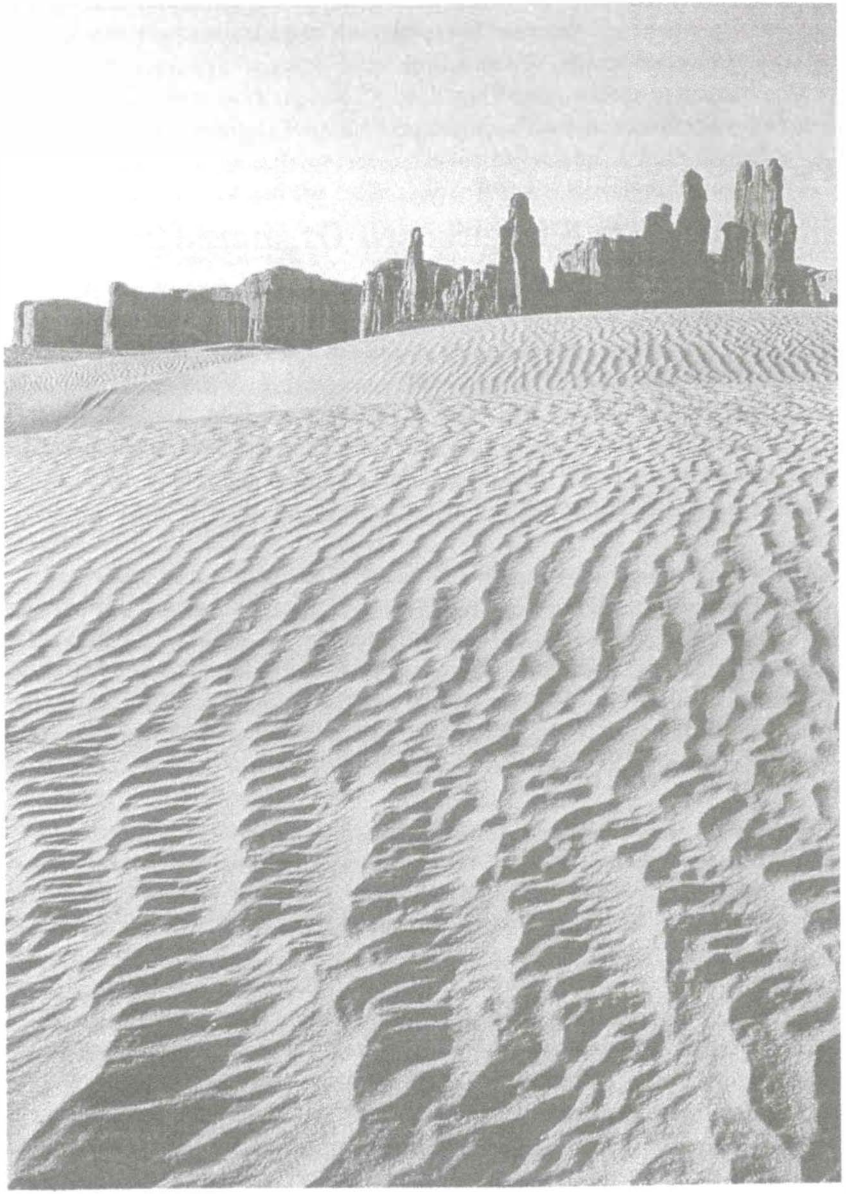


Figure 1.1 Self-organized pattern of wind-blown ripples on the surface of a sand dune. (Photo © 1994 Bob Barber/ColorBytes)

1

What Is Self-Organization?

Technological systems become organized by commands from outside, as when human intentions lead to the building of structures or machines. But many natural systems become structured by their own internal processes: these are the self-organizing systems, and the emergence of order within them is a complex phenomenon that intrigues scientists from all disciplines.

—F. E. Yates et al., *Self-Organizing Systems: The Emergence of Order*

Self-Organization Defined

Self-organization refers to a broad range of pattern-formation processes in both physical and biological systems, such as sand grains assembling into rippled dunes (Figure 1.1), chemical reactants forming swirling spirals (Figure 1.3a), cells making up highly structured tissues, and fish joining together in schools. A basic feature of these diverse systems is the means by which they acquire their order and structure. In self-organizing systems, pattern formation occurs through interactions internal to the system, without intervention by external directing influences. Haken (1977, p. 191) illustrated this crucial distinction with an example based on human activity: "Consider, for example, a group of workers. We then speak of organization or, more exactly, of organized behavior if each worker acts in a well-defined way on given external orders, i.e., by the boss. We would call the same process as being self-organized if there are no external orders given but the workers work together by some kind of mutual understanding." (Because the "boss" does not contribute directly to the pattern formation, it is considered external to the system that actually builds the pattern.)

Systems lacking self-organization can have order imposed on them in many different ways, not only through instructions from a supervisory leader but also through various directives such as blueprints or recipes, or through pre-existing patterns in the environment (templates).

To express as clearly as possible what we mean by self-organization in the context of pattern formation in biological systems, we provide the following definition: *Self-organization is a process in which pattern at the global level of a system emerges solely from numerous interactions among the lower-level components of the system. Moreover, the rules specifying interactions among the system's components are executed using only local information, without reference to the global pattern.* In short, the pattern is an emergent property of the system, rather than a property imposed on the system by an external ordering influence. Emergent properties will be defined in later chapters, but for now suffice to say that emergent properties are features of a system that arise unexpectedly from interactions among the system's components. An emergent property cannot be understood simply by examining in isolation the properties of the system's components, but requires a consideration of the interactions among the system's components. It is important to point out that system components do not necessarily have to interact directly. As described in Chapter 2, and Figure 2.4, individuals may interact indirectly if the behavior of one individual modifies the environment and thus affects the behavior of other individuals.

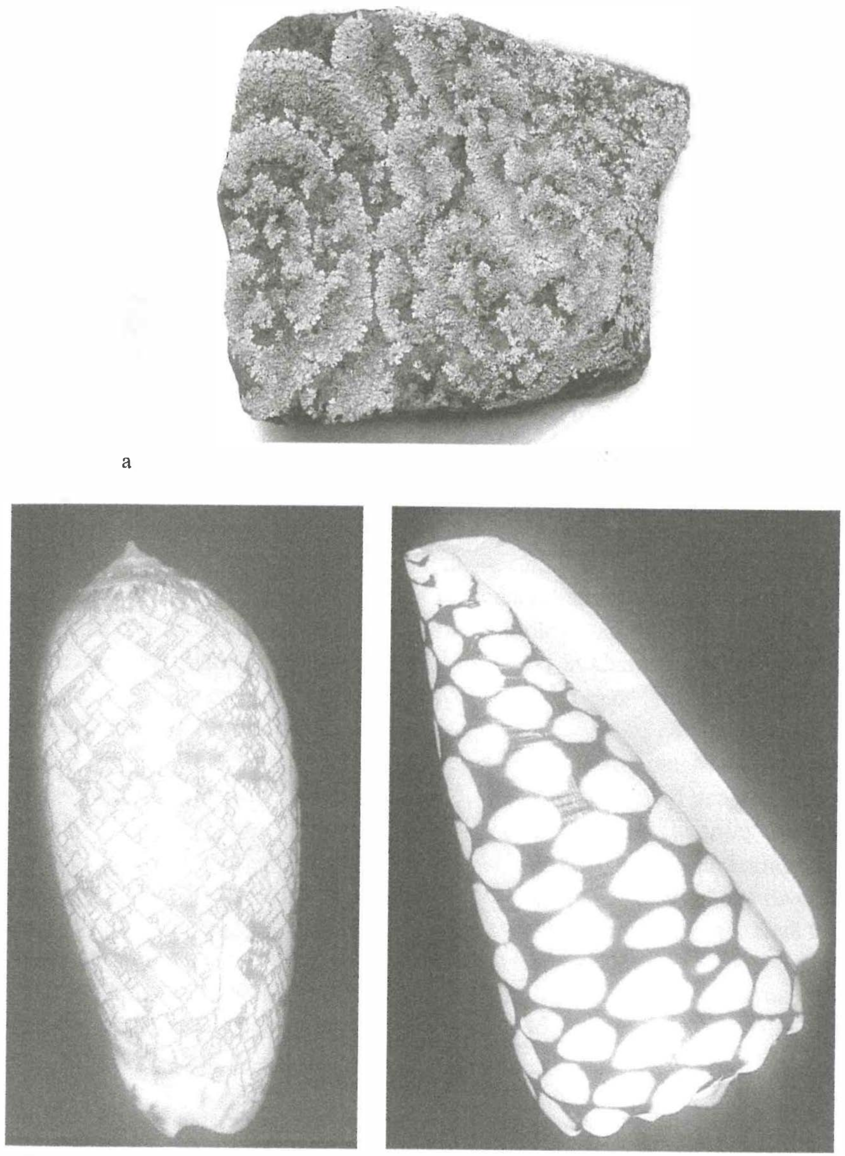
Pattern in Group Activities

Critical to understanding our definition of self-organization is the meaning of the term *pattern*. As used here, pattern is a particular, organized arrangement of objects in space or time. Examples of biological pattern include a school of fish, a raiding column of army ants, the synchronous flashing of fireflies, and the complex architecture of a termite mound. Examples of other biological patterns include lichen growth (Figure 1.2a), pigmentation patterns on shells, fish and mammals (Murray 1988, Meinhardt 1995), (Figures 1.2b,c,d) and the ocular dominance stripes in the visual cortex of the macaque monkey brain (Hubel and Wiesel 1977) (Figure 1.2e).

To understand how such patterns are built, it is important to note that in some cases the building blocks are living units — fish, ants, nerve cells, etc. — and in others they are inanimate objects such as bits of dirt and fecal cement that make up the termite mound. In each case, however, a system of living cells or organisms builds a pattern and succeeds in doing so with no external directing influence, such as a template in the environment or directions from a leader. Instead, the system's components interact to produce the pattern, and these interactions are based on local, not global, information. In a school of fish, for instance, each individual bases its behavior on its perception of the position and velocity of its *nearest* neighbors, rather than knowledge of the global behavior of the whole school. Similarly, an army ant within a raiding column bases its activity on *local* concentrations of pheromone laid down by other ants rather than on a global overview of the pattern of the raid.

The literature on nonlinear systems often mentions self-organization, emergent properties, and complexity as well as dissipative structures and chaos

Figure 1.2



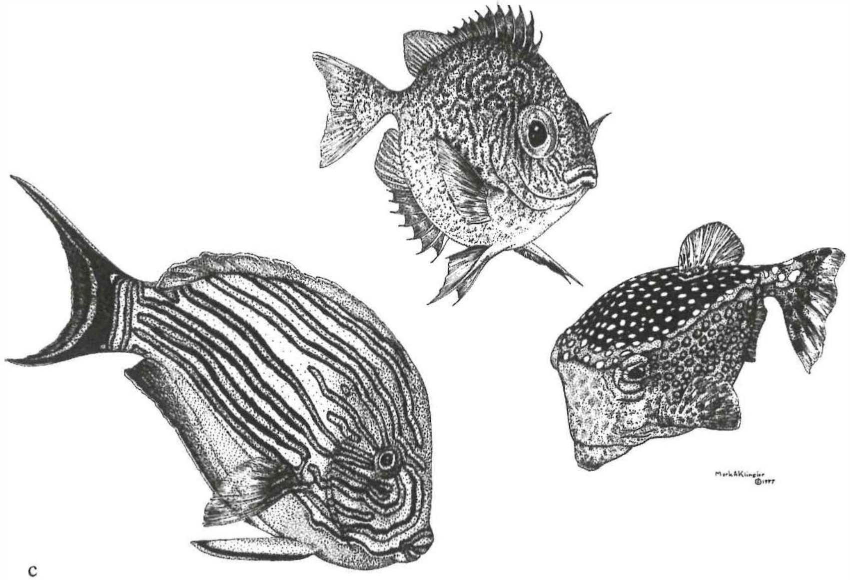
a

b(i)

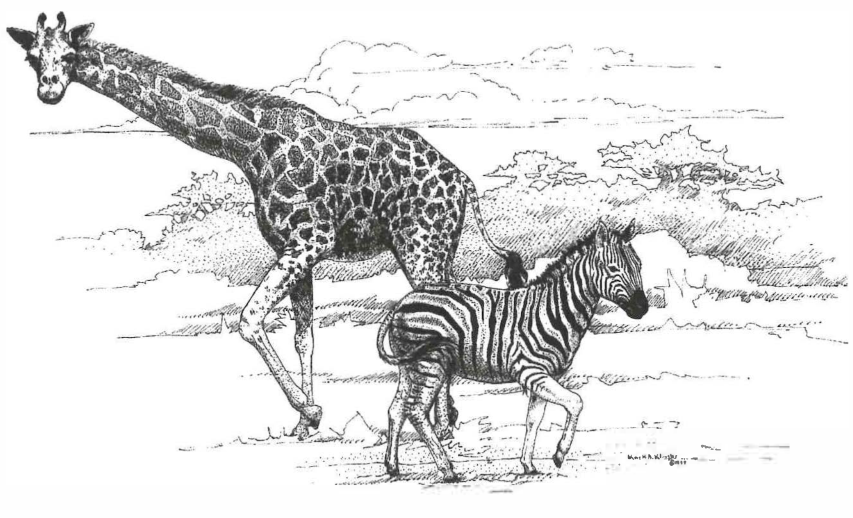
b(ii)

Figure 1.2 Self-organized patterns in biological systems include: (a) lichen growth; (b) pigmentation of a porphyry olive shell (*Olivia porphyria*) (i) and a marble cone shell (*Conus marmoreus*) (ii); (*Figure 1.2 continued next page*)

Figure 1.2 continued



c



d

(c) skin pigmentation on fish (clockwise from top—vermiculated rabbitfish (*Siganus vermiculatus*), male boxfish (*Ostracion solorensis*), and surgeonfish (*Acanthurus lineatus*)); (d) zebra and giraffe coat patterns. (*Figure 1.2 continued next page*)

Figure 1.2 continued

e

(e) ocular dominance stripes in the visual cortex of the macaque monkey (from Hubel and Wiesel 1977). Cortical regions receiving inputs from one of the monkey's eyes are shown in black while regions receiving inputs from the other eye are represented by white regions between the black stripes.

(Prigogine and Glansdorf 1971; Nicolis and Prigogine 1989). The terms *chaos* and *dissipative structures* have precise scientific meanings that may differ from popularized definitions, so it is important to discuss these terms at this point. To begin with, the term *complex* is a relative one. Individual organisms may use relatively simple behavioral rules to generate structures and patterns at the collective level that are relatively more complex than the components and processes from which they emerge. As discussed in Chapter 6 (see Box 1), systems are complex not because they involve many behavioral rules and large numbers of different components but because of the nature of the system's global response. Complexity and complex systems, on the other hand, generally refer to a system of interacting units that displays global properties not present at the lower level. These systems may show diverse responses that are often sensitively dependent on both the initial state of the system and nonlinear interactions among its components. Since these nonlinear interactions involve amplification or cooperativity, complex behaviors may emerge even though the system components may be similar and follow simple rules.

Complexity in a system does not require complicated components or numerous complicated rules of interaction.

Self-Organization in Biology

The concept of self-organization in biological systems can be conveyed through counterexamples. A marching band forming immense letters on a football field provides one such example. Here the band's members are guided in their behavior by a set of externally imposed instructions for the movements of each band member that specify in fine detail the final configuration of the whole band. A particular member of the band may know that the instructions are to march to the 50-yard line, turn left 90 degrees and march 10 paces. To the extent that the band member follows this recipe for contributing to the pattern and ignores local information, such as position relative to neighbors, this pattern formation would not be considered self-organized.

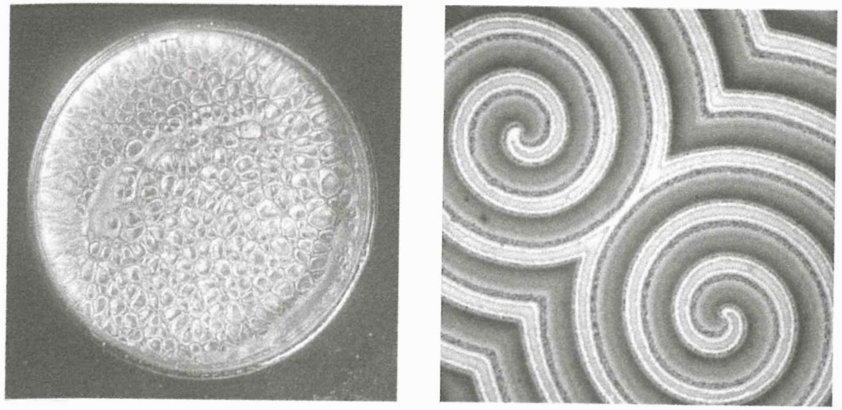
Similarly, a team of carpenters building a house is a pattern-formation process that functions without self-organization. Here members of the construction crew are guided in their collective behavior by predetermined externally imposed instructions expressed as blueprints, that precisely specify the final structure of the house. Letter formation by a marching band and house construction by a construction crew both involve pattern building in space.

Let us also consider two counterexamples to self-organization that involve pattern building over time. One such example is oarsmen in a rowing team pulling on their oars in perfect synchrony with one another and with appropriate adjustments of their stroke frequency. This pattern arises when each oarsman responds to the coxswain's shouted instructions indicating when to begin each stroke. Clearly, this is an example of a group generating a pattern by following explicit orders from a leader based on the overall state of the group members. The rhythmic contractions of muscle fibers in the heart are also a counterexample to self-organization. Here the pattern arises as the component building blocks (the muscle fibers), follow instructions from special excitable cells that act as an external pacemaker and send a rhythmic electrical signal to the fibers.[1]

We can easily see how a system can form a precise pattern if it receives instructions from outside—such as a blueprint, recipe, or signals from a pacemaker—but it is less obvious how a definite pattern can be produced in the absence of such instructions. A general answer to this puzzle is provided in the next chapter, while specific answers for particular biological patterns constitute the main body of this book. For now, it is merely asserted that pattern formation often is achieved by systems without external guidance.

The mechanisms of self-organization in biological systems differ from those in physical systems in two basic ways. The first is the greater complexity of the subunits in biological systems. The interacting subunits in physical systems are inanimate objects such as grains of sand or chemical reactants. In biological systems there is greater inherent complexity when the subunits are living organisms such as fish or ants or neurons.

The second difference concerns the nature of the rules governing interactions among system components. In chemical and physical systems, pattern is created through interactions based solely on physical laws. For example, heat applied evenly to the bottom of a tray filled with a thin sheet of viscous oil transforms the smooth surface of the oil into an array of hexagonal cells of moving fluid called *Bénard convection cells* (Figure 1.3) (Velarde and Normand 1980). The molecules of oil obey physical laws related to surface tension, viscosity, and other forces governing the motion of molecules in a heated fluid. Likewise, when wind blows over a uniform expanse of sand a pattern of regularly spaced ridges is formed (Figure 1.1) through a set of forces attributable to gravity and wind acting on the sand particles (Anderson 1990; Forrest and Haff 1992).



a b

Figure 1.3 Further examples of self-organized patterns in physical and chemical systems: (a) hexagonal Bénard convection cells created when a thin sheet of viscous oil is heated uniformly from below. Aluminum powder was added to the oil to show the convection pattern; and (b) spiral patterns produced by the Belousov-Zhabotinski reaction. The chemistry of the reaction is explained by Winfree (1972, 1984). (Image courtesy of Stefan C. Müller)

Of course, biological systems obey the laws of physics, but in addition to these laws the physiological and behavioral interactions among the living components are influenced by the genetically controlled properties of the components. In particular, the subunits in biological systems acquire information about the local properties of the system and *behave* according to particular genetic programs that have been subjected to natural selection. This adds an extra dimension to self-organization in biological systems, because in these systems selection can finely tune the rules of interaction. By tuning the rules, selection shapes the patterns that are formed and thus the products of group activity can be adaptive. What is also intriguing about pattern formation in biological systems and lends excitement to studies of self-organization in animal groups is the recent realization that interactions among system components can be surprisingly simple, even when extremely sophisticated patterns are built, such as the labyrinthine nests of termites, the spatial patterns of army ant raids, and the coordinated movements of fish in a school.

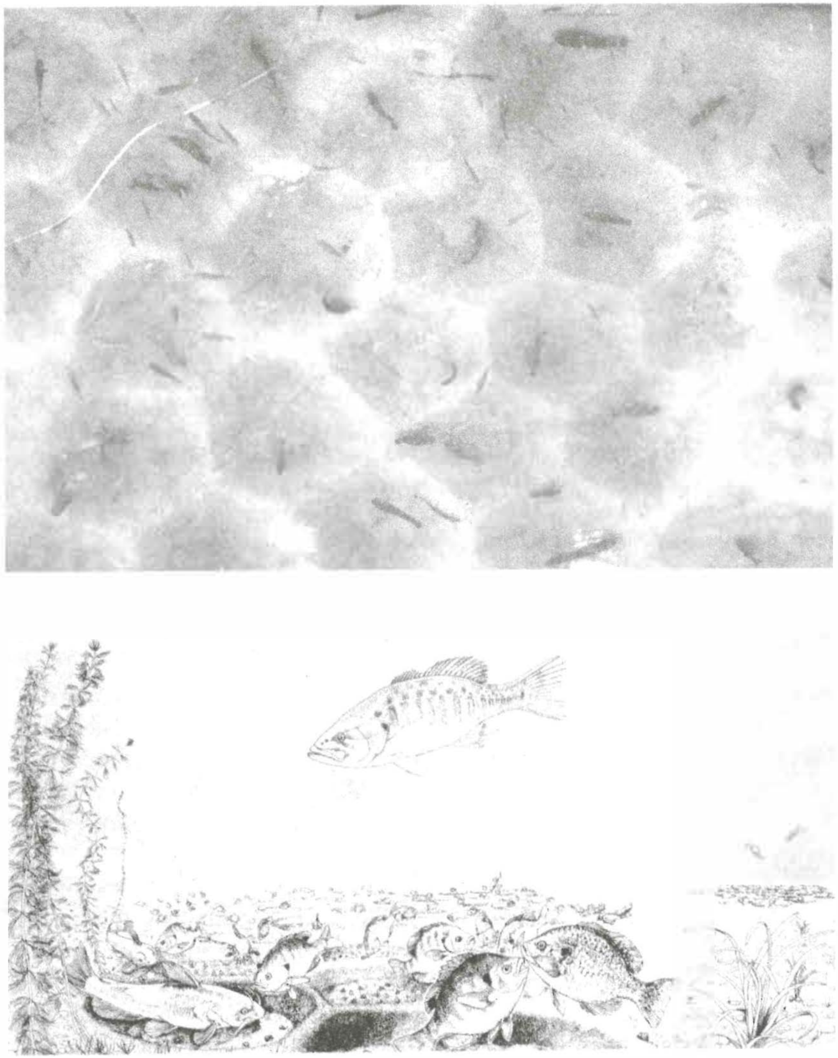


Figure 2.1 The upper portion of the figure is a top view of the polygonal pattern of male *Tilapia mossambica* nest territories. Each territory is a pit dug in the sandy bottom of the water. The rims of the pits form the boundaries of the territories and create a pattern of polygons that results from a combination of positive feedback and negative feedback (from Barlow 1974). Similarly shaped nesting territories of male bluegills are seen in the lower portion of the figure. Each colonial male defends a territory bordered by the nest sites of other males. Predators, such as bass (above), bullhead catfish (left), and pumpkinseed sunfish (right foreground) roam the colony in search of eggs. (Drawing © Matt Gross; used with permission)

2

How Self-Organization Works

Positive feedback isn't always negative.
—M. Resnick, *Learning about Life*

Self-organizing systems typically are comprised of a large number of frequently similar components or events. The principal challenge is to understand how the components interact to produce a complex pattern. The best approach is to first understand the two basic modes of interaction among the components of self-organizing systems: positive and negative feedback. The next step is to discuss information, since each component or individual must acquire and process information to determine its actions.

Feedback: Positive and Negative

Most self-organizing systems use positive feedback. This may be surprising since most biologists probably are more familiar with negative feedback, a mechanism commonly used to stabilize physiological processes (homeostasis) and avoid undesirable fluctuations. We are probably all familiar with the regulation of blood sugar levels, a process that proceeds smoothly in most people but functions abnormally in diabetics. Blood sugar levels are regulated by a negative feedback mechanism involving the release of insulin (Figure 2.2a) (Mountcastle 1974). An increase in blood glucose following ingestion of a sugary meal quickly triggers the release of insulin from the pancreas. Insulin has a number of physiological effects including the conversion of glucose to glycogen, an energy storage compound deposited in the liver. This negative feedback mechanism, counteracts increases in blood-sugar level. In this case, we see negative feedback acting to maintain the status quo by damping large fluctuations in blood glucose level. In diabetics, however, a failure of adequate insulin secretion results in elevated blood sugar levels.

A similar example involves the homeostatic regulation of body temperature. In warm-blooded mammals, internal body temperature is monitored by sensitive temperature receptors in the hypothalamic area of the brain (Brooks and Koizumi 1974). Arterial blood from throughout the body is monitored in the hypothalamus and if blood temperature is within a narrow range around the thermal setpoint, the organism feels comfortable. If, however, the organism

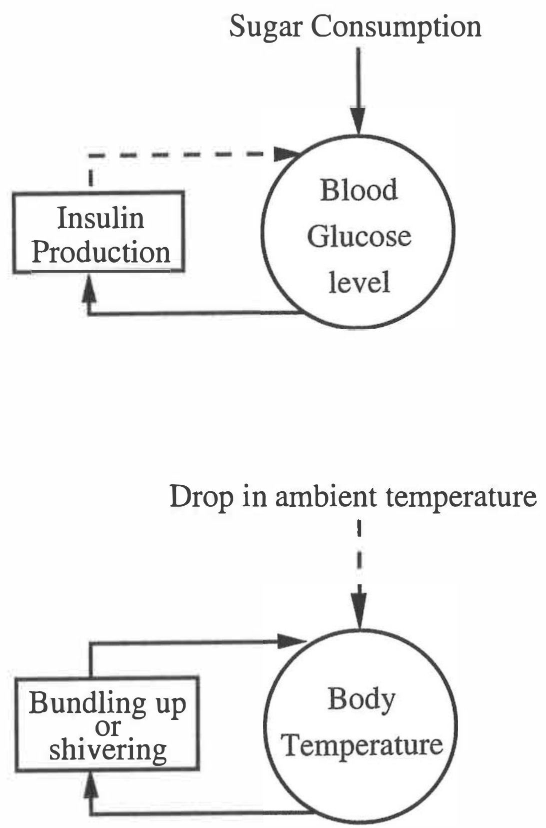


Figure 2.2 Examples of negative feedback regulation that compensates for a perturbation of the system and results in homeostasis: (a) a rise in blood glucose level (solid line) following the ingestion of food triggers the release of insulin and results in a drop (dotted line) in the glucose level; and (b) a drop in body temperature (dotted line) caused by exposure to cold weather, may cause a person to shiver or dress more warmly and experience a rise (solid line) in body temperature.

experiences a thermal stress, as would arise if a person stepped outdoors on a winter day without enough clothing (Figure 2.2b), then a discrepancy arises between the organism's actual body temperature and the thermal setpoint. The organism feels cold. The discrepancy triggers various behavioral and physiological responses, such as putting on a warm coat or shivering, that counteract the drop in body temperature.

In both instances, the individual acquires and processes information that elicits a negative feedback response: A small perturbation applied to the system triggers an opposing response that counteracts the perturbation. In the first case

an *increase* in blood glucose triggers a compensating response leading to a *decrease* in blood glucose. In the second case, a *decrease* in body temperature results in responses that *increase* body temperature. In these classical examples of regulatory systems, a single negative feedback loop performs the important role of counteracting changes imposed on a system.

Positive Feedback and the Creation of Pattern

In contrast to negative feedback, positive feedback generally promotes changes in a system. The explosive growth of the human population provides a familiar example of the effects of positive feedback (Figure 2.3). For the past several centuries, each generation has more than reproduced itself, so more births occur with each successive generation, which further increases the population and results in still more births and a yet greater population. The snowballing effect of positive feedback takes an initial change in a system and reinforces that change in the *same* direction as the initial deviation. Self-enhancement, amplification, facilitation, and autocatalysis are all terms used to describe positive feedback. The growth of the human population will also eventually be stabilized by negative feedback in the form of a lower birth rate (or a higher death rate) when the population becomes extremely large (Figure 2.3).

Consider another example of positive feedback—the clustering or aggregation of individuals. Many birds, such as seagulls (Kruuk 1964), herons (Krebs 1974), and blackbirds (Horn 1968) nest in large colonies. Group nesting evidently provides individuals with certain benefits, such as better detection of

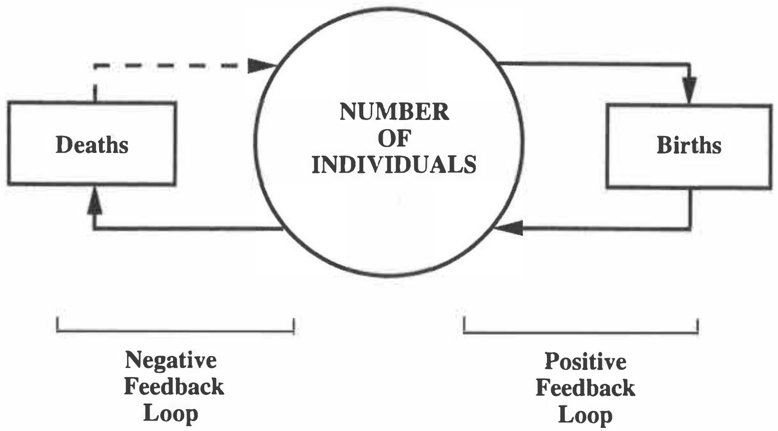


Figure 2.3 A simple model of population growth may involve a positive feedback loop of increased births and a negative feedback loop of increased deaths.

predators or greater ease in finding food. The mechanism by which colonial nesting arises is apparently that birds preparing to nest are attracted to sites where other birds are already nesting. This imitative behavior is a positive feedback process in which one individual follows the behavioral rule, "I nest close where you nest." As more birds nest at a particular site, the attractive stimulus becomes greater and the probability that newly arriving birds join the colony becomes greater, leading to an even larger aggregation. The key point is that the aggregation of nesting birds at a particular site is *not* purely a consequence of each bird being attracted to the site per se. Rather, the aggregation evidently arises primarily because each bird is attracted to *others*, hence because of interactions between individual birds in the system. In an environment with numerous, equally suitable nesting sites such as an array of islands, the birds aggregate on only a few of the many possible sites (see, for example, Krebs 1974).

Throughout this book, various forms of positive feedback are encountered that play a major role in building group activity. Fireflies flashing in synchrony follow the rule, "I signal when you signal," fish traveling in schools abide by the rule, "I go where you go," and so forth. In humans, the "infectious" quality of a yawn or laughter (Provine 1986, 1996) is a familiar example of positive feedback of the form, "I do what you do." Seeing a person yawning, or even just thinking of yawning, can trigger a yawn.

Positive Feedback and the Amplification of Fluctuations

Consider another example of colonial nesting. Male bluegill sunfish (*Lepomis macrochirus*) nest in colonies of up to 150 individuals (Figure 2.1b). This behavior presumably evolved as a defense against brood predators (Gross and MacMillan 1981), with each individual a member of a "selfish herd" (Hamilton 1971). By joining the group, and so surrounding its nest with the nests of others, each fish reduces the exposure of its brood to predators. But what is the mechanism that led to these aggregations? It may simply be that each male bluegill follows the behavioral rule, "I nest where others nest."

Now envision how the nesting pattern will appear in a large lake with a perfectly homogeneous bottom, hence an abundance of identical sites available for nesting. First, consider a scenario where the density of bluegills is very low. For lack of behavioral interactions among the males, the bluegills may end up nesting far apart over the lake bottom. A male may not find another nesting male in his vicinity, or even if it does find another male, it may be that a single adjacent male may not provide sufficient stimulus to nest nearby. Positive feedback under these conditions is insufficient to initiate the aggregation of nest sites, so a stable state will be reached in which nesting sites are randomly distributed. Next consider a scenario with a higher density of bluegills. Through a random process, several nesting sites occasionally will be close

enough to provide a sufficiently strong attraction to stimulate other bluegills to nest nearby, and form an aggregation nucleus. The random pattern of nest sites will now be unstable and a cluster of nest sites will grow. In the terminology of nonlinear dynamics, a stationary state became unstable through the amplification of random fluctuations. At a critical density of bluegills, a pattern arises within the system—a homogeneous, random array of nesting sites becomes a cluster. In fact, the nucleation of a cluster of nest sites in one area can lead to a self-organized regular spacing of clusters throughout the lake bottom.

Keeping Positive Feedback Under Control

The amplifying nature of positive feedback means that it has the potential to produce destructive explosions or implosions in any process where it plays a role. How can such snowballing be kept under control? This is where negative feedback plays a critical role, providing inhibition to offset the amplification and helping to shape it into a particular pattern. Given that male bluegills try to nest near one another, does one not find overcrowded colonies of fish? Although the details are unknown, it seems certain that negative feedback is involved. The fish have some limits in their behavioral tendency to nest where others nest. If too many male fish congregate within a given area, additional fish may be inhibited from nesting in this same area. Thus the behavioral rule may be more complicated than initially suggested, possessing both an autocatalytic as well as an antagonistic aspect: "I nest where others nest, *unless the area is overcrowded*." In this case both the positive and negative feedback may be coded into the behavioral rules of the fish.

In other cases one finds that the inhibition arises automatically, often simply from physical constraints. For instance, in a lake that contains only a small number of bluegills the buildup of males at a site is self-limiting. In this situation there is no need for the fish to employ a mechanism of negative feedback to avoid overcrowding because once all the fish have clustered in an area, the positive feedback ceases on its own. Exhaustion or consumption of the building blocks is often an important mechanism for limiting positive feedback.

There is nothing deeply thought-provoking about negative feedback that simply forces a process to a complete stop. But in the case of the bluegills (and other fish such as *Tilapia*) that assemble into a colony, negative feedback actually shapes the process and creates a striking pattern in the spatial array of nests. Through longer-range interactions, the fish aggregate in a positive feedback manner, resulting in colonial nesting. But in their short-range interactions the fish are influenced more by negative feedback: "Keep away! Don't nest where I am nesting." This occurs as each male fish builds a nest consisting of a depression in the sandy lake bottom, and diligently defends the nest area from intrusions by neighboring males. As a result of the interplay between the opposing tendencies to squeeze together yet maintain a personal territory, the breeding ground becomes a beautiful closely packed, polygonal array of nests (Figure 2.1a). It is likely, however, that a polygonal pattern itself serves no function and has no adaptive significance. Instead, the regular geometric spacing of nests probably is an epiphenomenon, an incidental consequence of each individual striving to be close, but not too close, to a neighbor. Mechanistically, it arises automatically through a self-organizing process similar to the hexagonal close-packing of round marbles placed in a dish.

A second example neatly illustrates the interplay between positive feedback, which is behaviorally coded, and negative feedback, which arises merely as a physical constraint. Consider a child making sand castles at the beach. Suppose the child wants to build a tall spire using dry sand. Naively, he employs a positive feedback rule: "Add more sand to where the sand pile is tallest." The pile starts out flat and initially gets steeper and steeper as it grows in size, but to the child's frustration he can never build the very steep tall tower he wants. Once the slope of the pile has reached a certain critical angle, the addition of more sand triggers a series of avalanches that brings the pile's profile back to the same angle (Bak et al. 1987; Jaeger and Nagel 1992). In this example, the positive feedback arises from the child's behavioral rule—"Add sand to sand."—but negative feedback arises automatically from the physical constraints of gravity and friction between the sand particles. On a particular beach with sand grains of a particular size, shape, and wetness, no matter how hard the child tries the slope of the pile always returns to the same self-organized angle of repose.

Self-enhancing positive feedback coupled with antagonistic negative feedback provides a powerful mechanism for creating structure and pattern in many physical and biological systems involving large numbers of components: the regular spacing of ridges and furrows in the surface of a sand dune (Figure 1.1), the pattern of ocular dominance stripes in the visual cortex of the brain (Figure 1.2e) or of zebra stripes (Figure 1.2d), and the skin pigmentation patterns of fish (Figure 1.2c) (Anderson 1990; DeAngelis et al. 1986; Forrest and Haff 1992; Meinhardt 1982; Miller et al. 1989; Murray 1981, 1988; Swindale 1980).

How Organisms Acquire and Act upon Information

The defining characteristic of self-organizing systems is that their organization arises entirely from multiple interactions among their components. In the case of animal groups, these internal interactions typically involve information transfers between individuals. Biologists have recently recognized that information can flow within groups via two distinct pathways—signals and cues (Lloyd 1983; Seeley 1989b). Signals are stimuli shaped by natural selection specifically to convey information, whereas cues are stimuli that convey information only incidentally. The distinction between signals and cues is illustrated by the difference between ant and deer trails. The chemical trail deposited by ants as they return from a desirable food source is a signal. Over evolutionary time such trails have been molded by natural selection for the purpose of sharing with nestmates information about the location of rich food sources. In contrast, the rutted trail made by deer walking through the woods is a cue. Almost certainly, deer trails have not been shaped by natural selection for communication among deer but are a simple by-product of animals walking along the same path. Nonetheless, these trails may provide useful information to deer.

Interactions within self-organized systems are based on both signals and cues. But whereas information transfer via signals tends to be conspicuous, since natural selection has shaped signals to be strong and effective displays, information transfer via cues is often more subtle and based on incidental stimuli in an organism's social environment (Seeley 1989b). The lack of prominence of cues means that many interactions within animal groups are easily overlooked, a fact that contributes to the seemingly mysterious origins of the emergent properties of self-organized groups.

Information Gathered from One's Neighbors

Chapter 11 discusses in some detail how fish coordinate their movements as they travel in a school. The following example of self-organization is briefly described here to illustrate that sometimes the most important information comes directly from an individual's neighbors, often its nearest neighbors. In coordinating their movements in a school, fish use both positive and negative feedback mechanisms (Huth and Wissel 1992; Partridge 1982; Partridge and Pitcher 1980; Partridge et al. 1980; Pitcher et al. 1976). Positive feedback operates as it does in the nesting colonies of seabirds; individuals are attracted to the presence of other individuals, resulting in the fish assembling into schools. Negative feedback functions in spacing fish within the school. A schooling fish that gets too close to a neighbor moves away to avoid a collision. It is as if each member were connected to its neighbor by a rubber band that pulls the individual toward a neighbor that gets too far away, but is also connected by a spring that pushes the individual away from neighbors that are too close. Here again, the behavioral rule, "Be most attracted to the largest group of fish," provides positive feedback to create a cluster of individuals. At close range, negative

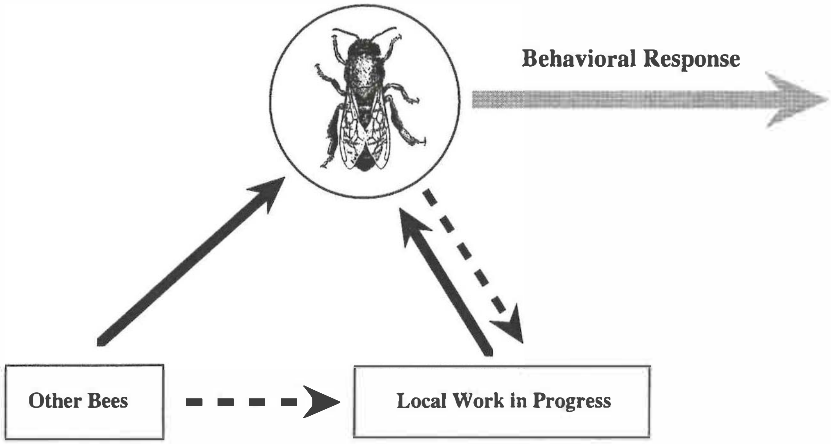


Figure 2.4 Information within an animal group may flow from one individual to another directly (generally via communication signals) or indirectly (generally via cues arising from work in process). Indirect flow is particularly important during the joint building of nests, for here individuals can efficiently coordinate their activities through information embodied in the structure of the partially completed nest. In the figure, the solid arrows show information from the environment or other individuals to the focal individual. The dotted arrows correspond to behavioral actions that may modify the environment and lead to a particular behavioral response by the focal individual.

feedback, "If too close, move away," imposes shape and pattern on the cluster.

Exactly how does each fish maintain the preferred spacing? Studies have shown that a school has no leader (Partridge 1982; Partridge et al. 1980). Indeed, in schools containing thousands of fish it is inconceivable either that one supervisory individual could monitor everybody's position and broadcast the moment-by-moment instructions needed to maintain the school's spatial structure, or that individual fish within the school could monitor the movements of the leader and follow accordingly. Coherence is achieved, instead, by each fish gathering information only about its nearest neighbors and responding accordingly. Many examples presented in this book show how individuals acquire only limited information, so that each individual's perception of group activity is myopic, not at all synoptic.

Such limited information acquisition presumably reflects the tremendous difficulty of acquiring a more complete knowledge of the group. Each fish traveling in a school, for instance, must constantly adjust its speed and direction of travel. Fish do not have time to gather more than momentary impressions of the movement patterns of their nearest neighbors before they must act. Any

delay in gathering, processing, and acting upon information will result in the fish bumping into others or being left behind. A fish must also contend with the sheer physical constraint of being surrounded by nearby fish, which surely blocks most stimuli from distant members of the school.

Members of a self-organized group often rely on simple behavioral rules of thumb to guide their actions (Krebs and Davies 1984; Stephens and Krebs 1986). The reason is that it is usually difficult, if not impossible, for an organism to obtain complete global information in a reasonable amount of time. These rules necessarily are often based upon local (hence incomplete) information, but this is generally sufficient. A member of a fish school does not need to know the long-range direction taken by the school or even the precise trajectories of all or any of its neighbors. It needs only apply a few simple rules of thumb, such as these: Approach neighbors if neighbors are too far away; Avoid collisions with nearby fish; If the first two rules have been obeyed and neighbors are at the "preferred" distance, then continue to move in the same direction.

The concept that individuals can function effectively with information acquired by monitoring just their nearest neighbors applies not only to fish schools, but to many self-organized systems. Another example of this is the coordinated rhythm of flashing fireflies that is discussed in Chapter 10. In this case each firefly primarily detects the flashes of immediately neighboring fireflies to adjust the timing of its own flash.

Information Gathered from Work in Progress (Stigmergy)

Information acquired directly from other individuals is only one source of information used by organisms in self-organizing systems. In situations where many individuals contribute to a collective effort, such as a colony of termites building a nest, stimuli provided by the emerging structure itself can be a rich source of information for the individual (Figure 2.4). In other words, information from the local environment and work-in-progress can guide further activity. As a structure such as a termite mound develops, the state of the building process continually provide new information for the builders.

In the study of social insects, the term *stigmergy* (Grassé 1959, 1967) has been used to describe such recursive building activity (See Chapter 4 for a more detailed discussion). "In stigmergic labor it is the product of work previously accomplished, rather than direct communication among nestmates, that induces the insects to perform additional labor" (Wilson 1971, p. 229).

There is good reason for many students of social insects to emphasize that workers rely on information derived from the environment rather than from fellow workers. Large colonies of social insects pose perplexing puzzles when viewed anthropomorphically. Maurice Maeterlinck (1927, p. 137), speaking of termites, wrote, "What is it that governs here? What is it that issues orders, foresees the future, elaborates plans and preserves equilibrium?" The mystery is how thousands of termites coordinate their activities during the building of a nest, a mound many thousands of times larger than a single individual. It seems certain that no termite possesses knowledge of the ultimate form of the structure, much less maintains an overview of the emerging structure as it takes shape. Furthermore, the duration of the building process spans several termite lifetimes, making it all the more mysterious how the work can progress smoothly over time.

For the reasons just mentioned, it seems clear that coordinated building activity does not depend on supervisor termites monitoring the construction progress and issuing instructions. The more likely explanation is a process of decentralized coordination based on stigmergic activity where individuals respond to stimuli provided through the common medium of the emerging nest. Instead of coordination through direct communication among nestmates, each individual can adjust its building behavior to fit with that of its nestmates through the medium of the work in progress. Each termite can communicate indirectly with its nestmates (or with itself) across both space and time by means of the small changes each one makes in the shared nest structure. More will be said about stigmergy in the next section, and in Chapter 4.

Positive Feedback, Stigmergy, and the Amplification of Fluctuations

During the initial stages of stigmergic activity, random fluctuations and chance heterogeneities may arise and become amplified by positive feedback to create the required structures. For example, consider the building activity of the termites described by Grassé (1959). When removed from their nest and introduced into a novel environment, such as a petri dish lined with a thin layer of soil, the termites will construct a series of pillars and arches made from pellets of earth and excrement (Figures 18.1 and 18.2). Grassé noticed a distinct period during the building process that he called "*la phase d'incoordination*," in which the workers randomly deposit pellets on the substrate. At this point they appear to work essentially independently and incoherently, with total indifference to the activities of their nestmates. In particular, the work appears incoherent because many individuals remove pellets of material from a particular location while others just as excitedly put them back in the same location.

Moreover, the same individual appears undecided about whether to build up or tear down its own work.

Eventually, however, small fluctuations in the deposition of pellets on the ground can generate a critical density of pellets in places, and the appearance of these incipient pellet piles induces an abrupt change in the building behavior of the termites. What was initially vague and diffuse activity suddenly becomes transformed into behavior infinitely more precise. But how exactly did this precipitous transition to *la phase de coordination* occur?

In the initial uncoordinated stage of activity, the relatively homogeneous substrate fails to provide a sufficient stimulus for deposition of material. Workers are stimulated both to deposit and remove pellets of earth and excrement. Therefore, nothing much gets done. Over time, however, and merely by chance heterogeneities in the substrate arise. A pellet placed haphazardly atop another pellet creates an inhomogeneity in the surface that provides an attractive stimulus for the deposition of yet another pellet. Once a critical density of pellets rises from the initial featureless plain, a snowballing effect takes control and the coordinated phase of activity ensues with many workers all building in the same place. Positive feedback serves to raise a pillar suddenly into the air. But even during the coordinated stage of activity, it is unlikely that the workers' actions are coordinated by means of direct communication between individuals. Rather, they are more likely coordinated through stigmergy creating positive feedback, such that many workers are attracted to build in the same location.

As discussed in greater detail in Chapter 18, the stigmergic mechanism may also account for an orderly spacing of pillars in the termite mound. Positive feedback acts over the short range to stimulate the deposition of more pellets, but outside this zone of attraction negative feedback evidently operates. Around each growing column the supply of earth is rapidly consumed as workers excavate material to add to the pillar. In so doing, they inhibit the initiation of nearby building activity. Overall, the building process starts with a homogeneous plain, then becomes focussed through a process of random fluctuations and nucleation, and then proceeds through an orderly array of positive and negative feedback zones. The sequence is entirely analogous to the positive and negative feedback that created the polygonal array of nests for the bluegill sunfish.

It is useful to consider the mechanistic origins of the positive and negative feedback in the termites' nest construction. The positive feedback process—expressed as the rule, "Build where there is already some building"—presumably is based on the termites' innate behavioral repertoire encoded in the termites' genes. However, there is no need to genetically encode the inhibitory feedback process that brakes and shapes the building. Instead, this inhibition is supplied by depletion of the number of termites in the vicinity.

There is no need to explicitly code for the behavioral rule, "Don't build one pillar near another." The diameter of the pillars and their spacing is probably determined through an interplay of many factors, including: strength of the positive feedback stimuli, which may include attraction pheromones added to structures as they are built, the amount and consistency of the soil, and the number and density of termites engaged in building. How column-building activity might progress to the eventual creation of precise and complex galleries and passageways will be discussed in greater detail in Chapter 18.

Summary

The preceding examples indicate that positive feedback is a powerful mechanism for building structure in biological systems. Without an antagonizing inhibitory mechanism, however, the process may become uncontrollable. Negative feedback brakes and shapes what could otherwise become an amorphous, overgrown structure. Positive and negative feedback mechanisms are set into motion when an individual acquires and acts on information gathered from other individuals, work in progress, or the initial state of the environment.

Where large numbers of individuals act simultaneously, a system can suddenly break out of an amorphous state and begin to exhibit order and pattern. All that is required sometimes for this transition is the implementation of a few simple rules based on positive feedback. Relatively little needs to be coded at the behavioral level and the information required for action by the individual is often local rather than global. In place of explicitly coding for a pattern by means of a blueprint or recipe, self-organized pattern-formation relies on positive feedback, negative feedback, and a dynamic system involving large numbers of actions and interactions.

With such self-organization, environmental randomness can act as the "imagination of the system," the raw material from which structures arise. Fluctuations can act as seeds from which patterns and structures are nucleated and grow. The precise patterns that emerge are often the result of negative feedback provided by these random features of environment and the physical constraints they impose, not by behaviors explicitly coded within the individual's genome.

Box 2.1 Negative Feedback, Positive Feedback, and the Amplification of Fluctuations

Consider two model systems consisting of interacting subunits, in one case positively charged particles and in another a group of male sunfish. Such a system yields different behaviors and spatial patterns of the subunits depending on whether the interactions between subunits include negative or positive feedback. In the case where all the particles are positively charged, the particles repel one another. When the particles are initially forced into one end of the chamber the interactions among subunits are governed by negative feedback; the more particles in a region, the greater the repulsive force on a particle. Such a system actively opposes any unequal distribution of particles in a region. In the second case, in which the subunits are male sunfish governed by a behavioral positive feedback, the greater the number of fish in a region the more attractive that region is for nesting. Here, even if the system initially starts out with a uniform distribution of fish, through fluctuations an instability may be reached in which one region experiences a moment in which it has significantly more fish than other regions, thus, permitting a symmetry-breaking amplification to occur. As the difference in numbers of fish between regions increases, the positive feedback becomes even stronger, allowing one region to capture all the fish. As discussed in the next chapter, whether all the subunits in a system cluster in one location will depend on the strength of the positive feedback as well as the initial density of system particles. (See the program Particles to explore systems of particles governed by negative or positive feedback. It can be downloaded at the following website address: http://beelab.cas.psu.edu.)