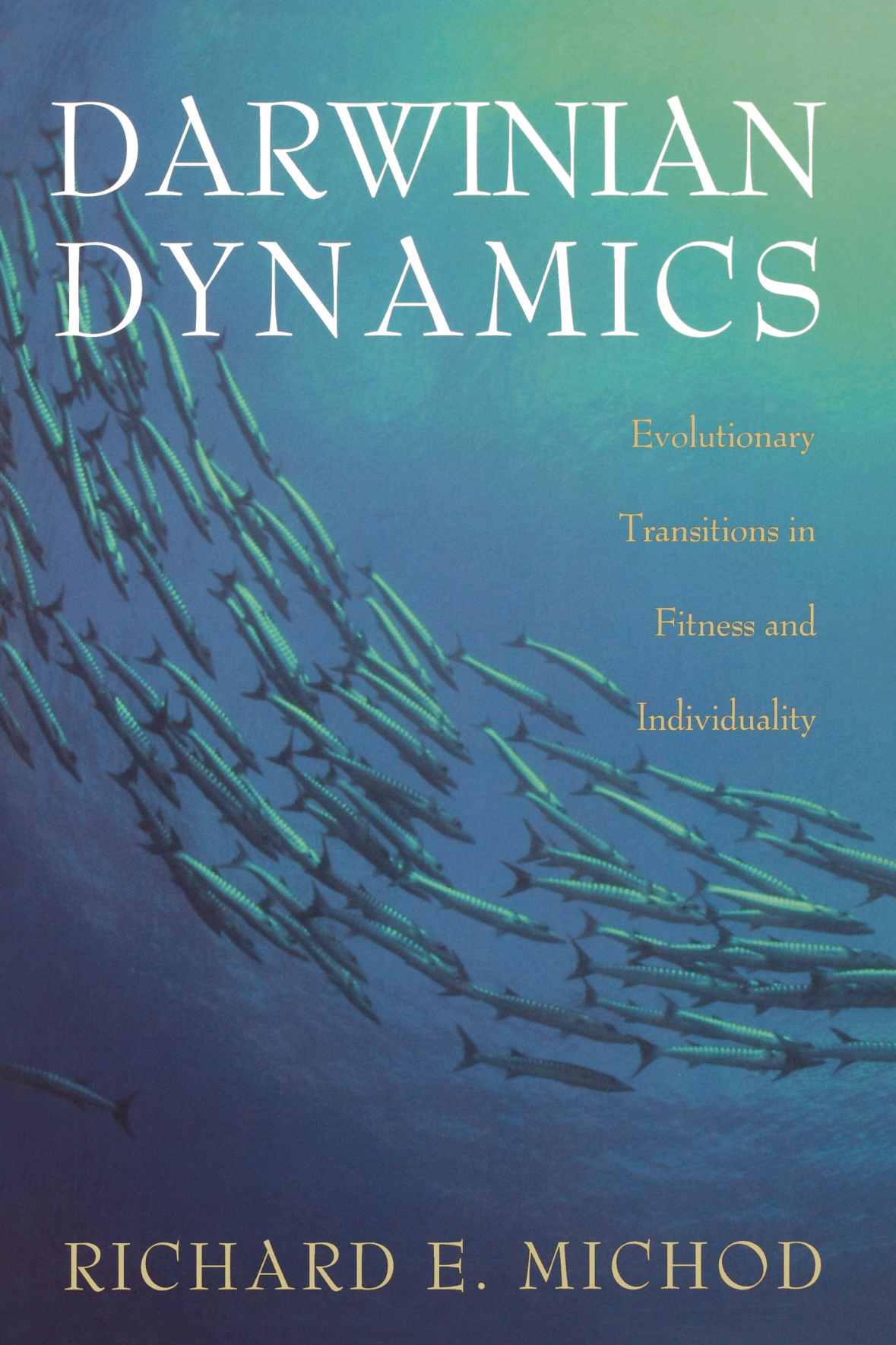




DARWINIAN DYNAMICS

Evolutionary

Transitions in

Fitness and

Individuality

RICHARD E. MICHOD

Darwinian Dynamics

Darwinian Dynamics

EVOLUTIONARY TRANSITIONS
IN FITNESS AND INDIVIDUALITY

Richard E. Michod

PRINCETON UNIVERSITY PRESS

PRINCETON, NEW JERSEY

Copyright © 1999 by Princeton University Press
Published by Princeton University Press, 41 William Street,
Princeton, New Jersey 08540
In the United Kingdom: Princeton University Press, Chichester, West Sussex
All Rights Reserved

Second printing, and first paperback printing, 2000

Paperback ISBN 0-691-05011-2

The Library of Congress has cataloged the cloth edition of this book as follows

Michod, Richard E.
Darwinian dynamics : evolutionary transitions in fitness and
individuality / Richard E. Michod.
p. cm.

Includes bibliographical references and index.

1. Natural selection. 2. Adaptation (Biology) I. Title.

QH375.M535 1999

ISBN 0-691-02699-8 (cl : alk. paper)

576.8'2—dc21 98-4166 CIP

This book has been composed in Times Roman

The paper used in this publication meets the minimum requirements of
ANSI/NISO Z39.48-1992 (R1997) (*Permanence of Paper*)

<http://pup.princeton.edu>

Printed in the United States of America

2 3 4 5 6 7 8 9 10

TO MY DAUGHTERS KRISTIN AND KAYLEY

Contents

<i>Preface</i>	xii
<i>Acknowledgments</i>	xv
CHAPTER 1	
The Language of Selection	3
<i>Plan of the Book</i>	3
<i>Darwinian Dynamics</i>	5
<i>Major Evolutionary Transitions</i>	7
<i>Cooperation and Conflict</i>	8
<i>Fisherian Fitness</i>	9
<i>Deconstructing Fitness</i>	11
<i>Selection as Fitness Covariance</i>	13
<i>Mathematical Models</i>	16
<i>Adequacy Criterion for Understanding Fitness</i>	18
<i>Definitions of Basic Concepts</i>	18
CHAPTER 2	
Origin of Fitness	19
<i>Complementarity</i>	19
<i>Spontaneous Creation</i>	20
<i>Self-Replication and the Origin of Fitness</i>	20
<i>Replicator Dynamics</i>	21
<i>Design Analysis of Molecular Replicator</i>	22
<i>Life History Evolution</i>	24
<i>Survival of the Fittest</i>	25
<i>Survival of Anybody</i>	26
<i>Overview of the Origin of Fitness</i>	27
CHAPTER 3	
The First Individuals	29
<i>Origin of Gene Networks</i>	29
<i>Cooperation and Conflict</i>	32
<i>Survival of the First</i>	33
<i>Evolutionary Transitions Are Inherently Nonlinear</i>	35
<i>Origin of Hypercycles</i>	35

CONTENTS

<i>Quasispecies</i>	37
<i>Population Structure</i>	39
<i>Kin Selection in Evolutionary Transitions</i>	40
<i>Conflict Mediation through Individuality</i>	42
<i>Further Evolution of the Cell</i>	43
<i>Heritable Capacities of Single Cells</i>	45
<i>Reconsidering Adaptedness and Fitness</i>	46
<i>Early Transitions in Evolution</i>	47
 CHAPTER 4	
Evolution of Interactions	49
<i>Gene Frequency Change</i>	49
<i>Population Growth</i>	50
<i>Frequency-Dependent Selection</i>	51
<i>Constant Selection</i>	51
<i>Adaptive Topography</i>	52
<i>Frequency Dependence Decouples Fitness in a Selection Hierarchy</i>	53
<i>Selection as Covariance</i>	55
<i>Fisher's Fundamental Theorem</i>	57
<i>Evolution in Hierarchically Structured Populations</i>	62
<i>Evolution of Multicellular Organisms</i>	64
<i>Kin Selection</i>	66
<i>Game Theory</i>	70
<i>Modification of Genetic Constraints</i>	71
<i>Population Dynamics and Natural Selection</i>	72
<i>Fitness Minima</i>	73
<i>Prisoner's Dilemma</i>	75
<i>Spatial Structure and the Evolution of Cooperation</i>	77
<i>The Problem of Frequency Dependence</i>	80
 CHAPTER 5	
Multilevel Selection of the Organism	81
<i>A Scenario</i>	81
<i>A Model for the Emergence of Organisms</i>	81
<i>Recurrence Equations</i>	84
<i>Within-Organism Mutation Selection Model</i>	86
<i>Mutation Rate</i>	87
<i>Covariance Methods</i>	89
<i>The Risk of Development</i>	90

<i>Increase of Cooperation</i>	91
<i>Level of Cooperation among Cells within Organisms</i>	93
<i>Fitness of Organisms</i>	95
<i>Effect of Sex and Diploidy on the Emerging Organism</i>	101
<i>Strengths and Weaknesses of the Model</i>	102
 CHAPTER 6	
Rediscovering Individuality	107
<i>Evolutionary Individuals</i>	107
<i>Two-Locus Modifier Model</i>	109
<i>Model Parameters</i>	112
<i>Equilibria of the System</i>	112
<i>Evolution of the Germ Line</i>	113
<i>Evolution of the Mutation Rate</i>	118
<i>Evolution of Self-Policing</i>	119
<i>Evolution of Adult Size</i>	121
<i>Effect of Transition on the Level of Cooperation</i>	122
<i>Increase of Fitness Covariance at Organism Level</i>	122
<i>Heritability of Fitness and the Evolution of Individuality</i>	124
<i>Sex and Individuality</i>	127
<i>Origin of Multicellular Life</i>	129
<i>Transitions in Individuality</i>	131
 CHAPTER 7	
Fitness Explanations	133
<i>Overview of Fitness and Natural Selection</i>	133
<i>Trading Fitness through Cooperation</i>	135
<i>Kinship and Population Structure</i>	136
<i>Conflict Mediation</i>	137
<i>Reconsidering Fitness</i>	137
<i>The "Tautology Problem"</i>	140
<i>Surrogates for Natural Selection</i>	142
<i>Evolution of Selfing</i>	145
<i>Cost of Sex</i>	146
<i>Immortality, Death, and the Life Cycle</i>	150
<i>Kin Selection of Altruism</i>	152
<i>Heterozygote Superiority</i>	154
<i>Sickle Cell Anemia</i>	156
<i>Darwin's Dilemmas</i>	158

CONTENTS

CHAPTER 8

A Philosophy of Fitness	161
<i>Dynamics of Design</i>	161
<i>What Makes Biology Different?</i>	163
<i>Success and Design</i>	164
<i>Long-Term versus Short-Term Measures of Fitness</i>	166
<i>Darwinian Dynamics</i>	167
<i>Natural Selection as a Biological Law</i>	169
<i>Paradigms for Natural Selection</i>	173
<i>Fitness in Darwinian Dynamics</i>	174
<i>The Insufficiency of Individual Fitness</i>	175
<i>Heritability and Natural Selection</i>	179
<i>Schema for Natural Selection</i>	181
<i>The Propensity Interpretation of Fitness</i>	183
<i>Brandon's Approach</i>	186
<i>Heritable Capacities as Components of Design</i>	189
<i>Overall Adaptedness of Organisms</i>	191
<i>Masking of Adaptiveness</i>	194
<i>Are Adaptation Concepts Necessary?</i>	196
<i>F-Fitness and Evolutionary Explanations</i>	197
<i>Explaining Fitness</i>	200
APPENDIX A	
Supporting Analyses	203
<i>Statistics of Fitness and Selection</i>	203
<i>Equilibria for Modifier Model ($G = 0$)</i>	217
<i>Cost of Sex in Diploids</i>	218
APPENDIX B	
Fitness Phrases	222
APPENDIX C	
Notation	226
Notes	233
References	237
Index	253

Preface

LIFE EXISTS as hierarchically nested levels of organization, in which higher-level units are composed of lower-level units (gene, chromosome, genome, cell, multicellular organism, society). How did this come about, and what are the implications of hierarchical organization for individuality and the meaning of fitness in evolutionary explanation? Cooperation among lower-level units is central to the emergence of new higher levels, because only cooperation can trade fitness from lower to higher levels. My book is concerned with the study of cooperation, and the principles that guide the emergence of higher levels of organization. I have tried to show that there is a common set of principles and problems that bind the study of levels of organization as disparate as the gene, the cell, the multicellular organism, and whole societies. I focus here on the early transitions in the history of life (from genes to networks of cooperating genes to that first individual, the cell) and on the transition from single-celled organisms to multicellular ones.

These are exciting times for the study of cooperation. In the past, the study of cooperation has usually received less attention than the other two forms of ecological interaction, competition and predation. In the past scholars have viewed cooperation to be of limited interest, of special relevance to certain groups of organisms to be sure—the social insects, birds, our own species, and our primate relatives—but not of general significance to life on earth. All that has changed with the study of evolutionary transitions and the emergence of new units of selection. What began as the study of animal social behavior some thirty-five years ago has now embraced the study of interactions at all biological levels. Instead of being viewed as a special characteristic clustered in certain groups of social animals, cooperation is now seen as the primary creative force behind ever greater levels of complexity and organization in all of biology.

The benefit of group living results from cooperative interactions among group members. To create new levels of selection and organization in evolution, cooperation must be promoted among lower-level units, while, at the same time, ways must be found of mitigating the inherent tendency of the lower-level units to compete with one another through frequency-dependent fitness effects. Because cooperation is usually costly to the fitness of individuals within the group, defecting mutants can arise and take over the

group, in the process destroying cooperation and the very conditions that made their increase possible in the first place. Cooperation is a critical factor in the emergence of new units of selection precisely because it trades fitness from the lower level (its costs) for increased fitness at the group level (its benefits). In this way, cooperation can create new levels of fitness (see tables 3-1 and 5-1).

The study of evolutionary transitions is the study of the emergence of new levels of fitness. Fitness is the most fundamental and unique concept in all of biology—pretty much everything else in biology is chemistry and physics, or a remnant of history. Although fundamental, it is difficult to define fitness and to explicate its role in evolutionary explanation, especially its role in evolutionary transitions. Fitness is both a cause and effect of evolutionary transitions. When it is traded between evolutionary units during cooperative interactions new levels of fitness and individuality may emerge. I hope to explain in the following pages how fitness is constructed out of evolutionary and population processes.

Understanding the emergence of higher levels of organization in evolution requires a population genetics theory of interaction in a multilevel context. I have tried to provide such a theoretical framework, and to apply it to evolutionary transitions from the molecular level to the whole organism. Further, because the study of evolutionary transitions is basically the study of the emergence of new levels of fitness, I have sought to clarify the role of fitness in this theory and in evolutionary explanation in general.

I take a dynamical point of view on evolution and on fitness concepts. Evolution has no enduring products—even organisms are of only fleeting existence, each born unique because of sex, each soon to die. Accordingly, I argue that to be construed correctly, fitness should apply to the process of genetic change (much as R. A. Fisher and G. Price envisioned) and not to products of evolution, such as organisms. I investigate fitness from the molecular level up to the level of the whole organism. With the understanding made possible by recent developments in ecology, multilevel selection theory, and the origin of life, it is now possible to present a theory of fitness. In so doing, I give special attention to fitness levels and their origins and transitions in the evolutionary process. Finally, I consider the philosophical implications of my theory of fitness for explanation in biology.

Before Darwin, design was understood as a product of either the human mind or a Creator. A watch implies a watchmaker, so argued William Payley in 1802. Darwin changed all that. Darwin argued that the design apparent in life arises out of processes intrinsic to life, not from extrinsic forces. Differen-

tial birth and death rates within populations of organisms—when systematically related to features in the environment—explain the well-designed features of organisms. The human eye, the grasp of the tiger's paw, the match of the pollinator with the flower, even the human mind—all must arise out of the blindly mechanistic process Darwin called natural selection.

Sounds simple, almost too simple, for there is a lot of explaining to do. How does the theory of evolution actually go about explaining design? One concept is central—fitness. Fitness is what makes biology different. But what is fitness and where did it come from?

The great philosopher Karl Popper dismissed biology as not being science, because he thought its central doctrine, “survival of the fittest,” was a tautology. Who are the fittest? he asked. Those who survive of course. Darwin's great principle becomes the tautology “survival of those who survive,” much to the exasperation of evolutionary biologists who have little fear that their science can be reduced to empty truisms. Popper's challenge has been heard by a generation of philosophers of biology who have come to the rescue of evolutionary science. By and large, these defenses have followed Darwin's lead and viewed fitness as a property of organisms.

It is easy to be confused by organisms, fitted as they are with such wondrous designs. Organisms are born and they die. In between this birthing and dying they may have offspring, some more than others according to the traits they possess and their environment. But this birthing and dying of organisms is only a part of the selection process, for the organism does not exist in isolation. In many situations, especially during evolutionary transitions, other factors dominate and interfere with the individual as the maximizing agent. Of particular concern to the major transitions in evolution are the frequency-dependent fitness effects within populations that frustrate emergence of higher levels of organization. The organism is not a maximizing agent, but this does not mean that the organism is not a unit of selection, as Dawkins argues;¹ rather it means that there is more to natural selection than maximizing individual fitness. Organizational factors like multiple levels of selection, genetic factors like epistasis, linkage, and recombination, and ecological factors like population density, frequency, and age structure can intervene and decouple organism fitness from evolution. I argue that a dynamically sufficient concept of fitness cannot relate to an overall property of organisms but instead must be associated with the dynamics of evolutionary change. The modern theory of evolution demands this dynamical view of fitness.

I develop a formal theory for the evolution of interactions using the dynamics of natural selection. Of course, the founding fathers of evolutionary

biology (Fisher, Wright, and Haldane) developed a basic selection theory—so what has changed? There have been three key developments in the last thirty or so years that make possible the synthesis I wish to make. First, the abstract selection coefficient of the old theory has been unpacked and connected to ecology and behavior, especially with regard to the role of interactions in affecting fitness. In Fisher's view, as embodied in his fundamental theorem of natural selection, the environment only deteriorates in time, undermining the state of adaptation of the population. What was once a black box, the environment, has now been given explicit ecological content. Population biologists and ecologists understand the environment far better and represent it explicitly in their models. Of central importance to evolutionary transitions is the role of interactions with other members of the population. Second, we understand in far greater detail the multilevel nature of selection and how natural selection occurs simultaneously at different hierarchical levels: gene, chromosome, cell, organism, group, and species. As a result of this multilevel approach, cooperation among different levels becomes not only possible but likely. I use the covariance approach to selection to embrace this multilevel setting. Finally, we have a sufficient (in principle) theory of the origin of life and genetic information. We understand where fitness comes from and how it emerged from chemistry and physics.

Armed with these recent developments and a dynamical theory of selection, I reconsider Popper's challenge and its fallout in the philosophical literature. How does evolutionary theory explain design and the fitness and individuality of evolutionary units?

Acknowledgments

I WISH to understand in a common theoretical framework evolutionary transitions between levels of organization in biology. I have been influenced by the research of many workers, most significantly R. A. Fisher, W. D. Hamilton, J. Maynard Smith, E. O. Wilson, and S. Wright. I have also been influenced by three previous works on evolutionary transitions (E. O. Wilson 1975; Buss 1987; Maynard Smith and Szathmáry 1995). I learned from Buss (1987) that the principles of conflict and cooperation can be applied to the sorting out of cell lineages during development. I read Wilson's book (1975) as a graduate student, and, although it focused primarily on the transition from multicellular organisms to societies, I appreciated its far-reaching and synthetic approach. My earlier interest in the theory of kin selection and the evolution of sociality in both organisms and molecular replicators (Michod 1984, 1980, 1979, 1983b, 1982; Michod and Anderson 1979; Michod and Hamilton 1980) stemmed from the excitement I felt from reading Wilson's book (1975) and from visiting with John Maynard Smith and the rest of the Population Biology Group at the University of Sussex in 1976. I am especially indebted to John Maynard Smith, and will always cherish the many discussions we have had together.

Over the years I have had many discussions with many people about the topics considered in this book, including W. Anderson, H. Bernstein, R. Brandon, H. Byerly, R. Ferriere, P. H. Gouyon, F. Hopf, S. Kleiner, C. Lavigne, J. Maynard Smith, D. Roze, D. S. Wilson, E. Szathmáry, and B. Wimsatt. The following colleagues commented on the manuscript and their criticisms and suggestions greatly improved it: A. Ariew, H. Bernstein, R. Brandon, H. Byerly, S. Gavrillets, C. Lavigne, D. Roze, and M. Wade. I appreciate the discussions and comments of the participants in my seminar on fitness in spring 1997 at the University of Arizona (H. Byerly, A. Ariew, M. Clauss, A. Corl, E. Hebets, M. McIntosh, J. Netting, J. Lie, J. Reiss). I thank D. Roze and J. Lie for allowing me to refer to their unpublished results. I appreciate the hospitality of E. Szathmáry and the staff at the Collegium Budapest/Institute for Advanced Study, and R. Ferrier and the Ecole Normale Supérieure de Paris, where I completed the book during my sabbatical in 1997–98. Grants from the National Science Foundation and the National Institute of Health funded the research upon which this book is based.

Darwinian Dynamics

The Language of Selection

PLAN OF THE BOOK

I have written this book for two kinds of readers, those interested in the theory of evolutionary transitions (to new levels of fitness and individuality) and those interested in the role of fitness in evolutionary explanation. I realize that the evolutionary biologist may find the excursions into philosophy tangential, while the philosopher interested in the nature of biological explanations may find the emphasis on formal mathematical models overly technical. I ask the indulgence of both types of readers to tolerate the needs of the other.

In chapter 1, I provide a general introduction to the basic terms and concepts of selection theory used in the book. I am more interested in the meaning of a few central terms and concepts and their use in evolutionary explanation than in providing an exhaustive compendium. A more formal introduction to the mathematics of selection theory as it relates to the evolution of interactions is given later in chapter 4.

Cooperative interactions are the basis of more inclusive evolutionary units. Because cooperation reduces the fitness of lower-level units, while increasing the fitness of the group, cooperation drives transitions to higher-level units. Defection, the antithesis of cooperation, is the bane of cooperative groups everywhere, because it is often favored within the group by its frequency-dependent advantages. In light of the central role of cooperation in evolutionary transitions, I pay special attention to the means by which cooperative interactions evolve and are later enforced during the emergence of individuality.

In chapters 2 and 3, I study the early evolutionary transitions, from chemical compounds to replicating molecules to gene networks, culminating in that first true individual, the cell. I emphasize the role and meaning of fitness during these transitions and how the dynamics of natural selection of these early evolutionary units may be studied using simple models from population biology. During an evolutionary transition, frequency-dependent selection within the group prevents the maximization of the fitness of the group. For this reason, simple fitness arguments cannot be used in the study of emergent complexity during evolutionary transitions. I find that

there is much more to the dynamics of natural selection than increase of better-designed individuals. The central problem during evolutionary transitions is how to move from groups of lower-level units to a new level of selection. In short, the group must become an individual. But how does this occur? Conflict mediation is the process by which lower-level change is modulated in favor of the new emerging unit.

In chapters 5 and 6, I study the transition from cells to multicellular organisms. Mutation and selection among cells during development provide variation both within and between the cell-groups, or proto-organisms. However, the level of cooperation and synergism attained is rather limited, even in genetically related cell-groups clonally derived from a single cell, the zygote. Within-organism mutation and selection frustrate the creation of the new higher-level unit. The evolution of greater levels of cooperation among cells, the proximate agent of design at the organism level, is frustrated by within-organism change. Individual organisms are more than groups of genetically related cooperating cells; they require higher-level functions that mediate conflict within and maintain harmony for the group. Conflict mediators evolve to modify the rules of interaction and selection at the cell and group levels. Conflict mediators facilitate the transition to the new level by increasing the covariance between fitness at the cell-group level and genes carried in the zygote, which increases the heritability of fitness at the new higher level.

In chapter 7, I begin by considering the meaning of fitness that emerges from my study of evolutionary transitions. The concept of design in biology must rest on the Darwinian principles underlying natural selection, because there can be no preexisting plan in evolution. When the consequences of Darwin's principles are fully understood as embodied in the dynamics of natural selection, there is no meaningful concept of the individual as a maximizing agent, especially when the units of selection are changing. Frequency-dependent fitness effects frustrate the creation of new evolutionary units and prevent the application of simple maximization arguments. The tension between lower and higher level units is never completely resolved in any evolutionary transition. Units of selection, such as genes, cells, or organisms, do not exist in isolation, nor are they completely interdependent. Instead, they exist in a hierarchy of nested but partially decoupled levels, and any focal level provides the context for lower-level units as well as the components for higher-level units. Because evolutionary units (genes included) play the roles of both context and component at the same time, the dynamics of natural selection at any level involves an interplay between the dynamics at all levels.

After considering the meaning of fitness that emerges from my studies, I consider touchstone cases of natural selection using my dynamical view of fitness: the so-called tautology problem, the evolution of sex and reproductive systems, the immortality of the germ line in contrast to the mortality of the soma, such old standbys as sickle-cell anemia and heterozygote superiority, and the existence of species as distinct entities. These studies of natural selection recommend a dynamical view of fitness. This conclusion is pursued in more philosophical vein in chapter 8, where I consider other interpretations of fitness and offer a general framework for the role of fitness in evolutionary explanation.

DARWINIAN DYNAMICS

Darwin proposed that evolution by natural selection occurs when a population of replicating entities possesses three characteristics: variation, heritability, and the “struggle to survive” (Darwin 1859). Darwin observed that all organisms have the potential to increase in numbers at an exponential rate and produce many more offspring than could possibly survive. Consequently, there must often be a competition in which some kinds of organism are better able to survive to reproduce. Such variations in survival and reproductive success (variations in individual fitness) provide the raw material for evolution by natural selection—so long as the traits are heritable (capable of being passed from parent to offspring). Darwin knew very little about how genes work, but he did appreciate that the tendency of offspring to resemble their parents is necessary for evolution. Today, we know that heritability results from the faithful, highly accurate replication of the nucleotide sequence information contained in DNA. Offspring resemble their parents because they possess copies of their parents’ genes.

Putting together Darwin’s properties of variation, the struggle to survive and reproduce, and heritability, we expect (Darwin certainly did) that heritable traits that aid in the struggle to survive and reproduce should increase in frequency in the population, and deleterious traits should decrease.¹ This is how natural selection is supposed to work. However, this expectation assumes that the unit of selection, usually taken to be the organism, is well established. During evolutionary transitions this is certainly not the case, and even after a new level has been established, lower-level change can produce results different than what we might expect. The view that more adapted traits always increase ignores many of the complicating factors that intervene during the life cycle of the organism—within-organism change, sex,

genetic factors such as linkage and pleiotropy, and ecological factors such as population frequency and density. This book should make it clear that there are many more outcomes contained in Darwin's conditions and the process of natural selection than simply the increase of more fit organisms.

My colleagues and I term dynamical equations based on Darwin's conditions "Darwinian dynamics" (Bernstein et al. 1983; Byerly and Michod 1991a,b; Michod 1986, 1984). Darwinian dynamics deserve special study as a general class of equations with special dynamical properties that may be used to understand the process of natural selection. In addition to their fundamental role in biology, Darwinian dynamics occur in the study of ordered phenomena in certain physical systems such as lasers. Darwinian dynamics provide an explicit well-defined context for understanding the role of fitness in evolutionary explanations, as will be shown in the last two chapters.

Many definitions of natural selection have been offered. I view natural selection as the process of change in gene and genotype frequencies resulting from Darwin's conditions. In offering this definition, my emphasis is on the conditions involved in the process rather than the outcome. Indeed, I think there are several, perhaps many, possible outcomes of natural selection consistent with Darwin's defining conditions.

Darwin's conditions of variation and heritability in fitness can, in principle, apply at any level in the hierarchy of life: genes, gene networks, chromosomes, bacteria-like cells, eukaryote-like cells, multicellular organisms, families, groups, and societies (Lewontin 1970). In this book, I am particularly interested in the progression of fitness relations as new levels of selection are created during evolution. The essence of a transition in evolutionary units is that lower-level units relinquish their claim to fitness, as it were, so that fitness may emerge at the new higher level. Cooperation drives the passage from one level of fitness to another, because cooperation trades increased fitness at the higher level for decreased fitness at the lower level. In chapters 2, 3, 5, and 6, I consider the conditions under which evolutionary transitions may occur. A more formal presentation of Darwin's conditions is given in chapter 8, in the section "Natural Selection as a Biological Law."

The orderly transformation of living systems through time depends on information encoded in the sequence of nucleotide base pairs in DNA. Genetic information must accomplish two seemingly contradictory feats, which baffled early geneticists: while accurately transferring itself from parent to offspring, the genetic material must be open to modification in the event that the environment changes. Informational noise—random changes

in the information sequence—is both a curse and a source of hope in this endeavor. Ultimately, all the variation underlying design in the living world comes from random changes to DNA, through either mutation or recombination.

Processes that produce informational noise should generally reduce fitness unless they also produce a benefit that offsets this deleterious effect. In living systems, informational noise is produced during the repair and replication of DNA (Bernstein et al. 1987)—the benefits of DNA repair and replication are self-evident. I have discussed elsewhere how recombination copes with genetic error while maintaining an open and flexible genetic system (Michod 1995). For natural selection to occur, the information in the genes must be perpetuated through time, or else the properties and relations of living things would not be heritable, that is, passed on from parent to offspring. Without the heritability of traits contributing to fitness, the life cycle would crumble, since offspring would no longer resemble their parents, and the flow of information underlying the fitness relations so necessary for the evolution of life would cease. In chapter 6 I pay special attention to how heritability of fitness may emerge at a new level.

MAJOR EVOLUTIONARY TRANSITIONS

Natural selection requires heritable variations in fitness. Levels in the biological hierarchy—genes, chromosomes, cells, organisms, kin groups, groups, societies—possess these properties to varying degrees, according to which they may function as units of selection in the evolutionary process (Lewontin 1970). From E. O. Wilson (1975) and the transition from solitary animals to societies, to Buss (1987) with the transition from unicellular to multicellular organisms, and more recently Maynard Smith and Szathmáry (1995; Szathmáry and Maynard Smith 1995), attention has focused on understanding transitions between different levels of selection.

The major transitions in evolutionary units are from individual genes to networks of genes, from gene networks to bacteria-like cells, from bacteria-like cells to eukaryotic cells with organelles, from cells to multicellular organisms, and from solitary organisms to societies (Buss 1987; Maynard Smith and Szathmáry 1995; Maynard Smith 1991, 1990, 1988). These transitions in the units of selection share two common themes: the emergence of cooperation among the lower-level units in the functioning of the new higher-level unit, and regulation of conflict among the lower-level units.

Eigen and Schuster proposed the hypercycle as a way to keep individual

genes from competing with one another so that cooperating gene networks could emerge (Eigen and Schuster 1979; Eigen 1992). Localizing genes in the cell keeps selfish parasitic genes from destroying the cooperative nature of the genome (Michod 1983b; Eigen 1992; Maynard Smith and Szathmáry 1995). These early transitions from genes to gene networks to cells are discussed in chapters 2 and 3. Chromosomes reduce the conflict among individual genes (Maynard Smith and Szathmáry 1993, 1995). Meiosis serves to police the selfish tendencies of genes and usually insures that each of the alleles at every diploid locus has an equal chance of ending up in a gamete. As a result of the fairness of meiosis, genes can increase their representation in the next generation only by cooperating with other genes to help make a better organism. Uniparental inheritance of cytoplasm may serve as a means of reducing conflict among organelles through the expression of either nuclear genes (Hoekstra 1990; Hurst 1990; Hastings 1992), or organelle genes (Godelle and Reboud 1995), or both. Finally, concerning the final transition—that from organisms to societies of cooperating organisms—the theories of kin selection, reciprocation, and group selection (introduced in chapter 4) provide three related mechanisms for the regulation of conflict among organisms: genetic relatedness, repeated encounters, and group structure. These are just a few of the ways in which the selfish tendencies of lower-level units are regulated during the emergence of a new higher-level unit.

As initially conceived, the field of sociobiology focused on the transition from solitary organisms to groups of organisms, or societies, and the emergence of cooperative functions at the social level, the level of the colony, say, in the case of eusocial behavior in insects (E. O. Wilson, 1975). However, the set of tools and concepts used in studying conflict and cooperation during the transition from organisms to societies has proved useful for studying the other major transitions.

COOPERATION AND CONFLICT

New evolutionary units begin as groups of existing units. Two issues are central to the creation of a new unit of selection: promoting cooperation among the lower-level units in the functioning of the group, while at the same time mitigating the inherent tendency of the lower-level units to compete with one another through frequency-dependent fitness effects. Cooperation represents the benefit of group living; groups of individuals can then behave in new and useful ways. Cooperation is a critical factor in the emer-

gence of new units of selection precisely because it trades fitness at the lower level (its costs) for increased fitness at the group level (its benefits). In this way, cooperation can create new levels of fitness (see, for example, tables 3-1 and 5-1).

Frequency-dependent interactions among evolutionary units are both a source of novelty for the group and a threat to its collective well-being. Because cooperation is usually costly to the fitness of the individuals involved, defection may reap the benefits of cooperation and spread in the population, thereby destroying the very conditions upon which its spread depended in the first place. As a result of the spread of defection, cooperation is lost and along with it any hope for the creation of a new higher level.

Certain conditions are required to overcome the inherent limits posed by frequency-dependent selection to the emergence of new levels of selection: kinship, population structure, and conflict mediation. Conflict mediation is the process by which lower-level change is modulated in favor of the new emerging unit.

The theory of cooperation and conflict presented here is concerned with populations of interacting and replicating entities (genes, cells, organisms) that share a common ecological and/or genetic context. For the most part, this means either a common resource base in the case of replicating molecules studied in chapters 2 and 3 or a common gene pool and group setting in the cases of cells within organisms studied in chapters 5 and 6. I study symbiosis (cooperation between genetic units that were once capable of independent existence) in the context of the origin of cooperating networks of genes in chapter 3, in the game theory of cooperation in chapter 4, and in the transition from cells to organisms in chapters 5 and 6. However, I do not study the symbiotic origin of mitochondria, chloroplasts, and microbodies that make up the eukaryotic cell (Margulis 1970, 1981). Symbiosis is of fundamental importance to the emergence of complexity during evolution, but there are also other ways in which evolutionary transitions may occur (Maynard Smith and Szathmáry 1995).

FISHERIAN FITNESS

There are many legitimate notions of "fitness." In discrete-generation population genetics models, fitness is often defined as the expected reproductive success of a type (reproductive output weighted by survival). I refer to this notion of fitness as individual fitness.² There are other meanings to the term "fitness," however. In his explorations into natural selection, R. A.

Fisher defined fitness as the rate of increase of a type, often expressed on a per capita basis (1930). I refer to Fisher's notion of fitness as *F-fitness*. It is difficult to commit to any one definition of fitness, because there are many legitimate definitions, each suited to a different purpose. On this topic, I have much more to say. However, at the outset let me say that I find Fisher's notion of fitness by far the most encompassing and dynamically sufficient concept of fitness, especially when the levels of selection are changing. For this reason, I return to Fisher's concept when discussing philosophical matters in the last two chapters.

Why did Fisher focus on the rate of increase? Because it "measures fitness by the objective fact of representation in future generations" (Fisher 1958, p. 37). The per capita rate of increase is the bottom line in population studies in both ecology and genetics. For a discussion of the central role of the per capita rate of increase in both population ecology and population genetics, see Ginzburg 1983, especially chapter 1. For an especially clear presentation of *F-fitness* in the context of genetic models, see Denniston 1978 (where *F-fitness* is termed r_{ij}). Fisherian fitness is given in equation (1-1), letting X_i denote the density or frequency of type i in a population and t denote time:

$$F_i \equiv \frac{1}{X_i} \frac{dX_i}{dt}. \quad (1-1)$$

A genotype's rate of increase expresses its reproductive success over time and ultimately determines its evolutionary success (at least for the short term, which tends to be how natural selection acts). Confusion may arise, however, because the rate of increase of a genotype does not usually depend on properties of the genotype in isolation. In addition to depending on the environment and the composition of the population, a genotype's rate of increase in a sexual population depends upon the properties of the genotypes of all potential mates.

Fisher referred to the rate of increase of a genotype as the "Malthusian parameter," denoted m . Later workers often represented m as if it were a property of the genotype alone, expressing it in terms of the genotype specific rates of birth and death as follows (Crow and Kimura 1970):

$$\frac{1}{X_i} \frac{dX_i}{dt} = m_i \stackrel{?}{=} b_i - d_i \quad (1-2)$$

The problem with the decomposition of fitness given in equation 1-2 is that the per capita rate of increase cannot usually be expressed as a function of individual genotypic capacities alone, capacities such as b_i or d_i . Because

this is misleading as a general analysis of fitness, I have put a “?” above the equal sign in equation 1-2. Later work has shown that the formulation given in equation 1-2 assumes fixed per capita birth and death rates (Charlesworth 1980), assumptions that are unlikely to hold if the genotypic composition of the population is changing, especially if genotypes interact in their effects on fitness, or if there is sex. Almost everything going on in the population affects the rate of increase of a type, and so Fisherian fitness cannot be regarded as the sole property of the individual or genotype.

Nevertheless, as we see in later chapters, Fisher’s term “Malthusian” is appropriate, because the decomposition of fitness embodied by the right-hand side of equation 1-2 holds in a meaningful sense, though not in the sense of the equality given in equation 1-2. When population growth is a linear function of density, exponential or Malthusian growth results. The goal embodied on the right-hand side of equation 1-2 is to express evolutionary success (the left-hand side of the equation) as a function of the individual capacities alone given on the right-hand side. When population growth is Malthusian (linear in density), the condition for mutant invasion involves only b_i and d_i (see equation 2-5 or equation 3-3 below). So the decomposition of evolutionary success suggested by equation 1-2 applies to mutant invasion (even though the equality in equation 1-2 does not generally hold). This is why I find Fisher’s term “Malthusian” especially appropriate.

The approach embodied in equation 1-2 formulates a goal of the theory of natural selection—to express evolutionary success of a type, say a genotype, as a function of the genotype’s individual capacities and characteristics. In equation 1-2, evolutionary success is represented by genotype i ’s fitness in Fisher’s sense as a rate of increase, $(1/X_i) (dX_i/dX_i)$, and the genotype’s capacities are represented simply by b_i and d_i . More generally, the genotype’s capacities can be any attributes of interest. In this respect, the decomposition of fitness studied in chapters 7 and 8 follows Fisher’s lead. The challenge is to express evolutionary change as a function of individual capacities in a way that is dynamically sufficient and accurately represents the underlying causal nexus of individual, genetic, ecological, and population factors, something that equation 1-2 fails to do.

DECONSTRUCTING FITNESS

Evolutionary explanations based on natural selection require the construction of models that involve the causal components of fitness for the prob-