ADAPTABILITY

The Significance of Variability from Molecule to Ecosystem

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PLENUM PRESS • NEW YORK AND LONDON

Library of Congress Cataloging in Publication Data

Conrad, Michael.
Adaptability: the significance of variability from molecule to ecosystem.

Includes bibliographies and index.
1. Adaptation (Biology). I. Title. [DNLM: 1. Adaptation, Physiological. 2. Ecology.
QT 140 C754a]
QH546.C65 1983 574.5 82-24558
ISBN 0-306-41223-3

A Division of Plenum Publishing Corporation
233 Spring Street, New York, N.Y. 10013

Printed in the United States of America

Preface and Acknowledgments

In order to survive and reproduce biological systems must be adapted to the specific features of their environment. They must also be adaptable, capable of functioning in an uncertain environment. The adaptability of biological matter is one of its most striking properties.

This adaptability may manifest itself at many different levels of organization, ranging from the molecular and cellular levels to the levels of the population and the community. One type of population, for example a microbial population, may rely on culturability and control of gene expression to cope with the uncertainty of the environment, while another of metazoan plants, may rely on genetic and developmental plasticity, or it may restrict itself to an environment which is not so uncertain. Still another population, say of metazoan animals, may rely on social organization or on behavioral plasticity mediated by its neuromuscular system. Indeed, over the broad spectrum of biological nature, one can find the most diverse mechanisms of adaptability and also the most diverse strategies for using these mechanisms.

This great diversity may invite a certain amount of pessimism as to the possibility of understanding, or even describing, the patterns of adaptability which actually exist in nature. Fortunately, however, the problem is simpler than it appears at first. This is because all the different mechanisms and modes of adaptability have one thing in common: they are all adaptations to the uncertainty of the environment. This means that we can expect all forms of adaptability, regardless of their diversity, to have some common denominator.

In this book I want to describe this common denominator and then show how it can be used to analyze patterns of adaptability in nature. In particular I want to answer four questions:

1. What is adaptability?
2. What are the major mechanisms of adaptability?
3. What are the major strategies with which biological systems use these mechanisms?

4. How do these strategies interlink in the development and evolution of the ecosystem as a whole?

The approach taken to these questions is formally quite straightforward. The first step is to describe the ecosystem as a biotic community and physical environment, each with a set of states and some probabilistic (and generally unknown) law governing the state-to-state transitions. The second step is to characterize the statistical properties of the biota in terms of suitable uncertainty (or entropy) measures and relate these to the uncertainty of the environment. This makes it possible to define adaptability and also to connect it to its mechanistic basis. Next I develop a convenient way of describing the complex organization of the biota in terms of its hierarchical (or, more precisely, compartmental) structure. This makes it possible to redescribe the statistical model of the ecosystem in hierarchical terms and therefore to consider the major factors which determine the allocation of various statistical properties to the different levels—in short, the factors which determine patterns of adaptability in nature. These are of crucial importance for the organization of the organism and for succession and evolution, both from the standpoint of the individual population and from the standpoint of the ecosystem as a whole.

The problem of adaptability also has a crucial conceptual connection to the problem of stability. The ability to cope with an uncertain environment is clearly a necessary condition for the maintenance of a relatively permanent form of organization, hence for stability. This is the reason for the connection between adaptability and ecological succession or evolution. Essentially, only those ecosystems with suitable adaptability properties have the "right to persist."

A number of deep and rather subtle issues arise. Adaptability involves the use of information about the environment. So information processing and reliability of information processing must be considered. Another fundamental connection is between adaptability and the structural and functional transformability of biological systems. Transformability turns out to be a generalization of reliability. A self-contained treatment requires a close analysis of fundamental biological concepts, such as information, complexity, efficiency, and fitness. Some questions of special importance concern the legitimate ways of using information measures in biology, the connection between energy and adaptability, and the relation between adaptability and various dynamical notions of stability, such as orbital stability and structural stability. To understand the relation between stability and complexity correctly it is necessary to understand the relation between stability and adaptability. There is also an important link between the adaptability of a system and the extent to which its dynamics is predictable.

My major objective, however, has been to use the theory developed to make testable statements about observable biological phenomena and to compare the concrete phenomena to the claims made about the adaptability structure of biological systems at different levels of organization. At the very lowest levels and at the very highest, decisions about which systems to focus on are easy to make. On the lower side I focus on genetic organizations, including the adaptability structure of individual genes and proteins. On the top side I focus on patterns of adaptability in populations, on the adaptability structure and successional development of communities, and on the long-term process of evolution. There are numerous specific physiological systems that could be considered in the zone between gene and population. Here I have attempted to state the general principles and to choose some examples which I believe are particularly illustrative. Examples include cyclic nucleotide and hormonal systems, ATP control systems, features of the immune system and the central nervous system, and basic morphological features of plants and animals insofar as they relate to the structure of adaptability. Features of some of the smallest objects in biology—such as genes—are deeply connected to features of large objects, such as communities. All biological objects are tied together by their contribution to the structure of adaptability, so it should not be surprising that a coherent account of adaptability would reveal new and interesting connections between superficially unrelated phenomena.

Needless to say, any formalism which is capable of coping with the full complexity of adaptability processes in nature must itself be complex. The formalism described in this book shares this feature. It would be impossible to arrive at correct conclusions without using a formal instrument. It is necessary to show the results in order to be in a position to say what they are. But I have in each case stated the results informally and have illustrated them with as many biological examples as practical. The informal statements are not as precise as the formal statements, but they are correct. As the philosopher Wittgenstein pointed out (in *Philosophical Investigations*) the concept of absolute precision cannot be useful. The suitable degree of precision must be chosen relative to the purposes at hand. The observation is remarkably apt for biological analysis. In the formal development I have chosen a degree of precision which I believe has been the most suitable for reaching useful conclusions.

But the theory is by no means all, or even primarily, mathematical formalism. Every biological theory is obliged to make a three-point landing, not only on the ground of mathematical self-consistency, but also on the ground of consistency with physical law, and most of all on the ground of consistency with and incorporation of fundamental biological principles and concepts. Thus the book requires some background of physical and thermodynamic ideas and of course a background of basic biology. I have tried to present this wide-ranging background in a way which indicates the breadth of connections, which is technical only on points relevant to adaptability, and which always gives a nontechnical description of these technicalities. As in the presentation of the formal structures of the theory itself, the nontechnical descriptions should make the book accessible to the reader who wants to familiarize himself with the main principles of adaptability in nature, but who would rather omit some of the details.

The possibility of elucidating these principles, of explaining as well as describing patterns of adaptability, is appealing from the naturalistic point of view. It is also appealing from the theoretical point of view because the generality of the problem is such that it is amenable to mathematical analysis. There is also a practical aspect. Many of the problems which arise in genetic engineering, medicine, agronomy, and ecological management are essentially ones of adaptability theory. The problem in these vital areas finally reduces to the problem of adequate adaptations to the uncertainty of the environment, of using these various adaptations to combat internal and external perturbations, and of interweaving them into stable forms of organization. I believe such practical applications would be best developed in the context of concrete situations. Of necessity this is a matter for the future. But in the concluding chapter I have used the principles to formulate a set of guidelines which should be applicable to a wide variety of practical situations. Living systems are evidently much more adaptable than present-day technical systems and have much greater potential for evolution and novel adaptation. Adaptability theory points up the features which underlie this. The design guidelines which it implies are simply guidelines for maintaining these features along with criteria for assessing whether they are in fact being maintained. The theory naturally extends from preeconomic ecosystems to ecosystems with a monetary economy. Here design is especially important and I therefore conclude the book with an application of the analysis to the adaptability structure of economic ecosystems.

Since adaptability involves both the functional organization of biological systems and their physiochemical constitution, it is inevitable that any adequate theory will include in its ancestry a number of lines of thought. It is necessary to abstract from a reality which dies when any of these lines becomes irrelevant. One important lineage is the theory of evolution. This is a line of thought which has its origins in biology itself and which is the source of basic notions such as adaptation, adaptability, and fitness. A second important lineage is physiology. This is the source of ideas about homeostasis and of analogies between physiological processes and technological control systems which have been at the same time fruitful and misleading. Ideas about feedback control and models of information processing which have their roots in automaton theory can, with some liberty, be placed here. A fourth important line of thought comes from physics and from irreversible thermodynamics. This provides the link between adaptability and energy–entropy processes and a conceptual underpinning which is necessary for the proper interpretation of the formalism. Two important sources of the underlying biology involve phenomena at the extreme scales of size. The large-scale source comes from studies of global ecosystems, particularly phenomena such as cycles and succession. The small-scale source is molecular biophysics and molecular genetics. Processes such as protein folding are fundamental for evolutionary adaptability. They are connected on the one hand with the virtually neutral sequence variability exhibited by some genetic structures and on the other to the topological transformability of biological structures which is the *sine qua non* for evolution by variation and natural selection.

The formalism itself has its origin in information theory and discrete systems theory. It captures enough of the reality to serve as a general and reliable instrument of deduction. Dynamical formalisms, another important lineage, are capable of mapping more detail. But I shall argue that for the questions addressed by adaptability theory they abstract away too much of the underlying biology (if they are constructed to be tractable) and that they predict more than is in principle predictable. Their real value (from the standpoint of adaptability) is as a tool for thinking about the stability of functional organizations. The conscious incompleteness of the formalism may dissatisfy those who have hopes for more powerful tools. But the tradeoff between completeness of description and generality of conclusion appears to be fundamental in biology. This does not mean that more completely descriptive tools cannot eventually be developed which give more complete answers to the questions posed. But it does mean that one cannot expect to develop these tools by attempting to fulfill traditional expectations. By posing more modest questions than are naturally posed with other tools, I believe it has been possible to obtain conclusions which are more generally applicable.

It is interesting to compare the point of view of adaptability theory to that of classical biostatistical analysis. Both are basically probabilistic approaches. The difference lies in how the variability of data is viewed. The adaptability theorist views variability as having functional significance, whereas the statistician seeks to extract, with a stated degree of confidence, a prototype correlation which the variability is presumed to mask. There are fundamental relationships in living systems and there are situations in which it has been useful to view variable observations as error which obscures these relationships. But I shall argue that for living matter the variability of data is at least as fundamental as any prototype relationships which could be extracted from it and that in the typical situation a more fruitful hypothesis can be constructed about the variability than can be extracted from it. This functional view of variability is already present in models of evolutionary processes having their origin in statistics. But by and large variability of data is still viewed as a nuisance by most experimental and field biologists. According to adaptability theory this nuisance phenomenon is especially pronounced in biological materials because of its great importance for life. There is an interesting analogy to the situation in physics. Originally the variability of data was viewed as an extraneous nuisance. But now it is known that at least some uncertainty in measurement is due to quantum fluctuations and that such fluctuations, rather than being a nuisance, are responsible for the forces which hold our universe together. The variabilities of biological systems are essential to their integrity in different but equally significant ways. In both physics and biology there must therefore be a point at which the paradigm of a prototype reality masked by error becomes inappropriate. This intrinsic importance of variability was recognized much earlier in the history of biology than in the history of physics, certainly not later than the appearance of the Darwin–Wallace theory of evolution. The problem is that this recognition has not extended to as many areas of biology as it should. It seems to me that an enormous amount of useful biological data is every day being ignored or discarded because of the great desire to extract prototype relationships from it and because of the absence of a suitable adaptability theoretical framework for interpreting it.

This book shares a profound public debt to the many individuals associated with the ideas which have contributed to it. The best place to acknowledge these debts—insofar as it is possible—is in the text itself. But the debt would be inadequately acknowledged if I did not point out a fundamental inaccuracy in the historical picture which I have so minimally outlined. It would be a mistake to imagine that these different lines of thought developed in isolation. I believe that a strong case can be made that they have intersected at the most pivotal junctures. Certainly cross-correlations between them have been the subject of deep studies. The problem is that they are isolated insofar as they have become attached to institutional structures. The imagery which they engender—life as a physical process, as a machine, as an expression of stable dynamical forms, as an evolution process, as an irreducible organization—are often antithetical as well. The lineage which can be identified as theoretical biology has in this respect played a special role. As a discipline basically without institutional support it has provided the necessary but all too narrow conduit of interchange and has served to maintain the thread of a tradition which at potentially pivotal times has played the pivotal role. I conjecture that careful evaluation of the historical evidence would show this claim to have merit.

Thinking back on the individuals with whom I have worked or have had the benefit of discussion I am struck by the extent to which they reflect these different lineages of thought.

The physiologist E. S. Castle sponsored my initial work on adaptability when I was a senior undergraduate in the Harvard Biology Department. I recall that the framework was an independent research course which I called Models and Analogs in Biology. I wrote a primitive version of the book during the summer of 1964, just before moving to the Biophysics Program at Stanford. H. H. Pattee was one of the individuals to whom I showed this manuscript and I am greatly indebted to him for numerous invaluable discussions starting at that time on the compatibility of physics and biology. I was also stimulated by discussions about morphology and organization with A. K. Christensen and by discussion of the automaton paradigm with Michael Arbib. At Stanford I emphasized computational modeling of evolutionary processes. This work is not in evidence in this book, but it served as a laboratory for testing and developing a number of ideas which play an important role in adaptability theory. I returned to the problem of adaptability in a concentrated way during two postdoctoral periods spent at the Center for Theoretical Studies at the University of Miami. I thank Behram Kursunoglu for sponsoring these fellowships and for encouraging me to give a seminar series on Biological Organization in 1969. The specific form of the theory grew out of this series. The formalism itself developed largely while I was a postdoctoral scholar in the Mathematics Department at the University of California at Berkeley. I am indebted to Hans Bremermann for many extremely valuable discussions on mathematical biology during this period and subsequently.

The first segment of the book was written in 1973 while I was a faculty member at the Institute for Information Science at the University of Tübingen and during subsequent visits to Tübingen. I thank Werner Güttinger for encouraging me to give a course on adaptability theory and for discussions of stability theory. I am very specifically indebted on many points over many years to Mario Dal Cin (first at Miami and later in Tübingen) and to Otto Rössler, located in the Theoretical Chemistry Institute at Tübingen. Dal Cin, Rössler, and I ran an informal seminar on adaptation in 1974 which served very effectively to sharpen the problems and to compare algorithmic, statistical, and dynamical approaches.

Segments were written while I was a faculty member in the Department of Biology at the City College of New York and while a member of the Department of Computer and Communication Sciences at the University of Michigan. I acknowledge discussions with members of both faculties, including discussion of a number of interesting statistical problems at CCNY. For perceptive suggestions I thank students who attended my course on adaptability theory at Michigan as well as the interdepartmental community which attended our theoretical biology tea. I acknowledge discussions with John Holland on the process of adaptation.

Major portions of the book as well as major additions to earlier chapters have been completed since joining the Computer Science and Biological Sciences Departments at Wayne State University. I thank colleagues in both departments for valuable discussion and acknowledge the unusually innovative milieu in the Computer Science Department and its Intelligent Systems Laboratory. I acknowledge discussions with M. A. Rahimi on technology and adaptability, collaboration with Roberto Kampfner on evolutionary adaptation from an algorithmic point of view, and discussions with students involved with my course on natural information processing.

For discussions of adaptability theory which have been especially valuable I thank Robert Rosen, Bernard Patten, Harold Hastings, and R. M. Williams. Chapter 10 was written in the summer of 1979, while I was a visiting scholar at Cavendish Laboratory, Cambridge University. I acknowledge intensely stimulating conversations with B. D. Josephson during this visit and at other times on the connection between physics and life phenomena and on the deeper problems connected with adaptive intelligence.

I did major work on Chapter 12 during an interacademy exchange visit to the USSR and major work on Chapter 13 during an interacademy exchange visit to East Germany. I thank the U.S. National Academy of Sciences for sponsoring both visits. I acknowledge collaboration with Efim Liberman on the cyclic nucleotide system of intraneuronal information processing as well as extensive exchange of ideas about the underlying mechanisms of biological computing while at his laboratory at the Institute for Problems of Information Transmission, Moscow. I had the pleasure of many perceptive discussions with Michael Volkenstein on information and evolution. I completed small but crucial pieces during shorter visits to the Institute for Cybernetics in Baku, the Institute for Biophysics in Tashkent, the Institute for High Molecular Compounds in Leningrad, and the Institute for Biological and Chemical Physics in Tallinn. I acknowledge discussion on physics and evolution with Werner Ebeling of the Humboldt University and also discussions of the dynamics and stability of agroecosystems with members of the Institute for Cybernetics and Information Processes in East Berlin. I did bits and pieces at the Institute for Biophysics and the Carl Ludwig Institute for Physiology at the University of Leipzig, at the Institute for Microbiology and Experimental Therapeutics in Jena, and during a visit to the Information Science Institutes at the Dresden Technical University. But I acknowledge these institutes and the many individuals with whom I had the pleasure of interacting less for the writing done at the time than for an important contribution to work done after returning to Detroit.

In the text I acknowledge discussions or articles which may have been stimulating and which draw attention to related work. I have given numerous talks on adaptability theory since 1969 and I am afraid there is no way of crediting all the sharp questions which have sent me home to clarify this or that point. For reading and commenting on the manuscript I would like to thank M. Dal Cin, H. Hastings, R. Kampfner, K. Kirby, R. Rada, O. Rössler, F. E. Yates, and B. Ziegler.

My deepest acknowledgment is to my wife, Deborah, who deciphered and critically examined each page, who drafted the diagrams, and who has been my companion in the laboratory as elsewhere.

I have learned a great deal as a result of working on this book in a number of different lands and in a number of different disciplinary frameworks. There are intense problems bearing on the world and everywhere there is pressure to achieve laudable goals in agriculture, industry, and medicine. This is true in both the capitalist and socialist countries. It occurred to me that the single-mindedness with which these goals are being pursued is so great that our treasury of potentialities—our adaptability—is being cultivated much less than it ought to be. Science is unifying and, properly viewed, our problems could be unifying as well.

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Important Symbols

Page numbers refer to page of first occurrence.

ω	Transition scheme of biota, p. 54
ω^*	Transition scheme of environment, p. 54
$\hat{\omega}$	Transition scheme of biota as determined in most uncertain allowable environment (stressed transition scheme), p. 56
$\hat{\omega}^*$	Transition scheme of most uncertain allowable environment, p. 56
$\underline{\hat{\omega}}$	Stressed transition scheme in information transfer picture, that is, defined over fine (selectively equivalent) states, p. 176; cf. also p. 63
$\hat{\omega}_{ij}$	Stressed transition scheme of compartment i at level j, p. 96
ω^*_{h0}	Transition scheme of region h of the environment, p. 93
$\hat{\dot{\omega}}_{ij}$	Stressed partial transition scheme of compartment i at level j, that is, with state of compartment c_{ij} specified in terms of its subcompartments at the next lower level, p. 96
$H(\hat{\omega})$	Potential behavioral uncertainty of biota, p. 56
$H(\hat{\omega}\vert\hat{\omega}^*)$	Potential behavioral uncertainty of biota given behavior of environment (anticipation entropy), p. 56
$H(\hat{\omega}^*\vert\hat{\omega})$	Potential behavioral uncertainty of environment given behavior of biota (indifference), p. 56
$H(\omega^*)$	Actual uncertainty of environment, p. 54
$H(\hat{\omega}_{ij})$	Potential behavioral uncertainty of compartment c_{ij}, p. 162; cf. also p. 93

$H_e(\hat{\omega}_{ij})$	Effective entropy of c_{ij} (modifiability of c_{ij} + dependence terms), p. 96; cf. also p. 94
$H_e(\hat{\omega}_{ij}\vert\Pi\hat{\omega}^*_{h0})$	Effective anticipation entropy of c_{ij} ($\Pi\hat{\omega}^*_{h0} = \omega^*$), p. 96
β^u	State u of biota, p. 51
ε^v	State v of environment, p. 51
E	Energy, p. 12
S	Entropy, p. 13
ε	Efficiency, p. 144

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