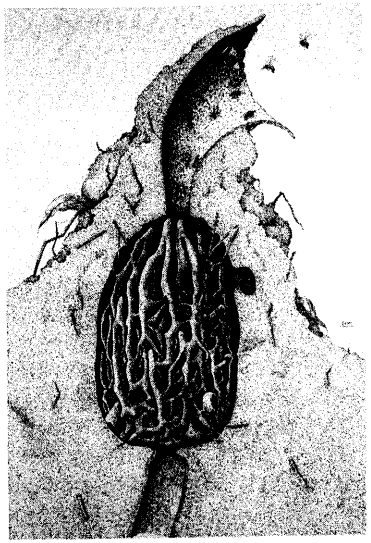

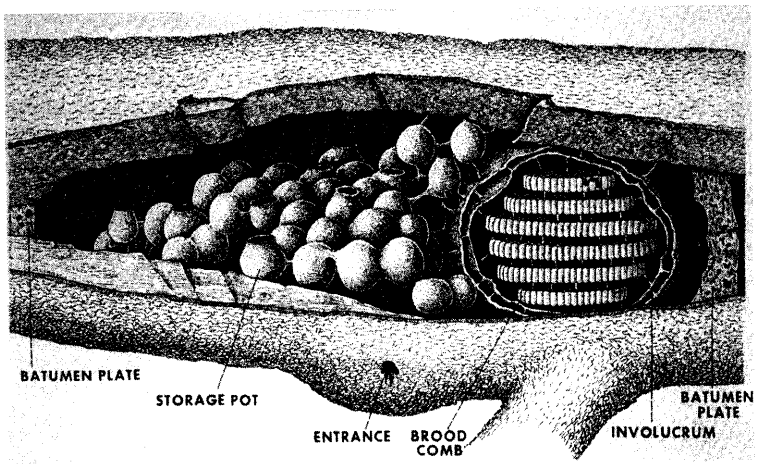

Figure 3.1 Typical examples of the diversity and regularity of structures in social-insect nests are the internal nest structure of the stingless bees. *Trigona testacea*, with its funnel-shaped entrance (top), and *Melipona interrupta grandis* in a hollow branch. The anastomosing rods (top) presumably provide resting space for the colony's defense force. Self-organization probably plays a role, at least partially, in the building of the nests. (Original drawings, courtesy J. M. F. de Camargo, from Michener 1974)

3

Characteristics of Self-Organizing Systems

> Simple and complex systems exhibit... the spontaneous emergence of order, the occurrence of self-organization.
> —S. A. Kauffman, *The Origins of Order: Self-Organization and Selection in Evolution*

We have defined self-organization and briefly discussed how it works. Now, we will describe some of the characteristics of self-organizing systems. What general features do these systems possess?

Self-Organizing Systems Are Dynamic

The multiplicity of interactions that characterizes self-organizing systems emphasizes that such systems are dynamic and require continual interactions among lower-level components to produce and maintain structure. This point is made more clearly by contrasting a dynamic process of pattern formation with an alternative, essentially static process illustrated by the assembly of a jigsaw puzzle. A jigsaw puzzle is a global structure with an intricate pattern constructed from lower-level subunits, the pieces of the puzzle. The pieces are put together in a precise manner to create a pattern. Each piece of the puzzle has a particular shape and set of markings that complements the shape and markings of the pieces to which it fits. To create the global pattern, one carefully matches the pieces together, and once the pieces of the puzzle are fit together the action stops. The pattern and structure are locked into place.

Edelman (1984, p. 120) provides a lovely metaphor for such a static mechanism of pattern formation in his discussion of the role of cell-adhesion molecules in regulating cell movements and morphogenetic processes during embryological development:

> There are two alternative ways patterns might be formed at the cellular level without the direct intervention of some kind of "little architect" or "construction demon." The first way would require prelabeling all cells with molecular markers (presumably proteins), each one spatially complementary to some other marker on a cell to be placed next to it in the pattern. This is essentially how parts of the great offshore abbey of Mont-Saint-Michel were built. Stones were cut and shaped on the mainland,

marked by their makers and reassembled on the island according to a plan. The Mont-Saint-Michel model is a metaphor for various "chemoaffinity" theories of cell adhesion. The major difficulty with such theories is that if the pattern to be formed is complex, has much variation in shape or has many elements and much local detail (as, for example, in the brain), then the number of specific surface markers determining each cell's location must be enormous. Inasmuch as such markers are most likely to be specific proteins, each encoded by a different gene, the number of genes would be correspondingly large.... Moreover, a pattern made this way is prefigured and essentially static: once the right markers come together, no further dynamism is necessary.

Several alternative, more dynamic ways of generating patterns have been described. Turing (1952), in what has been called "one of the most important papers in theoretical biology" (Murray 1988, p. 80), postulated a mechanism of generating animal coat patterns based on reacting and diffusing chemicals that he called morphogens (see Figure 1.2). The "Brussels school" extended these ideas of self-organized pattern formation to a variety of chemical and biochemical systems (Nicolis and Prigogine 1977, 1989). In these open systems, in which there is a continual influx of energy or matter, reactions occur far from chemical equilibrium, and structures emerge through interactions obeying nonlinear kinetics. Such structures are called *dissipative*. At about the same time, Haken (1978) introduced the concept of synergetics as a unifying approach to pattern formation in various disciplines. (See also reviews by Levin and Segel 1985 and Schöner and Kelso 1988.) Without going into a technical discussion of the similarities and differences among these different explanations of self-organized pattern formation, we again refer to Edelman (1984, p. 120) who provides a useful visual metaphor of this process:

There is an alternative and more dynamic way of generating patterns, akin to what might be observed in a mountain stream. In this kinetic, far-from-equilibrium situation, pattern results from the play of energy as it is dissipated into the environment against various constraints. To make the simplest case for this mountain-stream example, imagine a stream of water running down a mountainside and striking a submerged boulder whose temperature is below freezing. At first the flow of water will be influenced only slightly by the boulder and the stream will remain a single stream. In time, however, as water freezes onto the boulder, the enlarging structure may suddenly become a barrier causing the stream to split into two and assume a new shape as it runs down the mountain. All subsequent shapings of the stream will be influenced by the effect of the original freezing. Rivulets downstream may break into a variety of new and intricate patterns as they meet different constraints at lower levels. Seen from above, the entire stream will nonetheless have a definite shape.

As described in the next section, this dynamic process of pattern formation gives rise to emergent properties, an example of which is the sudden bifurcation of the stream as it courses down the mountain.

Self-Organizing Systems Exhibit Emergent Properties

In the first chapter self-organizing systems were shown to possess emergent properties. Emergence refers to a process by which a system of interacting subunits acquires qualitatively new properties that cannot be understood as the simple addition of their individual contributions. Since these system-level properties arise unexpectedly from nonlinear interactions among a system's components, the term *emergent property* may suggest to some a mysterious property that materializes magically. To dispel this notion, two examples are given that illustrate an emergent property of the system. The first is the biological phenomenon of clustering by larvae of the bark beetle, *Dendroctonus micans*. (We will consider this example in greater detail in Chapter 9.) The second is a physical phenomenon—Bénard convection—which was mentioned earlier (Figure 1.3a) but will be discussed again in more detail.

The eggs of *Dendroctonus* beetles are laid in batches beneath the bark of spruce trees. Larvae hatch from the eggs and feed as a group, side by side, on the phloem tissues just inside the tree bark (Deneubourg et al. 1990a). Previous studies have shown that the larvae emit an attractive pheromone (Grégoire et al. 1982). In a series of experiments (described in Chapter 9), the larvae were randomly placed on a circular sheet of filter paper 24 cm in diameter between two glass plates separated by 3 mm to allow the larvae free movement. The subsequent positions of the larvae were observed over time. The degree of clustering exhibited by the larvae was found to depend strongly on the initial larval density. At low density (0.04 larvae/cm^2), a loose cluster appeared, but it did so only slowly, in approximately 1 hour, and comprised only 25 percent of the population (Figure 9.4). In contrast, at high density (0.17 larva/cm^2) a single, tight cluster rapidly assembled (Figure 9.3). Within 5 min about 50% of the larvae were clustered in the arena's center and after 20 min some 90 percent of the larvae joined this cluster. The experiments demonstrated a simple emergent property—a cluster—in a group where the individuals initially were homogeneously distributed. At a certain density of larvae, the system spontaneously organizes itself.[1]

An even more dramatic example of spontaneous emergence of pattern is the well-known phenomenon of Bénard convection cells described in Box 3.1. Here an initially homogeneous layer of fluid becomes organized into a regular array of hexagonal cells of moving fluid (Figure 1.3a). The striking pattern of convection does not appear gradually but arises suddenly. At a certain moment determined by the amount of heat applied to the bottom of the fluid layer, the initially homogeneous regime becomes unstable and changes to a new pattern.

In the terminology of dynamic systems, this emergent pattern or property is called an *attractor* of the system. Under a particular set of initial conditions and parameter values, an attractor is the state toward which the system converges over time. In the Bénard convection system, one attractor (seen under conditions of a small temperature gradient) is the random motion of the fluid molecules. A different attractor appears when the temperature gradient is increased to a critical value.

The mere detection of a pattern in nature, however, is inadequate to distinguish self-organizing mechanisms from other mechanisms of pattern formation. Observing a pattern at a moment or even over a period of time does not enable one to identify the mechanism of that pattern's formation. One must understand the pattern-formation machinery inside the system and be able to observe its operation to know whether the pattern is self-organized. Most importantly, one needs to devise means of experimentally perturbing the pattern-formation system and to obtain evidence that supports models based on self-organization as opposed to other models based on greater degrees of centralized or external control.

Compare an aggregation of *Dendroctonus* larvae to a group of people huddled under a bus stop to get out of the rain. In both cases one observes a cluster of individuals, but in the first the cluster arises through a self-organized process involving interactions among the individuals, whereas individuals in the second case are independently attracted to a preexisting focus of aggregation.

A striking feature of self-organized systems is the occurrence of a bifurcation—a sudden transition from one pattern to another following even a small change in a parameter of the system. One speaks of "tuning" a parameter in the system to invoke the onset of a different pattern. In the *Dendroctonus* example, one tunable parameter is the initial density of the setup. In the Bénard convection system, a tunable parameter is the amount of heat applied to the lower surface of the dish. By making small adjustments in such parameters, one can induce large changes in the state of the system, since the system may now be on a trajectory that flows to a quite different attractor. Most self-organized systems have many tunable parameters. Let us explore this phenomenon of parameter tuning more closely.

Parameter Tuning

A mathematical model popularized by Robert May (1974; 1976) has become one of the premier examples in the field of chaos theory, and it is a classic example of population growth for a hypothetical organism with nonoverlapping generations. (Also refer to the less technical presentations by Crutchfield et al. 1986; Gleick 1987; Dewdney 1991.) This system is a useful one for gaining an intuitive understanding of how a system can undergo dramatic transitions

between two ordered states, or from an ordered state to a chaotic state or vice versa.[2]

As shown in Box 3.2, we can model the growth of a certain population with the logistic difference equation: $N_{t+1} = rN_t(1 - N_t)$. This equation has the single variable, N_t, which is the population size in the current generation, and varies between 0 and 1, where 0 is extinction and 1 is the population at the carrying capacity of the environment. The single parameter, r represents the intrinsic reproductive rate of the species. The population size in the next generation is given by N_{t+1}. To determine the population size over time, the equation is solved iteratively, starting with an arbitrary population value for N_t in the range of 0 to 1. The result of each iteration is the new population value N_{t+1}, which is then substituted in the equation as the population size in the current generation. The process can be repeated *ad infinitum*. One finds that if r is within a certain range ($0 < r < 1$), then repeated iterations result in extinction of the population regardless of the initial population size, N_t. This is to be expected for the obvious reason that each individual does not replace itself in the next generation. Similarly, if $1 \leq r < 3$, then the population again shows simple behavior, approaching a constant size after several generations, as one might intuitively expect for a population living under constant environmental conditions. Regardless of its initial size the population approaches the same final size, an *attractor*. But if we increase r slightly beyond 3, the population suddenly develops a new pattern; it enters a regime where it oscillates between two values. If we continue to increase r to more than 3.4, the system undergoes another abrupt transition where the oscillations between two population sizes change to oscillations between four population sizes. The system is now behaving in an unanticipated way. If r is raised yet again, beyond 3.57, the population exhibits deterministic chaos, changing erratically between generations with no regular pattern.

The appearance of a qualitative change in behavior when a parameter-value changes quantitatively is called a bifurcation. At the bifurcation between a single, stable population and oscillations between two different population values, r provides sufficient positive feedback in the system for the population size to undergo a cyclic rise and fall. The population size overshoots and then crashes.

Self-organizing systems, with nonlinear positive feedback interactions characteristically show bifurcations. In the *Dendroctonus* system, experiments reveal a bifurcation at a particular density of larvae; in the Bénard convection system, a bifurcation occurs as the amount of heat applied to the bottom of the fluid layer reaches a certain level. In many real-world systems, especially those in biology, it is difficult to control parameter values precisely enough to reveal such abrupt bifurcations, but in our hypothetical population we have complete control of the system. So in this situation it is easy to demonstrate the sudden emergence of novel behavior as one gradually tunes a system parameter.

Multistable Systems

Another type of behavior often exhibited by self-organizing systems is multi-stability, in which multiple possible stable states, or attractors may occur. This raises the question of what determines which of the various alternatives the system will exhibit. In the case of our hypothetical population, the behavior of the system is sensitive both to the parameter-value r and to the initial value of the population N_t. Figure 3.2 portrays the behavior of the system over the entire range of r, for all initial conditions. When different patterns arise in systems with multiple regimes there is usually no way of knowing a priori which particular regimes ultimately will be chosen. The final states attained by such systems usually depend on the initial conditions and a range of initial conditions that act as a *basin of attraction* for a particular attractor.

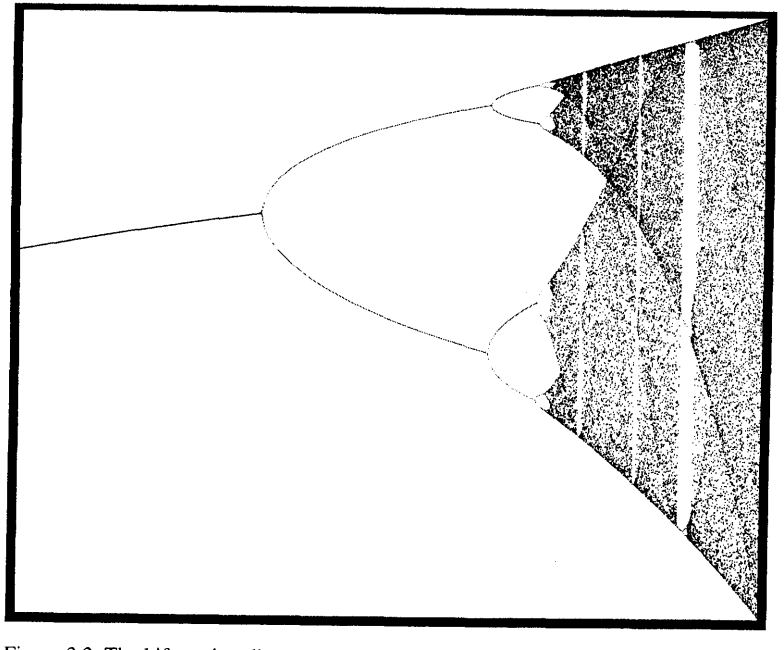

Figure 3.2 The bifurcation diagram above is for the logistic difference equation. Values along the x-axis are the tuning parameter, r, from 0 to 4. The corresponding population values (ranging from 0 to 1) are shown along the y axis. The diagram was generated with the program, Bifurcation Diagram, which can be downloaded at http://beelab.cas.psu.edu.

Biological and Physical Parameters

For the biological systems discussed in this book—what is meant by a "parameter"? In systems that can be described by a simple mathematical equation, we have no difficulty identifying the parameters, such as r in the above population equation. But of course, the situation is more complicated in actual living systems. As biologists interested in the behavior of living organisms, we may distinguish between two basic types of parameters in self-organized systems: those intrinsic to the organisms (the biological parameters) and those that arise from the environment or by physical constraints (the physical parameters). However, this distinction is irrelevant to the pattern formation process. For example, a parameter can affect the rules of thumb that describe the probability of performing a certain behavior under specified circumstances. The execution of a rule of thumb depends on information (about itself and the environment) that an organism acquires moment by moment, and on genetically encoded information that an organism possesses intrinsically. In formulating models of pattern formation in the examples in this book, we generally start out with a presentation of the behavioral rules of thumb used by the individuals in the system. For example, a rule of thumb for an army ant, "The more pheromone detected, the quicker the running speed," might translate to a differential equation such as $dx/dt = \nu C$, where dx/dt is the distance moved by the ant per unit time (its speed) as a function of the pheromone concentration, C. The parameter, ν, relates the walking speed to the pheromone concentration.

Physical parameters also play important roles in biological systems. Consider the example of trail-following by ants. We need to know how the concentration of the trail pheromone varies over time, not only as a function of the behavior of the ant depositing the pheromone, but also as a function of the evaporation rate of the pheromone. The evaporation rate is determined by the pheromone's chemical structure and the physical conditions, such as temperature and air flow. Natural selection can influence the evaporation rate by determining the chemical structure of the pheromone, but the volatility of a particular pheromone compound is governed by the laws of physics.

Consequences of Emergent Properties in Self-Organization

The striking phenomenon of tunable emergent properties can have important evolutionary consequences for self-organized systems. We have shown how a small change in a system parameter can result in a large change in the overall behavior of the system. Is it possible that such properties could provide self-organized systems with adaptive, flexible responses to changing conditions in the environment and to changing needs of the system? If so, how might this flexibility arise?

Let us assume that natural selection can tune a particular behavioral parameter to a range of values close to a bifurcation point. Then, small adjustments in

the parameter for each individual within a group may induce large changes in the collective properties of the group, thereby endowing the group with a wide range of responses and the ability to switch from one behavioral response to another.

Flexibility of this type may operate on a day to day basis, or over a longer time span, such as throughout the seasons. To take a hypothetical example: in the spring honey bee colonies undergo a transition from one mode of behavior to another as colonies switch from a nonswarming to a swarming state. The colony initially produces only worker bees, but eventually it begins to produce a batch of queens. The colony then divides, with approximately half the workers leaving (swarming) with the original queen to establish a new colony and the other half remaining at home with one of the new queens to continue the original colony. In some cases, however, the colony produces multiple swarms. What is responsible for these different swarming responses?

Rather than assuming that different behavioral rules determine the type of swarming outcome, let us suppose that the bees respond with the *same* set of behavioral rules to slightly *different* circumstances such as the initial colony size. In such a system, there may be an economy of behavioral complexity at the individual level required to switch from one kind of behavior to another. Thus, tunable parameters and bifurcations might provide an efficient mechanism for producing flexibility in biological systems.

Role of Environmental Factors

Environmental parameters may play a crucial role in shaping self-organized systems. The environment specifies some of the initial conditions, and positive feedback results in great sensitivity to these conditions. In particular, positive feedback can amplify initial random fluctuations or heterogeneities in the environment, and as a result the system may exhibit a number of different outcomes. A clear example is the raiding patterns of army ant colonies, analyzed in detail in Chapter 14. Deneubourg et al. (1989) examined models in which the *same* set of behavioral and physiological rules apply to *different* army ant species, but under different environmental conditions. Their striking finding was that distinct morphological patterns of army ant raids emerged merely by varying the initial distribution of food in the environment. It was not at all obvious, a priori, that the system would display multiple stable regimes as a function of variation in environmental parameters.

Biologists are accustomed to considering differences between species' behavior patterns as the phenotypic expressions of underlying genotypic differences that evolved over an evolutionary time-scale in response to environmental conditions. We suggest that certain species-specific patterns may be self-organized expressions of differences in environmental variables. Not surprisingly, differences in the raiding patterns of *Eciton burchelli* versus *E. rapax* may also reflect genetically based differences in pheromones or behaviors. Undeniably, such differences in biological parameters probably do exist, but a remarkable fact is that models of the raiding patterns demonstrate that differences between species in raiding patterns could arise simply from differences in the spatial distribution of each species' prey.

Self-Organization Can Promote Stable Patterns

We have emphasized transitions from one pattern to another as one or more of a system's parameters changes value. This may have given the impression that self-organizing systems are rather fragile, erratic, and susceptible to perturbations. However, most of the self-organizing systems described in this book are extremely robust, by which we mean they are stable over a wide range of parameter values. Although we have pointed out that natural selection may tune a particular parameter to the vicinity of a bifurcation point, it appears that most systems operate in a parameter range far from bifurcation points and, therefore, stubbornly resist transition from one pattern to another. The reason for this seems clear. Most of the patterns discussed in this book are adaptive and in most cases would be highly maladaptive if the behavior of the builders did not consistently produce the typical species-specific superstructure or pattern.

Consider again the example of the bark beetles (*Dendroctonus*). Although experimental situations can be contrived in which the larvae do not aggregate, under normal conditions the larvae almost always operate in a parameter range where strong aggregation occurs. This makes sense, for if this clustered feeding is an important adaptation for countering the tree's defensive production of sticky resin, then that clustering is expected to be consistently observed under natural conditions. Natural selection is expected to tune the larvae's behavioral and physiological parameters so that clustering occurs under the full range of conditions that the larvae would be expected to encounter.

Given that natural selection frequently favors a particular pattern for a system, many self-organizing systems are expected to resist perturbations and operate with great stability within a single regime. In such circumstances, the pattern exhibits the property of self-repair. In other words, the pattern is an attractor of the system. This phenomenon is discussed further in Chapter 16 with analysis of pattern formation on the comb of honey bee colonies.

Self-Organization and the Evolution of Pattern and Structure

Intuitively, it would seem easier for natural selection to make adjustments in the processes underlying an existing structure than to evolve a fundamentally new structure. It seems likely, therefore, that natural selection generates new adaptive structures and patterns by tuning system parameters in self-organized systems rather than by developing new mechanisms for each new structure.

Consider the wide range of different coat patterns of mammals or shell patterns of mollusks. Self-organized pattern formation mechanisms have been hypothesized for these systems (Ermentrout et al. 1986; Fowler et al. 1992; Lindsay 1977; Murray 1981; Murray 1988). An intriguing feature of this hypothesis is that fundamentally similar mechanisms may account for a wide variety of different patterns. In the past most biologists probably would have thought that the strikingly different color patterns on different shells or mammals arise through qualitatively different mechanisms. However, the concept of self-organization alerts us to the possibility that strikingly *different patterns* may result from the *same mechanism* operating in a different parameter range. This underscores the possibility that in evolution important changes in the properties of organisms and groups of organisms might result from slight changes in the tuning of parameters of the underlying developmental systems.

Simple Rules, Complex Patterns—The Solution to a Paradox

Biologists have been puzzled by the fact that the amount of information stored in the genes is much smaller than the amount of information needed to describe the structure of the adult individual. The puzzle now may be solved by noticing that the genes are not required to specify all the information regarding adult structure, but need only carry a set of rules to generate that information (Maruyama 1963, p. 171).

Most self-organizing systems, like biological systems in general, are highly complex and probably use multiple rules. Termites, for example, probably use more than a single simple set of rules for constructing their intricate mounds (Figures 18.1 and 18.2). Nonetheless, it should be stressed that simple nonlinear interactions between large numbers of individuals can lead to surprisingly complex patterns at the group level, patterns that often are unexpected even if detailed knowledge exists of the group's members and their interactions. An important goal of this book is to explore the question of how much—more to the point, how little—complexity must be built into the components of a self-organized system to generate the observed complexity at the group level. This question has important evolutionary implications.

As Maruyama (1963) points out, we know that it is impossible for each detail of an organism to be *explicitly coded* in the genome. For example, the human body can produce antibodies against a nearly unlimited number of foreign substances, yet the body has only about 100,000 different genes. An individual can synthesize more than 100 million distinct antibody proteins at any one time, so each protein obviously cannot be specified by a separate gene. Instead, natural selection led to a clever device for economizing on the information that needs to be genetically coded for the immune system. The device is a combinatorial scheme for generating diversity (Janeway 1993). Antibody genes are not distinct units; they are inherited as fragments joined together to form a complete gene within individual B lymphocytes, of which the body has about 10 trillion. One cannot improve on François Jacob's (1982, p. 38) elegant description of the process:

> [A] mammal can produce several millions or tens of millions of different antibodies, a number far greater than the number of structural genes in the mammalian genome. Actually a small number of genetic segments is used, but the diversity is generated during the development of the embryo by the cumulative effect of different mechanisms operating at three levels. First, at the *cell* level, every antibody-forming cell produces only one type of antibody, the total repertoire of antibodies in the organism being formed by the whole population of such cells. Second at the *protein* level, every antibody is formed by the association of two types of protein chains, heavy and light; each of these chains can be sampled from a pool of several thousand and their combinatorial association generates a diversity of several million types. Third, at the *gene* level, every gene coding for an antibody chain, heavy or light, is prepared during embryonic development by joining several DNA segments, each one sampled from a pool of similar but not identical sequences. This combinatorial systems allows a limited amount of genetic information in the germ line to produce an enormous number of protein structures with different binding capacities in the soma. This process clearly illustrates the way nature operates to create diversity: by endlessly combining bits and pieces.

This example shows that various mechanisms exist for economizing on the information that needs to be coded in a system. Self-organization is one type of mechanism for creating structure with a minimal amount of genetic coding. The antibody combinatorial mechanism is another. Let us now return to the original question: How much behavioral information needs to be coded explicitly in the genome of a self-organized system? Although we cannot provide a precise answer, we suggest that it is far less information than might have been assumed in the past.

Box 3.1 Bénard Convection

The Bénard convection system has become a classic example of a self-organizing system. It is simple to demonstrate and displays a complex emergent pattern (Figure 1.3a). Convection is a process of fluid flow that occurs when a liquid or gas is heated (DeAngelis et al. 1986; Velarde

and Normand 1980). When a fluid is heated from below, the bottom layer expands and becomes less dense. This lighter, warmer layer tends to rise and the heavier, cooler layer above tends to sink. The result is convective fluid transport.

At the turn of the last century the French investigator Henri Bénard studied a convective system that revealed unusual patterns. The system comprised a thin layer of spermaceti oil heated uniformly from below while its upper surface was kept relatively cool by contact with the atmosphere. As long as the vertical temperature gradient in the fluid was sufficiently small, no special pattern appeared; but when a gradual increase occurred in a system parameter—the amount of heat applied to the lower surface—the previously uniform surface of the fluid suddenly became a tesselated mosaic of polygons. The critical value of the tuning parameter depended on the fluid's viscosity, surface tension, depth, and other factors. Indeed, any of these factors can be taken as the tuning parameter, although it is most convenient to adjust the amount of heat. The following description of the Bénard convection system provides a good explanation of the phenomenon (Velarde and Normand 1980, p. 94–95):

> Consider a small parcel of fluid near the bottom of the layer. Because of the elevated temperature at the bottom, the parcel has a density that is less than the average density of the entire layer. As long as the parcel remains in place, however, it is surrounded by fluid of the same density, and so has neutral buoyancy. All the forces acting on it are in balance, and it neither rises nor sinks.
>
> Suppose now that through some random perturbation the parcel of fluid is given a slight upward motion. What effect does the displacement have on the balances of forces? The parcel now is surrounded by cooler and denser fluid. As a result it has positive buoyancy, so it tends to rise. The net upward force is proportional to the density difference and to the volume of the parcel. Thus an initial upward displacement of the warm fluid is amplified by the density gradient, and the amplification gives rise to forces that cause further upward movement. A similar analysis could be made for a slight downward displacement of a parcel of cool, dense fluid near the top of the layer. On moving downward the parcel would enter an environment of lower average density, and so the parcel would become heavier than its surroundings. It would therefore tend to sink, amplifying the initial perturbation. Natural convection is the result of these combined upward and downward flows, and it tends to overturn the entire layer of fluid.

The next description of the onset of instability is expressed in the terminology of self-organization and dynamic systems (Prigogine and Stengers 1984, p. 142):

> The "Bénard instability" is another striking example of the instability of a stationary state giving rise to a phenomenon of spontaneous self-organization. The instability is due to a vertical temperature gradient set up in a horizontal liquid layer. The lower surface of the latter is heated to a given temperature, which is higher than that of the upper surface. As a result of these boundary conditions, a permanent heat flux is set up, moving from the bottom to the top. When the imposed gradient reaches a threshold value, the fluid's state of rest—the stationary state in which heat is conveyed by conduction alone, without convection—becomes unstable.... The Bénard instability is a spectacular phenomenon. The convection motion produced actually consists of the complex spatial organization of the system. Millions of molecules move coherently, forming hexagonal convection cells of a characteristic size.

The development of hexagonal cells in the Bénard convection system may be comparable to the development of clustering in the *Dendroctonus* beetle system. In Bénard convection, random motion of the molecules (in which heat transfer is by conduction) competes with coherent motion of the molecules (when convection occurs). With the beetle larvae, random motion of the larvae occurs in the absence of any chemical cues, but motion becomes oriented when a pheromonal gradient is established by the larvae themselves. In both cases, the system exhibits a spontaneous transition to a more ordered state as a particular parameter is gradually increased beyond its bifurcation point.

It is easy to demonstrate Bénard convection in the classroom. Bénard used spermaceti (sperm whale) oil, and Velarde and Normand (1980) used silicone oil to which flakes of aluminum were added to make the flow visible. We can use ordinary vegetable oil to which we add very fine aluminum powder (called bronzing powder, available at art supply stores). A pinch of powder in a cup of oil is sufficient. We place a layer of this oil about 1 cm thick in a 10-cm-diameter glass petri dish. Rather than use an apparatus with which we could gradually and uniformly increase the temperature at the bottom of the dish, we simply place the dish briefly on a laboratory hot plate, then carefully remove the dish and place it on a table top. If the bottom of the dish is heated sufficiently, the charac-

teristic pattern will suddenly appear, and remain for several minutes. It is a temporarily stable, swirling pattern of polygonal Bénard convection cells.

Box 3.2 Tuning the Growth Rate Parameter in the Logistic Difference Equation

In many species of insect, such as certain butterflies, generations are nonoverlapping. Such species have eggs that hatch in the spring after overwintering. The adults live through the summer and then die after laying eggs in the fall. To describe the growth of such a population, one can use the so-called logistic difference equation:

$$N_{t+1} = rN_t(1 - N_t)$$

We can think of this equation as describing the population size in the next generation (N_{t+1}) as a function of the current population size (N_t) and a parameter, r. Population size is scaled to vary between 0 (no individuals) and 1 (the maximum number of individuals). Here the subscripts, t and $t + 1$, refer respectively to the current time and the time of the next generation. This equation tells us that the population reached in the next generation (N_{t+1}) depends on the number of individuals in the current generation (N_t), which makes sense since the current individuals are those that will be laying the eggs for the next generation. The parameter, r, corresponds to an intrinsic reproductive rate indicating the average fecundity (number of offspring surviving to adulthood) of an individual. The equation supposes that, in the absence of a limiting factor such as overcrowding, the population in the next generation will be rN_t. Greater values of r result in greater numbers of individuals in the next generation. The parameter r specifies the strength of the positive feedback in the system. The factor $(1 - N_t)$ plays an important role in the system: it provides the negative feedback. It also makes the equation nonlinear, giving it many of its unusual properties. In this model the population is scaled between the limits of zero (extinct) and one (the maximum carrying capacity of the population). Thus the factor $(1 - N_t)$ limits population growth as it nears its carrying capacity, because as N_t approaches 1, the factor $(1 - N_t)$ approaches zero. Expanding the right hand side of the equation yields $rN_t - rN_t^2$, which is the equation of a parabolic curve.

Without the factor $(1 - N_t)$, the right hand side of the equation is simply rN_t, the equation of a line with slope r.

In exploring this simple model of population growth, we wish to demonstrate how a system can suddenly go from one state to another through the gradual tuning of a parameter.[2] As described in the main text, the final population size reached after several iterations of the equation depends on the value of the reproductive parameter, r. Over certain ranges of r the population size reaches a single value, but as the parameter is increased the population size oscillates first between two values (so-called "period two behavior"), then four values, eight values and so on. In the terminology of nonlinear dynamics, the system exhibits a sequence of period-doubling bifurcations.

Another feature of nonlinear systems that can be explored with this equation is the transition to chaos. As r is increased beyond 3.57, the system not only fails to reach a stable value but also does not oscillate among a number of fixed values. Instead, no pattern occurs in the sequence of population levels from generation to generation. The system is said to be chaotic. Prior to Robert May's work, it is likely that such unpredictable behavior in an insect population would have been attributed to random external influences or noise in the measurements of population size. But in our hypothetical population governed by this simple deterministic equation, noise is not provided by the environment, the model, or by random errors in data collection that so often plague field studies. The chaotic behavior is called deterministic chaos. Here, the term *chaos* has a precise mathematical meaning that should not be confused with randomness or noise. Deterministic chaos is the unpredictable behavior of a nonlinear system within a certain parameter range. Deterministic means that subsequent population values are determined precisely by its equation. What is so unexpected, however, is that a deterministic equation can yield unpredictable results.

Chaos is not a topic emphasized in this book, largely because the systems dealt with here do not normally exhibit chaotic behavior. No doubt this is because natural selection tunes the parameters of living systems to avoid chaos. In most situations, it would probably be grossly maladaptive for a living system to exhibit chaotic, disorganized patterns.

Even a simple nonlinear equation can exhibit complex behavior, and so researchers have developed a graphical method for showing in a single figure the behavior of the system over a range of parameter values. This is called a bifurcation diagram (Figure 3.2). For the logistic difference equation, the diagram displays values of r on the x axis. The correspond-

ing population sizes appear on the y axis. For each value of r, many initial values of the population size, N_t, are iterated one by one, and after a large number of iterations, the population size for each N_t is plotted on the graph. We see that for certain values of r, a single steady state is reached regardless of the initial population size. Other regions show period two behavior and the transition to chaos, as well as parameter zones within the chaotic region where the population level suddenly switches to fixed population sizes.

Box 3.3 Toppling Dominoes: A Mechanical Example of Tuning a Parameter

The example of clustering by *Dendroctonus* beetle larvae illustrated how the initial density of the larvae was a parameter that could be tuned to generate sufficient positive feedback to initiate clustering. A simple mechanical analog of this system uses dominoes. Instead of tuning the initial density of larvae to affect a clustering process, the density of dominoes can be changed to affect a chain reaction of toppling.

Consider an arena of fixed size, say 1 m^2, seeded with a variable number of dominoes, each standing on its narrow end. If the density of dominoes is sufficiently low they will be sufficiently separated so that toppling a single one results in few, if any, subsequent topples. As the density of dominoes is gradually increased a density is eventually reached at which the fall of a single domino triggers a chain reaction of topples throughout the system. Experiments can be performed in which one counts the number of topples initiated by knocking over a single randomly chosen domino. If the experiment is repeated many times with different domino-densities, one can plot the average number of topples per experiment as a function of the domino density. The plot would be nonlinear, with a low number of topples up to a certain domino density, and then a rapidly rising portion of the curve at higher domino densities where the fall of a single domino results in a chain reaction of many topples.

Domino density is not the only parameter that can be tuned. The probability that a chain reaction propagates through the system is also a function of the height of a domino and the area of its base. The taller a domino, the more likely it will hit another domino when it falls. The smaller the area on which a domino stands, the more likely it will topple when hit

by another domino. Thus a parameter equal to (density × height)/area of base also can be tuned to specify the probability that a chain reaction propagates throughout the system.

In Chapter 6, this domino system is shown to be a mechanical analog of a cellular-automaton simulation of an epidemic. The spread of disease in a population resembles the propagation of topples in the domino system.