

# Human Social Evolution

THE FOUNDATIONAL WORKS OF  
RICHARD D. ALEXANDER



*Edited by*  
Kyle Summers • Bernard Crespi

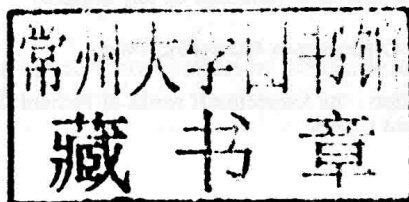
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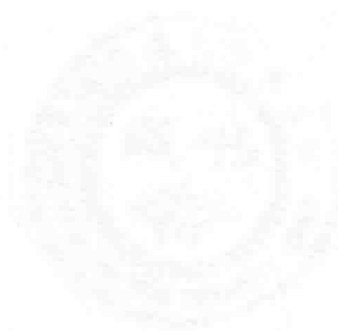
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RICHARD D. ALLEXANDER

Edited by Nick Soderstrom  
and  
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SAN DIEGO

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## PREFACE

This book is a tribute to one of the great minds in evolutionary biology, Richard D. Alexander. His help and encouragement during our graduate careers at the University of Michigan was invaluable to both of us, and we miss the penetrating discussions of complex topics in human and animal behavior and evolution that he loved to engage in. His contributions to science, and the humanities, should become standard reading for generations to come, and we hope this volume will help to make that goal a reality. Dr. Alexander provided unstinting help with various facets of the process of developing and producing this volume, and we thank him for his efforts.

We also would like to take this opportunity to thank all of the people who contributed to this volume—their contributions have served to highlight Dr. Alexander's work, and illuminate the many contributions he has made to our understanding of human social evolution. These contributors also illustrate how Dr. Alexander's legacy is being passed on through the scientists that he trained and influenced during the course of his career. He taught so many of us how to think about evolution, and humanity, and how to turn these thoughts into productive science.

We also thank our families, who have tolerated our absent-mindedness, and absences during the long hours and late nights required to complete this volume.

K.S. and B.C.



# CONTENTS

Contributors ix

Preface xi

Introduction – Kyle Summers and Bernard Crespi 1

## PART I} General Foundations

### 1. Insect Behavior and Social Evolution 21

Introduction: From Cricket Taxonomy to a Darwinian Philosophy of Man by Mary Jane West-Eberhard, Smithsonian Tropical Research Institute 23

Excerpt from Alexander, R. D. 1969. Comparative animal behavior and systematics. In: *Systematic Biology. Proceedings of the International Conference on Systematics* (Ann Arbor, Michigan, July 1967). National Academy of Sciences Publication 1962: 494–517. 29

### 2. Cooperation 39

Introduction: A New Theory of Cooperation by Steven Frank, University of California at Irvine 40

Excerpt from: Alexander, R.D. 1986. *The Biology of Moral Systems*. New York: Aldine Press. 48

### 3. Eusociality in Naked Mole-Rats 53

Introduction: Richard Alexander, the Naked Mole-Rat, and the Evolution of Eusociality by Paul Sherman, Cornell University 55

Excerpt from Alexander, R.D., Noonan, K.M. and Crespi, B.J. 1991. The Evolution of Eusociality. In P. Sherman, J. Jarvis and R.D. Alexander (eds.). *The Biology of the Naked Mole-Rat*: 3–44. Princeton, NJ: Princeton University Press. 63

### 4. Parent-Offspring Conflict and Manipulation 70

Introduction: The Evolution of Social Behavior by David Queller, Washington University 71

Excerpt from Alexander, R.D. 1974. The evolution of social behavior. *Annual Review of Ecology and Systematics* 5:325–383. 77

PART II } **Human Social Evolution**

**5. Biology and Culture 93**

Introduction by Mark Flinn, University of Missouri 95

Excerpt from Alexander, R.D. Evolution and culture. In *Evolutionary Biology and Human Social Behavior: an Anthropological Perspective*.

N. Chagnon and W.G. Irons (eds.): pp. 59–78. North Scituate, MA: Duxbury Press. 104

**6. Intergroup Competition and Within-group Cooperation 123**

Introduction: Thinking about Human Aggression, Past and Present:

Alexander and Tinkle's (1968) Review of Lorenz and Ardrey by Bobbi Low, University of Michigan 125

Excerpt from Alexander, R.D. and Tinkle, D.W. 1968. Review of *On Aggression* by Konrad Lorenz and *The Territorial Imperative* by Robert Ardrey. *Bioscience* 18:245–248. 130

**7. Kinship, Parental Care, and Human Societies 138**

Introduction: Concealed Ovulation in Humans: Further Evidence by Beverly Strassmann, University of Michigan 139

Excerpt from Alexander, R.D. and Noonan, K.M. 1979. Concealment of ovulation, parental care, and human social evolution. In N.A. Chagnon and W.G. Irons (eds.). *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective*. 436–453. North Scituate, MA: Duxbury Press. 152

**8. Human Childhood 171**

Introduction: Altriciality, Neoteny, and Pleiotropy by Paul Turke, University of Michigan 173

Altriciality: Why are human babies helpless? In Alexander, R.D. 1990. *How Did Humans Evolve? Reflections on a Uniquely Unique Species*. University of Michigan Museum of Zoology Special Publication 1:1–38. 182

**9. Indirect Reciprocity 197**

Introduction: The Basis of Morality, Richard Alexander on Indirect Reciprocity by Karl Sigmund, University of Vienna 199

Excerpt from Alexander, R.D. 1986. *The Biology of Moral Systems*. New York: Aldine Press. 209

**10. The Evolution of Intelligence 232**

Introduction: Reflections on the Evolution of the Human Psyche by R.I.M. Dunbar, Oxford University 235

Alexander, R.D. Evolution of the Human Psyche 1989. In P. Mellars and C. Stringer (eds.). *The Human Revolution. Behavioral and Biological Perspectives on the Origins of Modern Humans*: pp. 455–513. Princeton, NJ: Princeton University Press. 244

## 11. Evolution of Morality 305

Introduction: Twelve (More) Things about the Evolution of Morality that Make People Nauseous by David Lahti, City University of New York 307  
Alexander, R.D. Biology and the Moral Paradoxes. *Journal of Biological Structures* 5:389–395. 325

## 12. Evolution and Humor 334

Introduction: The Adaptive Significance of Humor by Stan Braude, Washington University 337  
Alexander, R.D. Ostracism and Indirect Reciprocity: The Reproductive Significance of Humor. 1986. *Ethology and Sociobiology* 7:253–270. 345

## 13. Ecological Constraints and Human Cooperation 364

Introduction: Darwin's Question: How Can Sterility Evolve? by Laura Betzig, The Adaptationist Program 365  
Excerpt from Alexander, R.D., Noonan, K.M. and Crespi, B.J. 1991. The Evolution of Eusociality. In P. Sherman, J. Jarvis and R.D. Alexander (eds.). *The Biology of the Naked Mole-Rat*: pp. 3–44. Princeton, NJ: Princeton University Press. 375

## 14. Evolution and Religion 379

Introduction: The Concept of God as a Metaphor for Social Unity: Richard Alexander's Hypothesis by William Irons, Northwestern University 381  
Religion, Evolution and the Quest for Global Harmony—Original essay for this volume 384

## 15. Evolution and the Arts 426

Introduction: Cornerstone to Capstone: Richard Alexander on Social Selection and the Arts by Kyle Summers, East Carolina University & Bernard Crespi, Simon Fraser University 429  
Excerpt from Alexander, R.D. 2003. Evolutionary Selection and the Nature of Humanity. Chapter 15. In: V. Hosle and Ch. Illies (eds.). *Darwinism and Philosophy*. South Bend, IN: University of Notre Dame Press. 440

## Index 453

# Introduction

Kyle Summers and Bernard J. Crespi

After decades rife with science strife  
It seems appropriate to join  
The slice of life that plies the knife  
Along the flip side of the coin

R. D. ALEXANDER, 2011

Richard D. Alexander is a farmer and rancher, horse trainer, poet, story teller, folk singer, song writer, musician, author, and a philosopher, as well as a husband (to Lorrie Alexander), a parent, and a grandparent. He and his wife have run a large farm in Manchester, Michigan for more than thirty-five years. Alexander grew up in rural Illinois, the child of two school teachers turned livestock farmers. His childhood passed without many of the conveniences of modern life, such as electricity and indoor plumbing. His mother cooked on a wood stove, and light after dark came from kerosene lamps. His family raised cows, pigs, and chickens on feed they grew themselves, selling meat, eggs, and cream. Alexander grew up doing "chores" that most people would consider hard labor, such as working his own threshing team of draft horses on different farms across the county. He went to school in a one room country schoolhouse with a single teacher for all grades. In 1946, Alexander attended Blackburn College, where he was consigned to a single dormitory with a mix of new high school graduates and veterans of World War II who were returning to school. In high school, Alexander had no thought of attending college, and when he first went to college he had no thought of a career in academia. From these rural origins sprang an intellect that has transformed our understanding of human social behavior and evolution and, we propose, ourselves.

Alexander's intellectual curiosity about human evolution probably sprang from his early experiences in church, where he found himself fascinated by the questions raised concerning human nature, yet dissatisfied by the answers proffered. Early in his college career, during his time at Blackburn College, he realized that in academia he could pursue any questions he thought were of interest. Although he pursued coursework in philosophy at Illinois Normal University after transferring from Blackburn, Alexander was struck by the lack of a model of human nature, and ultimately turned to biology to pursue his interests. Before entering graduate

school, he did not have the opportunity to take a course in evolutionary biology, and even after deciding to pursue graduate study in biology at the University of Ohio, where he studied entomology (see ch. 1), there were few courses in evolutionary biology available. Nevertheless, over time his interests in evolution crystallized and motivated Alexander to pursue three of the most difficult and important questions in biology: how the diversity of life came into being through the process of speciation, how natural selection has shaped the complexity of life (including our own minds), and the meaning of the extreme social attributes of humans (e.g., art, music, dance, religion) from an evolutionary perspective. Alexander was able to pursue groundbreaking research on the first two questions as a graduate student working on singing insects, but it was only after he had become a faculty member at the University of Michigan that he began to focus on sociality, and particularly on human social behavior.

Over a long career at the University of Michigan, Alexander became, we would argue, the world's leading thinker on human social behavior from an evolutionary perspective. His publications on this topic trace back to a remarkable review in 1968 (with Donald Tinkle) of two books (*On Aggression* by Konrad Lorenz and *The Territorial Imperative* by Robert Ardrey), where he laid out a hypothesis concerning the influence of intergroup competition on human social behavior that continues to be influential today. It was obvious from this review that Alexander had been thinking about these issues for a long time, and from these beginnings sprang a long series of publications on human social evolution that have continued throughout his career at the University of Michigan, and beyond.

A key watershed occurred with the publication of Alexander's first book on human social evolution: *Darwinism and Human Affairs*, in 1979 (The University of Washington Press). In developing his ideas for this book, Alexander was greatly influenced by the profound insights of three contemporaries: George Williams, who taught biologists how to think about selection at the level of individual rather than species benefit, William Hamilton, whose inclusive fitness theory, and evolutionary stable strategy reasoning, taught us how to apply selection thinking at the levels of genes, families, and evolving traits, and Robert Trivers, who first explained how kin cooperation and kin conflict are necessarily enmixed, and how reciprocity can evolve, especially in species with powerful cognitive abilities, such as humans. This was a time of Darwinian revolution for the study of behavior, when the conceptual tools for understanding behavioral phenotypes, especially conflicts and confluences of interest, first came together. In *Darwinism and Human Affairs*, Alexander first applied many of the key theoretical approaches that these three researchers had developed—and many of his own—to human social behavior in a comprehensive and systematic way, providing the most complete and rigorous overview of the entire scope of human social behavior from an evolutionary perspective achieved to that point.

After the publication of *Darwinism and Human Affairs*, a veritable flood of research on human social behavior was initiated by evolution-minded scientists, not only in biology but in many other fields. The major themes that Alexander laid out in his first book continue to be the focus of intense interest and debate in the study of human social behavior today, including kinship and nepotism, direct and indirect reciprocity, ontogeny, life history and senescence, the evolution of culture, deceit and self-deception, innate and learned behavior, morality, law and justice, and the evolution of artistic expression, among others.

Many years have passed since *Darwinism and Human Affairs*, and in this time Alexander, his students and colleagues, and many others, have been constructing a new evolutionary synthesis upon these themes, a synthesis that has grown to encompass anthropology, psychology, psychiatry, economics, sociology, the arts, humanities, and religion. This volume is a celebration of Richard Alexander's work, and his diverse, enduring influences in the study of virtually all aspects of humanity. For each chapter we have chosen an excerpt from a key paper or chapter that represents a particular theme that Alexander wrote about over the course of his career. Each chapter is introduced by an expert in the field, most of whom are former students or colleagues of Dr. Alexander, who provides perspective on how his ideas have advanced scientific thought.

We believe this structure for the book is appropriate because Alexander constantly strove to inspire his students and colleagues to think carefully about evolution and human behavior, and to develop and test novel, integrative hypotheses. In his classic "Evolution and Human Behavior" course, taught for decades at the University of Michigan, Alexander would challenge any and all students (undergraduate and graduate) to try and find errors in his arguments, and to develop their own alternative hypotheses. Alexander would carefully read hundreds of essays, and provide firm yet helpful comments to all the students in this very popular (and hence very large) class. That some of his students took him up on this challenge is apparent from this volume. Beverly Strassmann, for instance, wrote a paper in this class as an undergraduate that has itself become a classic in the field of human social evolution (Strassmann 1981). But this is just a start—all of the students and colleagues of Alexander who have written introductory essays for this volume have gone on to develop their own research programs in social evolution, and those authors who did not directly interact with Alexander were nonetheless inspired by his published work as they developed their own theories. Even the essays themselves reveal the profound influence of Alexander's philosophy. For example, Paul Turke, in his essay, proposes a novel hypothesis connecting altriciality and neoteny to the delayed senescence that characterizes the human species relative to other primates. Even in the short space of an introduction, Alexander's associates cannot help but explore novel connections and new ideas. This is a major part of Alexander's legacy—a cadre of evolutionary thinkers who, inspired by his example, have spent their lives developing and testing hypotheses

concerning social evolution, and especially the social evolution of that most complicated of species, ourselves.

## One

Chapter 1 by one of Alexander's first graduate students, Mary Jane West-Eberhard, provides an overview of Alexander's early work on communication and mating behavior. West-Eberhard is a staff scientist at the Smithsonian Tropical Research Institute. She is one of the world's leading experts on the behavior and evolution of social wasps, and has also published on sexual and social selection in general, and in relation to speciation, as well as a groundbreaking body of theory connecting developmental mechanisms to evolutionary phenomena, including morphological and behavioral change under selection, and population divergence and speciation. The chapter provides a brief synopsis of some of Alexander's early work on communication, mating behavior, and speciation in insects, and some of his early thoughts on human evolution. West-Eberhard shows how one of his papers was a bridge between his earlier writings and the later ones on human evolution. She argues that Alexander's exceptional abilities to illuminate the evolutionary basis of human social behavior stemmed from his strong background in the systematics and evolutionary biology of the singing insects, and his pioneering work on Darwinian approaches to behavior in nonhuman animals.

## Two

In chapter 2, Steven Frank explores a new view of the evolution of cooperation that was developed by Alexander, as illustrated by an excerpt from his second book on human social evolution, *The Biology of Moral Systems* (1987). Frank, a professor of evolutionary biology at the University of California at Irvine, is one of the world's leading evolutionary theoreticians. His work has transformed our understanding of inclusive fitness, multilevel selection, sex ratio evolution, parasite-host coevolution, and genetic conflict, among many other topics. Frank began his pursuit of a career in evolutionary biology after taking Alexander's class in animal behavior as an undergraduate. He was a graduate student of the late William Hamilton, but was also advised by Alexander. He points out that the extensive cooperative networks that are part and parcel of the vast nation-states that characterize human society are not easily explained by the twin pillars of cooperation developed in evolutionary biology: kinship and reciprocity. He argues that Alexander's work led to a new view of how these cooperative networks could evolve and remain stable: group suppression of conflict. Alexander's ideas in this vein followed from two parallel themes that he pursued over the course of his career: the evolution of morality and justice, and the evolution of individuals at different levels in the

hierarchy of life over the course of evolution. These ideas were stimulated by the work of other great thinkers (such as John Rawls in the case of morality, and Egbert Leigh in the case of conflict suppression in the evolution of the hierarchy of life), yet he developed a unique synthesis that made the generality of the concepts clear. The theoretical underpinnings of this mechanism have now been developed and refined (by Steven Frank and others), and it has become another general principle upon which our understanding of the evolution of cooperation rests. The idea has far-reaching implications. For example, as Alexander stresses in the *Biology of Moral Systems*, the reproductive opportunity-leveling characteristic of large democratic nation-states may have led to their notable success at warfare and territorial expansion at the expense of more despotic regimes. In fact, the collapse of despotism (which was the rule rather than the exception during the long course of human history following the development of agriculture) may well have been driven by this dynamic. After all, the prospect of fighting and risking one's life for king and country is less appealing when the royal elite have monopolized most of the women.

### Three

In chapter three, Paul Sherman introduces an excerpt from a classic paper on the evolution of eusociality (by Alexander, Noonan, and Crespi), published in 1991 in an edited volume entitled *The Biology of the Naked Mole-Rat*. Sherman, a professor of biology at Cornell University, is a world-renowned researcher in the field of animal behavior, having carried out groundbreaking studies on the social behavior of ground squirrels, naked mole rats, and wood ducks, among other organisms. He is also a leader in the field of evolutionary medicine, publishing innovative studies of spices as antimicrobial agents, allergies as anticancer mechanisms, and morning sickness as a toxin-avoidance mechanism, among many other topics. Sherman was a graduate student of Alexander, and they later worked together to establish the first naked mole-rat colonies in the United States, at the University of Michigan and at Cornell University. Sherman relates the story of how Alexander conceived of the key characteristics of a eusocial vertebrate as a thought experiment and prediction before anyone was aware of the existence of such an animal. Remarkably, Alexander's description almost perfectly described the naked mole-rat, which was the subject of research by the biologist Jennifer Jarvis in South Africa. The discovery of a eusocial vertebrate allowed profound insights into the ecological and evolutionary mechanisms that drove the evolution of eusociality, and in turn this led to a flood of research and publications, culminating in *The Biology of the Naked Mole-Rat*. Sherman points out that Alexander had been thinking about the evolution of eusociality for a long time before writing the chapter, beginning with a strong interest in the phenomenon as an entomologist studying social behavior. He notes that Alexander et al. (1991) made several key points with respect to the evolution

of eusociality: First, the haplo-diploid system that characterizes the major eusocial insect groups (ants, bees, and wasps) is not a sufficient explanation for the evolution of eusociality; second, eusociality is a much more general phenomenon than initially appreciated, evolving convergently across vast spans of the tree of life; and third, both intrinsic (genetic and developmental) and extrinsic (ecological) factors must have been crucial for the evolution of eusociality. Alexander et al. (1991) argued that both “ecological constraints” (environmentally imposed constraints on the ability of individuals to breed on their own) in the form of the need for nest site protection from predation (an extrinsic factor), and levels of genetic relatedness (kinship, an intrinsic factor), are crucial for the evolution of eusociality. Sherman emphasizes that the arguments presented in Alexander et al. (1991) have become widely accepted, and the chapter has become an indispensable guide to understanding the evolution of eusociality.

#### Four

Chapter 4, by David Queller, introduces an article that represents Alexander’s (1974) first exposition of general theory for the evolution of social behavior across all animals, including humans. Queller was a doctoral student with Alexander, and has since gone on to become one of the foremost researchers working on social evolution, in organisms from plants to wasps to slime molds to humans. He describes how Alexander’s (1974) paper, integrating nepotism, reciprocity, and his new idea—parental manipulation—served as a nexus for future theory and research, which included extensions, inspiration, presages of much-later developments such as skew theory, and ultimately constructive assaults. Alexander (1974) also marks his transition from mainly studying crickets, to mainly focusing on the evolution of sociality, and his effective combining of studies of specific taxa and big questions in social evolution is mirrored in the work of many of his students.

#### Five

The fifth chapter, by Mark Flinn, expands on a paper elucidating Alexander’s conception of how culture, long a bastion defended against biology, evolves in the contexts of the human psyche, human conflicts and confluences of interest, and human beliefs concerning how best to respond to particular social and material contingencies. As an evolutionary anthropologist who has also survived, and prospered, in the biology-versus-culture debate that was catalyzed by the changes in evolutionary theory that Alexander, Hamilton, Trivers, Williams, and others developed, Flinn is uniquely suited to describe how Alexander provides a novel behaviorally based perspective on human culture. Alexander’s analysis opened the door for future researchers to study culture from the perspective of evolutionary biology. Flinn was one of the first through this door. He was influenced by