1 must appear on a second gene, and when allele A_{-1} appears on the first gene, allele B_{-1} must appear on the second gene. We can write these high fitness organisms with the notation $(1, 1)$ and $(-1, -1)$; the organisms with lower fitness (for simplicity, $\lambda = 0$) are $(1, -1)$ and $(-1, 1)$. It is clear that there are two stable states of the population with $(1, 1)$ or with $(-1, -1)$. If we start with exactly 50% of each allele, then there is an unstable steady state. In every generation, 50% of the organisms reproduce and 50% do not. Any small bias in the proportion of one or the other will cause there to be more and more of one type over the other, and the population will eventually have only one set of alleles.

We can solve the example directly. It simplifies matters to realize that the reproducing parents must contain the same proportion of the correlated alleles (A_1 and B_1) so that:

$$\begin{aligned} P_{1,1}(t) + P_{1,-1}(t) &= P_{1,1}(t) + P_{-1,1}(t) = P_1(t) \\ P_{-1,1}(t) + P_{-1,-1}(t) &= P_{1,-1}(t) + P_{-1,-1}(t) = P_{-1}(t) = (1 - P_1(t)) \end{aligned} \quad (6.6.9)$$

The reproduction equations are:

$$\begin{aligned} P_{1,1}(t) &= P_1(t-1)^2 \\ P_{1,-1}(t) &= P_{-1,1}(t) = P_1(t-1)(1 - P_1(t-1)) \\ P_{-1,-1}(t) &= (1 - P_1(t-1))^2 \end{aligned} \quad (6.6.10)$$

The proportion of the alleles in the generation t is given by the selected organisms:

$$P_1(t) = \left(P_{1,1}(t) + P_{-1,-1}(t) \right) \quad (6.6.11)$$

Since the less fit organisms $(1, -1)$ and $(-1, 1)$ do not reproduce this is described by:

$$P_1(t) = P_{1,1}(t) = \frac{1}{P_{1,1}(t) + P_{-1,-1}(t)} P_{1,1}(t) \quad (6.6.12)$$

This gives the update equation:

$$P_1(t) = \frac{P_1(t-1)^2}{P_1(t-1)^2 + (1 - P_1(t-1))^2} \quad (6.6.13)$$

which has the behavior described above and shown in Fig. 6.6.1. This problem is reminiscent of the ferromagnet at low temperature as studied in Section 1.6. Starting from a nearly random state with a slight bias in the number of UP and DOWN spins, the spins align, becoming either all UP or all DOWN.

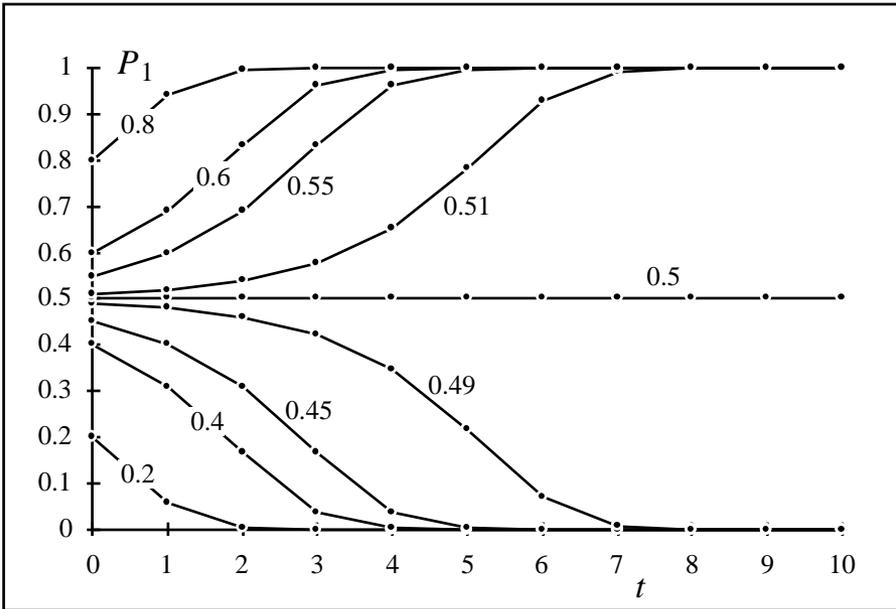


Figure 6.6.1 Time evolution of the allele population in sexual reproduction when selection enforces a correlation between alleles on two genes, Eq. (6.6.13). The proportion of the first coupled pair of alleles $P_1(t)$ in successive generations is shown by the dots, and connecting lines are included for clarity. The starting proportions $P_1(0)$ are indicated by the labels. The figure shows that the pair of alleles which starts with a larger proportion eventually dominates. For $P_1(t) = 0.5$ there is an unstable equilibrium. The text discusses a species that has nonuniform composition in physical space. In one area one allele pair dominates and in another area the second allele pair dominates. Under the influence of correlated selection linked to correlated reproduction, two distinct populations arise. ■

In order to relate the examples and assumptions we have used to a more general formulation of sexual reproduction, we write a two-step general model for sexual reproduction:

$$\{N(s;t)\} = R[\{N(s;t-1)\}] \tag{6.6.14}$$

$$\{N(s;t)\} = D[\{N(s;t)\}] \tag{6.6.15}$$

The first equation describes reproduction. The number of offspring $N(s;t)$ having a particular genome s is written as a function of the reproducing organisms $N(s;t-1)$ from the previous generation. The second equation describes selection. The reproducing population is written as a function of the offspring. The brackets on the left indicate that each of these equations represents a set of equations for each value of the genome. The brackets within the functions indicate, for example, that each of the offspring populations depends on the entire set of parent populations.

A mean field approximation is performed by assuming that the reproduction step depends only on the proportion of alleles and not on their specific combinations in the reproducing population. This proportion can be written as:

$$P(s_i; t) = \frac{1}{N_0(t)} \prod_{j=1}^i N(s_j; t) \tag{6.6.16}$$

where we use $s = (s_1, \dots, s_N)$ to represent the genome in terms of alleles, and the sum is over all gene alleles keeping s_j fixed. $N_0(t)$ is the total reproducing population at time t . According to our assumption about reproduction, the same offspring would be achieved by a population with a number of reproducing organisms given by

$$\tilde{N}(s, t) = N_0(t) \prod_i P(s_i; t) \tag{6.6.17}$$

since this has the same proportions as Eq. (6.6.16). The form of this equation indicates that the probability of a particular genome is a product of the probabilities of the individual genes—they are independent. Thus complete reproductive mixing assumes that:

$$R[\{\tilde{N}(s; t)\}] = R[\{N(s; t)\}] \tag{6.6.18}$$

Once this is assumed, then a complete step including both reproduction and selection can also be written in terms of the allele probabilities in the whole population. The update of an allele probability is:

$$P(s_i; t) = \frac{1}{N_0(t)} \prod_{j=1}^i D[R[\{\tilde{N}(s; t-1)\}]] \tag{6.6.19}$$

Given the form of Eq. (6.6.17) we could write this as an effective one-step update

$$P(s_i; t) = \tilde{D}[\{P(s_i; t-1)\}] \tag{6.6.20}$$

which describes the allele population change. Thus the assumption of complete mixing allows us to write the evolution of a single allele in this way. However, because Eq. (6.6.20) is a function of all the allele populations, the fitness of an allele is coupled to the evolution of other alleles.

Eq. (6.6.17) describes the neglect of allele correlations in reproduction consistent with a mean field approximation. It should be apparent that this is only a rough first approximation. It is valid only when the gene appears with sufficiently many different combinations of other genes so that correlations are unimportant. In more realistic models, correlations between genes affect both reproduction and selection.

We can provide a specific example of breakdown of the mean field approximation using the previous example of selection of gene combinations leading to Eq. (6.6.13). In this example, if there is a spatial variation in the organism population that results in a starting population that has more of the alleles represented by 1 in one region and more of the alleles represented by -1 in another region, and reproduction

is correlated by region, then we will form patches of organisms that have (1,1) and (-1,-1) after several generations. This symmetry breaking, like in the ferromagnet, is the usual breakdown of the mean field approximation. Here, we see that it creates correlations in the genetic makeup of the population. When the correlations become significant, then the species has a number of types. The formation of organism types depends on the existence of correlations in reproduction that are, in effect, a partial form of speciation—what is important is whether interbreeding occurs, not whether it is possible.

Thus we see that the most dramatic breakdown of the mean field approximation occurs when multiple organism types form. This is consistent with our understanding of ergodicity breaking, phase transitions and the mean field approximation from Section 1.6. Interdependence at the genetic level is echoed in the population through the development of subpopulations. We should emphasize, that this symmetry breaking required both selection and reproduction to be coupled to gene correlations. Moreover, if there is a small bias in the fitness of (1,1) over (-1,-1) then the formation of the two varieties will not persist due to competition between them over many generations. Thus we still need the existence of multiple resources, as discussed in the previous section, to enable the distinct types to persist.

Even if we assume that there exist multiple resources, interbreeding of organisms may continue to mix and force them to remain a single type with diverse individuals. However, the more correlations are important during selection, the more ineffective this becomes. When viable organisms are a small subset of the organisms formed by reproduction, a large number of offspring are required in order to maintain the population. Specifically, the number of offspring grows exponentially with the number of genes whose alleles are coupled to each other in selection. Strong genomic correlations in selection eventually make reproductive mixing impossible. The actual situation is not quite so extreme, because meiosis does not result in complete mixing of parent DNA. Only limited crossover occurs, so that chromosomes do not lose much of the preexisting allele correlations.

The existence of sexual reproduction implies that from a fitness perspective it is beneficial. Our next objective is to understand how it might be beneficial and what this says about fitness. In sexual reproduction, organisms are paired and their offspring are not copies of the original organisms but rather composites of them. We use the term “composites” in the same sense as used in Chapter 2, and its significance there is related to its significance in the present context. The implication is that organisms are composites of partially independent components, designed to correspond to partially independent aspects of the fitness. Specifically, distinct physiological or behavioral attributes have varying degrees of interdependence in selection. The approach of trying composite states of previously successful combinations applies in this case, as it did in the learning of patterns in neural networks. This, however, does not entirely explain the existence of sexual reproduction.

We have discussed various aspects of the problem of sexual reproduction however, these have not indicated why sexual reproduction itself improves organism fitness. By conventional argument, sexual reproduction should be a physiological or

behavioral attribute that increases the ability of an organism to produce surviving offspring. On the face of it this seems ludicrous. Asexual reproduction does not depend on the existence of a mate, and therefore an organism that can reproduce asexually is more likely to reproduce. Moreover, asexual reproduction seems to require a much smaller overhead in terms of physiological machinery. This physiological machinery uses resources that could be utilized for other purposes. In other words, an organism that had all of the physiological traits of a sexually reproducing organism but could reproduce itself asexually (e.g., by cloning) would seem to have a fitness advantage.

There are difficulties with this picture that illustrate problems with simple formulations of the theory of evolution. The first is that the ability to produce surviving offspring depends on a time-varying fitness landscape rather than a static one. Of particular significance in this variability is the evolution of competing organisms. An organism that evolves more slowly has a lower probability of producing surviving offspring than an organism that evolves more rapidly. This sentence, however, does not make sense, since an organism does not evolve, only a population of organisms evolve. In order to understand this we must improve the language that we use to describe evolution.

We often say that fitness-based selection implies that an organism exists because of its ability to survive and have offspring. The problem with this statement is that an organism does not exist because of what happens in the future but rather what happened in the past. The two are only the same when every generation is the same. Thus the organisms that exist at any one time are offspring from organisms that survived, who in turn were offspring of a set of organisms that survived. Thus we must write an iterative equation of the form

$$N(s, t) = R[D[R[D[R[D[R[D[\dots\{N(s;0)\}\dots]]]]]]] \quad (6.6.21)$$

representing the selection of organisms at every generation. Because selection applies not to a particular organism but to a chain of ancestors, the rate of fitness improvement is essential to the selection. We see that this causes conceptual problems, because selection is no longer based only upon the fitness of an organism but rather on the rate of fitness change, which is a property of generations of organisms.

The process of sexual reproduction accelerates evolution because of the same reason that composite states are useful in pattern recognition. As long as the genes on an organism cause partially independent effects, it is advantageous to attempt possible composites and establish more definite relationships only as the correlations are established by selection. This process, however, describes not selection of an organism but selection of the collectively evolving species. Thus we return to the discussion at the end of the last section, where selection acts not upon an organism but upon species that evolve in parallel and compete for resources. This should not be overly troubling because, after all, sexual reproduction does inherently involve the coupling of past and future generations of any organism with the other organisms that are reproductively coupled. We will return to this issue in the next section.

Our remarks about the relevance of sexual reproduction to fitness suggest that evolution is a process that is far from equilibrium, which is quite reasonable. In such

a far-from-equilibrium process, we are not only selecting for the static properties but also for the dynamic properties. Earlier our treatments assumed that selection applied to a persistent property rather than a dynamical property. Thus, to include the dynamic property in Section 6.4 we would assume that different parts of the landscape have walkers that take steps at different rates. In section 6.5.3 we would assume that organisms have higher or lower rates of mutation as determined by part of the genome itself. An analogy to a car race may be helpful. Our previous discussion assumed that the race is won by the car that is farther along on the road, as opposed to the car that is faster. Of course it makes sense that the faster car is farther along the road, since we assumed in evolution, like in a usual car race, that all started from the same place. The point is that the nature of selection causes the properties of the organism not only directly through fitness but also self-consistently through the process of selection itself.

Question 6.6.1 Criticize the following statement: Since we can define the proportion of a gene in generation t and in generation $t + 1$, we can always write an expression for the allele evolution in the form:

$$\begin{aligned}
 P(s_i; t) &= \lambda_{s_i} P(s_i; t - 1) \\
 \lambda_{s_i} &= 1
 \end{aligned}
 \tag{6.6.22}$$

so that we always have evolution that can be described in terms of genes. Does it matter if Eq. (6.6.17) applies?

Solution 6.6.1 The difficulty lies in the dependence of the coefficients λ on time t through its dependence on the changing population. In steady state, λ values would not change. Of course, in steady state there is no need to describe the dynamics. The equation is only useful as a description of the dynamics if the values of λ are slowly varying in time compared to the changes in P . When Eq. (6.6.17) is not valid, neglecting the subpopulation correlations is formally equivalent to considering the average gene dynamics over all of the organisms on earth despite their differences and the lack of mixing of species. This is the ultimate form of the gene-centered view of evolution. Eq. (6.6.17) applies to the two examples given in the text. The coefficients λ can be written explicitly. They can be seen to vary significantly when the gene population is changing. For the first example we obtain the value $\lambda_1(t) = \lambda_{1,1}P_1(t) + \lambda_{1,-1}(1 - P_1(t))$ from Eq. (6.6.5). For the second example we read the value $\lambda_1(t) = P_1(t)$ from Eq. (6.6.13). ■

Question 6.6.2 Discuss the existence of nonreproducing organisms such as mules in light of Eq. (6.6.21).

Solution 6.6.2 The problem with nonreproducing organisms is understanding why they should exist, since they do not have offspring and therefore by usual concepts are completely unfit—nonviable. Eq. (6.6.21) solves the formal problem of their existence by indicating logically that the exist-

tence of a mule depends only on the existence of its parents. However, it does not explain why evolutionary changes have not caused horses and donkeys to avoid coupling. By coupling, their ability to produce reproducing offspring and therefore their fitness would seem to decrease. In this light we can only remark that the existence of mules suggests the importance of the dynamics of the evolutionary process over the equilibrium view. ■

There are several concepts that relate to sexual reproduction that we briefly mention here. An implicit issue in sexual reproduction is identifying the region of genome or phenome space that can interbreed, which defines the boundaries of possible spread of a single species. We generally assume that for each species this is a well-defined domain separate from other species. In principle, the domains might interleave; however, the large size of phase space suggests otherwise.

A related issue is the relevance of sexual reproduction to our earlier discussion of interactions between organisms in the space. We first recognize that sexual reproduction represented in terms of walkers in the genome space on a fitness landscape corresponds to a step that starts by selecting two walkers at different locations and creates new walkers that are related to the original walkers in that some coordinates are from one and some from the other. The notion of composite states suggests that the landscape is quite rough; however, the selection of composites tends to place organisms into valleys that may be separated from each other by high ridges. Such steps are efficient nonlocal Monte Carlo moves. In effect these steps enable the population to move and spread in what is likely to be a fragmented space. Indeed, if the space were smooth the formation of composites would not be an improvement over standard Monte Carlo steps.

We can think about the impact of sexual reproduction on the effective interactions such as attraction and repulsion. Because of the boundaries of the domain of sexual reproduction, the species inherently evolves together. This corresponds to an attractive interaction within this domain and a repulsive interaction outside of it. Organisms that are similar but located outside the domain of reproduction would be impeded from reproducing if they are present in small numbers because of the prevalence of organisms with which they cannot reproduce. The need to identify organisms with which one can reproduce may be a motivation for the creation of patterns on animal skins discussed in Chapter 7, as well as bird calls and mating behavior.

6.6.2 *Genes, organisms and groups— the evolution of interdependence*

The partial independence of genic evolution in the evolution of sexually reproducing species has led to a gene centered view of evolution where the gene, rather than the organism of which it is a part, is the “entity of interest.” One way to react to this is to consider this approach as the result of a too seriously taken mean field approximation. However, there are important philosophical issues that are raised in discussions of this point that have direct relevance to our understanding of complex systems, so we will spend some time discussing them.

The fundamental philosophical difficulty that appears to give impetus to the focus on gene evolution is the concept of interdependence. Ironically, interdependence that is so essential to the concept of a complex system appears to be at odds with the evolutionary concepts of competition and selection that are supposed to create them. If we consider phenomenologically the evolution of molecular fragments (e.g., genes), or molecules, or cells, or organisms, we find the formation of collections of interdependent individuals. The real problem is understanding the reason for the emergence of interdependence in the context of evolution. Why, after all, would the selection of fit individuals give rise to the appearance of a collective interdependence? We see this problem in discussions of altruism and selfish or even aggressive social behavior. Why would organisms develop altruistic behaviors in a competition for survival? It appears straightforward to assume that selfish or aggressive social behavior provides selective advantage and altruism selective disadvantage when competition for a resource determines survival. The same problem arises at the molecular fragment level when we consider why genes should assemble into interdependent chromosomes. We might easily imagine that the gene that is responsible for coding a replicase could replicate itself many more times with the available resources without the other genes of a complex organism. Until this point we have been concerned with the processes of incremental modification of organisms and speciation. In order to develop an understanding of evolution, we must also understand the formation of interdependent communities of organisms.

In order to make progress, we use the language of organisms evolving on a fitness landscape and the interactions between them as discussed in Section 6.4.5. We considered interactions between organisms that caused either a mutual lowering or a mutual raising of fitness. We argued that organisms would aggregate in regions of space where there was a mutual raising of fitness. We can understand this simply in the context of genic interactions or human social interactions: when there are similar organisms, that help each other, this mutual assistance increases their fitness or success. This model of a mutually supportive community of organisms is not, however, complete, as we now discuss.

Let us imagine introducing into this community a single selfish or aggressive individual (gene, cell, organism or human). The selfish individual benefits from the help that others give, while not providing help to them. Instead it utilizes the additional effort for self-benefit. It is important to recognize that in the language of interactions this is an asymmetric interaction. The existence of the selfish individual does not improve the success of the other individuals, while their existence improves the success of the selfish individual. Similarly, an aggressive biological organism is assumed to decrease the fitness of the other organisms, while they do not decrease its fitness. We might also add that an altruistic individual is assumed to increase the fitness of other organisms while decreasing its own.

This interaction asymmetry means that analysis of this problem does not fit within the framework of energies and equilibria. Instead it must be analyzed as a dynamical system such as a predator-prey problem. This conclusion has important consequences for the idea that selfish or aggressive behavior cause benefits for the

individual. It is not generally reasonable to analyze a dynamical system with the concepts of a model of energies and equilibrium. In the latter we assign definite steady state properties to the entities involved. In the former this is not generally possible. For example, in what way can we compare the fitness of a predator and its prey? However, just because we cannot analyze the model in the same way does not mean that we can avoid dealing with this problem.

With this in mind, let us continue our introduction of selfish individuals. Assuming there is benefit to the individual in being selfish, then such individuals will proliferate. The fitness and success of mutually supportive individuals will decrease. Moreover, as the proportion of the selfish individuals in the population increases they encounter each other, and their fitness and success will also decrease even as their advantage over the mutually supportive individuals continues to exist. We should not analyze this as a static situation but rather introduce a dynamic model that describes possible fluctuations in the numbers of the different types of individuals. However, we can take a step further without considering the dynamic aspect of the model.

We know from direct consideration of the interactions that a completely mutually-supportive collection of individuals consists of individuals that are more fit than the mixed community that has been created by introduction of selfish individuals. Nevertheless, we also know that the former is unstable to the introduction of such selfish individuals. Thus, if we can modify the community of mutually supportive individuals in such a way that can stabilize it to the introduction of selfish individuals, then the mutually supportive group will be more successful win—in a competition with the mixed group.

What is completely essential to realize in this discussion is that we have made the step to the competition between communities of organisms rather than competition between individuals. It is only at the level of community competition that the success of mutual support is sufficient to eliminate the selfish individuals. Thus, it is only when we have several communities of organisms, some of which have selfish individuals in them and some of which do not, that we will have selection in favor of the community of mutually-supportive individuals over the communities with selfish individuals.

How can we stabilize the community of mutually supportive individuals to the introduction of selfish or aggressive individuals? Social behaviors that prevent the introduction of selfish individuals are not necessarily individually based, because they only arise in the context of the selection of collections of individuals. However, they may be individually-based behaviors such as recognition and rejection (ostracism) of selfish individuals. As has often been noted, this rejection causes extrinsic consequences to the selfish behavior. Rejection is not inherent in the selfish behavior. Its presence results from feedback through the process of community selection that promotes such extrinsic consequences. In the context of the individual, these consequences may not appear causally related to the behavior itself but are manifest as indirect social consequences. One way to think about this is that the action of selection at the higher level of organization modifies the influence of selection at the lower level of organization. This is because inherently the environment of the individual includes

the social environment, and selection cannot be considered independently of this social environment.

We can see such social mechanisms at all levels of collective organization. Cellular systems provide for regulation of gene expression or replication. Physiological systems provide for prevention of cancerous growths. More generally we can consider the immune system as combating selfish or aggressive individual cells that appear as infections. Social systems ranging from spousal selection in sexual reproduction to ostracism to human legal systems provide for regulation or reward of individual behaviors.

Once a collective community identity is formed and it is competing for resources and survival at the next level of organization, then various other properties of the collective entity may be introduced through incremental evolutionary change. These include specialization and more elaborate forms of interdependence that are found in complex systems. These arise as improvements in the capabilities of the community.

In this discussion we have given support to the emergence of mutually supportive behaviors and the elimination of selfish or aggressive behaviors. However, we must emphasize that in our argument these behaviors arise only when there is competition and selection at the higher level of organization. Specifically, only when there is competition between communities of organisms. There is no direct mechanism to suppress selfish or aggressive behaviors at the highest level of organization present at a particular time. Ultimately, this is also tied to the statement that evolution applies to members of a population—a single organism cannot evolve by itself.

Questions 6.6.4 and 6.6.5 focus on these concepts in the context of human societies. This follows from the recognition that social evolution has similar properties to biological evolution through the existence of heritable behavioral traits that are transmitted by education. This should not be too much of a surprise, since biological selection is also based on information. It is not the atoms that are selected, but rather the sequence of base pairs—information—that is selected.

Question 6.6.3 What is wrong with this seemingly logical statement: “Survival of the fittest is based upon a competition for survival. Therefore an organism that competes by eliminating its competitors is more likely to survive”?

Solution 6.6.3 The solution was articulated in this section as a difficulty with analyzing a dynamical system with equilibrium concepts. The analysis shows that a system of mutual support is unstable to the introduction of an organism or individual that acts aggressively. The problem is that this situation is not stable either. From an equilibrium model we can only say that mutually supporting individuals are better off than mutually destructive individuals. Once there are asymmetric relationships, the system has a dynamic population that may, for example, display population fluctuations like the predator-prey model unless the system is stabilized by additional interactions that create social consequences for the behavior of “eliminating its competitors.” ■

Question 6.6.4 Consider bravery and altruism in the context of human societies. Discuss these behaviors in the context of the discussion of the appearance of collective social behaviors. How do they persist from generation to generation? For simplicity, define “altruism” as a behavior that increases the reproductive success of others at the expense of reproductive success of the altruistic individual.

Solution 6.6.4 Bravery is actually an example of altruistic behavior, since it implies facing danger to oneself for a cause that is generally of collective benefit. The soldier facing danger in war is a prime example. Such behavior causes a lower probability of individual survival. It should thus be selected against and disappear from civilization. As discussed in Chapter 3, human behavior has both a genetic and a learned component. In order to promote the existence of bravery, there appear to be social behaviors that promote its presence. If we assume a persistence of bravery, the social behaviors that promote bravery must be sufficiently strong to compensate for both the genetic losses (death before reproduction) and the loss due to experience (cessation of bravery due to learning). In general, spousal selection may promote altruistic behaviors by increasing the probability of reproduction or average number of offspring of subgroups that are less likely to survive. Socialization in pedagogy may serve to compensate for the effects of experience, and social rewards for altruistic behavior may mitigate their effects. As discussed previously, these must manifest their benefit in the action of competition and selection of groups. ■

Question 6.6.5 Consider war in the context of human societies. Is war necessary for the creation of altruistic behavior?

Solution 6.6.5 It is not clear that competition between groups requires war. However, war is a mechanism of group competition that, by the arguments presented here, should promote interdependence within societies. Thus it can also promote altruistic behavior. Some other mechanisms such as mass starvations due to competition for resources are not more appealing. Our arguments suggest that whatever the mechanism, the emergence of complex social behaviors must arise as a result of competition of populations that can only be manifest in the (selective) demolishing of whole populations. In this regard we note that wars are manifest in ants, which have complex social structures, sometimes called superorganisms. When social behaviors are learned rather than genetically based, then other possibilities for competition arise. This is because one form of reproduction is the transfer of learned social behaviors. Defeat in economic competition can cause one group to adopt social behaviors of a second group, which is equivalent to its reproduction. ■

Question 6.6.6 Evolution is often separated into two parts; the formation of self-reproducing organisms from molecules and the evolution of

these organisms into their present form. Argue that a distinction is not necessary. Why would it seem a natural distinction if it is not really one?

Solution 6.6.6 Under certain environments, molecules can also be self-reproducing organisms. However, these conditions are much more limited than the conditions under which individual cells can self-reproduce. This is because the cell membrane creates a distinction between inside and outside environments that allows an artificial environment for reproduction of molecules to exist. If the internal environment of the cell was typical of the fluid in which the cells were found, then the cell membrane would not be necessary. We can imagine that at some time and place there was such an environment that was conducive to molecular reproduction. Molecules evolved within this environment, forming various molecular types. At some point the molecules formed collective entities that were able to move out of this limited environment in the same way that organisms left the ocean for the land. Several stages of such processes gave rise to cells. The formation of cells expanded greatly the possible environments/resources that could be consumed by self-reproducing organisms. ■

We have focused on the formation of collectives in order to describe interdependence. In a sense, the interdependence was already explained previously in this chapter in two steps. First we noted the necessity of increasing complexity through increasing the genomic space. This provided a selective advantage for long genomes but did not explain the existence of subcomponents. The second step was arguing that there are partially independent traits of organisms and therefore that a composite genome would be effective in accelerating evolution. This completes our argument, because we now have both an argument for the creation of collective communities and an argument for the retention of substructure.

The development of higher levels of organization might be thought to create additional problems for our discussion of the global evolutionary process in the context of a single fitness parameter. Do we need to introduce a separate parameter to consider the fitness of the collective? Actually this is not the case. Any parameter that describes replicative proliferation of a collective organism which has a well-defined number of components is the same parameter as that of any one of its components. In a sense this manifests exactly what we mean by a complex system that is collectively and individually interdependent.

6.7 Conclusions

Our primary effort in this chapter has been to develop an understanding of the context in which incremental evolutionary processes relate to global phenomena of evolution. A problem we encountered is that it is hard if not impossible to define fitness so that it can compare *E. coli* and human beings. We began with a model of Monte Carlo walkers on a fitness landscape. While there were problems with this model, we were able to discuss incremental changes including trait divergence and augment the

model to include population interactions. Difficulties with global phenomena were compounded, however, when we introduced models of reproduction and selection through competition. Specifically, we were left with the problem of understanding trait divergence when competition would eliminate distinct organisms. We came to the conclusion that in order to think about fitness we must limit the scope of selection by considering multiple resources. When selection occurs with multiple resources, it acts more broadly than in the Monte Carlo model and in a more limited fashion than in a single-resource model. The introduction of multiple resources suggests that in order to understand global evolution we must have a clear understanding of the properties of resources as well as organisms, and a consideration of the latter separately is not adequate. At every stage of our discussion we found that interactions between organisms were an essential part of understanding evolution. Mean field approaches that may be used in incremental evolutionary theory break down and are deceptive if we want to understand global evolution. In particular, in the context of discussing sexual reproduction and collective behavior we developed an understanding of the creation of various levels of structure and interdependence in organisms.

How can we develop a better understanding of the processes associated with the evolution, and thus creation, of complex systems? In recent years several additional examples of evolution have been studied. In our immune system, an evolutionary process enhances the recognition and removal of antigens—foreign and/or harmful cellular or molecular entities. The immune system creates molecular receptors and antibodies that bind antigens and enable them to be eliminated. To achieve this, receptors undergo reproduction and selection for high-affinity binding. This process includes rapid genetic mutation of immune cell DNA that codes for the receptors. Our understanding of this process and the development of mechanisms for rapid replication of DNA in a test tube have led to recent implementation of artificial molecular evolution. In this process DNA or RNA is itself used as a reacting molecule or enzyme. The desired molecular action is obtained by repeated test tube selection and replication. There is hope that molecular evolution will enable the formation of targeted medical drugs. Finally, there are increasing efforts to implement evolutionary processes for the creation of software algorithms. This requires representation of algorithms in a manner that allows them to undergo mutation and selection. The immune system maturation, test tube molecular evolution and software evolution all provide opportunities for further study and for application of knowledge gained about evolution.