



## BOOKS: SYSTEMS BIOLOGY

## Unveiling Mechanisms of Collective Behavior

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The way humans build things is not typical of nature. Perhaps because we do things so differently, our initial encounters with self-organization in nature are often disorienting. When information and control are distributed among many interacting agents, organization can seem to arise spontaneously from disorder. There is no architect or manager, and the agents neither plan nor perceive the whole of the emerging pattern, which may bear no obvious relation to the relatively simple interactions that produced it. Furthermore, self-organized biological structures are typically in use from the moment construction begins, and they are often repaired by the same mechanisms that created them. Despite these seemingly severe constraints, self-organization can lead to surprisingly complex functional structures. Those structures that develop through interactions among organisms—such as the massive, elaborate nests built by colonies of the fungus-growing termite *Macrotermes*—are the focus of *Self-Organization in Biological Systems*.

The concept of self-organization originated in the study of nonlinear physical and chemical systems, such as convection flows and chemical reactions that form waves. In these systems, global patterns emerge from local interactions among many subunits. The interactions are typically shaped by multiple feedback loops, including positive ones that amplify emergent dynamics and negative ones that modulate and constrain them. As Scott Camazine and his co-authors point out, biological self-organization differs from these nonliving systems in two important ways: The subunits are more complex, and the local rules of interaction can be tuned by natural selection to produce larger-scale patterns that are adaptive.

The range of self-organizing systems in biology is quite broad, but the scope of this

book is much narrower than its title implies. Despite the authors' recognition that "self-organization is a familiar concept in development and neurobiology," they focus exclusively on social behavior. Unlike many earlier accounts of the topic, the book is written by and for empirical scientists. It contributes to the current trend in which ideas about self-organization have moved from abstract theorizing toward providing useful tools for field and laboratory biologists.

Given the book's empirical emphasis, it is not surprising that the first section, seven chapters that introduce the concepts of biological self-organization, is the weakest. Rigorous definitions of key terms such as "organization" and "pattern" are lacking, technical terms such as "bifurcation" are not always defined accurately, and the concept of self-

why in biological systems self-organization would be favored over other means of pattern formation. The authors' principal answer, presented in five pages, is that alternatives to self-organization are usually unavailable. Surprisingly, they do not mention some properties of self-organized systems that they discuss elsewhere in the book, such as economical encoding of information, robustness and the capacity for self-repair, and flexibility in the face of varying environmental conditions.

These are relatively minor flaws, however, because the heart of the book, filling more than three fourths of its length, is a collection of 13 case studies. These chapters are drawn mainly from the work of the six authors. One examines aggregation in microbes; another, schooling in fish; and the rest, insects (especially highly social ants, bees, and wasps). This section could serve as a primer on how to use models to generate and test hypotheses about the mechanisms underlying self-organization. Early models of pattern formation used a "top-down" approach, in which the parameters of the model describe the system-level properties. In contrast, the models the authors present specify only local interactions, so that global properties emerge as results of the model rather than enter as assumptions. The authors do not offer general models of self-organization in the ab-

### Self-Organization in Biological Systems

by Scott Camazine,  
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**Bees by the number.** By marking worker bees, researchers can follow the activities of individuals and investigate the stimulus-response "rules" that determine their behavior.

organization itself is described mainly through counter-examples. Some examples intended to illustrate basic ideas are also not as clear as they should be. The discussion of bifurcations and chaos in the logistic difference equation is marred by confusion between carrying capacity and limits on current population size. In the example of how to build a differential equation model, it is hard to get from the assumptions to the equations without positing an underlying probability model that the authors do not discuss.

We were also struck by the brevity of the chapter that addresses the question of

abstract. Instead, each model is closely tied to a particular system under empirical study, and key parameters are usually estimated from observations or experiments.

In each case study, the authors start by identifying the emergent group-level pattern that is to be explained. They consider alternatives to self-organization, mechanisms that they classify into four categories: leaders, blueprints, recipes, and templates. After hypothesizing a set of individual rules that might explain the observed system-level patterns, they build mathematical or computational models to test those hypotheses. The case studies illustrate several

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different modeling approaches, including differential equations, cellular automata, and stochastic individual-based models (which the authors refer to as “Monte Carlo” models). Some chapters use an iterative procedure for improving models. The chapter on honeybee comb patterns addresses a single system with three entirely different modeling approaches, thus providing an opportunity to compare their relative strengths and weaknesses. The value of these case studies is further enhanced by a companion Web site where many of the computer simulations can be downloaded (in Macintosh format only).

The case studies provide concrete examples of ideas about self-organization that might otherwise seem nebulous. The formation of ant foraging trails illustrates the flexible group behaviors that can result from fixed individual rules. The distribution of honey, pollen, and brood in honeybee combs demonstrates robustness and self-repair. Several of the studies highlight concepts such as the interplay of positive and negative feedback or the capacity for self-organization to produce complex emergent patterns by specifying only a few relatively simple rules.

Although, in keeping with their emphasis on empirical questions, the authors skirt most of the theoretical debates surrounding self-organization, they tackle one central controversy in the field: can adaptation arise solely through the process of self-organization, without requiring natural selection? (Some versions of the “Gaia hypothesis,” the notion that the global ecosystem functions as an adaptive organism-like entity, rest on this belief.) The authors label as a basic misconception the idea that self-organization and natural selection are alternative explanations of adaptive evolution. They present a more sophisticated scenario, one in which natural selection exploits the efficient information-coding that self-organization makes possible and molds interaction rules to create adaptive emergent patterns.

We suspect that the ideas associated with self-organization will play an increasingly prominent role in biology for some time to come, particularly as biologists strive to use new genomic data to comprehend the fundamentally self-organizing process of development. *Self-Organization in Biological Systems* presents a unique opportunity to watch a group of active researchers apply these intriguing concepts to formerly mystifying feats of social organization in animals. We know of no better guide for those who wish to understand how modeling can be used to dissect the mechanisms of self-organized biological systems.