

Prologue

Aims and Scope of the Book

This book examines biological structures built through mechanisms involving self-organization. The structures of interest are those that develop through interactions among organisms, hence we focus on objects built by (or of) groups of organisms. Moreover, we focus our attention on those products of group activity which are group-level adaptations, not merely incidental by-products of the behaviors of a group's members (Williams 1966).

A prime example of an adaptive structure is a nest built by a colony of the fungus-growing termite *Macrotermes* (Figure 18.1). With its thick protective walls and labyrinth of ventilation ducts, this air-conditioned castle of clay confers large positive fitness effects on the genes of its termite builders, by providing them with a safe and stable environment. One aim of this book is to understand how such structures are built, and the role in their construction played by mechanisms involving self-organization.

The book is divided into three parts. Part I is an introduction to self-organization as it relates to the biological systems that are the subject matter of this book. It provides both the conceptual basis and tools for understanding the examples of self-organization that constitute the remainder of the book. In Part II, we present certain examples that show how self-organized structures arise in groups of organisms that are gregarious for at least a portion of their lives. The structures built by these groups are generally less sophisticated than the highly adaptive structures that are built by insect societies—also the subject matter of Part II. In Part III we summarize the lessons learned from self-organization, identify new avenues of research, and suggest how the self-organization approach will improve our understanding of the building of biological structures in general.

Even though the study of self-organization is a relatively new field, there is already a large literature on numerous topics. However, most concern the fields of physics, chemistry, biochemistry, and developmental biology (Prigogine and Glansdorf 1971; Haken 1977; Nicolis and Prigogine 1977, 1989; Murray 1988, 1989; Kauffman 1993; Kapral and Showalter 1994; Nicolis 1995; Goldbeter 1996; Bak 1996) rather than organismal biology, our focus in this book. Although we devote one chapter of the book to the well-studied aggregation patterns formed by unicellular slime molds, most of the book concerns itself with groups of more complex multicellular organisms which utilize self-organizing

mechanisms of pattern formation, decision-making, and collective behavior. Some examples include the coordinated movements of fish in a school, the synchronized flashing of fireflies, and the collective foraging and building behavior of social insects.

What is of special interest to us are the *mechanisms* by which such structures develop and are maintained. Recent research has begun to reveal that even the most sophisticated structures that we will consider, such as the nests of termite colonies, are self-organized structures built through the iteration of surprisingly simple behaviors performed by large numbers of individuals that rely only on local information. Our primary goal in writing this book is to demonstrate, for a wide range of examples, the link between the rather simple behavioral programs of the individuals in a group and the sophisticated structures and patterns that emerge from their collective activity. This goal raises a number of questions to be addressed throughout the book: (1) To what extent can mechanisms of pattern formation based upon self-organization account for biological structure? (2) What are the alternative mechanisms of biological pattern formation? (3) Under what circumstances do organisms use self-organization versus these alternatives? (4) What level of complexity at the individual level is required to generate the observed complexity at the group (collective) level? (5) How much of the observed complexity at the group level is a reflection of complexity of the environment rather than complexity at the level of the individual? (6) To what extent have widely differing organisms adopted similar, convergent strategies of pattern formation?

We wish to emphasize one more important idea at the start of this book: Much of the complexity of self-organized structures seen in biology arises because the rules governing the interactions among the components of biological systems have evolved through natural selection. The process of evolution has generated an enormous diversity of behavioral and physiological interactions, far surpassing the diversity of interactions possible in chemical and physical systems. This makes the study of biological self-organization particularly exciting and challenging. Furthermore, it guarantees that the study of biological self-organization will not simply be a reworking of chemical and physical models of self-organization using the same equations with the variables simply carrying different names.

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