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.

Acknowledgments

We have many people to thank for their contributions to our thoughts and writings on self-organization. Foremost among these are Rüdiger Wehner who initiated this project when he invited Scott Camazine, Jean-Louis Deneubourg, Nigel Franks and Tom Seeley to spend a year at the Wissenschaftskolleg in Berlin, Germany. Although our interactions were far from self-organized, the Wissenschaftskolleg provided us with an ideal milieu for working closely, and
sharing our thoughts about the role of self-organization in biological systems. We greatly appreciate the opportunity afforded by the Wissenschaftskolleg, and the generous assistance of the staff at the institute.

For their support at various times during this project or for certain aspects of the experimental work reported here, Nigel Franks wishes to thank the Wissenschaftskolleg, Rüdiger Wehner, Tom Seeley, Ana Sendova-Franks, The Department of Biology and Biochemistry of the University of Bath, Iain Couzin, The Leverhulme Trust and the Smithsonian Tropical Research Institute.

Jean-Louis Deneubourg would like to thank Claire Detrain, Arnaud Lioni, Jesus Millor, Grégoire Nicolis, Jacques Pasteels, Ilya Prigogine and Philippe Rasse for the fruitful discussions, and The Solvay Institutes and the FNRS for their support.

Guy Theraulaz and Eric Bonabeau acknowledge grants from the GIS (Groupement d’Intérêt Scientifique) Sciences de la Cognition and from the Conseil Régional Midi-Pyrénées. Guy Theraulaz wishes to thank Stéphane Blanco, Vincent Fourcassié, Richard Fournier, Bob Jeanne and Jean-Louis Joly for their friendship and many fruitful discussions. Eric Bonabeau wishes to thank the Santa Fe Institute for support through the Interval Research Fellowship.

Scott Camazine would like to thank Bob Jeanne for comments on an early version of the manuscript, and for the helpful feedback during discussions with several of his students. In addition, he would like to thank Tom Seeley for countless hours of advice and stimulating discussions as his Ph.D. advisor and colleague. At Penn State, Camazine thanks Albert Rozo for assistance with many tasks related to preparing the manuscript. I offer special thanks to my wife, Susan Trainor, for technical and emotional support during the writing of this book.

At Princeton University Press, many people participated in bringing this book to fruition. Among them are Sam Elworthy, Brigitte Pelner, Jack Repcheck, Michelle McKenna, Malcolm DeBevoise, and Heidi Sheehan. Bob Bernhard did an excellent job of reading through the entire manuscript, and providing valuable suggestions for improving the readability, grammar and technical aspects of our writing.

We would like to thank Bill Thies for his skills in developing the StarLogo simulations mentioned in the book. Scott Camazine learned a great deal from Bill, who enthusiastically worked on these programs as a high school student, the year before entering M.I.T. Among the artists who contributed illustrations for the book, we thank William Ristine, Mary Ellen Didion, Mark A. Klingler, Anne-Catherine Mailleux and Stephane Portha.

There are undoubtedly many others who we have inadvertently omitted from our acknowledgments. We thank everyone who contributed to this book directly, and to those who provided research, data, and insight into the ideas presented here.