

# HOLISTIC DARWINISM

---

*Synergy, Cybernetics, and the Bioeconomics of Evolution*

Peter A. Corning

*The University of Chicago Press • Chicago & London*

## Contents

---

	Introduction: The New Evolutionary Paradigm	<i>1</i>
<b>Part I</b>	<b>Synergy and Evolution: From the Origins of Life to Global Governance</b>	
1	Synergy: Another Idea Whose Time Has Come?	<i>11</i>
2	Holistic Darwinism: Synergistic Selection and the Evolutionary Process	<i>17</i>
3	The Synergism Hypothesis: On the Concept of Synergy and Its Role in the Evolution of Complex Systems	<i>47</i>
4	Synergy versus Self-Organization in the Evolution of Complex Systems	<i>89</i>
5	The Re-Emergence of Emergence: A Venerable Concept in Search of a Theory	<i>123</i>
6	Synergy, Cybernetics, and the Evolution of Politics	<i>141</i>
7	Devolution as an Opportunity to Test the Synergism Hypothesis and the Cybernetic Theory of Political Systems	<i>165</i>
8	Synergy and the Evolution of Superorganisms: Past, Present, and Future	<i>187</i>
<b>Part II</b>	<b>Bioeconomics and Evolution</b>	
9	Evolutionary Economics: Metaphor or Unifying Paradigm?	<i>215</i>
10	Bioeconomics as a Subversive Science	<i>237</i>
11	Biological Adaptation in Human Societies: A Basic Needs Approach	<i>253</i>

<b>Part III</b>	<b>From Thermodynamics and Information Theory to Thermoeconomics and Control Information</b>	
12	To Be or Entropy: Thermodynamics, Information, and Life Revisited	313
13	Thermoeconomics: Beyond the Second Law	335
14	Control Information: The Missing Element in Norbert Wiener's Cybernetic Paradigm?	361
<b>Part IV</b>	<b>Evolution and Ethics</b>	
15	Evolutionary Ethics: An Idea Whose Time Has Come?	379
16	The Sociobiology of Democracy: Is Authoritarianism in Our Genes?	403
17	Fair Shares: A Biological Approach to Social Justice	417
	Acknowledgments	449
	Notes	453
	References	473
	Index	529

## Introduction

# The New Evolutionary Paradigm

A major paradigm shift is currently underway in evolutionary theory. Neo-Darwinism—the reductionist, mechanistic, gene-centered approach to evolution epitomized by the selfish gene metaphor of Richard Dawkins—has come under assault from various quarters. These attacks have included the following:

- **A growing appreciation for the fact that evolution is a multilevel process, from genes to ecosystems;** coevolution has come to be recognized as a many-faceted phenomenon.
- **A revitalization of group selection theory,** which was banned (too hastily) from evolutionary biology more than thirty years ago.
- **An increasing recognition that symbiosis is an important phenomenon in nature and that symbiogenesis is a major source of innovation in evolution.**
- **A broad array of new, more advanced game theory models,** which support the growing evidence that cooperation is commonplace in nature and not a rare exception.
- **New research and theoretical work that stresses the role of developmental dynamics, “phenotypic plasticity,” and organism-environment interactions in evolutionary continuity and change;** an inextricable relationship between nature and nurture are the rule, rather than the exception.
- **A flood of publications on the role of behavior, social learning, and cultural transmission as pacemakers of evolutionary change,** a development that is especially relevant in relation to the evolution of humankind.
- **New insights into the nature of the genome,** and increasing respect for the fact that the genome is neither a “bean bag” (in biologist Ernst Mayr’s caricature)

nor a gladiatorial arena for competing genes but a complex, interdependent, cooperating system.

- **The emergence of hierarchy theory**, which stresses that the natural world is structured and influenced by hierarchies of various kinds.
- **The rise of systems biology**, a new field that emphasizes the systemic properties of living organisms; one scientist, writing in the journal *Science*, called it “whole-istic biology.”
- **The claims advanced by various theorists for the role of autocatalysis, self-organization, network dynamics, and even “laws” of evolution (though I remain guarded about them).**

The crux of the debate, however, has to do with the evolution of complexity. An individualistic, gene-centered theory seems insufficient to account for the evolution of more complex, multileveled biological systems over time. It is increasingly evident that the selfish gene metaphor is inadequate. A more appropriate metaphor is the cooperative gene (see Corning 1996a; Ridley 2001). Thus, a major challenge for evolutionary theory is to develop a better understanding of cooperation and complexity in the natural world. Many theorists are now looking beyond the individualistic, mutation-competition-selection paradigm.

Accordingly, the term *Holistic Darwinism* is not an oxymoron. Nor does it refer to some metaphysical abstraction. It is a candidate name for the new paradigm that is emerging as an alternative to Neo-Darwinism. It also involves a theory about the role of “wholes” in evolution.

First and foremost, Holistic Darwinism views evolution as a dynamic, multilevel process in which there is both “upward causation” (from the genes to the phenotype and higher levels of organization) and “downward causation” (phenotypic influences on differential survival and reproduction), and even “horizontal causation” (between organisms). In this paradigm, the emergence of higher-level “individuals” (in Michael Ghiselin’s characterization) are not epiphenomena; they *act* as wholes and exert causal influences as distinct evolutionary units. They may constrain, control, and even differentially determine the fate of various parts (genes). To borrow a metaphor from the biologist Egbert Leigh (1977), selfish genes are subject to the “parliament of the genes.” I call it the “selfish genome” model, but the principle applies equally well to selfish groups, selfish colonies, selfish packs, selfish bands, and even selfish nation-states, as we shall see (see also Corning 1997a).

A second major feature of Holistic Darwinism is that it serves as an umbrella for a broad theory of cooperation and complexity in nature first

proposed in *The Synergism Hypothesis* (Corning 1983). This theory has recently been gaining support among biologists and social scientists. Both the historical background and more recent developments relating to this theory are detailed in chapter 1.

A critique of Neo-Darwinism and the case for Holistic Darwinism are presented in chapter 2, along with a brief introduction to the Synergism Hypothesis. The hypothesis, in brief, is that synergy—a vaguely familiar term to many of us—has been a wellspring of creativity in the natural world and has played a key role in the evolution of cooperation and complexity at all levels of living systems. This theory asserts that synergy is more than a class of interesting and ubiquitous effects in nature. It has also been a major *causal agency* in evolution; it represents a unifying explanation for complexity at all levels of living systems.

Moreover, this theory is fully consistent with Darwin's theory. It involves only a different perspective on the evolutionary process. In contrast with gene-centered theories, or postulates of self-organization and emergent "laws" of complexity, the Synergism Hypothesis represents, in essence, an economic (or, more precisely, bioeconomic) theory of complexity. It is postulated that the functional payoffs produced by various kinds of synergy have been the drivers of this important evolutionary trend. After a brief survey of the many different kinds of synergy in the natural world (including examples drawn from a variety of disciplines), the case for the Synergism Hypothesis is presented in detail in chapter 3, along with some ways of testing the theory.

A third major feature of Holistic Darwinism is that it fully acknowledges the "teleonomy" (purposiveness) of living systems and incorporates this important aspect of the natural world into the causal dynamics of the evolutionary process itself. This pertains especially to behavior, which has often served as a "pacemaker" of evolutionary change (in Ernst Mayr's famous characterization). Sometimes this is referred to as the "Baldwin effect" (see chapter 2), but credit for the idea that a change in an organism's "habits" can influence the course of evolution should properly be given to Jean Baptiste de Lamarck (even though he guessed wrong about the "mechanism" involved). The role of teleonomy and self-determination in evolution, as well as the relationship between synergy and self-organization, are discussed in chapter 4.

A fourth feature of Holistic Darwinism is that it also encompasses the phenomena associated with emergence—the recently rediscovered nineteenth century term for the idea (traceable back to Aristotle) that wholes may have distinct properties that transcend their parts. The re-emergence of

emergence is reviewed in some detail in chapter 5, along with a discussion of how emergence relates to synergy and the Synergism Hypothesis.

Another important aspect of Holistic Darwinism is that it also applies to human evolution and to the evolution of human cultures and their political systems. In fact, synergy played a key causal role in the evolution of humankind, and so did cybernetic (political) processes—decision making, social communications, social control, and feedback. Nor are such processes unique to our species. Analogous cybernetic processes are found in slime molds, leaf-cutter ants, naked mole rats, killer whales, and our closest primate relatives, among others; they are a fundamental feature of social life. The intimate relationship between synergy, cybernetics, and the bioeconomics of sociality is discussed in chapter 6. Devolution, which provides a major opportunity for testing this theory, is defined and explored in chapter 7.

Finally, Holistic Darwinism embraces the recently revitalized “superorganism” concept, which has regained respectability in evolutionary biology after a long, ideologically tainted period in the wilderness. Actually, the so-called organismic analogy has ancient roots. It was first articulated by the classical Greek theorists as a way of characterizing human societies, and it has been utilized by many other political theorists over the past two thousand years. However, the term *superorganism* itself was coined by the nineteenth century polymath Herbert Spencer, who focused especially on the division of labor and the problem of functional integration in complex systems. The history of this concept is briefly reviewed in chapter 8, along with a survey of the many examples found in nature. It is also stressed that cybernetic processes are essential concomitants of superorganisms of all kinds. More important, this broad evolutionary perspective also applies to the ongoing political evolution of human societies, including the prospects for global governance.

Part 2 of this volume comprises three chapters on the subject of bioeconomics—a key element of the paradigm shift identified with Holistic Darwinism. Over the years, much has been made of the relationship between “the economy of nature” (a term of art that Darwin borrowed from Linnaeus) and human economies. More recently, there has also been much cross-fertilization between biology and economics, especially in areas such as behavioral ecology, evolutionary game theory, evolutionary economics, ecological economics, and the like. However, the connection between biology and economics goes beyond analogies, and beyond methodologies. There is also a deeper-level homology, which the new interdiscipline of

bioeconomics is helping to illuminate. In a nutshell, the fundamental linkage between biology and economics derives from the fact that humans share with all other living species the fundamental problems of survival and reproduction. This bedrock challenge is multifaceted, ongoing, and inescapable; it can never be permanently solved. Indeed, whether we are aware of it or not, the overwhelming majority of our activities as a species are devoted to various aspects of the survival problem (either directly or indirectly). A human society represents, quintessentially, a “collective survival enterprise.” This important metatheoretical issue is addressed in chapter 9 in the course of a review essay on how the new interdisciplinary of evolutionary economics should be defined and developed.

Chapter 10, “Bioeconomics as a Subversive Science,” elaborates on this theme and mounts a frontal challenge to the basic premises of traditional (neoclassical) economics. In effect, bioeconomics redefines the nature and purpose of a society, and an economy. The “ground-zero premise” (so to speak) of the life sciences is that survival and reproduction represent the basic problem for all living organisms, and this bedrock challenge applies also to human societies. It is the “paradigmatic problem” for all economies, and economic performance must ultimately be judged in these terms, not in relation to economic growth or gross domestic product or other conventional economic measures. Indeed, even traditional income and standard of living measures may be woefully inadequate. Chapter 11, an expansion on an essay that originally appeared in the *Journal of Bioeconomics* (Corning 2000), follows through on this theme. It applies the concept of biological adaptation specifically to human societies and develops a detailed framework of fourteen basic needs that define the parameters of the survival/reproduction problem for humankind. There is also a brief introduction to the “Survival Indicators” program, which represents an effort to deploy an array of concrete measuring rods, or gauges, for adaptation similar to the economic and social indicators that are already widely used by social scientists and policy makers.

Part 3 then addresses the theoretical foundations of evolutionary theory in general—and Holistic Darwinism in particular—at a much deeper level. Two major areas of modern physics, namely thermodynamics and information theory, have made significant incursions into evolutionary theory over the past twenty years or so, and some major claims have been made on behalf of both the so-called entropy law and Claude Shannon’s statistical information theory. In chapter 12, based on a paper coauthored by the late Stephen Jay Kline (emeritus professor of engineering at Stanford University



and a leading expert on thermodynamics), the pretensions of these theoretical schools are sharply criticized. Major alternatives to these formulations are then developed in chapter 13 (on thermoeconomics) and chapter 14 (on control information). These new formulations are entirely compatible with Darwin's theory and with the teleonomic, cybernetic approach to the role of information in evolution that is described in part 1. The term *thermoecconomics* refers to the use of economic criteria to understand the role of energy in evolution, and *control information* describes a new, cybernetic (functional) kind of information that is measured in terms of the energy that can be controlled in a given context. Examples are provided to illustrate each concept.

Finally, part 4 includes some writings that examine the long-standing and vexed debate over evolutionary ethics—an inescapable aspect of any paradigm shift in evolutionary theory. The history of this debate is briefly summarized in a review essay (chapter 15), and it is argued that evolutionary ethics is indeed an idea whose time has come. Once the narrow, constricted, individualist caricature associated with Neo-Darwinism is replaced by the more balanced, ecumenical, economically oriented paradigm of Holistic Darwinism (not to mention a more balanced view of human nature and the role of cooperation in human evolution), the main theoretical impediment to a robust evolutionary ethics is removed. In chapter 16, this perspective is applied specifically to a critique of a recent volume on the sociobiology of democracy. The authors of that work hold a dour view of democracy's prospects, but I disagree with their analysis.

The ethical implications of Holistic Darwinism are more fully articulated in a final essay entitled "Fair Shares" (chapter 17), which seems especially relevant in light of recent economic trends. The two major twentieth century political ideologies are critiqued and the durable concept of fairness—now a "hot" research area in the social sciences—is advanced as a more balanced alternative. The important advantage of this middle-ground alternative is that it is grounded in an evolutionary and biological framework; it has a strong empirical basis. (This is reflected in the subtitle, "a biological approach to social justice.") Chapter 17 could also have been subtitled "beyond John Rawls," for it does not rely on an artificial philosophical construct; it grounds (and justifies) the concept of fairness in the biological sciences, and it implies certain specific principles for how to apply this criterion in human societies. It reaches the conclusion that we cannot avoid making ethical choices and that many of these have significant consequences for our ultimate survival and reproductive success. As the biologist Garrett Hardin (1972, p. 360) pointed out:

We cannot *predict* history but we can *make* it; and we can *make* evolution. More: we cannot avoid making evolution. Every reform deliberately instituted in the structure of society changes both history and the selective forces that affect evolution—though evolution may be the farthest thing from our minds as reformers. We are not free to avoid producing evolution; we are only free to close our eyes to what we are doing.

One final note: Many of the chapters in this volume previously appeared in peer-reviewed journals during the past few years, though they have been edited and updated in various ways. Others served as the basis for presentations at professional meetings, including the International Society for the Systems Sciences, the New England Complex Systems Institute, the Human Behavior and Evolution Society, the International Society for Human Ethology, the International Society for Endocytobiology, and the Association for Politics and the Life Sciences. The relevant citations and acknowledgments are included at the end of the book. However, it should be stressed that this is not simply a disparate collection of writings on various subjects. Each chapter forms an essential part—a building block—for the theoretical structure that I have called Holistic Darwinism; each chapter is a part of a synergistic whole that, it is hoped, will help to advance the emerging new, post-Neo-Darwinian evolutionary paradigm. Three of the major aspects of this new paradigm, to reiterate, are synergy, cybernetics, and bioeconomics. More important, in this paradigm, selfish genes are the servants, not the masters. To borrow a punch line from a later chapter, many “engines” have been proposed to account for the evolution of complexity, but the engine is nothing without the car. It is time to focus on the car.

## Synergy: Another Idea Whose Time Has Come?

### Catching the Flood Tide

Shakespeare's famous metaphor has been borrowed by many modern authors, perhaps because it captures an eternal truth. In the 1930s the historian Arthur Schlesinger (senior) used this image in a widely acclaimed article called "Tides of American Politics" (1939). In the 1960s, the French historian Jacques Pirenne wrote a magisterial volume that was translated and published in English as *The Tides of History* (1962). Political scientist Karl Deutsch also used the metaphor in the title of his classic text *Tides among Nations* (1979).

More recently, a search of the Internet bookseller amazon.com produced a total of 274 current titles that include the word "tides." There are books on corporate tides, the tides of power, tides of migration, tides of change, the tides of reform, China against the tides, NATO and the tides of discontent, the tides of war, the tides of love, and political tides in the Arab world, as well as, of course, many volumes related to ocean tides.

Our everyday lives are also subject to such tidal influences, especially in the business world, in the arts, and in politics. This year's fad is often next year's remainder or closeout sale item. This year's titanic blockbuster movie will be available for rental next year for a pittance. And this year's hot political issue may be ignored by the media next year, even though the underlying problem still exists.

Although we like to think that science is free from such extraneous influences, of course this is not so. Thomas Kuhn, in his celebrated volume *The Structure of Scientific Revolutions* (1962), argued that science is very much influenced by the tidal effects associated with different paradigms. Ideas and theories that fit within or support the currently dominant framework of basic

assumptions and theories in a given discipline are more likely to be favorably received. On the other hand, conflicting work, especially if it challenges the dominant paradigm, is often ignored or rejected. Kuhn's specific scenario for scientific revolutions has been much debated. Nevertheless, there seems to be widespread agreement that Kuhn's core idea is valid, even if the dynamics may be somewhat different from his original formulation.

A classic case in point is biologist Barbara McClintock's work on the so-called jumping genes—genetic rearrangements during ontogeny via what are now called transposons (or transposable elements) that can produce variations in the phenotype of an organism (such as the different color patterns in maize). This phenomenon, painstakingly documented by McClintock over twenty years, remained in the shadows until late in her life. The reason was that it contradicted the then-reigning central dogma of molecular biology—namely, that the genome is expressed during ontogenesis in a linear, deterministic fashion (DNA to RNA to proteins). Now, of course, it is recognized that ontogeny is a much more complex process and that a variety of nonlinear, feedback-dependent influences may affect the outcome (see E. F. Keller 1983).

In a similar fashion, the dominant paradigm in the social sciences for the better part of the past century utilized as its core premise the assumption that human behavior and cultural processes are determined (caused) by the socio-cultural environment, and that biological influences are largely irrelevant. According to the widely quoted dictum of Emile Durkheim, one of the founding fathers of sociology, "Every time that a social phenomenon is directly explained by a psychological phenomenon, we may be sure that the explanation is false" (1938, p. 104). Among the many consequences of this dogmatism was a wall of prejudice against any purported facts that conflicted with socio-economic and cultural explanations. Accordingly, Edward O. Wilson's paradigm-shattering textbook, *Sociobiology: The New Synthesis* (1975), was greeted by many mainstream social scientists with great hostility. This is not surprising; Wilson threatened their core assumptions and challenged the hegemony of their explanatory apparatus. (The term *sociobiology* was actually coined by the pioneer biopsychologist John Paul Scott, but Wilson made it famous.)

Now it seems that another, somewhat less contentious tide change is underway, one that is affecting both evolutionary biology and the social sciences. It is a shift that, hopefully, will result in a more balanced, multileveled, interactional perspective on the evolutionary process generally and the ongoing evolution of the human species in particular. Over much of the past twenty-five years, evolutionary theory has been dominated by the "selfish gene" (or Neo-Darwinian) paradigm, so named after biologist Richard Dawkins's famous 1976 book by that title. The selfish gene metaphor epitomizes a reductionist perspective in which atomistic individual competition is viewed as the predominant, if not exclusive, shaping force in evolution. In this view, cooperative

phenomena are not only very limited in scope but are reducible to gene self-interest; higher-level cooperative relationships are even considered by some theorists to be epiphenomena that are not causally important in their own right.

Given this predisposition among many evolutionary theorists of the 1980s, a new theory about the role of synergy in evolution—about cooperative effects of various kinds as a causal mechanism in the evolution of complexity—was, in retrospect, launched on a strongly unfavorable tide. The theory was developed in a book-length monograph called *The Synergism Hypothesis: A Theory of Progressive Evolution* (Corning 1983), and it was largely ignored at the time that it was published. Not only did this theory challenge the dominant Neo-Darwinian paradigm, shifting the focus from competition to cooperation (or, better said, to competition via cooperation), but it directed attention away from genes and stressed the functional dynamics of living systems at various levels of organization—that is, the functional effects produced by the phenotypes. As a corollary, this theory also proposed to shift the explanatory focus to the economics of survival and reproduction.

Paradoxically, at the time this theory was first proposed, the concept of synergy was already widely used in biochemistry, physiology, pharmacology, and related disciplines. (A search of a biological database for the year 1988 using the keyword “synerg” identified 613 references, of which 95 percent were related to these hard sciences.) However, in evolutionary theory and the behavioral sciences the concept of synergy was largely ignored during those years—aside from a few eccentric uses by the anthropologist Ruth Benedict, the engineer-inventor Buckminster Fuller, and a handful of others. Of course, the term *synergy* is often used—and misused—in the business world, most notably in relation to corporate mergers and the like.

### A Tide Change in Evolutionary Theory

Today there is every indication that the tide has turned. One early sign was the adoption of the synergy concept by biologist John Maynard Smith (1982a, 1983, 1989), who developed a synergistic selection model to characterize the interdependent functional effects that may arise from altruistic cooperation. (Maynard Smith later broadened the concept to accord with a strictly functional interpretation, whether altruistic or not.) The work of political scientist Robert Axelrod and biologist William Hamilton (1981; also see Axelrod 1984) on the evolution of cooperation, which relies on the game theory methodology pioneered by Maynard Smith, was also important.

Another significant contribution was made by biologist Leo Buss in his 1987 book on the evolution of higher levels of organization, which invoked the concept of synergy, albeit in a narrow sense and without much elaboration. The biologically oriented psychologist David Smillie (1993) has also utilized the

concept of synergy in relation to social interactions in nature. Biologist David Sloan Wilson and various colleagues have also played a role with their dogged efforts over the past twenty-five years to put the concept of group selection on a new footing (D. S. Wilson 1975, 1980; Wilson and Sober 1994; Wilson and Dugatkin 1997; Sober and Wilson 1998). Although Wilson's paradigm remains gene-centered, he stresses the role of what he calls a "shared fate" among individual cooperators, which implies a functional interdependency.

Especially important, though, is the work of biologist Lynn Margulis on the role of "symbiogenesis" in evolution (particularly in relation to the origin of eukaryotic cells). Now recognized as a major theoretical contribution, this concept has focused attention on an area in which synergistic functional effects have played a key role (see Margulis 1981, 1993; Margulis and Fester 1991; Margulis and Sagan 1995). Indeed, the relatively new discipline of endocytobiology—inspired in part by Margulis's work but centered in Europe—is concerned especially with investigating symbiotic and synergistic phenomena of various kinds at the cellular level.

Perhaps the most significant sign that a favorable tide now exists for the synergy concept is the publication of two books coauthored by John Maynard Smith and Eörs Szathmáry on the evolution of complexity, *The Major Transitions in Evolution* (1995) and *The Origins of Life* (1999), which feature the role of synergy at various levels of biological organization. Maynard Smith came to recognize the universal importance of functional synergy (personal communication), as did Ernst Mayr (personal communication). Nowadays, articles about synergy in evolution are routinely accepted for publication, whereas fifteen years ago they were routinely rejected.

Complexity is also recognized by many theorists these days to be a distinct emergent phenomenon that requires higher-level explanations. In fact, there is a rapidly growing literature in complexity theory—much of it powered by the mathematics of nonlinear dynamical systems theory—that is richly synergistic in character; it is primarily concerned with collective properties and collective effects. To be sure, much (but not all) of the work in complexity theory involves a radically different view of the evolutionary process from the functional, selectionist paradigm within which the Synergism Hypothesis fits. For instance, the biophysicist Stuart Kauffman's work (e.g., 1993, 1995, 2000) is directed toward trying to identify overarching laws of biological order. His metatheoretical premise is that much of the order found in nature is self-organized—"order for free" as he puts it. (Ultimately, I believe that both self-organizing influences and synergistic functional influences will be recognized as important mechanisms in the evolution of complex systems. For more on this issue, see chapter 4.)

Even the concept of progressive evolution—lately denigrated as an outmoded idea (see especially Nitecki 1988; S. J. Gould 1996)—has also been resuscitated. For instance, John Stewart (1997) proposes that progressive evolu-

tion, meaning the trend toward the emergence of higher levels of organization, has been catalyzed and sustained by the functional advantages of cooperation and the ability of managers to control cheaters and free riders. Stewart boldly projects this process forward with a futuristic vision of government on a “planetary scale.” A similar vision can be found in Robert Wright’s *Non Zero* (2000). There is also much work in biology these days on emergence and the evolution of higher-level individuals (e.g., Michod 1997, 1999; Frank 2003; also see Ghiselin 1997). Again, we will explore these matters further in chapters 2 to 5.

So, the question is, will the rising tide lead on to fortune for the concept of synergy? A firm prediction would be risky, of course, but there do seem to be a number of favorable indications. One is the case for it made by Maynard Smith and Szathmáry in their two volumes on major transitions theory. Several of my recent publications also seek to advance the concept (see especially Corning 1995, 1996a, 1998, 2003).

There is also a recognition, only now emerging, that synergistic functional effects are a fundamental aspect of virtually every scientific discipline (see chapter 3). The reason why the universality of this functional principle has not been widely appreciated in the past is that synergy has traveled under many different aliases: emergent effects, cooperativity, symbiosis, a division of labor (or, more precisely, a combination of labor), epistasis, threshold effects, phase transitions, coevolution, heterosis, dynamical attractors, holistic effects, mutualism, complementarity—even interactions and cooperation.

Finally, there are currently several convergent theoretical developments that focus in various ways on synergistic phenomena, even though they may not employ the term *synergy* explicitly. These developments include, among others, (1) *network theory and network dynamics* (see, for example, Barabási 2002; Buchanan 2002; Strohmán 2002; Fewell 2003; Strogatz 2003); (2) *niche construction theory* (Laland et al. 2000; Odling-Smee et al. 2003); (3) *emergence theory* (J. Goldstein 2002; S. Johnson 2001; Morowitz 2002); (4) *evolutionary developmental systems theory* or evo-devo (Rollo 1995; Oyama 2000; Pigliucci 2001; W. Arthur 2002; West-Eberhard 2003); (5) *systems biology* (Kitano 2001, 2002; Chong and Ray 2002; Csete and Doyle 2002); and (6) *gene-culture co-evolution theory* (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985; Durham 1991; Thompson 1994; Weingart et al. 1997; P. R. Ehrlich 2000; Hammerstein 2003; Richerson and Boyd 2004).

Of course, it is one thing to recognize synergy as a ubiquitous phenomenon. It is another thing to assign to it a major causal/explanatory role in various domains, particularly biological evolution, human evolution, and the evolution of complex societies. This is what the Synergism Hypothesis encompasses, and the case for this theory, along with an argument for using synergy as a unifying concept for cooperative effects of all kinds in various scientific disciplines, will be presented in chapters 2 and 3.



Often the most important contribution a scientist can make is to discover a new way of seeing old theories or facts.

—Richard Dawkins

The power and majesty of nature in all its aspects is lost on one who contemplates it merely in the detail of its parts and not as a whole.

—Pliny the Elder

**SUMMARY:** “Holistic Darwinism” is a candidate name for a post-Neo-Darwinian evolutionary paradigm. When two functionally linked genes are selected together, or when two symbionts (say a ruminant and its gut bacteria) are jointly favored, or when a group of communally nesting female wasps reproduce in greater abundance, the unit of differential survival and reproduction (in functional terms) is the whole—the combined (synergistic) effects produced by the cooperating parts. Holistic Darwinism is not a different theory; it involves a different perspective on the evolutionary process. To borrow Richard Dawkins’s image, it is an alternative way of viewing the theoretical Necker cube. Holistic Darwinism is distinctive in that it is concerned especially with the bio-economics—the functional costs and benefits—of cooperative phenomena of all kinds. It does not contradict the Neo-Darwinian assumption of gene self-interest but highlights the paradoxical interdependence of genes and their “ves-sels.” Indeed, it is argued that the units of replication (genes, genomes, gene pools) and their genetic relationships are less important as determinants of cooperative phenomena than are the functional properties and survival consequences of cooperation, as the data on such interactions clearly suggest. (Maynard Smith has termed it “synergistic selection.”) Many hypotheses have been advanced to explain the evolution of complexity—an undisputed historical trend if not a “law” as some theorists have claimed. Holistic Darwinism focuses on the causal role of functional synergy.



## 2

---

### Holistic Darwinism: Synergistic Selection and the Evolutionary Process

#### Introduction: The Perils of Group Selection

The emotionally charged group selection debate in biology—which will celebrate an unofficial thirty-ninth anniversary in 2005—provides a classic example of a controversy based largely on a misconception. To Darwin and many of his contemporaries, group selection was a perfectly respectable concept. Indeed, it was Darwin who first proposed, in 1871 in *The Descent of Man*, the then-unexceptional idea that differential group selection may have played an important role in human evolution, along with what he called family selection (now known as inclusive fitness or kin selection theory) and individual reciprocities (now variously called mutualism and reciprocal altruism). Darwin's tripartite explanation of human evolution was quite subtle, but his view of the role played by group selection is illuminated in this brief passage: "All that we know about savages, or may infer from their traditions and old monuments, the history of which is quite forgotten by the present inhabitants, show that from the remotest times successful tribes have supplanted other tribes" (1874 p. 147). Herbert Spencer, one of the outstanding theorists of the nineteenth century, expressed a similar view in *The Principles of Sociology* (1897), and many of the pioneer anthropologists of that period also seem to have agreed.

In the first half of the twentieth century, the founding fathers of modern genetics and population biology, notably including Haldane, Wright, Fisher, Morgan, and Dobzhansky (plus some non-geneticists such as Huxley, Mayr, and Simpson) redefined evolutionary theory in quantitative genetic terms. However, the so-called modern synthesis was also deemed to

be compatible with group selection of various kinds. For instance, Sewall Wright (1968–78) at the University of Chicago coined the term *interdemic selection*—i.e., selection between discrete breeding groups, or demes—and developed what he called a shifting balance model, which he believed was of the utmost importance in producing evolutionary changes. Ernst Mayr, likewise, spoke of evolutionary change as a population-level phenomenon, meaning that populations and species are the ultimate units of evolutionary change, not individuals. Mayr also developed what he called the founder principle, which envisions small, reproductively isolated groups as a significant source of evolutionary innovation (Mayr 1963, 1976). More recently, the paleontologist Niles Eldredge (1995) and the paleontologist-popularizer Stephen Jay Gould (2002) have championed a higher-level species selection paradigm. Meanwhile, various students of animal behavior, such as William Morton Wheeler and Warder C. Allee, stressed the cooperative aspect of animal behavior and social life. Wheeler (1927) also promoted the idea of emergent evolution, and he borrowed from Spencer the idea that a socially organized group can be likened to a superorganism (Wheeler 1928; see chapter 8).

However, a theoretical punctuated equilibrium occurred in 1962. In his subsequently much-maligned book *Animal Dispersion in Relation to Social Behaviour*, Vero C. Wynne-Edwards (1962) made himself a stalking horse, in Edward O. Wilson's characterization, by propounding a seriously overstated version of the group selection hypothesis. Wynne-Edwards asserted that group-living animals regularly display behaviors that involve the curtailment of their own personal fitness for the good of the group (for example, through conventional controls on personal reproduction that serve to limit population densities). "The great benefit of sociality," he claimed in a companion article in *Nature* (1963), "arises from its capacity to override the advantage of individual members in the interest of the survival of the group as a whole." Some of Wynne-Edwards's critics, playing loose with the facts, accused him of a Pollyanna-like naivete that violated Darwinian theory, but in fact he clearly stated that altruistic, group-serving behaviors could arise only if natural selection were to operate between social groups "as evolutionary units." Notwithstanding, Wynne-Edwards became a pariah in evolutionary biology and has been routinely chastised for his heresy ever since—rather like the treatment accorded to Lamarck.

Although the assault on group selection theory began with William D. Hamilton's now-classic papers on "The Genetical Evolution of Social Behavior" (1964a, 1964b), it was fully elaborated in George C. Williams's New Testament, *Adaptation and Natural Selection* (1966). Williams's near-

legendary book was in many respects a therapeutic cold bath that served to purge evolutionary theory of some sloppy thinking. However, Williams also took an extreme position, from which he has since retreated, to the effect that selection at any level higher than that of an individual is essentially “impotent” and is “not an appreciable factor in evolution” (1966, p. 8; cf. Williams 1992).

Edward O. Wilson was more moderate by comparison in his discipline-defining volume, *Sociobiology* (1975), but he also (inadvertently) propagated a conceptual muddle that caused much confusion and inadvertent mischief in evolutionary theory.<sup>1</sup> Wilson launched his massive synthesis with the startling assertion that altruism is “the central theoretical problem of sociobiology” (p. 3). The implication, which guided much subsequent work in this new interdiscipline, was that social life is founded on altruism. Therefore, cooperative behaviors are inherently a theoretical problem that can be overcome only under extraordinary circumstances—such as via group selection, kin selection, and maybe Robert Trivers’s (1971) “reciprocal altruism.” In opposition to Wynne-Edwards, Wilson considered “pure” group selection—that is, among non-kin—to be highly improbable, a rare occurrence confined to humans and perhaps a few other species. His detailed, chapter-length discussion of group selection included a review both of the available evidence and of various formal models, but his conclusion was preordained by the assumption that “pure” group selection necessarily implied genetic altruism (E. O. Wilson 1975, pp. 106–29).

Another broadside against group selection theory came in 1976 in the form of Richard Dawkins’s ideologically tinged popularization with the cunningly anthropomorphic title *The Selfish Gene*. “I think ‘nature red in tooth and claw’ sums up our modern understanding of natural selection admirably,” Dawkins wrote with evident relish (1989, p. 2). Not surprisingly, *The Selfish Gene* became a controversial best seller. In retrospect, the selfish gene metaphor has proven to be a powerful heuristic tool. It has led to many new insights about the interactions within and among various functional units in nature and to much productive research. On the other hand, it also introduced a simplistic and seriously distorting perspective into evolutionary theory.

The short-term consequence of this rancorous theoretical debate was a wholesale rejection of the concept of group selection. Nevertheless, as noted earlier, for the past twenty-five years or so David Sloan Wilson (lately with the collaboration of Elliott Sober and with parallel efforts from a growing number of other workers) has been attempting to resurrect group selection on a new foundation. What Wilson calls “trait group selection” (D. S. Wilson

1975, 1980; Wilson and Sober 1989, 1994; Sober and Wilson 1998) refers to a model in which there may be linkages (a “shared fate” in Wilson’s term) between two or more individuals (genotypes) in a randomly breeding population, such that the linkage between the two becomes a unit of differential survival and reproduction. Initially, Wilson assumed that one of the two was an altruist, for he was then intent on accounting for the evolution of altruism without recourse to kin selection. As noted earlier, John Maynard Smith developed a similar model, which he dubbed “synergistic selection.” (See also Matessi and Jayakar 1976; Wade 1977, 1985; and the discussion in Dugatkin et al. 1992.)

The current revival of group selection theory may perhaps be attributed, in considerable measure, to the growing recognition that it can also entail win-win processes. Cooperating groups might provide mutual advantages for their members, so that the net benefits to all participants outweigh the costs. In other words, cooperation is not equivalent to altruism and does not by definition require sacrifices, or genes for altruism. I refer to it as “egoistic cooperation,” to distinguish it from altruism. This, in essence, is what game theory models of cooperation (such as the classic prisoner’s dilemma game) tacitly postulate (see Maynard Smith 1982b, 1984, 1989; Axelrod and Hamilton 1981), which is why game theory formulations are largely indifferent to the degree of relatedness, if any, between the cooperators. And game theory models of cooperation (along with experimental research on the subject) have been growing exponentially in number over the past decade or so (see especially Sigmund 1993; Binmore 1994a, 1994b; Gintis 2000a; Stephens et al. 2002; Sigmund et al. 2002; Bowles et al. 2003). (More on this below.)

Moreover, game theory provides a window into a vastly larger galaxy of cooperative phenomena that, I submit, reduces the group selection controversy to a tempest in a teapot. This alternative formulation was originally developed in *The Synergism Hypothesis: A Theory of Progressive Evolution* (Corning 1983) and will be summarized in chapter 3. It was also developed independently by Maynard Smith and Szathmáry (1995, 1999), and it is supported by an accumulating body of research findings across many different specialized disciplines, from molecular biology and microbiology to behavioral ecology, primatology, and sociobiology—not to mention the social sciences. This alternative paradigm might be characterized as Holistic Darwinism. (See also Dugatkin and Reeve 1994, and Dugatkin and Mesterton-Gibbons 1996, on indirect “by-product mutualism” in evolution; and D. S. Wilson and Dugatkin 1997, on the role of “assortative interactions,” or behavioral selection, as a mechanism of group selection.)

## Holistic Darwinism Defined

Holistic Darwinism—to repeat—is not an oxymoron. The term was coined as a way of highlighting the paradox that selfish genes are, without exception, selected in the context of their functional consequences (if any) for various wholes. Holistic Darwinism is strictly Darwinian in its underlying assumptions about natural selection and the evolutionary process. It has no fundamental quarrel with the theoretical premise of gene selfishness. Rather, it involves a different perspective on the causal dynamics of evolution. In his preface to the second edition of *The Selfish Gene*, Dawkins uses the metaphor of a Necker cube—a two-dimensional drawing of a three-dimensional object that can be perceived in different ways—to characterize the intent behind his inspired metaphor: “My point was that there are two ways of looking at natural selection, the gene’s angle and that of the individual. . . . It is a different way of seeing, not a different theory” (1989, pp. x–xi).

Actually, there are more than two ways of looking at natural selection, and Holistic Darwinism focuses not on genes, or individuals, or even groups as units of selection but on the functional relationships among the units at various levels of biological organization, from genomes to ecosystems, and on their consequences for differential survival and reproduction. It involves refocusing the Necker cube on the interactions between genes, between cells, between organisms, and between organisms and their environments. Perforce, Holistic Darwinism is also about the role of synergy—the combined effects produced by phenomena that cooperate (operate together)—as a major cause of evolutionary continuity and change.

A word is in order here about my use of the word *holism*. To some the term may seem problematic—perhaps idealistic or vaguely metaphysical. To the contrary, my intent is to characterize a theoretical shift of focus to the combined (synergistic) effects produced by various combinations of parts (wholes) at various levels of biological organization. In contrast with such early holists as Jan Smuts (1926), who evidently coined the term *holism* and who discerned an inherent “driving force” in nature toward the emergence of wholes, Holistic Darwinism represents a functional, Darwinian approach. Living wholes are contingent products of evolution, and of natural selection.

It should also be stressed that the term *cooperation* will be used here in a strictly functional sense; it refers to functional interactions. In this conceptualization, cooperation may or may not also be considered selfish or altruistic, mutualistic or parasitic, positive or negative. Such attributes involve additional, post hoc judgments about the consequences of a cooperative

relationship with respect to some separately specified goal or value. (Of course, in Darwinian theory the operative value is survival and reproductive success.) By the same token, a cooperative relationship may or may not be voluntary. Slavery, in nature and in human societies alike, involves a form of involuntary cooperation, and so (presumably) does the host's role in a parasitic relationship.

Accordingly, a key point about cooperation as a functional concept is that it is found at every level of living systems. Beginning with the very origins of life, it is a common denominator in all of the various formal hypotheses about the earliest steps in the evolutionary process (reviewed in Corning 1996a). All share the common assumption that cooperative interactions among various component parts played a central role in catalyzing living systems.

Similarly, at the level of the genome, it goes without saying that genes do not act alone, even when major single-gene effects are involved. Indeed, the human genome sequencing project has established, among many other things, that there are in fact 1,195 distinct genes associated with the human heart, 2,164 with white blood cells, and 3,195 with the human brain (see Little 1995). The functional (morphogenetic) implications behind those numbers are awesome to contemplate. As Richard Dawkins himself so eloquently put it in a later book, *The Blind Watchmaker*:

In a sense, the whole process of embryonic development can be looked upon as a cooperative venture, jointly run by thousands of genes together. Embryos are put together by all the working genes in the developing organism, in collaboration with one another. . . . We have a picture of teams of genes all evolving toward cooperative solutions to problems. . . . It is the "team" that evolves. (1987, pp. 170, 171)

The origin of chromosomes, likewise, may have involved a cooperative/symbiotic process (see Maynard Smith and Szathmáry 1993). Sexual reproduction, one of the major outstanding puzzles in evolutionary theory, is also a cooperative phenomenon, as the term is used here. Although there is still great uncertainty about the precise nature of the benefits, it is assumed that sexual reproduction is, by and large, a mutually beneficial joint venture.

As one moves upward in "the great chain of being" (to borrow a durable anachronism), one finds further variations on the theme of functional cooperation. Once upon a time bacteria were considered to be mostly loners, but no longer. It is now recognized that large-scale, sophisticated cooperative efforts—complete with a division of labor—are commonplace

among bacteria and can be traced back at least to the origin of the so-called stromatolites (rocky mineral deposits) that, it is believed, were first constructed by bacterial colonies some 3.5 billion years ago (J. A. Shapiro 1988; J. A. Shapiro and Dworkin 1997; Margulis 1993; Bloom 1997). Shapiro suggests that bacterial colonies can be likened to multicellular organisms.

Eukaryotic cells can also be characterized as cooperative ventures—obligate federations that may have originated as symbiotic unions (parasitic, predatory, or perhaps mutualistic) between ancient prokaryote hosts and that have now become the cytoplasmic organelles, particularly the mitochondria, the chloroplasts and, possibly, eukaryotic undulipodia (cilia) and certain internal structures that may have evolved from structurally similar spirochete ancestors (Margulis 1993). The phenomenon of symbiosis, by definition a category of cooperative relationships in nature, provides yet another example. Not only has the darker side of symbiosis—parasitism—gained new prominence over the past decade or so but more benign commensalistic and mutualistic forms of symbiosis are also more widely appreciated (see below).

Sociobiology is also, by definition, concerned with cooperative relationships among conspecifics, interactions that can provide a variety of adaptive consequences for the participants. As shown by the many field studies and laboratory experiments that were inspired by inclusive fitness theory and game theory, the social interactions that occur in nature among members of the same species may be perturbed by “free riders,” defectors, exploiters, conspecific parasites, and so on, yet the fact remains that within-species cooperative behaviors are fairly common and encompass a broad array of survival-related functions, including (1) hunting and foraging collaboratively, which may serve to increase capture efficiency, the size of the prey that can be pursued, or the likelihood of finding food patches; (2) joint detection and avoidance of, and defense against, predators, using behaviors that range from mobbing and other kinds of coordinated attacks to flocking, herding, communal nesting, and synchronized reproduction; (3) shared protection of jointly acquired food caches, notably among many insects and some birds; (4) cooperative movement and migration, including the use of formations that increase aerodynamic or hydrodynamic efficiency, reduce individual energy costs, and/or facilitate navigation; (5) cooperation in reproduction, which can include joint nest building, joint feeding, and joint protection of the young; and (6) shared environmental conditioning.

Neo-Darwinian theory—as purified by the selfish gene perspective—attributes evolutionary change to competition among the replicators—the

ultimate units of information transfer in evolution. In the classical Neo-Darwinian model, cooperation plays a decidedly subsidiary role. But if we shift our perspective and view evolution as an ecological and economic process—a survival enterprise in which living systems and their replicators are embedded—then differential reproductive success may be viewed as the result of a complex interplay of competitive and cooperative interactions (along with a variety of other factors), both within and among functionally interdependent units of ecological interaction. Our focus shifts to the activities of the “vehicles” (in Richard Dawkins’s terminology) or the “interactors” (in the terminology of David Hull 1980)—and, more important, to the bioeconomic consequences of their functional interactions. (For a classic paper on this subject, see Paine 1966.)

It has been a cardinal assumption of Neo-Darwinism that cooperation in nature is a phenomenon that is at odds with the basic principle of gene competition, and that extraordinary conditions are required to overcome the inherent selective bias against the evolution of cooperation. This assumption is what accounts for the importance attached to inclusive fitness theory (or “kin selection,” in Maynard Smith’s usage) and to game theory. However, a functional/bioeconomic perspective on the evolutionary process challenges that point of view. Not only is cooperation (broadly defined) fairly common in nature, but synergistic effects (the functional consequences of cooperation), it is argued, have played an important causal role in evolution, especially in relation to the evolution of complexity. To put it baldly, functional synergy explains the evolution of cooperation in nature, not the other way around. In other words, functional groups (in the sense of functionally integrated teams of cooperators of various kinds) have been important units of evolutionary change at all levels of biological organization; functional group selection is thus a ubiquitous aspect of the evolutionary process.<sup>2</sup> This is obviously a highly contentious assertion. In the next section, I will briefly summarize the evidence.

### Consider the Evidence

If cooperation in nature is not largely dependent on inclusive fitness, we would expect to find a significant degree of decoupling in the natural world between genetic relatedness and cooperation, and, in fact, there are at least four sources of evidence for this proposition. First, there is the entire domain of symbioses. Here we can observe a wide range of cooperative relationships that can only be accounted for in bioeconomic, cost-benefit terms. Kinship is largely irrelevant. Indeed, many types of symbioses—such as the



estimated 20,000 species of lichen partnerships involving approximately 300 different genera of fungi and algae, or the rhizobia and similar bacteria that form root nodules with some 17,500 species in 600 genera of plants—reflect a plethora of independent inventions. In other words, many different species may discover and utilize the same functionally advantageous cooperative relationships. As Maynard Smith (1989) has noted, extreme non-specificity is the rule among mutualists, whereas parasitism is highly specific. The case for symbiogenesis as a significant factor in evolution was documented by participants at a 1989 conference on the subject and in a subsequent volume edited by Margulis and Fester (1991). (Symbiogenesis will be discussed in more detail in chapters 3 and 4.) The following is some of the extensive evidence that was presented at the conference:

- Mutualistic or commensalistic associations (not to mention parasitism) exist in all five kingdoms of organisms, as defined by Whittaker and modified by Margulis and Schwartz (1982). Most extant species may, in fact, be either a product of or currently involved in (or both) endo- or ecto-symbioses. Elsewhere, Bermudes and Margulis (1987) documented that twenty-seven of seventy-five phyla in the four eukaryotic kingdoms (or 37 percent) exhibit symbiotic relationships.
- Over 90 percent of all modern land plants establish mutually beneficial associations with the mycorrhizal fungi that are ubiquitous in fertile soils (Lewis 1991), and Silurian and Devonian plant fossils have been found to contain structures closely resembling the symbiotic vesicles produced by modern mycorrhiza (D. C. Smith and Douglas 1987).
- Land plants may have arisen through a merger between fungal and algal genomes, as sort of inside-out lichens. In any case, it is evident that modern land plants represent a joint venture between fungi and green algae (Pirozynski and Malloch 1975; Atsatt 1988, 1991).
- Approximately one third of all known fungi are involved in mutualistic symbioses (e.g., lichens), many of which have conferred on their partnerships the ability to colonize environments that would not otherwise have been accessible to each one alone (Kendrick 1991).
- Virtually all species of ruminants, including some two thousand termites, ten thousand wood-boring beetles, and two hundred Artiodactyla (deer, camels, antelope, etc.), are dependent upon endoparasitic bacteria, protoctists, or fungi for the breakdown of plant cellulose into usable cellulases (P. W. Price 1991).
- Within the teeming communities of organisms that have recently been discovered in proximity to various sea floor hydrothermal vents, there are a

number of symbiotic partnerships between chemoautotrophic (sulfur-oxidizing) bacteria and various invertebrates, which rely on the bacteria for their carbon and energy requirements (Vetter 1991).

- Most bacterial cells congregate and reproduce in large, mixed colonies with many endosymbionts (virus-like plasmids and prophages) and ectosymbionts (metabolically complementary bacterial strains). These congregations call into question the classical notion of a species, in the sense of competitive exclusion and reproductive isolation (Sonea 1991; also J. A. Shapiro 1988; J. A. Shapiro and Dworkin 1997).

A second body of supporting evidence can be found in the various game theoretic models of cooperation between *unrelated* individuals, along with the substantial research literature that these models have inspired. (These will be discussed further below.) Third, there is the entire category of outbreeding reproduction, a class of cooperative behaviors that, by definition, falls outside of the inclusive fitness model. Finally, over the past decade or so there have been many field and laboratory studies of cooperation among conspecifics that are inconsistent with inclusive fitness theory and suggest that the particular behaviors in question are more satisfactorily explained in bioeconomic terms, although cooperation remains more likely to occur in closely related, or at least familiar, animals.

A detailed summary of this discordant evidence (including twenty-eight recent field and laboratory studies and seven reviews of the older literature) can be found in Corning (1996a); see also the careful analysis by Goodnight and Stevens (1997). One particularly well-documented illustration is the food-sharing behavior among vampire bats (*Desmodus rotundus*), which clearly demonstrates the power of functional/bioeconomic factors to transcend the influence of genetic relatedness in shaping cooperative behaviors (G. S. Wilkinson 1984, 1988, 1990). If gene competition were of overriding importance, the sharing of blood among vampire bats (their exclusive food source) would be confined to close relatives. The reason is that blood sharing in this species has very high fitness value; an individual bat that fails to feed for two nights in a row will die. In field studies as well as in controlled observations in captive groups over a ten-year period, Wilkinson found that blood sharing both between relatives (matrilines) and nonrelatives was extensive. Both relatedness and prior association proved to be important facilitators. Moreover, quantitative cost-benefit analyses showed that the cost to donors was relatively low (in effect, they were sharing their surpluses), whereas the fitness benefits to recipients was relatively high. When this was combined with the fact that the donors' generosity was

usually reciprocated later (i.e., reciprocal altruism *sensu* Trivers 1971), there was a significant increase in the mutualists' joint fitness. Wilkinson concludes, "Reciprocity is likely to be more beneficial than kin selection—provided that cheaters can be detected and excluded from the system" (1990, p. 82). (For a more recent example of non-kin cooperation, in red-winged blackbirds, see Olendorf and Getty 2004.)

Two themes stand out in the many other examples that are described in Corning (1996a, 2003): (1) the importance of bioeconomic cost-benefit considerations in cooperative relationships and (2) the presence of synergy—combined functional effects (payoffs) that are jointly produced and provide benefits to the cooperators that are greater than would otherwise be possible. As Maynard Smith and Szathmáry put it in *The Major Transitions in Evolution* (1995), if an individual can produce two offspring on its own but by cooperating in a group consisting of  $n$  individuals can produce  $3n$  offspring, it pays to cooperate. (An application of this perspective to avian species can be found in Emlen 1996.)

### Game Theory Revisited

Game theory models of cooperation, viewed in the proper light, are also consistent with Holistic Darwinism. Game theory suggests that the evolution of cooperative behaviors depends on an appropriate set of strategic circumstances. Although the focus has always been on the behavioral context and the strategies of the players, if one looks closely at the various game theory formalizations they tacitly depend on an interaction between the behavior of the players and the structure of the payoff matrix. And if one looks closely at the payoff matrices in some of the classic formulations, such as tit-for-tat, the cooperative strategies in turn depend on synergy. In Axelrod and Hamilton's (1981) model, mutual defection yielded one point each, asymmetrical cooperation (parasitism?) yielded five points for the defector and none for the cooperator, and mutual cooperation yielded a total of six points, evenly divided. Furthermore, defectors would be penalized in subsequent rounds (it was conceived as an iterated game) so that mutual cooperation becomes an increasingly rewarding option over time. In effect, this amounts to a quantification of synergy; the implicit economic benefits of the game are critically important.

But what about the problem of cheating or defection (the prisoner's dilemma)? Maynard Smith and Szathmáry (1995) have proposed a response in terms of game theory, as illustrated in the two diagrams in figure 1. (I have taken the liberty of revising the payoff values that were utilized by Maynard

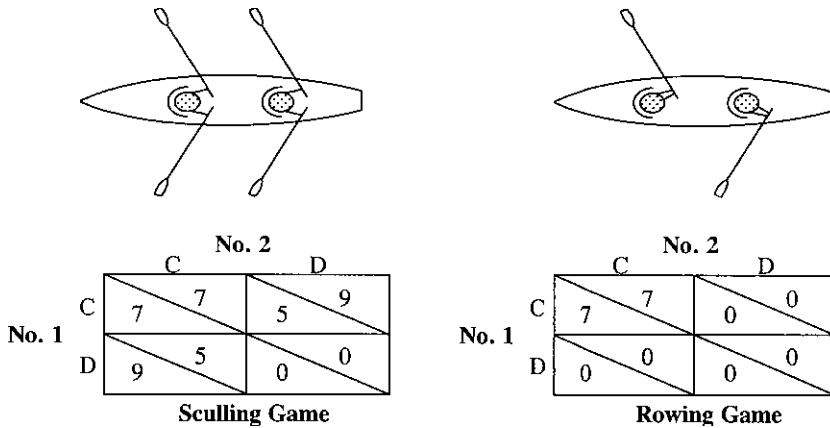


Figure 1. Sculling game versus rowing game. The matrices show the payoff values for each oarsman if he cooperates (C) or defects (D).

Smith and Szathmáry to accord with a more explicit assumption about the object of the game, namely, that the oarsmen are both seeking to cross a river.) The left-hand diagram involves a sculling model, in which two oarsmen each have a pair of oars and row in tandem. In this situation, it is easy for one oarsman to slack off and let the other one do the heavy work. This corresponds to the classical two-person game. However, in a two-person rowing model, as depicted in the right-hand diagram, each oarsman has only one opposing oar. Now their relationship to the performance of the boat is interdependent. If one oarsman slacks off, the boat will go in circles. In this case, mutual cooperation becomes an evolutionarily stable strategy and defection is totally unrewarding; in the absence of teamwork, the boat will not reach its goal.

Maynard Smith and Szathmáry conclude that the rowing model is a better representation of how cooperation evolves in nature: “The intellectual fascination of the Prisoner’s Dilemma game may have led us to overestimate its evolutionary importance” (1995, p. 261). Indeed, as Peck (1993, p. 195) observed, “The position of [stable] equilibria (and hence the frequency of cooperators) depends on the size of the various payoffs that define the Prisoner’s Dilemma game.” (See also Dugatkin et al. 1992; Brembs 1996.)

### An Evolutionary Theory of Government

If many forms of cooperation are functionally interdependent and thus self-policing, many more are not. The problems of cheating, defection, and free

riders—phenomena that the selfish gene metaphor has helped to illuminate—are real. But, in retrospect, the problem may have loomed much larger in theory than it does in fact; our models may have been too pessimistic about the constraints on errant behavior in cooperative relationships. In effect, the games may have been unintentionally rigged. Consider some of the common assumptions in classical two-person games: The games are always voluntary and democratic; each player is free to choose his or her own preferred strategy, and the opposing player has no means available for coercing choices or compliance. Also, the players are not allowed to communicate with one another in an effort to reduce the uncertainties in the interactions. Furthermore, defectors are usually rewarded handsomely for cheating while the cooperators are denied the power to prevent defectors from enjoying the rewards, much less to punish them for defection. Such grade inflation for defection biases the game in favor of cheating. Worse yet, in iterative games the players are forced to continue playing; they cannot exclude or ostracize a defector. They can only retaliate by themselves defecting and hoping thereby to penalize the other player (see also Binmore 2004).

A tacit rebuttal to this formulation was incorporated into a new kind of prisoner's dilemma model developed by Nowak and Sigmund (1993) called Pavlov, which the authors suggested can outperform tit-for-tat. They called their strategy "win-stay, lose-shift," and the significance of this innovation is that, in contrast with an iterated game in which the players must continue playing regardless of the outcome, in Pavlov they have the choice of leaving the game if they don't like the results. In other words, a player may also have the power to exercise some control over the behavior of a defector by denying to that player future access to the game and its potential benefits. Punishments as well as rewards may be utilized as a means of keeping the game honest and, more important, as a means of restricting the game over time to mutual cooperators.

In addition to such suggestive formalizations, there is increasing evidence that a policing function does in fact exist in nature. Indeed, there may even be altruistic punishment. (Among the outpouring of publications on this subject, see especially Boyd and Richerson 1992; Clutton-Brock and Parker 1995; Frank 1995, 1996; Michod 1996; Fehr and Gächter 2000a, 2000b, 2002; Gintis 2000b; Falk et al. 2001; Henrich and Boyd 2001; Bowles and Gintis 2002; Boyd et al. 2003; Gintis et al. 2003; Binmore 2004.) As Clutton-Brock and Parker point out in the summary of their review article on the subject, "In social animals, retaliatory aggression is common. Individuals often punish other group members that infringe their

interests, and punishments can cause subordinates to desist from behaviour likely to reduce the fitness of dominant animals. Punishing strategies are used to establish and maintain dominance relationships, to discourage parasites and cheats, to discipline offspring or prospective sexual partners and to maintain cooperative behaviour” (1995, p. 209). Evidence of a policing function has also been documented in, among others, social insects (Ratnieks and Visscher 1989), naked mole rats (Sherman et al. 1991), primates (de Waal 1996), and, needless to say, *Homo sapiens*.

From a functional (synergy) perspective, if cooperation offers sufficient benefits it may be in the interest of some individuals to invest in coercing the cooperation of others. Inclusive fitness provides one possible explanation for punishment as a successful strategy in social groups. Another explanation might be the sort of individual fitness trade-offs referred to above. Group selection may also provide a mechanism. The enforcement of cooperation might have significant fitness-enhancing value for groups that are in competition with other groups, or other species. Maynard Smith’s (1982a, 1983, 1989) “synergistic selection” model is relevant here. The model suggests that, if cooperative interactions among two or more individuals—related or unrelated—produce selectively advantageous synergistic effects for all parties (on average), the cooperating players may become a unit of selection. A synergistic functional group might be favored in competition with other groups or with ecological competitors from other species. Or a cooperating group may gain an advantage in comparison with the statistical probability of its survival and reproduction in the absence of cooperation. More broadly, synergistic selection can be defined in terms of gene combinations that enable or induce synergistic functional effects at various levels of biological organization. (See Michod 1996 for a model related to the multicellular level.) The evolution of “government” will be considered more fully in chapter 6.

### Synergistic Selection

The concept of functional group selection, or synergistic selection, can be illustrated by returning to Maynard Smith and Szathmáry’s sculling and rowing models, as described previously (and shown in figure 1). What if the objective of the game were changed? Rather than wanting to merely cross a river (say), now the two oarsmen in each boat share the objective of winning a race against the other boat. Now it has become a functional group selection game (see figure 2). In this situation, if either oarsman were to defect, their team might lose the race; only all-out cooperation would provide

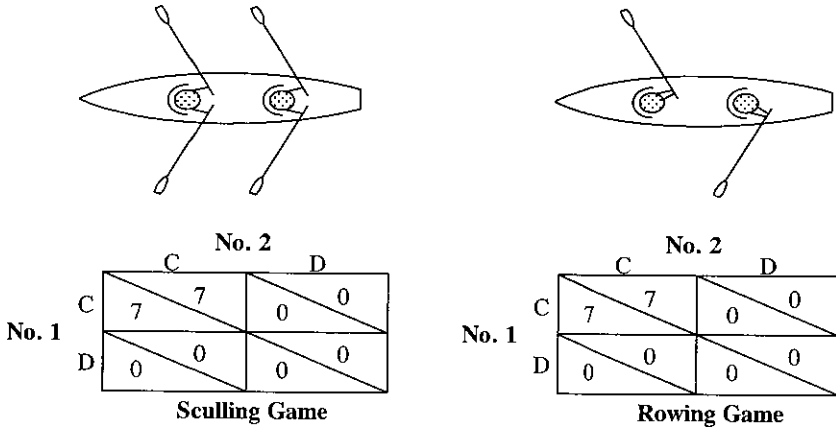


Figure 2. A group competition or group selection game. The matrices show payoff values for each oarsman, under the assumption that the goal is winning a race against the other boat.

rewards for either player. (Note that the two payoff matrices are now identical.) Now the sculling and the rowing games are functionally equivalent in the sense that the performance of either boat depends upon both of its oarsmen; each set has become a functional group; there is “synergistic selection.” Furthermore, it is irrelevant whether or not the oarsmen are related to one another.

The following are a few specific examples of synergistic selection:

- In insects, Page and Robinson (1991) conducted an analysis of their own and other researchers’ data on the division of labor in honeybees, including a number of computer simulations, and concluded that natural selection operated on colony-level parameters. Oldroyd and others (Oldroyd et al. 1992a, 1992b) also studied the genetics of honeybee colonies and concluded that colony performance was also influenced by the interactions among subfamilies, a colony-level parameter. Fewell and Winston (1992) conducted a study that examined the relationship between pollen storage levels in honeybee colonies (a group-level parameter) and individual forager efforts; not only was the correlation strong, but the researchers detected evidence of a homeostatic “set point.” And Guzmán-Novoa and others (1994) reported on a study that focused on the relationship between colony-level natural selection and the level of effort associated with various components of the division of labor in honeybee colonies (see also Calderone and Page 1992).
- An older study by Hoogland and Sherman (1976) examined in detail the influence of six possible disadvantages and three potential advantages of

colonial nesting in 54 colonies of the bank swallow (*Riparia*), ranging in size from 2 to 451 members. Hoogland and Sherman concluded that the disadvantages were not very burdensome and, more important, that the maintenance of coloniality was most strongly associated with group-level defensive measures, which differentially benefited the larger colonies. Although potential predators were not more frequent visitors to large groups, they were detected much more quickly and were mobbed by greater numbers of defenders; predators were also subject to more vocal commotion, and, bottom line, larger colonies were more effective overall in deterring predators.

- Scheel and Packer (1991), in a study of female African lions, found that the average degree of relatedness among the animals had no bearing on their propensity to engage in group hunting. The key variable was the potential for synergy; successful hunting of larger prey required group hunting. In a separate study by Packer and others (1990), it was concluded that the dynamics of female lion grouping were also strongly influenced by the need to defend their cubs (often a group-level function) and to compete against neighboring prides. In both situations, larger groups had an advantage.
- Maynard Smith illustrated his 1982 article on synergistic selection with, among others, the following examples: groups of fifteen to twenty female orb-web spiders (*Metabus gravidus*) that cooperate in building a joint web to span a stream where prey are abundant, tropical wasps (*Metapolybia aztecoides*) that establish joint nests, and coalitions of male lions (*Panthera leo*) that cooperate in taking over and holding a pride.
- Finally, a recent study of spotted hyenas (*Crocuta crocuta*) by Russel Van Horn and his associates (2004) showed that, contrary to kin selection theory, individual matriline commonly aggregate into larger “clans” of unrelated groups when confronted with dangerous competitors—including even matrilines that are closely related. It should also be noted that D. S. Wilson and Sober (1994), in an in-depth target article on the subject, provide a compendium of over two hundred references on group selection, of which thirty-five are identified as field or laboratory research efforts. See also the in-depth study of group selection in social bees in Moritz and Southwick (1992).

### Downward Causation

Closely related to the notion of functional group selection, or synergistic selection, as an evolutionary phenomenon is the concept of “downward causation.” The term was actually coined by psychobiologist Roger Sperry



(1969, 1991) in connection with the functional organization and operation of the human brain—that is, cybernetic control processes. (It may be that psychologist Donald Campbell [1974] developed the concept independently.) Sperry was fond of using as an illustration the metaphor of a wheel rolling downhill—its rim, all of its spokes, indeed all of its atoms, are compelled to go along for the ride.

We will use the term here in a slightly different sense. Downward causation in this context refers to the selective influences that have shaped the evolution of cooperative phenomena generally and complexity in particular. Why do selfish genes cooperate in ways that produce teamwork, which, in turn, leads to interdependency? What compels them to subordinate their interests to the interests of the whole? To be specific, how did morphological castes and a division of labor evolve in army ants? How do reproductive controls evolve in mutualistic symbioses where, as Margulis (1993) points out, there must of necessity be reproductive synchronization if the relationship is to remain stable? (See also the discussion of sociogenesis in E. O. Wilson 1985; also Buss 1987; D. C. Smith 1992; and the examples cited in Leigh 1991.) Equally important, how can the potential for cheating among selfish genes (or selfish individuals) be constrained?

Downward causation in an evolutionary context refers to the fact that the functional (synergistic) properties of the whole become a selective screen—a significant influence on the differential survival and reproduction of the parts. Sometimes individual parts are disadvantaged (e.g., nonreproductive workers), and kin selection may help us to understand how such sacrifices for the common good may occur. But, as the evidence previously cited indicates, kinship is not a *sine qua non*. The whole may also be sustained by fitness trade-offs; that is, the costs may be offset by commensurate benefits. For instance, an animal that is at risk from predators may suffer a reduction in its relative reproductive fitness in a social group setting, but it may also enjoy greatly enhanced odds of survival and absolute fitness. (This may help to explain why defeated contenders for breeding privileges sometimes stay on in the group and may even serve as helpers.) To quote Dawkins again, “In natural selection, genes are always selected for their capacity to flourish in the environment in which they find themselves. . . . But from each gene’s point of view, perhaps the most important part of its environment *is all the other genes that it encounters* [emphasis in original]. . . . Doing well in such environments will turn out to be equivalent to ‘collaborating’ with these other genes” (1987, pp. 170–71).

In some cases, the whole may represent an unalloyed benefit for the parts with little or no cost. Many cases of mutualistic symbioses seem to fit

into this category. For instance, Margulis (1993) is adamant about the cooperativeness, promiscuity, and evolutionary significance of bacterial colonies. (See also the parallel argument of J. A. Shapiro 1988.) Thus, an isolated bacterium would be cut off from access to the extensive gene swapping and the collective environmental intelligence (information) that commonly exist in bacterial colonies, not to mention the advantages of a division of labor and various collaborative efforts. Social mammals may also exhibit many of these higher-level properties. Some of the most compelling recent field research has illuminated the surprisingly sophisticated social organization, mutualism, and even “culture” in whales and dolphins (see especially Würsig 1988, 1989; Mann et al. 2000; Gyax 2002; Yurk et al. 2002; Whitehead and Rendell 2004). Conversely, the power of a social group to isolate or ostracize a free rider can be a significant deterrent and an agency of negative (downward) selection.

In any case, the synergies that result from cooperation may selectively reinforce cooperative behavior (to use the terminology of behaviorist psychology), and this may in turn differentially favor the evolution of relevant morphological and psychological characteristics over time. Thus, army ant submajors have acquired anatomical specializations that facilitate their role as porters, and humans have evolved psychological predispositions that help us to orchestrate (and even enjoy) our participation in group activities.

In sum, the relevant factors for explaining cooperative phenomena in nature (and in human societies) may include genetic relatedness, but kinship is neither necessary nor sufficient. The key lies in functional synergy and its bioeconomic consequences for differential survival and reproduction in a specific context; functional synergy is the frequently unappreciated common denominator in various models of cooperative behavior in sociobiology.

### **From Evo-Devo to the Baldwin Effect**

Four convergent developments in theory and research, mentioned earlier, should also be highlighted briefly. One is the work on what has been variously called developmental systems theory (Oyama 2000), phenotypic plasticity theory (Rollo 1995; Pigliucci 2001; West-Eberhard 2003), and, simply, evolutionary development theory, or evo-devo (various authors but see especially S. J. Gould 2002). In effect, this movement represents an effort to meld the traditional, gene-centered evolutionary theory with the expanding body of evidence that developmental processes—which involve an inextricable interaction between an organism and its environment—can also be an important source of evolutionary novelties.

Some adherents claim this is the path to a new evolutionary synthesis, much like the so-called “modern synthesis” of the 1930s, which melded Mendelian genetics and Darwinian theory. However, this claim falls short because it excludes another important development in evolutionary theory—a renewed focus on the role of behavior, and “mind,” as an innovative agency in evolution. The roots of this idea can be traced back to Jean Baptiste de Lamarck’s 1809 *Zoological Philosophy* (1963). Lamarck argued that, in the evolutionary process, changes in an animal’s “habits” often come first and that morphological changes may then follow. At the turn of the twentieth century a movement arose that attempted to Darwinize Lamarck’s insight, postulating that behavioral changes could reshape the context and the criteria for natural selection. This phenomenon—renamed the Baldwin effect by paleontologist George Gaylord Simpson (1953) after one of the leading advocates of what was originally known as organic selection theory, psychologist James Mark Baldwin—has gained an increasing number of adherents over the years (see, among others, Roe and Simpson 1958; E. Mayr 1960; Corning 1983, 2003; P. P. G. Bateson 1988; Plotkin 1988; Avital and Jablonka 1994, 2000; Deacon 1997; Weber and Depew 2003). I prefer to call this mechanism neo-Lamarckian selection, in honor of the theorist who first recognized its importance. But, under any name, behavioral innovations have often been the “pacemakers” of evolutionary change—in Ernst Mayr’s (1960) characterization.

Another convergent trend in evolutionary theory involves the important work by Odling-Smee and his colleagues on “niche construction theory” (Laland et al. 2001; Odling-Smee et al. 2003). These models, and the supporting evidence, show clearly that living organisms at all levels are not passive recipients of environmental conditions but actively shape their environments—and even the entire biosphere—to suit their needs.

Finally, there is a rapidly expanding body of work—most relevant to human evolution but not exclusively so—that is referred to as gene-culture coevolution theory. Theoretical work on this goes back to the 1980s (see especially Cavalli-Sforza and Feldman 1981; Corning 1983; Boyd and Richerson 1985; Durham 1991). However, the last few years have seen a rapid increase in empirical work that is supportive of this paradigm, along with further theoretical refinements. This has been stimulated in part by a growing recognition that culture (broadly defined as the social transmission of adaptive behavioral information) also exists in other species—from songbirds to cetaceans and, especially, our primate relatives. (For more extensive discussions, see Weingart et al. 1997; Dunbar et al. 1999; Corning 2003; Hammerstein 2003; Richerson and Boyd 2004.) Indeed, a case can be made

for the view that, in some species (most notably humans), it might be more accurate to call it culture-gene coevolution theory. We will have more to say on this subject in the next section and in chapter 6.

### The Selfish Genome

All of this rampant holism begs a question, however. Do wholes have goals that transcend the goals of the parts? Can wholes come to exercise a degree of autonomous control as wholes? In other words, can we postulate a “selfish genome?” The Neo-Darwinian response, it appears, is a somewhat equivocal “no.” Richard Dawkins (1989) became famous for the assertion that organisms are merely “robot vehicles” that have been blindly programmed to serve the interests of the genes, yet (as noted earlier) he also allowed that genes can be selected for their ability to serve the interests of the gene team. And George Williams (1966), although acknowledging the wholeness and unity of organisms, characterized many of the claims regarding superorganisms as figments of a “romantic imagination” (p. 220). In truth, some of these superorganismic claims were inflated, but Williams’s view of this issue was perhaps a bit too jaundiced: “A wolf can live on elk only when it attacks its prey in the company of other wolves with similar dietary tendencies. I am not aware, however, of any evidence of functional organization of wolf packs” (pp. 217–18).

In contrast, Holistic Darwinism postulates that wholes at various levels of biological organization may evolve mechanisms that permit partially autonomous control over the parts and their actions. Some insight into how superordinate controls can evolve in nature is provided in Egbert Leigh’s various discussions (as noted earlier) of how groups might act to contain or override individual advantages for the good of the group—what he calls the “parliament of the genes” (Leigh 1971, 1977, 1983, 1991; see also Michod 1996, 1997, 1999; Frank 2003; Rainey and Rainey 2003). Leigh’s argument, in essence, is that if the potential payoffs (synergies) for each of the participants in a cooperative relationship are high enough, this could also provide an incentive for the imposition of “government” in the “public interest.” Leigh even draws on Adam Smith’s reasoning, not from his 1776 *The Wealth of Nations* but from his earlier and less well-known *The Theory of Moral Sentiments* (1759). Although it has not been widely appreciated until quite recently, Smith argued for the necessity of a system of laws and appropriate means of enforcement in human societies to resist the dangers of unfettered self-interest. (1976, pp. 86, 88–9, 340–41)—a theme that has

gained many adherents of late. Government is, in fact, an essential functional element in any socially organized group.

A key to understanding the evolution of government at various levels of biological organization may lie in what could be called the “paradox of dependency.” Although cooperative interactions may produce individual fitness-enhancing synergies, a trade-off may be that the more valuable the benefits the more likely it is that the parts will become dependent upon the whole. As the benefits of cooperation increase, so may the costs of not cooperating. Wholes may then become obligatory survival units, one consequence of which may be that a decrement in the performance of the whole might result in the demise of the parts. An example can be found in a long-term study by Jeon (1972, 1983). A strain of *Amoeba proteus* was initially infected with bacterial parasites that were resistant to the hosts’ digestive enzymes. After two hundred generations, or eighteen months, a mutualistic relationship had become established, and after ten years the symbionts had developed complete interdependence. (Jeon [1992] has also illuminated some of the biochemistry of these changes.) It should also be noted that Margulis (1993) makes a similar argument with respect to the integration of symbiotic organelles in the ancestral eukaryotic cells. An obvious implication is that the incentives (both proximate and ultimate) for imposing government over the parts are likely to increase in relation to the degree of interdependency among the parts, and the advantages of operating as a superorganism (more on this in chapters 6 and 8).<sup>3</sup>

In fact, in what may appear to be an utter contradiction of classical Neo-Darwinism, it may often be the case that it is in the interest of a gene, or an individual, to promote the well-being of an interdependent other, simply because functional interdependence means just that; it’s “one for all, and all for one,” to borrow a legendary slogan. Consider this hypothetical example: If one of the two oarsmen in the rowing game (depicted in figure 1) should suffer from thirst and dehydration in the summer heat (he forgot his water bottle), his partner might decide to share his water supply, in the interest of reaching their joint goal. Or, to cite an example from nature, consider the exquisitely complex energy-production services that the mitochondria provide for eukaryotic cells, in their own direct self-interest. Or, for that matter, consider the innumerable situations in human societies where our well-being depends, unequivocally, upon the performance of others—airline pilots, railroad engineers, surgeons, and the other motorists that we encounter on the highways, to name a few. How do we explain these cooperative relationships? They have nothing to do with altruism, kin selection,

reciprocal altruism, or even (strictly speaking) tit-for-tat mutualism. They are sustained by pure self-interest.

One final point related to the concepts of downward causation, government, and the selfish genome. At the most basic level of biological organization (the genome itself), there is mounting evidence that the genes do not inhabit a “bean bag” (to reiterate Ernst Mayr’s felicitous caricature), and that morphogenesis is not a mindless process. Rather, it is an organized, cybernetic process that entails the extensive use of superordinate feedback controls (the very essence of a teleonomic system). In other words, selfish genes are only citizens on good behavior in the selfish genome, and the outlaws, tax evaders, and parasites among them do not have a license to pursue their antisocial interests *ad libitum*.

### Evolution as a Multilevel Process

There is one other aspect to Holistic Darwinism that should be mentioned briefly. It relates to the traditional distinctions between parts and wholes, individuals and groups, even the concepts of “self-interest” and the “public interest” in political theory. During the past decade or so, there has been a growing appreciation of the fact that evolution is a multilevel, hierarchical (some prefer the term *holarchical*) process, just as survival (and reproduction) is a multifaceted problem (see especially Koestler 1967; Corning 1983; Brandon and Burian 1984; Eldredge and Salthe 1984; Salthe 1985; Eldredge 1985, 1995; Buss 1987; Grene 1987; D. S. Wilson and Sober 1994; Maynard Smith and Szathmáry 1995; Michod 1996; Sober and Wilson 1998; S. J. Gould 2002). In essence, there is a recognition that natural selection operates at various levels of biological organization—from genes to ecosystems—often simultaneously. Indeed, Eldredge and Salthe (1984; also Eldredge 1995) have shown that there are different kinds of hierarchies in the natural world and that these may be in conflict with one another. One implication of this more complex view of evolution is that both competition and cooperation may coexist at different levels of organization, or in relation to different aspects of the survival enterprise. There may be a delicately balanced interplay between these supposedly polar relationships. The following examples illustrate this interplay.

- Eusocial insect species can generally occupy a broader spectrum of habitats and are often able to dominate and even exclude potential competitors among solitary and primitively social species, as noted earlier (see Hölldobler and Wilson 1990). Nevertheless, eusocial insect societies are not

the harmonious communities that we once supposed. Among other things, there may be intense competition for breeding rights among potential queens and there is evidence of nepotism among the patriline in polyandrous species.

- A number of ant species establish pleometrotic colonies; multiple foundresses cooperate in initial nest construction and brood production. In at least one case, the desert seed-harvester ant *Messor pergandei*, a study by Rissing and Pollack (1991) has shown that pleometrotic colonies are able to prevail in direct ecological competition with single-foundress colonies; multiple-foundress colonies are able to produce a larger raiding force more quickly, and this apparently provides a decisive competitive advantage (group selection). However, other studies of these colonies suggest that one trade-off may be internal competition among co-foundresses and their offspring—all very suggestive of human societies.
- Members of African lion prides cooperate and compete with one another in a variety of ways: Females typically hunt large prey in groups, share food, and even share in guarding cubs and defending the pride. As Packer and Rutten (1988) observe, there is evidence of synergy. For instance, a group of females can more effectively defend a kill against scavengers, including other lion groups. Likewise, a group of males can successfully defend access to a group of females, whereas single males cannot. However, there is also much intra-coalition competition among the males for mating privileges.
- One of the more dramatic examples of the interplay between competition and cooperation concerns the northern elephant seals (*Mirounga angustirostris*). Males of this species, which can weigh up to 4,500 kg, are legendary for their prolonged and bloody battles for dominance and mating privileges when they come ashore to breed in the winter and early spring. However, the males will only fight when estrous females have formed “harems” of fifty or more. And when the fighting is over, the alpha males commonly form coalitions with a half-dozen or more beta males, who will defend the perimeter of the harem against other marauding males (in return for which the beta males get limited mating privileges for themselves). Elephant seals generally feed at sea alone, and at great depths, but whenever they are ashore they congregate peacefully in tightly packed rookeries that facilitate defense and heat sharing (a critically important function in these animals). Males collaborate in this way during their summer molting season; nonbreeding males also aggregate into loser groups during the breeding season; females huddle closely together to share heat and defend their pups during the breeding season; and pods of weanling pups huddle for warmth and mutual self-defense before setting off on their initial feeding expeditions (Le Boeuf 1985; Le Boeuf and Laws 1994).

## The Evolution Of Humankind

Human evolution may provide a singular illustration of the synergistic, functional group selection hypothesis, and of Holistic Darwinism. In effect, the principles that were elucidated in the previous section can also be observed in the evolution of the human species, and in our cultural evolution as well. For various reasons, the evolution of humankind has often been portrayed as a process that is *sui generis*. Of course, this overlooks the fact that all of evolution can be said to be *sui generis*, given its historical and situation-specific causal dynamics. As Darwin himself put it in *The Descent of Man* (1874), any evolutionary innovation depends upon many “concurrent favorable developments” that are always “tentative” (p. 150). Nevertheless, the evolution of humankind is undeniably one of the more remarkable episodes in evolutionary history. (This matter will be discussed briefly here and considered further in chapters 6 and 17.)

A number of suggestive and thoughtfully argued theories of human evolution have been advanced over the years. These theories were reviewed and critiqued in depth in Corning (1983), and a synthetic explanation was offered there that, in effect, combined Darwin’s tripartite selection theory of human evolution—that is, family (kin) selection, mutualism (including reciprocity), and group selection—with the concept of functional synergism. As Darwin pointed out—and this point is crucial—the three modes of selection need not be opposed to one another; they can be complementary and mutually reinforcing. In addition, the Synergism Hypothesis posits, in essence, that it was the bioeconomic payoffs (the synergies) associated with various forms of social cooperation that produced—in combination—the ultimate directional trend over a period of several million years, from the earliest bipedal hominids to modern *Homo sapiens*. That is, the synergies produced by various collaborative behavioral innovations provided proximate rewards or reinforcements (as the behaviorists would say) that were substantial enough to create a behavioral “pacemaker” (*sensu* Ernst Mayr 1960) for the progressive evolution over time of our distinctive wardrobe of biological characteristics. In other words, we invented ourselves (in effect) in response to various ecological pressures and opportunities—a paradigm that may be more widely applicable to evolutionary change than is generally appreciated (see Corning 1996a, 2003). Here I can only summarize the argument.<sup>4</sup>

The traditional approach to explaining human evolution has been to propose a “prime mover” theory, which is typically portrayed as the “engine” that has powered the course of human evolution. Darwin, in *The Descent of*



*Man* (1874), singled out the role of toolmaking. E. O. Wilson (1975) stressed our primate “preadaptations” and speculated about the possible role of an unspecified “autocatalysis.” Bipedalism, which we now know preceded the development of the “big brain,” is currently viewed by many theorists as the “breakthrough” development (e.g., Donald Johanson, Richard Leakey, Timothy White, etc.). Major climate changes during the Miocene and Pliocene have also been suggested as important precipitating factors (e.g., Yves Coppens, Elizabeth Vrba). Then there are the various competing group theories: group hunting (Dart, Washburn, Ardrey, Thompson, Stanford and others); group scavenging (Potts, Blumenshine, Shipman, etc.); female gathering (Zihlman and Tanner); the nuclear family and male provisioning (Lovejoy); collective defense against predation (Kruuk, Kortlandt, Alexander, etc.); and the ever-popular group conflict hypothesis, which traces back to Darwin and Spencer and which has been championed in the past century by Dart, Keith, Ardrey, Lorenz, Bigelow, Otterbein, and Alexander, among others. In the latter stages of human evolution, climate change, population growth, food surpluses, the adoption of fire, language development, increased intelligence, and warfare have also been singled out as prime movers by various theorists at various times.

Holistic Darwinism suggests the contrarian view that all of these factors were important but that none was sufficient. To repeat, the engine is nothing without the car. The answer lies in the unique combination of factors that produced, over time, many compatible and mutually supportive cooperative effects (functional synergies). Indeed, objections can be mounted against every one of the factors cited above, taken individually. For example, bipedalism is not unique to humans; birds are bipedal, and kangaroo forelimbs have atrophied rather than becoming instruments for the skilled manipulation of tools. In fact, hominid bipedalism existed for some millions of years before the “big brain” emerged. Toolmaking is also an insufficient explanation; we now know that many species make and use tools, especially our closest relatives the chimpanzees. Also, crude stone tools were used by our hominid ancestors for perhaps a million years before the more refined and standardized Acheulean toolkit appeared (Leakey 1994; Tattersall 1995). Group hunting and scavenging are also inadequate explanations, for the same reasons; our ancestors were hardly unique in this regard. The primeval gathering scenario and the nuclear family scenario are appealing, though difficult to support empirically; yet they are in any case insufficient because they overlook other factors—namely, the often serious threat from potential predators and the premium associated with meat getting (via scavenging, hunting, or both) in the more open and diversified

environments in which some of the later hominid developments most likely occurred. Even the conflict hypothesis—which Alexander (1979) asserts is both necessary and sufficient—begs the question: why are there no nation-states composed of chimpanzees, which we now know can be quite warlike? The very absurdity of that idea highlights the fact that there had to be many other factors that worked together to propel the process. Indeed, the extensive hominid migrations out of Africa over time suggest that conflict avoidance might well have been a common adaptive strategy.

In a major critique of cultural evolution theories, anthropologist Elman Service (1971) came to this emphatic conclusion: “down with prime movers!” (p. 25). The same can be said, equally emphatically, of the larger process of human evolution. Prime mover arguments invariably take for granted some, or all, of the other requisites for survival and reproduction. Very often they reflect a kind of ecological naivete; they discount the many life-and-death challenges associated with living (and evolving) in a demanding and changeable environment over a period of several million years. But if no one factor alone can provide a sufficient explanation for the evolution of humankind, then what is sufficient? The answer is that all of the important human traits were necessary and none were sufficient. In effect, there was a mutually reinforcing synergy among the key innovations—combined effects that would not otherwise have been possible.

### “Man Makes Himself”

However, the dominant theme of human evolution may have been the expansion of various modes of social cooperation (including cooperative modes of competition), which have been rewarded with commensurate bioeconomic benefits. To reiterate, competition and cooperation are not mutually exclusive explanations for human evolution; each played an important role in shaping our evolution. Nevertheless, the thesis here is that increasingly potent (and selectively advantageous) forms of social cooperation may have given our ancestors their competitive edge.

As Edward O. Wilson (1975, 1985) has noted, a multifaceted group-living ecological strategy is a relatively rare occurrence in nature. We rightly admire the complex social organization of honeybees, naked mole rats, army ants, killer whales, and a small number of other highly social species, including some of our close primate relatives. The synergies that have made such collective survival strategies rewarding for various social species are increasingly well documented. We are among that select company, and it has been the key to our evolutionary success. A human society can be characterized

as a “collective survival enterprise.” We meet our basic survival needs through elaborate networks of social cooperation.

We do not know, and likely never will know, the full story of our evolution as a species, although we are gradually adding more details to the outline and making better-informed guesses. However, there is reason to believe that behavioral changes in the direction of greater social cooperation for specific functional purposes were the “pacemakers” that precipitated supportive morphological changes. In a very real sense, as anthropologist V. Gordon Childe (1951) put it in the title of his famous 1936 book on the rise of civilization, the human species may have “invented” itself. The real key to human evolution, accordingly, was not any single prime mover but the entire suite of cooperative behavioral, cultural, and morphological inventions—a synergy of synergies.

An oft-used (and important) illustration of this dynamic is the adoption by evolving hominids of the controlled use of fire (or, more broadly, various exogenous forms of energy). This is a uniquely human cultural invention and is still a major factor in our ongoing evolution—a point that various energy-oriented theorists have thoroughly documented (e.g., L. A. White 1943, 1949; Cottrell 1953; H. T. Odum 1971; Adams 1975, 1988). The earliest strong evidence for the use of fire by our hominid ancestors is identified with the Middle Pleistocene, perhaps 200 to 400,000 years ago. However, some theorists argue on plausibility grounds, albeit with more fragmentary evidence, for a much earlier date. (See especially the cautious review by James [1989] and the offsetting commentary by Lewis in the same volume.) The controlled use of fire by hominids (in effect, a cooperative animal-tool symbiosis) had enormous long-term benefits. Over the course of time, fire was most likely used as an effective means of defense against predators; it was a source of warmth that facilitated migration into colder climates; it might well have served as an insect repellent and as a means for obtaining honey from bee hives (as a bee suppressant); it probably became a weapon for driving and capturing prey animals; it was a means for shaping and hardening tools; it could be used for conditioning the environment (as in slash and burn horticulture); and, not least, it enabled our ancestors to add to their diets many foods that would otherwise have been toxic, indigestible, or infectious if eaten raw (Leopold and Ardrey 1972; Stahl 1984). See also the case that is developed in Wrangham et al. (1999) for what they call the “cooking hypothesis” (also Wrangham 2001).

In any event, fire represented the functional equivalent of a major morphological development. With the acquisition of fire, our ancestors were able to greatly expand their niche, which in turn changed the selective forces

to which our ancestors were subject. Furthermore, fire most likely became another focal point of social cooperation. Fire-keeping was a collective good that required a division of labor—for gathering firewood, fire tending, fire transport, and, eventually, fire-making. In other words, this primordial hominid technology, like most human technologies, was at once a source of bioeconomic benefits and a generator of social cooperation and social organization.

How can this synergistic theory of human evolution be tested? One way is to try a few thought experiments: Take away fire (along with other energy sources in modern societies); we are utterly dependent upon exogenous forms of energy. Or, take away language, or bipedalism, or tools and technology. In short, there is no major adaptive modality that we could do without; they are all necessary parts of an interdependent, synergistic system.<sup>5</sup>

### **Conclusion: A Post-Neo-Darwinian Paradigm?**

I believe that Holistic Darwinism can plausibly be viewed as a candidate for a post-Neo-Darwinian theoretical paradigm. It refocuses evolutionary theory on the “vessels” and their functional properties as the vanguard of evolutionary change. In fact, that is where natural selection as a causal dynamic actually occurs; to use an older turn of phrase, it is the phenotypes that are “tested” in the environment. Holistic Darwinism shifts our focus from the anthropomorphic purposes of selfish genes in theoretical isolation to the evolved, emergent purposiveness of the living systems as wholes, and to the functional interactions and relationships (adaptations in specific environments) that result in differential survival and reproduction. It also stresses the “synergistic selection” of various combinations.

Equally important, Holistic Darwinism de-emphasizes (without denying) the role of genetic mutations, recombinations, transpositions, etc., as sources of creativity in evolution and emphasizes purposeful innovations which may occur at the behavioral, cognitive, even social levels (inclusive of symbiogenesis). In this model, proximate “neo-Lamarckian selections” by wholes (i.e., adapting organisms and, in some cases, adapting groups) assume a much more important role in evolutionary change than is acknowledged in Neo-Darwinism.

Finally, and perhaps most contentious of all, I maintain that Holistic Darwinism also encompasses human evolution and, indeed, the ongoing biocultural evolution of our species. (Again, see the further discussion in chapters 6 and 17.) It is a seamless theoretical framework that does not require any additional causal principle or “mechanism” to account

for humankind.<sup>6</sup> We must recognize human culture, human economies, even human political systems for what they truly are—an augmentation of adaptive modalities that can be found in rudimentary form in many other species. (In this paradigm, the activities of humankind virtually everywhere on earth are viewed as an integral part of the evolutionary process, not something that is separate from it.) But, having recognized that, we must also acknowledge our uniqueness as a species. Complex human societies are as different from those of honeybees or naked mole-rats or even chimpanzees as complex multicellular organisms are from single-celled protists. The cumulative, synergistic effects of many differences in degree have produced a difference in kind—and a dynamic of rapid change at the behavioral/cultural level that is obviously unique. This is an evolutionary development that Holistic Darwinism can fully comprehend. It is not even conceivable in a theoretical world that barely recognizes the existence of wholes.

I believe that it is time to refocus the Necker cube on the problem of explaining the evolution of complex systems in a way that is fully consistent with Darwin's vision. In the long run, I believe that the Darwinian, functional explanation of complexity will prevail over various orthogenetic theories of self-organization—in reality a teleological black box that begs the “how” question (see chapter 4), or theories that postulate a random “drunkard's walk” (S. J. Gould 1996). Gould's argument is especially surprising, coming as it does from such a sophisticated and articulate student of evolution. It is a formulation which tacitly ignores the functional costs and benefits related to the evolution of biological complexity; complexity is not a free lunch but a cumulation of adaptive innovations over the eons. I can only second the conclusion of George Williams in the peroration of his famous book (1966, p. 273): “It may not, in any absolute or permanent sense, represent the truth, but I am convinced that it is the light and the way.”