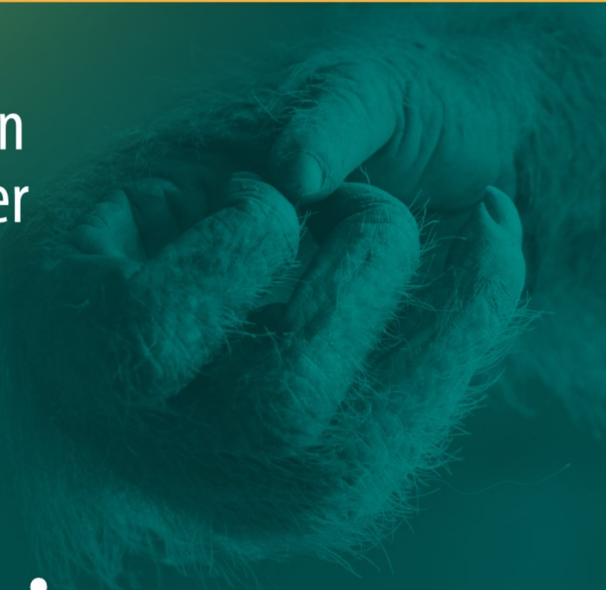
Developments in Primatology: Progress and Prospects

*Series Editor:* Louise Barrett



Robert W. Sussman
C. Robert Cloninger
*Editors*

# Origins of Altruism and Cooperation

Springer

# Developments in Primatology: Progress and Prospects

**Series Editor**

Louise Barrett

For further volumes:
http://www.springer.com/series/5852

Robert W. Sussman · C. Robert Cloninger
Editors

# Origins of Altruism and Cooperation

Springer

*Editors*
Robert W. Sussman
Department of Anthropology
Washington University
St. Louis, MO 63130, USA
rwsussma@artsci.wustl.edu

C. Robert Cloninger
Department of Psychiatry
Washington University
School of Medicine
St. Louis, MO 63110, USA
clon@wustl.edu

ISBN 978-1-4419-9519-3 e-ISBN 978-1-4419-9520-9
DOI 10.1007/978-1-4419-9520-9
Springer New York Dordrecht Heidelberg London

Library of Congress Control Number: 2011932917

Printed on acid-free paper

Springer is part of Springer Science+Business Media (www.springer.com)

*We dedicate this book to Walter Goldschmidt who reminded us at the conference that: "You talk about cooperation and altruism, but what you really mean is LOVE. We shouldn't be afraid to use the word LOVE. That is what makes us truly human."*

# Preface

This book is derived from a conference entitled "Man the Hunted and the Origin and Nature of Human Sociality, Altruism and Well-Being" held at Washington University, March, 2009. Authors include academics from around the world and across multiple disciplines—anthropology, psychiatry, human evolution, biology, psychology, religion, philosophy, education, and medicine—to focus on the evolution of cooperation, altruism, and sociality and possible factors that led to the evolution of these characteristics in nonhuman primates and humans.

The traits of altruism and cooperation often are assumed to be among humanity's essential and defining characteristics. However, it has been difficult to account for the origins and evolution of altruistic behavior. Recently, scientists have found data on altruistic behavior in many animal species, as well as in human societies, that do not conform to evolutionary models based solely on competition and the evolutionary drive to pass on selfish genes. In this volume, recent debates about the nature and origins of cooperative behaviors are reviewed. The hypothesis that unselfish cooperative behavior has evolved in animals that live in social groups is discussed. Many of the mechanisms that primates and humans have evolved for protection against predators, including cooperation and sociality are explored.

Social animals, including primates and humans, are not forced to live socially but do so because it benefits them in numerous ways. Through natural selection, primates and humans have developed areas of the brain that respond to being cooperative or altruistic as pleasant and satisfying activities. Data are presented supporting the idea that the normal pattern for most diurnal primates and for humans is to be social. People who develop the need for psychiatric intervention are those who have become alienated and antisocial. It is human nature to want to work together and cooperate. A hypothesis is developed that well-being is inseparable from positive social interaction.

All diurnal primates live in social groups. This is widely recognized as a predator protection mechanism. The more eyes and ears to detect predators and the more animals to mob them, the better the group is protected. Early humans have traditionally been thought of as hunters. However, because of their relatively small size, dental morphology, lack of hunting tools, and a number of other factors, it is more likely that the earliest humans, like most other primates, were prey species rather than predators. Sociality, cooperation, inter-individual dependency, and mutual protection are all part of the toolkit of social-living prey.

Watching the 5 o'clock news regularly, you might think that humans were born to be destructive, violent, and antagonistic. But this is not the case. The evidence leads to the conclusion that cooperative and altruistic behaviors are not just by-products of competition but rather are essential ingredients in evolution, ecology, and development, and are the glue that underlies the ability for primates and humans to live together in groups. The paleontological, behavioral, neurobiological, and psychological evidence provided in this book gives a more optimistic and realistic view of human nature than the more popular, conventional view of humans being naturally and basically aggressive and warlike. Competition and aggressive self-preservation are a definite part of the behavioral repertoire of all mammals, but they are primitive tendencies that are progressively regulated by higher cognitive processes increasing the capacity for cooperation, which emerged in a stepwise fashion in the evolution of nonhuman primates and human beings from their common ancestors. The evidence described in this book from many fields indicates that cooperation and altruism are the statistical norm and represent the more typical, "normal," spontaneous (or natural) and healthy behavioral pattern in primates. In fact, cooperative sociality is a necessity for well-being in anthropoid primates.

In this volume, the authors review recent debates about the nature and origins of cooperative behavior. They test the hypothesis that unselfish cooperative behavior has evolved in group-living animals. Finally, they explore this hypothesis and many of the mechanisms nonhuman primates and humans may have evolved as protection against predators, including cooperation and sociality. The authors discuss how behavioral, hormonal, neuropsychiatric, and developmental mechanisms related to our evolution as a prey species might be affecting modern human and nonhuman primate behaviors.

Social scientists and biologists are learning that there is more to cooperation and generosity in both human and nonhuman group-living animals than an investment in one's own nepotistic patch of DNA. Research in a great diversity of scientific disciplines is revealing that there are many biological and behavioral mechanisms that humans and nonhuman primates use to reinforce pro-social or cooperative behavior. For example, there are specific neurobiological and hormonal mechanisms that support social behavior. There are also psychological, psychiatric, and cultural mechanisms. However, there has been little interaction among researchers working on these subjects from different disciplines. Given that little interchange has taken place among the scientists conducting this research, there have been few attempts to synthesize this material or to carry out interdisciplinary projects on this subject. In this book, the authors will describe interdisciplinary research and synthesize currently available information.

The book moves theoretical anthropology forward by integrating, synthesizing, and providing new hypotheses and a better understanding of the proximate and evolutionary underpinnings of human cooperative behavior, altruism, and sociality. There is abundant evidence for both social cooperation and violence in human history. Alternative theories make different predictions about the determinants of both social and antisocial behaviors in primates. Some primatologists suggest that humans are naturally aggressive and violent in most situations, so that cooperation is infrequent and externally forced. Others suggest that human beings are "bipolar apes" with conflicting dispositions for waging war (like aggressive chimpanzees) and making love (like sociable bonobos), so that human beings must constantly strive to engage in emotional reconciliation to maintain social harmony. We suggest that human beings are naturally cooperative when healthy and only revert to violence under abnormal conditions, as when stressed, abused, neglected, or mentally ill. Readers will have an opportunity to consider the evidence needed to distinguish among these alternative theories of human nature. In a shrinking world, the proper mechanisms for future peaceful global interactions necessitate a better understanding of how, when, and why humans cooperate. Anthropology should provide a synthesis of this diverse body of knowledge and we hope that this volume helps moves us in a more optimistic direction.

The book is intended both for the general reader and for students at a variety of levels (graduate and undergraduate): it aims to provide a compact, accessible, and up-to-date account of the current scholarly advances and debates in this field of study, and it is designed to be used in teaching and in discussion groups. The conference from which this volume originated was sponsored by N.S.F., the Wenner-Gren Foundation for Anthropological Research, the Washington University Committee for Ethics and Human Values, and the Anthropedia Foundation for the study of well-being.

St. Louis, Missouri

Robert W. Sussman
C. Robert Cloninger

# Contents

**Part III Altruism and Cooperation Among Humans: The Ethnographic Evidence**

**Part IV Neurological and Hormonal Mechanisms for Cooperation and Altruism**

**Part V Human Altruism and Cooperation: Needs and the Promotion of Well-Being in Modern Life**

# Contributors

**Marc Bekoff** Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO, USA, marc.bekoff@gmail.com

**Peter Benson** Department of Anthropology, Washington University, St. Louis, MO 63130, USA, pbenson@artsci.wustl.edu

**Dan G. Blazer** Departments of Psychiatry and Behavioral Sciences and Community & Family Medicine, Duke University Medical Center, Durham, NC 27710, USA, blaze001@mc.duke.edu

**C. Robert Cloninger** Department of Psychiatry, Center for Psychobiology of Personality, Washington University School of Medicine, St. Louis, MO 63110, USA, clon@wustl.edu

**Kevin Cloninger** Anthropedia Foundation, 1033 Corporate Square Drive, St. Louis, MO 63132, USA, kcloninger@anthropedia.org; www.anthropedia.org

**R. Brian Ferguson** Department of Sociology and Anthropology, Rutgers University, Newark, NJ 07102, USA, bfergusn@andromeda.rutgers.edu

**Douglas P. Fry** BARA, University of Arizona and Åbo Akademi University, P.O. Box 311, FIN-65101, Vasa, Finland, dfry@abo.fi

**Agustín Fuentes** Department of Anthropology, University of Notre Dame, Notre Dame, IN 46556-5611, USA, afuentes@nd.edu

**Paul A. Garber** Department of Anthropology, University of Illinois, Urbana, IL 61801, USA, p-garber@illinois.edu

**Walter Goldschmidt** Department of Anthropology, University of California, Los Angeles, CA 90095-1553, USA, rwsussma@artsci.wustl.edu

**Donna Hart** Department of Anthropology, University of Missouri, St. Louis, MO 63121, USA, hartd@umsl.edu

**David Hay** Department of Divinity and Religious Studies, School of Divinity, History and Philosophy, King's College, University of Aberdeen, Aberdeen AB24 3UB, UK, j.d.hay@abdn.ac.uk

**Helen Herrman** Centre for Youth Mental Health, The University of Melbourne, Parkville, VIC 3052, Australia, h.herrman@unimelb.edu.au

**Sita Kedia** Department of Pediatrics, University of Colorado School of Medicine, Denver, CO 80220, USA, sita.kedia@uchsc.edu

**Bruce M. Knauft** Department of Anthropology, Emory University, Atlanta, GA 30322, USA, antbk@emory.edu

**Martin K. Kowalewski** Estación Biológica de Usos Múltiples de Corrientes (EBCo), Museo Argentino de Ciencias Naturales-CONICET, Buenos Aires, Argentina, mkowalew@uiuc.edu

**Katherine C. MacKinnon** Department of Sociology and Criminal Justice, Center for International Studies, St. Louis University, St. Louis, MO 63103, USA, ackinn@slu.edu

**Juan E. Mezzich** International Center for Mental Health, Mount Sinai School of Medicine, New York University, New York, NY 10029, USA, juanmezzich@aol.com

**Lauren E. Munsch** Anthropedia Foundation, Mt. Sinai School of Medicine, New York, NY 10029-6574, USA, lmunsch@gmail.com

**Mary S.M. Pavelka** Department of Anthropology, University of Calgary, Calgary, AB T2N 1N4, Canada, pavelka@ucalgary.ca

**Jane Phillips-Conroy** Department of Anatomy and Neurobiology, and Anthropology, Washington University School of Medicine, St. Louis, MO 63110, USA, baboon@pcg.wustl.edu

**Telmo Pievani** Department of Human Sciences, University of Milan II, Milan, Italy, telmo.pievani@gmail.com

**Seth D. Pollak** Department of Psychology, University of Wisconsin, Madison, WI 53706-1696, USA, spollak@wisc.edu

**James K. Rilling** Departments of Anthropology and Psychiatry and Behavioral Sciences, Emory University, Atlanta, GA 30322, USA, jrillin@emory.edu

**Charles T. Snowdon** Department of Psychology, University of Wisconsin, Madison, WI 53706, USA, snowdon@wisc.edu

**Karen B. Strier** Department of Anthropology, University of Wisconsin, Madison, WI 53706-1393, USA, kbstrier@wisc.edu

**Robert W. Sussman** Department of Anthropology, Washington University, St. Louis, MO 63130, USA, rwsussma@artsci.wustl.edu

**Ian Tattersall** Division of Anthropology, American Museum of Natural History, New York, NY 10024, USA, iant@amnh.org

# Chapter 1
# Introduction: Cooperation and Altruism

**Robert W. Sussman and C. Robert Cloninger**

This book is about the evolution and nature of cooperation and "altruism" in social-living animals, focusing especially on nonhuman primates and on humans. Although cooperation and altruism are often thought to be simply remedies to competition and aggression within groups or related to the action of "selfish genes," there is increasing evidence that these behaviors are the result of biological mechanisms that have developed through natural selection in group-living species. This evidence leads to the conclusion that cooperative and altruistic behaviors are not just by-products of competition but rather they are essential ingredients in evolution, ecology, and development (Weiss and Buchanan, 2009) and are the glue that underlies the ability for primates and humans to live in groups. The paleontological, behavioral, neurobiological, and psychological evidence provided in this book gives a more optimistic and realistic view of human nature than the more popular, conventional view of humans being naturally and basically aggressive and warlike. Competition and aggressive self-preservation are definite parts of the behavioral repertoire of all mammals, but they are primitive tendencies that are progressively regulated by higher cognitive processes increasing the capacity for cooperation, which emerged in a stepwise fashion in the evolution of nonhuman primates and human beings from their common ancestors. The evidence described in this book from many fields indicates that cooperation and altruism are the statistical norm and represent the more typical, "normal," and healthy behavioral pattern in primates. In fact, cooperative sociality is a necessity for well-being in anthropoid primates.

This book is intended both for the general reader and for students at a variety of levels (graduate and undergraduate): it aims to provide a compact, accessible, and up-to-date account of the current scholarly advances and debates in this field of study, and it is designed to be used in teaching and in discussion groups. This book is derived from a conference that took place at the Charles F. Knight Conference Center, Washington University on March 12–14, 2009. It was sponsored and funded by N.S.F., the Wenner-Gren Foundation for Anthropological

---

R.W. Sussman (✉)
Department of Anthropology, Washington University, St. Louis, MO 63130, USA
e-mail: rwsussma@artsci.wustl.edu

R.W. Sussman, C.R. Cloninger (eds.), *Origins of Altruism and Cooperation*,
Developments in Primatology: Progress and Prospects 36, DOI 10.1007/978-1-4419-9520-9_1,

Research, the Washington University Committee for Ethics and Human Values, and the Anthropedia Foundation for the study of well-being.

As stated by Darwin (1874), “It has often been assumed that animals were in the first place rendered social, and that they feel as a consequence uncomfortable when separated from each other, and comfortable whilst together, but it is a more probable view that these sensations were first developed, in order that those animals which would profit by living in society, should be induced to live together (97) . . .The feeling of pleasure from society is probably an extension of the parental or filial affections, since the social instinct seems to be developed by the young remaining for a long time with their parents; and this extension may be attributed in part to habit, but chiefly to natural selection” (102).

All diurnal primates, except orangutans, live in social groups. Their group-living is widely recognized as a predator-protection mechanism. The more eyes and ears to detect predators and the more animals to mob them, the better the group is protected. Early humans have traditionally been thought of as hunters. However, because of their relatively small size, dental morphology, lack of hunting tools, and a number of other factors, it is more likely that the earliest humans, like most other primates, were more often in the position of being the prey rather than the predator. If this is true, then sociality, cooperation, interindividual dependency, and mutual protection among humans, again like in most other primates, might all have their origins as part of the toolkit of social-living prey.

The concept of cooperation or of altruism (i.e., disinterested concern for another’s welfare) is often assumed to be one of humanity’s essential and defining characteristics. It has also been difficult to account for the origins of altruistic motives and behavior. Evolutionary biologists, primatologists, and anthropologists and other social scientists have found data on seemingly altruistic behavior in many animal species, as well as in human societies, that do not conform with models of kin selection and altruism based solely on competition and on the evolutionary drive to pass on selfish genes. For example, Clutton-Brock (2002) has provided ample evidence that the benefits of cooperation in vertebrate societies, generally, show parallels to those in human societies, where altruism between unrelated individuals is frequent, and social institutions are often maintained by generalized cooperation and reciprocity.

If social animals and humans can be cooperative and altruistic without benefiting their own (or their own genes’) survival, how can this be explained? Can individuals be cooperative without being selfish? If so, are they risking their own fitness? Also, there are differences in opinion about the definition of the term “altruism.” As discussed by Blazer (Chapter 24), in evolutionary biology the term often has been used to describe a behavior that an organism has that benefits another at a cost to itself. On the other hand, many believe that an action can only be considered altruistic if it involves the conscious intention of helping another. In the latter case, many would argue that only humans can be altruistic, even though the biological preconditions might be seen in nonhuman animals. The discrepancy between these positions can be constructively resolved by recognizing that there are many precursor functions that underlie the conscious expression of intentional altruistic behavior in human beings. Rather than lumping all these cooperative behaviors into broad terms, such as fairness or altruism, we suggest that the understanding of the similarities and differences in cooperation among different groups of mammals will be facilitated by more precise and well-differentiated terminology based on an integrated understanding of phylogeny, neurobiology, cognition, and behavior. That way we can begin to evaluate more objectively whether the differences between different species of mammals are differences of degree or of kind.

In this book, the authors review recent debates about the nature and origins of cooperative behavior and of altruism. They test the hypothesis that unselfish cooperative behavior has evolved in group-living animals. Finally, they explore this hypothesis and many of the mechanisms nonhuman primates and humans may have evolved as protection against predators, including cooperation and sociality. The authors also discuss how behavioral, hormonal, neuropsychiatric, and developmental mechanisms related to our evolution as a prey species and/or other factors might be affecting modern human and nonhuman primate behavior, and how these factors affect individual well-being.

Social scientists and biologists are learning that there is more to cooperation and generosity in both human and nonhuman group-living animals than an investment in one’s own nepotistic patch of DNA. Research in a great diversity of scientific disciplines is revealing that there are many biological and behavioral mechanisms that humans and nonhuman primates use to reinforce pro-social or cooperative behavior. For example, there are specific neurobiological and hormonal mechanisms that support social behavior. There are also psychological, psychiatric, and cultural mechanisms. These mechanisms can affect the well-being of individuals and societies. However, there has been little interaction among researchers working on these subjects from different disciplines. Given that little interchange has taken place among the scientists conducting this research, there have been few attempts to synthesize this material or to carry out interdisciplinary or transdisciplinary projects on this subject. In this book, the authors will describe interdisciplinary and transdisciplinary research, and synthesize currently available information. This book will move theoretical anthropology and evolutionary psychology forward by integrating, synthesizing, and providing new hypotheses and a better understanding of the proximate and evolutionary underpinnings of human cooperative behavior, altruism, and sociality, and how these factors might relate to improved well-being. In a shrinking world, the proper mechanisms for future peaceful global interactions necessitate a better understanding of how, when, and why humans cooperate. Anthropology and evolutionary psychology need a rigorous scientific synthesis of this diverse body of knowledge in order to avoid the “just so” stories that otherwise dominate sociobiological speculation.

## The Contents of This Book

This book is divided into five parts, each providing background and evidence from different perspectives and disciplines, that cooperation and/or altruistic behavior are pivotal, and central components to nonhuman primate and human social existence. Each part begins with a short introduction summarizing and synthesizing the contents of that part.

## *Part I: Cooperation, Altruism, and Human Evolution*

In this part, the authors discuss the evolutionary underpinnings of cooperative and altruistic behavior in nonhuman primates living in habitats occupied by our earliest hominid ancestors. These, and the fossil evidence of the earliest humans, provide a potential model for human evolution that does not support the more common "Man the Hunter/Man the Killer" view of human evolution and nature. The overwhelming evidence points to a rather smallish species that, although an omnivore who does some opportunistic hunting of small prey (insects, birds, and an occasional rabbit, for example), is not a systematic, big-game hunter (Hart and Sussman). Rather than being on the top of the food chain, these early humans appear to have been a prey to a large number of predators. Much like other nonhuman primates living in similar habitats today, early humans developed a number of mechanisms to limit their vulnerability to predators. Among these mechanisms is being highly social, cohesive, cooperative, and altruistic. Pievani provides a theoretical overview of how altruism could develop as an exaptation during early human evolution. Cloninger and Kedia describe the phylogenesis of the behaviors and brain systems that serve as functional precursors and components of cooperation and altruism in modern human beings. This provides an integrated evolutionary model of both the component structures and functions that underlie complex behaviors like cooperation and altruism. The basis for similar outward behavior in different branches of mammals cannot be rigorously described and classified without such a model. For example, how can anyone say that the functional capacities of primates differ only in degree and not in kind if there is no systematic model of the evolution of the functions and their components?

## *Part II: Altruism and Cooperation Among Nonhuman Primates*

In Part I, the authors provide an evolutionary model (hypothesis) or scenario for the development of cooperation and altruism in early hominins based on fossil evidence and reference to the literature on nonhuman primates as prey species using behavioral mechanisms to help avoid high rates of predation. When we describe primates as a prey species, we recognize that they may sometimes also be predators under some conditions. In Part II, the authors provide further theoretical models of this hypothesis. They also give specific data and evidence of non-kin-based cooperation and possible "altruistic" behavior among free-ranging nonhuman primates from long-term field studies of identified individuals. The authors, in this part, examine the notion that cooperative behavior among group-living, often non-kin individuals, is the norm and is not simply based on reducing aggression or as a reaction to competition.

## *Part III: Altruism and Cooperation Among Humans: The Ethnographic Evidence*

In this part, ethnographic evidence is presented by noted cultural anthropologists. Knaupf presents evidence that rates of violence differ greatly in different societies and, from his work in New Guinea, he describes how statistics on violence in one group of people that he studied has changed radically over time from a very violent society to one with extremely little violence. The idea of an uncontrollable genetic propensity for violence among humans is not supported by this evidence. From his review of ethnographic literature, Fry presents evidence from a comparative view of foraging societies indicating that these societies are extremely cooperative and fit a "Man the Hunted" model. There is much more evidence among these societies for cooperative, egalitarian, peaceful existence than for highly agonistic and warlike societies. Humans have developed a number of mechanisms that are employed to avoid agonistic encounters and war; they appear to have a propensity for peace. Further comparisons are made by Ferguson between human intergroup interactions and views that humans and chimpanzees are naturally aggressive or are natural killers. Neither the ethnographic evidence nor the evidence from chimpanzee research supports this often-depicted view. In his piece, one of the most respected elders of cultural anthropology, Walter Goldschmidt investigates the idea and reviews the evidence that humans, and other social primates, have a biological need for affect and that this pervades most of the behavior of social-living primates and humans. Professor Goldschmidt died on September 1, 2010, and we mourn the loss of one of the most respected and eloquent social anthropologists and thinkers of our time. We feel extremely privileged to have had him with us at this conference. His thoughtfulness, insight, wit, and humor were among the major highlights of the meeting (Fig. 1.1).

## *Part IV: Neurological and Hormonal Mechanisms for Cooperation and Altruism*

In Part IV, the authors provide a number of specific examples of neurological and hormonal mechanisms that have evolved among nonhuman primates and humans that underlie sociality, cooperation, and altruistic behavior. These mechanisms enable social-living animals to interact in a social manner and essentially seem to give credence to Darwin's view, stated above, that "The feeling of pleasure from society is probably an extension of the parental or filial affections, since the social instinct seems to be developed by the young remaining for a long time with their parents; and this extension may be attributed in part to habit, but chiefly to natural selection." Rilling shows that pleasure centers of the brain are activated when people cooperate, except in individuals who, in independent measures, show characteristics of psychopathy. Snowden examines hormonal underpinnings of fathering and other cooperative behaviors in nonhuman primates. Pollak examines hormonal and

**Fig. 1.1** Dr. Goldschmidt with other participants of the symposium. *From right to left*: R. Sussman; T. Pievani; Goldschmidt; Shawn Longino (Goldschmidt's assistant); B. Wood (*in the background*); D. Blazer

neurological differences in maltreated versus "normally" treated young monkeys and children. Cloninger and Kedia in Part I provide a direct link between the paleontological section and this one by relating neurobiological mechanisms to normal human personality and the evolution of cooperation and altruism. These studies outline many of the underlying biological factors indicating that cooperation and altruism are major components of our normal biological makeup.

## *Part V: Human Altruism and Cooperation: Needs and the Promotion of Well-Being in Modern Life*

The authors, in this part, examine how cooperation and altruism are a necessary, normal, and healthy component of normal modern human existence and that they are essential to human well-being. The major focus of this part is to show how the paleontological, behavioral, and neurobiological evidence is not only relevant to a better understanding of human evolution and behavior in an academic sense but that it also has immediate and practical ramifications. K.M. Cloninger provides evidence of the negative effects on children and on our education system of the pessimistic paradigm of man as naturally aggressive and warlike, as opposed to a more positive paradigm of man as having natural cooperative and altruistic characteristics. Hay provides a historical perspective of the resistance in Western Culture to the idea of altruism as an aspect of rational consciousness. Using information from cross-cultural health data, Munsch and Herrman illustrate how cooperation and sociality are extremely important aspects of normal health and well-being in human populations. Blazer shows how interdisciplinary and especially transdisciplinary research, such as that covered in this book, provides an example of the type of research promoted by the National Institutes of Health, and how an understanding of complex phenomena can only be obtained by a synthesis of research from many different fields of science working on interrelated problems.

In 2001, the American Association for the Advancement of Science (AAAS) Program for Dialogue on Science, Ethics, and Religion (DoSER), under the direction of A. Chapman, began a series of symposia exploring the question of the evolution and nature of human sociality (Sussman and Chapman, 2004). Since that time, a number of symposia on this and related topics have been given at the meetings of the AAAS, American Anthropological Association, and American Association of Physical Anthropologists, in which some of the participants of the current volume have taken part. For example, in a 2006 AAAS meeting convened in St. Louis, Missouri, a number of us participated in a symposium that brought together researchers from diverse fields (primatology, socio-cultural anthropology, zoology, paleontology, psychiatry, psychology, neurobiology, and genetics) to consider substantive evidence about violence versus cooperation as hard-wired human behaviors. Along with other scientists, we synthesized current research supporting the behavioral, hormonal, and neuropsychiatric evolution of human cooperation. This volume originated from this symposium and is a formal extension of these meetings and interactions. Here and in continued transdisciplinary research and communication, we hope to formalize some of the ideas presented and to continue to carry out research that will further inform us on these topics. Finally, we hope that this research will help to formulate a new paradigm on the topic of the evolution of cooperation, altruism, and well-being. We believe that professionals in many fields seeking alternative explanations for cooperative behavior and altruism will find this book extremely useful and we hope that it will stimulate discussion, controversy, and an impetus for other researchers to delve into theories that are at odds with some of those currently in vogue.

## References

Clutton-Brock, T. 2002. Breeding together: kin selection and mutualism in cooperative vertebrates. *Science* 296:69–72.

Darwin, C. 1874. *The Descent of Man*, *Revised Edition*. The Henneberry Company, Chicago.

Sussman, R.W. and A.R. Chapman (eds.). 2004. *The Origin and Nature of Sociality.* Aldine de Gruyter, New York.

Weiss, K. and A. Buchanan. 2009. *The Mermaid's Tale: Four Billion Years of Cooperation in the Making of Living Things.* Harvard University Press, Cambridge.

# Part I
# Cooperation, Altruism, and Human Evolution

# Chapter 2
# Cooperation, Altruism, and Human Evolution: Introduction Part I

**Ian Tattersall**

There can be no doubt that *Homo sapiens* is an unusually cooperative species—in both senses of the adjective, because while all primates are social and thus at least minimally cooperative, *H. sapiens* is social in a very particular manner. Human beings will patiently endure long, uncomfortable back-of-the-cabin flights in hideously cramped aircraft or stand meekly in long, slow lines at soup kitchens: conditions that would undoubtedly provoke unbridled aggression in any other higher primate. This odd proclivity provokes the question of just what it is about us humans that permits or even obliges us to cooperate (most of the time) in this way, subjugating ourselves to the necessities of public order. Furthermore, whatever that factor may be, when did we acquire it? Answering questions such as these is vital in developing any comprehensive understanding of our species as a biological and social entity; despite the elusiveness not only of the answers but also of the very questions themselves the contributions to this book constitute an important if necessarily preliminary step in the direction of developing such an understanding.

In the quest to comprehend and reconstruct the history of our most singular behavioral attributes, we immediately encounter one enormous difficulty. This is, of course, the fact that *H. sapiens* processes information about the physical and social worlds in which we live in an entirely unique way: one that is without parallel, or even obvious precedent, in Nature, today or in the past. We alone are symbolic animals, disassembling our surroundings into a complex vocabulary of mental symbols which we can shuffle according to rules to provide alternative versions of the world we inhabit—both as it is and as it *might* be. Other animals live in the environment more or less as Nature presents it to them, reacting to its stimuli with varying degrees of sophistication and nuance. In stark contrast, we live to a remarkable extent in environments that we re-create in our heads. And although clearly grafted on to a preexisting substrate of purely intuitive intelligence that mediated some very complex behaviors indeed, including such impressive accomplishments as making stone tools and exchanging objects over long distances, the exceptional human cognitive

---

I. Tattersall (✉)
Division of Anthropology, American Museum of Natural History, New York, NY 10024, USA
e-mail: iant@amnh.org

R.W. Sussman, C.R. Cloninger (eds.), *Origins of Altruism and Cooperation*,
Developments in Primatology: Progress and Prospects 36, DOI 10.1007/978-1-4419-9520-9_2,

capacity that permits us to operate in this way was apparently acquired very recently and quite abruptly (Tattersall, 2004, 2008).

Today, ours is the only hominid species on the planet; and although we tend not to reflect on the fact, our lonely state is actually highly unusual. For the fossil record tells us in no uncertain terms that, throughout the long history of our family, several different hominid species typically coexisted. Indeed, we have clear evidence that as recently as some 40,000 years ago, the world was occupied by at least four different hominid species, and the arrival and spread of fully symbolic *H. sapiens* is almost certainly implicated in the rapid departure from the scene of such contemporaneous relatives as *Homo neanderthalensis*, *Homo erectus*, and *Homo floresiensis*. Uncomfortable as it may be, this reality undoubtedly tells us a great deal about ourselves as a species that (presumably as a result of our cognitive singularity) is not only intolerant of competition but also in a position to impose that intolerance.

In terms of self-knowledge, the thought is sobering. And, as just hinted, on an epistemological level it also means we are faced with the problems of context that are familiar in any attempt to explain the unique. Numerous questions about the behavioral nature of *H. sapiens* are, at best, only partially answerable on a strictly comparative basis. Is our extreme form of cooperativeness solely a function of our special and unprecedented cognitive facility? Or is it part of the necessary and preexisting substrate upon which that facility is grounded? Is it the result of long-term burnishing, by natural selection, of a property that has thus been finely honed in our lineage over the eons? Or is it an emergent quality that was acquired in a single event, through the chance addition of an otherwise unremarkable ingredient to a preexisting cognitive base that had, up to that point, functioned on an entirely different level of complexity? Is it related to what we perceive as altruistic or more generally cooperative behaviors in other primate and mammalian species? Or is it something entirely independent of those behaviors, something truly new? Is what we perceive as altruism in other primates directly comparable to whatever it is that we understand as altruism in our own social context? Or is it a by-product—or perhaps a facet—of something else entirely that we misconstrue in anthropomorphic terms? Indeed, does the recent radical reorganization of our cognitive system disqualify many aspects of our behavior, or even all, from direct comparison with their presumed counterparts in nonsymbolic precursors? This last question, particularly, demands our serious attention from the very outset. For, as Robert Cloninger (Chapter 5, this volume) observes, human beings simply cannot have the "same affective experiences" as those they "imagine [other species] might be having."

Still, despite its obvious inherent limitations, the only avenue we have for answering questions such as those just raised is through looking not simply at ourselves in isolation, but also in the context of what is known of the behaviors of organisms closely related to us. It is certainly tempting to consider that, by comparing behavioral repertoires, we will be able to see which among our behaviors are primitive, inherited from a very remote ancestor, and which are derived and thus recently acquired. But while the procedure itself might seem straightforward, even among living forms, compartmentalizing observed behaviors and sorting them into neatly comparable categories turns out, alas, to be a difficult task indeed. To complicate matters further, it is far from evident that the same categorizations apply validly across ranges of species. Behaviors displayed both by individuals and by local populations of the same higher primate species often turn out to be wildly variable, and their expression highly dependent on ecological circumstances. Among our extinct relatives the same presumably applied, with the additional difficulty that those behaviors cannot be observed but have to be inferred, frequently from very tenuous evidence. All of this makes it doubly unfortunate that the creatures believed to be our closest living relatives, the chimpanzees and bonobos, are not only quite remote from us—both an entire highly diverse hominid family, and the apes' own largely unknown evolutionary histories, lie between us and them—but also live in ecological circumstances that are radically different not simply from our own but also from those inferred for our very early ancestors.

Traditionally, the great apes—specifically chimpanzees—have been considered the most appropriate behavioral "models" for very early human relatives. In a broad cognitive sense, this may be fairly accurate: in all probability we can justifiably assume that, as the cognitive scientist Daniel Povinelli has put it, hominid ancestors were, like today's great apes, "intelligent, thinking creatures who deftly attend[ed] to and learn[ed] about the regularities that unfold[ed] in the world around them. But . . . they [did] not reason about unobservable things: they [had] no ideas about the 'mind,' no notion of 'causation'" (Povinelli, 2004:34). So far so good: the apes are not modern humans, and neither were our own ancient ancestors. But if we try to go beyond this, to identify specific past behaviors to which we can trace back modern equivalents, we find ourselves in highly speculative territory. For a start, living *H. sapiens* turns out to be even more variable and situational in its behavior patterns than the apes are. It is hard to establish behavioral norms in a species in which it is no problem at all to find examples to illustrate both poles of any pair of behavioral antitheses you can imagine—something that amply illustrates the assertion by Donna Hart and Bob Sussman in Chapter 3 that "we are . . . what we learn to be." Far less than members of *any* other species, are we condemned by our evolutionary past to any particular behavioral propensity in the present.

Clearly, though, we could not be the creatures we have become in the absence of a long and accretionary evolutionary history that includes our common ancestor with the apes. In reconstructing that history we are, of course, bedeviled by the unfortunate fact that behaviors rarely if ever preserve directly. What is more, rather few behaviors are even reflected in proxy evidence from which they might be reliably inferred. Still, the handful of proxies available, for a rather narrow range of social/behavioral features, is all we have to go on; and among those few potential proxies, ecological pressures are almost certainly more reliable than strict phylogenetic propinquity as predictors of behavior. Closely related primates may show dramatic differences in social organization, whereas creatures of the same general sort appear more likely to respond, or to accommodate, in broadly similar ways to similar environmental pressures. And, as forms that are physically adapted to forest existences, the apes—even the fairly eurytopic chimpanzees—do not provide close environmental analogs to the early hominids.

Nonetheless, "ape models" have traditionally dominated views of early hominid behavior, and they have been particularly conducive to Peterson and Wrangham's

(1997) "Demonic Males" version of the "Killer Ape" scenario of human evolution articulated in the 1940s and 1950s by Raymond Dart (e.g., 1957). Something in models of this kind seems to exert an innate appeal to the reductionist human storytelling mindset. But as Hart and Sussman cogently point out, in Chapter 3 and elsewhere (e.g., Hart and Sussman, 2005, 2009), early hominids were largely defenseless creatures of small stature and had body structures that would have made them not only less efficient terrestrially than we are but also less agile in the ancestral arboreal milieu than are chimpanzees. These attributes hardly suited them well to be predators in either setting; indeed, in many respects, these early relatives must have been the very antithesis of the predator. Subsisting on largely plant-based diets, and living mostly in a mosaic of forest-edges-to-woodland, they much better fit the profile of prey species, vulnerable to a large variety of terrestrial and semi-arboreal large cats and other carnivores. To close this largely circumstantial case, there is also substantial direct evidence from the fossil record that early hominids were heavily predated upon.

From this, Hart and Sussman draw several important conclusions about probable social organization among early hominids. They include the high likelihood that these creatures lived in large groups for protection (just as modern baboons and macaques do in comparable environments), and that, within those groups, individuals were highly social and cooperative. And it would almost certainly have been in social contexts of this kind that the groundwork was laid for the later extraordinary cooperativeness of *H. sapiens*. This is not to say that very early hominids would have exhibited anything like the extremely unusual form of extensive and nuanced cooperation (and its partial inverse, subtle, and often disguised and indirect antagonism) that we see in *H. sapiens* today. To be expressed in their modern form, both of these attributes—in many ways opposite ends of a single spectrum—almost certainly necessitate symbolic cognition. But the ultimate roots of the modern human brand of sociality—its requisite biological underpinnings—were nonetheless more than probably laid down in those very early times.

One unusual aspect of cooperation, not reported in humans alone, is altruism, whereby individuals act in ways that appear to be contrary to their own interests while benefiting someone else. Ignoring the fact that human beings often act in self-destructive ways while benefiting nobody, advocates of the notion that natural selection is in the business of fine-tuning all aspects of behavior have sought to find direct evolutionary advantage in apparently altruistic behaviors, most commonly discovering such advantage in benefits that accrue to (genetically similar) kin. In this way, individual "fitness" is extended to embrace the "inclusive fitness" of the kin group. Such "kin-selection" models require the assumption that larger evolutionary outcomes result virtually exclusively from the working of natural selection directly or indirectly to promote particular genotypes. This is the kind of selection that is nowadays usually referred to as "darwinian," although Pievani (Chapter 4, this volume) intriguingly points out that, in the social context, Charles Darwin himself (1871) expanded his definition of natural selection beyond the individual level to include the "tribe"—which would invoke something akin (sorry) to what is usually referred to today as "group selection:" an unfashionable mechanism that is often seen as entirely distinct, or sometimes even antithetical, to natural selection.

Pievani (Chapter 7, this volume) goes on to examine the history of study of altruism more closely, in the process demonstrating that evolutionary change has to be driven by much more than simply the promotion or elimination of particular genotypes at the individual level. His preference is for a "multi-level" view that sees larger scale evolutionary outcomes, including such social attributes as cooperativeness and altruism, as products of much more complex histories. At the finer end of the spectrum of influences, the multi-level approach takes into account the significant reality that organisms have economic lives as well as roles as replicators, and in the broader context it recognizes that individuals and populations belong to species that are parts of dynamic wider communities that in turn live and change in sometimes dramatically fluctuating environments. Pievani emphasizes that, in the long term, the success of the ephemeral individual is inextricably bound up with the success of the group—and ultimately, of course, of the entire species, for it is of little evolutionary advantage to be the most splendidly adapted member (whatever that might in practice mean) of a species that is being outcompeted into extinction.

Pievani thus advocates that we extricate ourselves from purely "adaptationist" views of the evolutionary process (or, more properly, processes). He urges us to acknowledge the fact that any innovation (behavioral, genetic, or physical) must come into existence spontaneously, without regard to its function, and that the "current usefulness" of an attribute should hence be seen as independent of its "historical origin." Once we have made this conceptual separation, we are relieved from the necessity of seeing such behavioral features as altruism as driven by inexorable generation-by-generation pressures.

Pievani emphasizes the ubiquity in documented evolutionary histories of "exaptation," whereby heritable novelties come into existence entirely independently of any use to which they might eventually be put (he mentions birds' feathers, which are essential for flight but that for many millions of years were not exploited in this way). The fixation of any novelty in a population may even be a random event, although it will presumably be facilitated if the characteristic in question is highly advantageous. In the case of altruism, however, we also have to bear in mind that this is not a discrete feature. All developmentally normal humans have big brains; all are bipedal; all have small canine teeth. These are all truly human characteristics and all are functionally discrete. But altruism is not. Not all individual human beings are equally altruistic—or even altruistic at all—and altruism is simply one potential expression of a much larger general capacity for cooperation. To the extent that it works, kin-selection theory only explains why natural selection has not eliminated the "altruistic" extreme of the spectrum of cooperative behaviors.

Pievani notes that, whatever it may otherwise be, evolution is not a matter of optimization: it does not strive toward the perfect but instead "tinkers with structural constraints." By the nature of the hereditary apparatus, the new must always come about by modification of the old, and thus there can be no wholesale elimination of the old to facilitate the adoption of the newer and better. Which is why, Pievani suggests, we show many "ambiguous and contradictory behaviors" of "former prey and predators at the same time." Our socially cooperative comportments, and our erratic individual ones too, are functions of a long and complex historical inheritance that can only be understood in this light. In the specific context of human behavioral evolution, the scenario Pievani favors is that altruism and cooperativeness of the human kind had their origins in an earlier tendency toward reciprocity, a tendency that proved advantageous in early human groups exposed to the hazards of woodland environments. A succession of circumstances then followed in which this tendency became exaptively amplified in a series of stages.

This scenario coincides well with what we know about the pattern of other behavioral acquisitions among our precursors, and it also fits comfortably with the fact that we still perceive echoes of our untidy origins in our dealings with each other and with the world around us. Because, as already emphasized, the new is founded on the old and is thus inextricably entangled with it. Optimization, however desirable from an engineering perspective, is rarely if ever an option in evolution, which at any moment can capitalize only on the best of whatever is available. If we seek to regard any of our behaviors, whether cooperative or aggressive, as fine-tuned by evolution for a specific function and thus as innate within us, we will miss the most important aspect of our uniqueness—namely, our almost infinite capacity to respond to circumstances. Members of *H. sapiens* may share a deep longing to understand "the human condition" in which they participate, but this does not mean that we all share an obligate behavioral state. To return to Hart's and Sussman's pithy formulation, to a very considerable extent we learn as individuals to be who and what we are.

Cloninger (Chapter 5, this volume) looks in some detail at various aspects of human learning and at the epistemological problems that arise from the complex and additive nature of human cognition and the resulting behaviors. He puts forward an ingenious model whereby major variables of human learning and personality arise from the following three distinct cognitive systems: behavioral conditioning, semantic learning, and self-aware learning. In Cloninger's scenario, these systems arose sequentially in human evolution, much as Pievani's model might predict. They and their sub-components interact to produce personality, the attribute that defines each of us as an individual. Cloninger finds that one character dimension (self-transcendence, the ability to step outside oneself and to know when rules apply) is a key to the fully modern mind; but his approach emphasizes the role of multiple feedbacks in the ultimate determination of the individual psyche. And even though his model is ultimately a "modular" one, in terms of the gradual acquisition of a set of discrete components of self-awareness over the long history of mammalian evolution, it also draws attention to the remarkable extent to which individual personality is shaped by multiple influences, among which situational and thus environmentally mediated stimuli are prominent.

Although there is plenty of evidence that symbolic cognition and its correlates are of remarkably recent origin, it is nonetheless fully evident that this capacity of ours is founded upon a very long and accretionary evolutionary history. No part of what we are, and so greatly prize ourselves for being, could have been acquired in the absence of any aspect of that long history. Cloninger courageously sketches in an evolutionary sequence in which those acquisitions might have been made. He identifies "precursor functions for symbolism" in living great apes, and sees these as the underpinnings for advanced degrees of cooperation in early hominids. In early *Homo*, he finds proxy evidence for initial enhanced function of the terminal association areas; these only later expanded into the "proactive fronto-temporo-parietal circuit" that promotes "autobiographical memory and self-aware consciousness in modern *H. sapiens*." The details of any such scenario are bound to be argued; but Cloninger's notion is compelling that not only our own senses of self but also the ways in which we perceive and process information about the world around us are dependent on self-aware consciousness of the kind he describes, mediated by "the specific functional abilities that emerged in human ancestors."

Again, we arrive at the notion that there is something very peculiar about modern human beings. We cannot legitimately seek to understand other animals, even close relatives, as less complex versions of ourselves; neither can we regard our own species as simply a more sophisticated version of them. Yes, we do indeed have ape brains inside our heads; but the added ingredient that Cloninger has striven to identify in us has produced an entirely new cognitive edifice, a structure with emergent and unprecedented properties. And this means that, as he is careful to point out, we have to be very cautious with our terminology. Humans have "self-transcendence," while other primates do not. As a result, such terms as "altruism" or even "cooperation" (inevitably possessing anthropomorphic overtones) are words we should not apply lightly, or without implicit qualification, to other species. Our anthropoid relatives may have immediate goals; and may even be aware of them, but they clearly do not process information, or make plans, or harbor motivations, in the same sense that human beings do.

Modern human beings are cooperative; and they would certainly never have become so had the biological underpinnings not already been present – not just in the hominid ancestor, but in a succession of precursor species among which, on average, behaviors we can at some level call cooperative had become more complex over time. Still, a yawning cognitive gulf was crossed when symbolic reasoning was acquired, well within the tenure of our species as diagnosed anatomically (Tattersall 2004, 2008). Certainly, our close(ish) relative *Homo neanderthalensis* indulged in a variety of behaviors, ranging from burial of the dead to the hunting of fearsomely large animals, that clearly required an advanced degree of coordination among individuals. Cognitively and socially these were impressive hominids, quite possibly the most intellectually complex beings that had ever existed before cognitively modern *H. sapiens* came along. But their social cooperation was almost certainly not mediated by mental information-processing in the modern human style. And we should be careful not to be misled by the terminology we use into thinking it might have been.

## References

Dart, R.A. 1957. The osteodontokeratic culture of *Australopithecus prometheus.* Mem. Transvaal Mus.10:1–105.

Darwin, C. 1871. *The Descent of Man*, 2 vols. London: John Murray.

Hart, D. and R.W. Sussman. 2005. *Man the Hunted: Primates, Predators, and Human Evolution*. New York: Westview/Perseus.

Hart, D. and R.W. Sussman. 2009. *Man the Hunted: Primates, Predators, and Human Evolution: Expanded Edition*. New York: Westview/Perseus.

Peterson, T. and R. Wrangham. 1997. *Demonic Males: Apes and the Origins of Human Violence*. New York: Mariner Books.

Povinelli, D. 2004. Behind the ape's appearance: Escaping anthropocentrism in the study of other minds. Daedalus 133(1):29–41.

Tattersall, I. 2004. What happened in the origin of human consciousness? Anat. Rec. (New Anat.) 267B:19–26.

Tattersall, I. 2008. An evolutionary framework for the acquisition of symbolic cognition by *Homo sapiens*. Comp. Cogn. Behav. Rev. 3:99–114.

# Chapter 3
# The Influence of Predation on Primate and Early Human Evolution: Impetus for Cooperation

**Donna Hart and Robert W. Sussman**

> *What brought the ape out of the trees, and so the man out of the ape, was a taste for blood. This is how the story went, when a few fossils found in Africa in the 1920s seemed to point to hunting as the first human activity among our simian forebears – the force behind our upright posture, skill with tools, domestic arrangements, and warlike ways. Why, on such slim evidence, did the theory take hold? (Harvard University Press, 1993)*

There have been many attempts to reconstruct the behavior and ecology of our earliest ancestors. The most common theory and the one that is widely accepted today is the "Man the Hunter" hypothesis. Cultural anthropologist Laura Klein expresses the current situation well: "While anthropologists argue in scientific meetings and journals, the general public receives its information from more popular sources . . . In many of these forums, the lesson of Man the Hunter has become gospel" (2004:10). However, this theory of early hominin behavior is still widely debated within the anthropological community and, as we will show, the evidence to support it remains controversial.

Raymond Dart launched the killer ape-man scenario in the mid-twentieth century with the help of the playwright Robert Ardrey and his best selling book, *African Genesis* (1961). Dart had interpreted the combined accumulation of fossilized long bones from savannah herbivores and damaged hominin skulls found in South African caves as evidence of an entrenched human hunting culture. The fact that the skulls were battered in a peculiar fashion led to Dart's firm conviction that violence and cannibalism on the part of killer ape-men formed the basis from which our own species eventually evolved. In his words, early hominins were "carnivorous creatures that seized living quarries by violence, battered them to death, tore apart their broken bodies, [and] dismembered them limb from limb, greedily devouring livid writhing flesh" (Dart, 1953:201).

---

D. Hart (✉)
Department of Anthropology, University of Missouri, St. Louis, MO 63121, USA
e-mail: hartd@umsl.edu

R.W. Sussman, C.R. Cloninger (eds.), *Origins of Altruism and Cooperation*,
Developments in Primatology: Progress and Prospects 36, DOI 10.1007/978-1-4419-9520-9_3,

Man the Hunter, as a vignette of our species' ecological status, purports to be based on science. But if Man the Hunter is truly a scientific theory, then what is the evidence? Is it really possible that smallish, upright creatures with flat nails instead of claws and relatively tiny canine teeth, with no tools or weapons for millions of years, could have been deadly predators?

Mammalian terrestrial predators—the carnivores—are taxonomically, skeletally, physiologically, and behaviorally distinct from primates. There are 7 families, 92 genera, and approximately 240 species in the order Carnivora which includes the customarily meat-eating dogs, bears, raccoons, weasels, mongooses, hyenas, and cats. Carnivores possess four- or five-clawed digits per limb and a non-opposable and sometimes absent pollex and hallux (Nowak, 1991). Wrist bones are fused together forming the strong scapholunar bone, unlike primates in which the bones remain independent (Macdonald, 1984). Temporalis and masseter muscles of the carnivore jaw can exert tremendous force for stabbing prey and cutting flesh (Macdonald, 1984). Dentally, canine teeth in carnivores are strong, recurved, pointed, and elongate; premolars are adapted for cutting; molars have sharp, pointed cusps; and carnassials—a key feature of the Carnivora—are specialized shearing mechanisms composed of the last upper premolar and the first lower molar (Nowak, 1991). A few species of the Carnivora (e.g., pandas) are largely vegetarian and their molars have reverted to the grinding surfaces found in primates (Macdonald, 1984). Unlike the visual cues used by the haplorhine primates, scent is an important intraspecific communication method in carnivores; urine, feces, and exudate from odorous skin glands convey information (Macdonald, 1984). Most carnivores are solitary or associate in pairs or small groups (Nowak, 1991). Although social predators exist—such as lions, wolves, spotted hyenas, and some mongoose species—their sociality is complex and no one selective pressure is the sole force for formation of groups (Macdonald, 1984).

Many human traits, such as bipedalism, monogamy, territoriality, tool use, technological invention, male aggression, group-living, and sociality, are often linked to the perspective of Man the Hunter. However, while theories and associations of human aggressive hunters abound, they are rarely based on the following three evidentiary approaches that shed light on early hominin ecology and behavior: living primate models, extant human hunter-gatherers, and the fossil record. When we investigate these three, a different view emerges.

As we have detailed elsewhere (Hart and Sussman, 2005, 2009), the diversity of large carnivores was extensive in African prehistory. Many groups of carnivores that are now extinct (e.g., huge short-faced bears and sabertoothed cats) preyed on hominins in Africa, especially between 6 and 3.5 million years ago. Then at about 3.5 million years ago, eight new genera of carnivores evolved to join the previous groups, resulting in potentially as many as eight to ten different species of sabertoothed cats, false sabertoothed cats, conical-tooth cats (large felids still represented today by leopards and lions), giant hyenas, large wolf-like canids, or short-faced bears roaming the same African sites where we now find hominin fossils (Treves and Palmqvist, 2007, see Fig. 3.1).

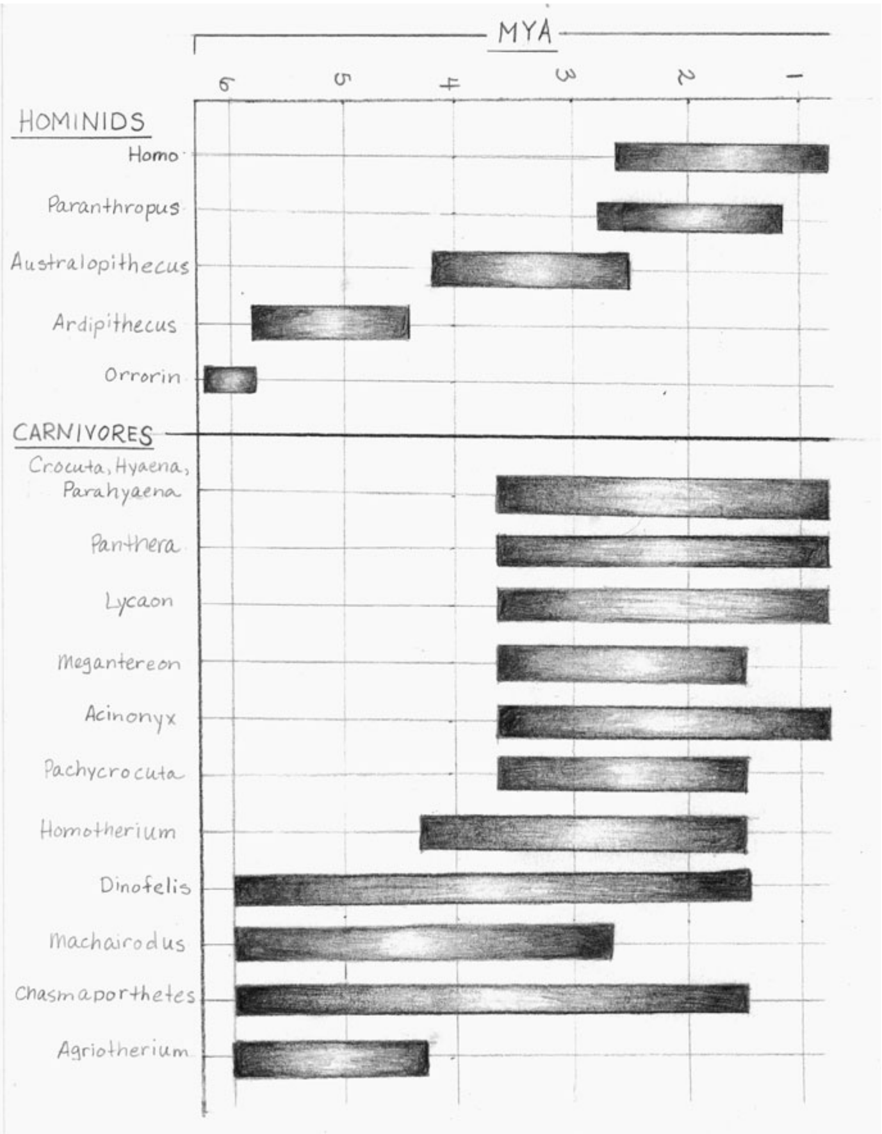


**Fig. 3.1** A time span comparison of ancient African predators and hominins. (C. Rudloff, redrawn from Treves and Palmqvist 2007 expressly for this chapter)

At about 1.8 million years ago, the archaic flesh eaters, such as the sabertoothed cats, went extinct probably due to climate change, but that did not leave a dearth of large carnivores to prey on early hominins. Consider the fossil evidence for predation that has been so far discovered: C. K. Brain, a South African paleontologist like Dart, started the process of relabeling “Man the Hunter” as “Man the Hunted” when he slid the lower fangs of a fossil leopard into matched punctures in the skull of a 2-million-year-old australopithecine (Brain, 1981). The paradigm change initiated by Brain continues to stimulate reassessment of hominin fossils. Dart's initial find, the cranium of an australopithecine (called the Taung child), who died approximately 2.5 million years ago, has been reassessed repeatedly (Berger and Clarke, 1995). Relying on new African crowned hawk eagle (*Stephanoaetus coronatus*) predation research carried out in the Tai Forest, Côte d'Ivoire by McGraw et al. (2006), the Taung cranium was compared to the remains of similarly sized African monkeys eaten today by these powerful raptors. The eagles are known to clutch their prey's head with sharp talons, leaving consistent grooved signatures on the remains. New features, based on analyses of monkey prey never before described, include punctures and ragged incisions in the base of the eye socket where the raptors have ripped out the eyes of dead monkeys with their talons and beaks to get at the brains. The identification of these same singularly curious marks on the Taung cranium has provided substantiation for theories of raptor predation on this famous fossil (AP, 2005) (Fig. 3.2).

As shown in Table 3.1, the list of fossils showing evidence of predation continues to grow. *Orrorin tugenensis*, a hominin who lived over 6 million years ago, shows signs of having died from leopard predation. *Ardipithecus ramidus* remains found in the early 1990s at Aramis, Ethiopia, indicate that many predatory animals were sharing the site with these 4.4-million-year-old hominins. A review of

**Fig. 3.2** New evidence from crowned hawk eagle studies has provided substantiation that raptor predation was involved in the Taung child's demise

**Table 3.1** Hominin fossils evidencing predation

| Fossil | Site | Approximate age | Evidence | Assumed predator | References |
|---|---|---|---|---|---|
| *Orrorin tugenensis* | Tugen Hills, Kenya | 6 mya | Tooth marks on several bones | Leopard-like carnivore | Senut (2001) |
| *Ardipithecus ramidus* | Aramis, Ethiopia | 4.4 mya | Tooth marks on cranial and postcranial elements | Carnivore | WoldeGabriel et al. (1994) |
| *Australopithecus africanus* | Taung Quarry, South Africa | 2.5 mya | Punctures and incisions at base of eye sockets; talon rakings on cranium | Extinct raptor (*Stephanoaetus* spp?) | Berger and Clark (1995), Associated Press (2005), McGraw et al. (2006) |
| *Paranthropus robustus* | Swartkrans, South Africa | 1.8–1.5 mya | Canine tooth indentations at base of cranium | Fossil leopard (*Panthera* spp.) | Brain (1981) |
| *Homo erectus* | Dmanisi, Rep. of Georgia | 1.8–1.7 mya | Canine tooth indentations on cranium; gnaw marks on mandible | Sabertoothed cat | Gore (2002), Wong (2003) |
| *Homo?* | Orce, Spain | 1.6 mya | Cranium fragment excavated from fossil hyena den | Short-faced hyena (*Pachycrocuta breviostris*) | Borja et al. (1997) |
| *Homo erectus* | Zhoukoudian, China | 450,000 ya | Crushing of facial bones, maxilla, and mandible; enlargement of foramen magnum | Short-faced hyena (*Pachycrocuta breviostris*) | Boaz and Ciochon (2001), Boaz et al. (2000, 2003) |
| *Homo?* | Olorgesailie, Kenya | 900,000 ya | Bite marks on left browridge | Carnivore | Small (2005), Fox (2004) |
| Archaic *Homo sapiens* (*“helmei”*) | Florisbad, South Africa | 260,000 ya | Canine tooth depression on forehead | Hyena | Deacon and Deacon (1999) |
| *Homo neanderthalensis* | Mt. Cicero, Italy | 50,000 ya | Fractures on cranium; enlargement of foramen magnum; gnaw marks on mandible | Hyena | Bahn (2005) |

*A. ramidus* noted: “We interpret the physiographical setting to have been a flat plain with little topography where scattered carcasses of medium and large mammals were ravaged by carnivores . . . Carnivore tooth marks scar the hominid cranial and postcranial elements and are ubiquitous on medium and large mammal bones in general” (WoldeGabriel et al., 1994:332). (The full list of predators found in conjunction with *A. ramidus* fossils includes crocodiles, pythons, hyenas, wild dogs, conical-toothed cats, sabertoothed cats, and short-faced bears.)

The Dmanisi site in the Republic of Georgia entombed a 1.75-million-year-old hominin skull exhibiting punctures from sabertoothed cat fangs. At Orce, Spain, what appears to be hominin remains dated at 1.6 million years have been found in the den of an extinct hyena species. A 900,000-year-old member of the genus *Homo* from Olorgesailie, Kenya, shows carnivore bite marks on the browridge. Cannibalism as a lifestyle for one species of human ancestors was inferred by the disfigurement of faces and foramina magna found in a 450,000-year-old cache of *Homo erectus* skulls from the Zhoukoudian cave in China. The initial explanation of these strange manipulations was through the lens of the “Man the Hunter” paradigm. Nevertheless, studies by Boaz and Ciochon (2001) show that a more substantive explanation involves predation by extinct giant hyenas (*Pachycrocuta breviostris*) that crunched their way into the lipid-rich brains of hominin prey. Yet another hyena casualty may be the South African “Florisbad cranium,” a late archaic *H. sapiens* approximately 260,000 years old. A Neanderthal skull from 50,000 years ago found at Monte Circeo, Italy, is also apparently the victim of hyena predation. While previously classified as a fatality from cannibalism, the fossil man of Monte Circeo was deposited at death in an active hyena den; the skull displays fractures consistent with hyena’s tooth marks, evidences an enlargement of the foramen magnum consistent with hyena predation, and exhibits gnaw marks on the jawbone.

The world of ancient hominins was replete with large mammalian predators, raptors, and reptiles, and there are strong indications that hominins were regularly hunted. In a seemingly uninterrupted legacy of our past, it can be documented that, outside the West, no small amount of predation has occurred on humans in modern times. We may not have seen these figures in newspaper headlines, but 612 people were killed by tigers in the Sundarbans Delta of India and Bangladesh in the decade from 1975 to 1985 (McDougal, 1991), and over 200 humans were attacked by leopards in one Indian state between 1988 and 1998 (Uprety, 1998). Chinese biologists suspected that brown bears killed 1,500 farmers annually in the Tibetan Plateau when it was opened up to agriculture (Domico, 1988), while an estimated 3,000 individuals are seized or eaten by crocodiles each year in sub-Saharan Africa (Alderton, 1991). After researching death records, zoologist Hans Kruuk (2002) could document that wolf predation is still a fact of life in Belarus and several other Eastern European nations.

Besides the fossil record, another reliable source to consult about our evolutionary past is extant nonhuman primates. A study of predation on nonhuman primates found that 178 species of predatory animals included primate prey in their diets (Hart, 2000). These ranged from fierce, tiny birds to huge 500-pound crocodiles and scores of animals in between—tigers, lions, leopards, jaguars, jackals, hyenas, genets, civets, mongooses, pythons, komodo dragons, eagles, hawks, owls, and even toucans. The level of predation endured by chimpanzee and gorilla populations provides another layer of authenticity to our background as prey—after all, these are our closest genetic relatives. The evidence of a gorilla meal found in leopard feces in the Central African Republic (Fay et al., 1995) proved that the largest primates are subject to predation. Chimpanzees, despite their obvious intelligence and strength, are no match for leopards or lions; 5–6% of chimpanzee populations are consumed annually by these wild cats at two African sites where predation was studied (Boesch, 1991; Tsukahara, 1993).

Our fossil relatives are said by many to have focused on acquisition of meat to the point that all major evolutionary adaptations can be traced to that particular craving. Nevertheless, as explained previously in this chapter, hominins cannot be categorized as carnivores; we and our fossil relatives have dentition and gut tracts very like our omnivorous but mainly like fruit-eating, primate relatives. Inflated importance for meat in the early hominin diet may have been derived from reports of increased red colobus monkey hunting and meat eating observed in selected chimpanzee populations (Fourrier et al., 2008). Yet, in one study of overall chimpanzee diets, meat from mammal prey was found to be less than 0.5% (Hladik, 1977); this was confirmed at Gombe and Tai Forest research sites by Boesch and Boesch-Achermann (2000) who state that meat is necessary neither for survival nor normal growth. In captivity, chimps are not meat eaters, possessing neither the oral nor dental morphology to chew meat efficiently (Milton and Demment, 1989).

Unless the meat is cooked, hominins do not possess the teeth or the gut tract to digest herbivore muscles (i.e., the raw meat that has typically been imagined as acquired through hunting or scavenging), and red meat cannot be cooked unless fire is available on demand and weapons exist to regularly kill large animals. Our teeth have remained much the same throughout the 7 million years of hominin evolution, and they are not the teeth of carnivores. Teaford and Ungar stress that “The early hominids were not dentally preadapted to eat meat—they simply did not have the sharp, reciprocally concave shearing blades necessary to retain and cut such foods” (2000:13509). Humans do not depend on their canine teeth to tear off or chew meat, and like other plant eaters, the human jaw can easily move backwards and forwards and from side to side for biting and grinding plant material, unlike carnivores who have fixed lower jaws permitting only open-and-shut movement thus adding stability and strength to their bites (Nowak, 1991).

Our gut tract is also basically the same design as fruit-eating primates (Hladik et al., 1999). We fall into the category of unspecialized frugivores when our digestive tract and body size are compared with other primates and meat-eating mammals; this nonspecialization allows for the large variations found in human diets (Hladik et al., 1999). Cooking allows humans to masticate and digest muscle fiber, but meat could neither be cooked nor become a regular dietary component for hominins until fires could be readily ignited and controlled. The first verifiable archaeological evidence of controlled fire has been found in Israel and dates to approximately 790,000 years ago (Goren-Inbar et al., 2004); prior to that time there were only tenuous indications of fire that can be as logically explained by natural phenomena as they are by hominin fabrication. Dates as early as 1.8 million years ago for Swartkrans in South Africa and 1.5 million years ago for Koobi Fora and Chesowanja in Kenya have been offered as substantiation of early hominin mastery over fire for light, heat, and cooking, but exhaustive critiques have found that without the unequivocal evidence of hearths, the early sites cannot be attributed to anything but to naturally ignited fires and smoldering vegetation (James, 1989; Klein, 1999).

There is little possibility that tools were available to include much meat as a dietary component before the advent of weapons. The first evidence of a javelin-like spear (which might be thrown as a hunting weapon) is 400,000 years old, but the effectiveness of the Schöningen spear against large herbivores is questionable since it has been likened to an "oversized toothpick" (Klein and Edgar, 2002:160). In fact, conservative interpretations of the archaeological evidence do not uphold the appearance of human hunting until the fairly recent past. Klein (1999) states that true large-scale, systematic hunting may not have made an appearance in human history until 60,000–80,000 years ago. While the Schöningen spear was found with the bones of horses, many of which showed evidence of butchery, Klein and Edgar (2002) maintain that artifacts at Schöningen demonstrate that the ancient people living there obtained some large animals but they question whether this was a regular event. To assess how successful the alleged hunters might have been, it is necessary to place the butchered bones in the context of all the bones at the site that do *not* evidence human manipulation and that *do* evidence carnivore teeth. Precise investigations suggest that as relatively recently as 500,000 years ago, human ancestors were not obtaining large mammals very often (Klein and Edgar, 2002). The previously proclaimed "kill" sites in Africa and Europe from this period, when subjected to rigorous analysis, do not substantiate large-scale human hunting. Klein and Edgar (2002) offer Duinefontein 2 (a 300,000–year-old South African site) as an example of the misleading cues posed by human tools and animal bones lying side by side. After meticulous examination of the bones and artifacts at Duinefontein 2, it became clear to the researchers that tool marks on animal bones were rare compared to carnivore tooth marks. These data were cross-checked against a much older South African site (Langebaanweg, dated at 5.5 million years) located only 36 miles away where no hominin presence has been found (and millions of years prior to the advent of tools). Data from the two sites are similar; carnivores were definitely eating large mammals, but ancient humans at Duinefontein 2 were having a negligible impact. Fresh examination of Ambrona and Torralba in Spain and Elandsfontein in South Africa demonstrates the same paucity of tool-marked bones and lack of real evidence for hunting (Klein and Edgar, 2002).

In the early 1980s, at Olduvai Gorge in Tanzania, Bunn (1981) and Potts and Shipman (1981) discovered large mammal bones with both carnivore tooth marks and cut marks that appeared to have been made by hominins with stone tools approximately 2 million years ago. These findings reinforced the idea that meat eating by early hominins, either from hunting or from scavenging, played an important role in human evolution. While "Man the Hunter" enjoyed popularity in the scientific community for many years, in the period of post-1980s "Man the Scavenger" garnered ardent supporters. Many archaeologists have relied on taphonomy to determine whether the distribution pattern of cut marks and tooth marks could tell us if hominins were hunters, aggressive power scavengers (i.e., hominins who mobbed carnivores and stole kills), or passive scavengers, but interpretations were often poles apart. For example, Blumenshine (1988, 1995) believed the evidence showed that large carnivores had first crack at the carcasses, indicating that hominins were passive scavengers. To Dominguez-Rodrigo (1997, 1999), the distribution of cut marks implied that early hominins had first access to the bones and thus the bones were the remains of hunting or aggressive scavenging. (Of course, passive scavenging and power scavenging are not mutually exclusive, and neither are hominins as scavengers and hominins as prey.)

More recently, however, Lupo and O'Connell (2002) have reexamined all the evidence used in these earlier studies. They compared the cut marks and tooth marks on the fossil bones with data on real-life hunting and scavenging carried out by modern East African foragers, the Hadza of Tanzania. While there is some relationship between cut mark and tooth mark distribution as well as order of consumer access (humans first versus carnivores first), it is not as clear cut as had been previously suggested, and there are a number of reasons why. First, cut marks and tooth marks have not been defined in the same way by the various researchers seeking to collect evidence for "Man the Scavenger." Secondly, procedures for reporting frequencies of tooth or cut marks are not standardized. Finally, there are significant differences between patterns observed in modern control samples and those reported on the bones from fossil sites.

In light of difficulties such as these, it is apparent that verification of a "Man the Scavenger" hypothesis is elusive—not because the studies are deficient but because the situation is terrifically complex. On this subject, Klein has said: "Again we must turn to logic, supplemented in this instance by studies of recent hunter-gatherers. These studies suggest that Oldowan people [two million years ago] relied mostly on plants and perhaps on other gathered foods such as insects. In light of this, their day-to-day food quest was probably far less bloodthirsty than some popular accounts have proposed" (1999:248).

An experiment in scavenging was carried out by Louis S. B. Leakey in the 1960s when he and his son Richard tried to forcibly take kills from predators (Munger, 1971). Leakey reported that it was impossible for them to keep the lions away, and the hyenas could only be held at bay for a very short time. As the Leakeys' discovered, stealing carcasses would be an extremely involved activity. The process increases the likelihood of becoming prey and so entails the need for threatening actions that carnivores and other scavengers will respect; it also requires processing the carcass while defending it and necessitates transporting the meat chunks while being pursued by irate predators and other scavengers (Treves and Palmqvist, 2007).

Another complexity not factored into "Man the Scavenger" scenarios is the reality of the condition of dead animals. DeVault et al. point out, "Contrary to widespread belief, vertebrate scavengers consume very few carcasses from predator kills because predators usually consume entire animals or guard their prey. Therefore, most scavengers rely on animal deaths due to malnutrition, disease, exposure, parasites, and accidents" (2003:226). "Man the Scavenger" has support in the scientific arena even though hominins possess none of the internal physiology or external structure necessary to ingest putrid meat, which is what real and facultative scavengers manage to do with the anatomical equipment they possess. These species have evolved detoxifying enzymes along with bodily structures and metabolic processes that protect them from harmful bacteria (DeVault et al., 2003). As stated by Ragir et al.:

> The primate digestive strategy combines a rapid passage through the stomach and prolonged digestion in the ileum of the small intestine and caecum, and this combination increases the likelihood of colonization of the small intestine by ingested bacteria that are the cause of gastrointestinal disease. Carrion is very quickly contaminated with a high bacterial load because the process of dismemberment of a carcass exposes the meat to the bacteria from the saliva of the predator, from the digestive tracts of insects, and from the carcasses' own gut. Thus, the opportunistic eating of uncooked carrion or even unusually large quantities of fresh-killed meat by nonhuman primates or humans is likely to result in gastrointestinal illness (2000:477).

Hominins may be opportunists who eat a variety of things, but with the exception of modern Westerners and Inuits, most of humanity does not eat much meat. Inuits, who have adapted over thousands of years to the coldest Arctic climates, are among the few populations who have diets high in meat, but they traditionally consume as much blubber as flesh from marine mammals (Hayden, 1981). Modern foragers outside the Arctic, such as the hunting and gathering !Kung San of the Kalahari Desert, have a diet that consists of as little as 4% meat (Tanaka, 1976). Among traditional hunter-gatherers studied in tropical and mid-latitude habitats, the most common feeding strategy was a high daily consumption of fruit, cooked rootstocks, and occasional bulbs, shoots, and young leaves supplemented by protein from all sorts of animals—turtles, lizards, insects, birds' eggs, and larger mammals (Vincent, 1985; Blurton Jones et al., 1989; Bailey, 1993; Blurton Jones, 1993; Sept, 1994; Hawkes et al., 1995; Marlowe, 2005; Speth, 2010).

If we were not meat eaters, then are there other fallacies that are linked to the commonly accepted "Man the Hunter" answer to our past? Were our early ancestors violent, natural born killers of other species and of their own kind?

> The blood-bespattered, slaughter-gutted archives of human history from the earliest Egyptians and Sumerian records to the most recent atrocities of the Second World War accord with early universal cannibalism . . . and with worldwide scalping, headhunting, body-mutilating and necrophilic practices of mankind in proclaiming this common bloodlust differentiator, this predaceous habit . . . (Dart, 1953:201).

The quote above lays out a trail that seems to lead from meat eating to hunting, then cannibalism, and ultimately into a morass of repellent activities. But the question we keep returning to after every misanthropic description asks whether views taken from a "Man the Hunter" position are supported by any scientific evidence. Often, connections to cannibalism are inferred from fossil assemblages. We find that almost all of the so-called cannibalistic sites have been lacking in evidence to support this claim. Recent less sensational analyses have not found substantiation of cannibalism but instead find evidence of natural disasters, including predation on the hominins involved. Australopithecines in South African caves and *H. erectus* in the Zhoukoudian Cave were thought to have been scenes of cannibalism but, as stated earlier, both involved the remains of hominins preyed on by large carnivores. At Atapuerca in Spain, the famous "Pit of Bones," (dated at approximately 800,000 years before the present) cannibalism has been alleged to be the cause of bone deposits (Mosquera Martínez, 1998). New analyses find that the hominin bone accumulations were the result of a natural catastrophic event and—while there is skepticism for such a conclusion—the site may even represent trapping of hominins by bears (Monge and Mann, 2007).

Neanderthals, in particular, have been tarnished with the stain of cannibalism almost since their fossil remains were first discovered. "As for Neanderthals, scholars in the early part of this [20th] century assumed almost routinely that they practised cannibalism, an idea that fitted the prevailing view of Neanderthals as shambling, uncultured brutes . . ." (Bahn, 2005:330). Trinkaus (2000) estimates that there is only one confirmed instance of violence in the Neanderthal fossil record. He noted, "The identification of traumatic injury in human fossil remains has plagued paleontologists for years. There has been a tendency to consider any form of damage to a fossil as conclusive evidence of prehistoric violence between humans . . ." (p. 133). As an example of what Trinkaus describes, a single Neanderthal cranium found at Monte Circeo, Italy in a "ring of stones" had been attributed to ritual cannibalism. A more recent theory, however, suggests that the "ring" was the result of a landslide; Monte Circeo was found to be a hyena den at the time the hominin bones were deposited, and damage to the single cranium is consistent with the method used by hyenas to crush skulls and extract brains (Bahn, 2005).

There is a full century behind accusations regarding cannibalism at the Krapina Neanderthal site in Croatia. Neanderthal bones were first discovered between 1899 and 1905 when crude methods were used to excavate and preserve hominin fossils. Cannibalism was the immediate explanation for the bone deposits, but wolf, bear, and hyena remains at the site also point to predators being responsible for the hominin cache (Klein and Edgar, 2002). Although media reports continue to identify Neanderthal remains at Krapina as a confirmed "cannibal feast," Bahn comments: "This gruesome image does not stand up to scrutiny. The bones display no evidence of the impact fractures characteristic of marrow extraction by humans. Instead, the extensive fragmentation can be explained by roof-falls, crushing by sediments, and the use of dynamite during excavation" (2005:330).

While accusations of cannibalism stretch back to Greek myths and seem to titillate the human mind, it is satisfying to find that cannibalism among humans is rare and extraordinary—in every way an exception to normal human behavior. It is prompted only by the most singular of circumstances, such as the famous instance when survivors of a plane crash in the Andes consumed their dead fellow passengers. Careful studies have found there are no reliable witnesses to ritual or habitual cannibalism, and reports of it are based on hearsay (Bahn, 2005).

In a recent volume, we have developed the hypothesis that, rather than being a predator with inherited tendencies to be excessively violent, humans evolved as a prey species (Hart and Sussman, 2005, 2009). In this theory, we propose that both nonhuman primates and humans, as well as other social-living animals, may have developed mechanisms of cooperation and sociality through natural selection. Looking at early humans as a prey species rather than as a top-level predator gives a rather different perspective to the evolution of sociality and cooperation. Independently, Treves and Palmqvist have come up with a similar conclusion: "Given the existence of numerous ambush predators between 3.6 and 1.8 ma, hominins would have experienced strong selection for efficient vigilance" (2007:370). They thus propose that early hominins "would have adopted more cohesive and calmer social organization to maintain vigilance and reduce conspicuousness to carnivores. . ." (p. 370). Inconspicuous groups "within which individuals cooperate in anti-predator behavior can survive under heavy predation pressure. . . . High levels of cooperation and reciprocity appear critical under heavy predation pressure" (p. 372).

To assess human behavior, researchers look at our primate roots where sociality may have its origin in the general benefits of mutual cooperation, strong mother–infant bonds, and the evolution of an extended juvenile period in which developing young ones are dependent on other group members. Naturally occurring opiates in the brain, whose effects are not unlike the restfulness and lessening of unease attained through opium-based narcotics (but without highs, withdrawals, or addiction), may be at the core of innate cooperative social responses (Carter, 1999; Taylor et al., 2000). These could finally explain the evolution not only of cooperation among nonrelated humans or nonhuman primates but also of true altruistic behavior and general well-being. Going one step further, recently Hauser (2006), and Bekoff and Pierce (2009), in separate volumes, have provided ample evidence of a moral toolkit in the human brain, a biological mechanism for acquisition of moral rules.

In a recent review, Sussman and Garber (2011) found that diurnal primates (lemurs, monkeys, and apes) devoted less than 10% of their daily activity budget to direct social interactions. The overwhelming majority of these interactions were affiliative and cooperative behaviors such as grooming, food sharing, huddling, and alliance formation. In contrast, aggression was rare and episodic, typically accounting for less than 1% of all social interactions. They concluded that cooperative and affiliative behaviors commonly accounted for over 90% of direct social interactions. Clearly cooperative interactions represent the overwhelming majority of primate social interactions and form the basis of individual social bonds.

Even in species in which social interactions typically account for only 2–4% of the activity budget and adult group members are not related (such as in howler monkeys, *Alouatta* spp.), individuals are found to exhibit consistent partner preferences from year to year (Bezanson et al., 2002; Chapters 8 and 9, this volume). These preferences are based on patterns of spatial proximity and affiliation enabling individuals to feed together in the same food patch and to develop social and mating bonds. In chimpanzees, both adult males and females have been observed to adopt unrelated infants whose mothers had died. Care of the orphaned infant by an adult in these cases was often very costly both in time and effort. Field researchers concluded that this was a clear sign of altruism (Boesch et al., 2010).

Sussman and Garber (2011) believe that researchers need to focus on the benefits of cooperation and mutualism in understanding the evolution of primate sociality. Several recent studies of primate social behavior have highlighted the role of cooperation and affiliation in determining the benefits to individuals in forming groups or subgroups of particular size and composition (cited in Sussman and Garber). Cooperation and affiliation represent behavioral tactics that can be used by individual group members to obtain resources, maintain or enhance their social position, or increase their reproductive opportunities.

Looking at physiological mechanisms that might relate to cooperative behavior, researchers have identified a set of neuroendocrine mechanisms in humans that may lead to cooperation among related and nonrelated individuals. In experiments using MRIs, mutual cooperation has been associated with consistent activation in two areas of the brain (specifically the anteroventral striatum and the orbitofrontal cortex, or OFC) that have been linked with reward processing. Rilling et al. (2002) and Rilling (Chapter 17, this volume) have proposed that activation of this neural network positively reinforces cooperative social interactions. Even more compelling, the strength of the neural response increases with the persistence of mutual cooperation over successive trials; it is, therefore, cumulative and self-reinforcing. Activation of the brain's reward center may account for why we tend to feel good when we cooperate. On the other hand, another area of the brain, the dorsolateral prefrontal cortex (DLPFC), is involved in the exertion of cognitive efforts to overcome prepotent response tendencies**.** This became evident in recent experiments related to cheating, when Rilling et al. (2007) and Rilling (2008, Chapter 17, this volume) found that most subjects activated OFC when choosing to cooperate but activated DLPFC when defecting. This suggests that cooperation was the prepotent emotional response tendency and cognitive effort was required to override this tendency and cheat. However, those subjects who scored highest on a measure of psychopathic personality showed a pattern of overriding the prepotent emotional response tendency. Thus noncooperation appeared to be a function of psychopathy.

Both of the above-mentioned locations in the brain linked with reward processing are rich in neurons that respond to dopamine, the neurotransmitter known for its role in addictive behaviors. The dopamine system evaluates rewards—both those that flow from the environment and those conjured up within the brain. When the stimulus is positive, dopamine is released. In experiments with rats in which electrodes are placed in the anteroventral striatum, the animals continue to press a bar to stimulate the electrodes, apparently receiving such pleasurable feedback that they will starve to death rather than stop pressing the bar (Angier, 2002). Therefore, it appears that in some ways we may be wired to cooperate with each other (Angier, 2002:24).

Another physiological mechanism related to friendly affiliation and nurturing is the neuroendocrine circuitry associated with mothering in mammals. Orchestrating the broad suite of these bio-behavioral feedback responses is the hormone oxytocin (OT). OT has been related to every type of animal bonding imaginable—parental, fraternal, sexual, and even the capacity to soothe oneself. It has been suggested that although OT's primary role may have been in forging the mother–infant bond, its ability to influence brain circuitry may have been co-opted to serve other affiliative purposes that allowed the formation of alliances and partnerships, thus facilitating the evolution of cooperative behaviors (Angier, 1999; Carter, 1999; Taylor et al., 2000; Carter and Cushing, 2004; Young et al., 2005). In humans OT also has been linked with increased trustworthiness (Kosfeld et al., 2005) and with the reduction of stress and anxiety (Kirsch et al., 2005).

Studies on cotton-top tamarins reveal other hormonal mechanisms critical to cooperation and affiliative behavior (Ferris et al., 2001; Snowdon, 2003; Ferris et al., 2004; Lazaro-Perea et al., 2004; Snowdon et al., 2006; Snowdon and Cronin, 2007; Chapter 18, this volume). In these small South American monkeys, males and older siblings provide essential infant care. Elevated levels of the hormone prolactin, usually associated with lactation, may be the impetus behind maternal care giving exhibited by males and siblings. Correlations of OT and prolactin levels with amounts of friendly social behavior between one adult and another also have been found. Experiments by Snowdon et al. (2006) and Snowdon (Chapter 18, this volume) indicate that high levels of affiliative hormones could result in good-quality social interactions, suggesting a reward system for positive behavior.

Many cooperative behaviors observed in primates can be explained by individual behaviors that benefit several group members (Clutton-Brock, 2002; Silk, 2002; Silk et al., 2003; Sussman and Garber, 2004, 2011). Coordinated behaviors such as resource or range defense, cooperative foraging and food harvesting, alliance formation, and predator vigilance and defense can be explained in terms of immediate benefits to both the individual and other group members. Even if the rewards for these behaviors are low level, we should expect cooperation to be common. Thus, many types of social interactions may be best understood in terms of a non-zero-sum game with multiple winners. Low-risk coalitions in which all participants make immediate gains are widespread in primates (Watts, 2002; Sussman and Garber, 2011) and may explain why nonhuman primates live in relatively stable, cohesive social groups and solve the problems of everyday life in a generally cooperative fashion. Charles Darwin had this idea long before scientific studies of animal behavior, primatology, or cooperation when he noted that natural selection would opt for "the feeling of pleasure from society" (1874:102).

Even though most nonhuman primates are highly social, investigations into the evolution of primate sociality have tended to focus on aggression and competition instead of cooperation. However, many results from behavioral, hormonal, and brain imaging studies offer a new perspective of primates and their proclivities for cooperation, sociality, and peace. For example, after 16-years research on the behavior and ecology of wild savanna baboons, Silk et al. conclude that social integration even enhances reproductive capabilities in female baboons: "Females who had more social contact with other adult group members and were more fully socially integrated into their groups were more likely than other females to rear infants successfully" (2003:1231). de Waal (2006) contends that chimp societies emphasize reconciliation and consolation after conflict; his 40 years of primate behavior observations have documented that concern for others is natural conduct for our closest primate relatives.

It appears that social animals are wired to cooperate and to reduce stress by seeking each others' company. If cooperation and physical proximity among group-living animals are rewarding in a variety of environmental and social circumstances and if physiological and neurological feedback systems reinforce social tolerance and cooperative behavior, then social living can persist in the absence of any conscious recognition that material gains might also flow from mutual cooperation. Based on the latest research, friendly and cooperative behaviors provide psychological, physiological, and ecological benefits to social primates which are positively reinforced by hormonal and neurological systems.

On a more general level, in a recent volume, Weiss and Buchanan (2009) show that the conventional wisdom focusing on relentless competition as the primary mover of evolution is largely an artifact of a restricted view of evolutionary time scales. They provide ample evidence that evolution, development, and ecological interactions generally work on the basis of cooperation.

How can this research on cooperative behaviors apply to humans when we consider violence and war? There is a cultural acceptance in the West that humans are innately aggressive and that we characterize our aggressive feelings through violent actions. The general primate physiology does not support this view and leads instead to a belief that cooperation is innate to humans. Why the disconnect? Sometimes putting things in perspective is a helpful exercise. There are more than 6 billion humans alive today—all are social animals having constant interactions with other humans. The overwhelming majority of our 6-billion conspecifics are having days, weeks, even entire lives devoid of violent interpersonal conflicts. This is not to naively underplay crimes, wars, and state-level aggression found in modern times, but it puts them in the domain of the anomalous.

Murder rates vary greatly from nation to nation and from culture to culture (Chapter 12, this volume). Are war, crimes, and violence the genetic, unalterable norm, or might they be specific to stresses that occur when too many people want too few resources? After an exhaustive examination of ethnographic research on modern societies ranging from nomadic foragers to urban industrialized societies, Fry (2006; Chapters 13 and 14, this volume) documented the human potential for cooperation and conflict resolution. He stresses that virtually all early studies defining man by his capacity for killing appear to be flawed: "War is either lacking or mild in the majority of cultures!" (p. 97). Counter to assumptions of hostility between groups and among individuals and recurring warfare over resources, the typical pattern is for humans to get along rather well, relying on resources within their own areas and respecting resources of their neighbors. After an examination of the primary ethnographic information on nomadic foragers, Fry found the proposition that human groups are pervasively hostile toward one another is simply not based on facts but rather on "a plethora of faulty assumptions and over-zealous speculation" (2006:183). According to Fry, "Conflict is an inevitable feature of social life, but clearly *physical aggression is not the only option for dealing with conflict*" (p. 22). He summarized his findings by acknowledging the human propensity to behave assertively and aggressively but adamantly stating that just as inherent is the human propensity to behave prosocially and cooperatively, with kindness and consideration for others. Indeed, Fry's work has convinced him that the very existence of human societies is dependent on the preponderance of prosocial tendencies over assertive and aggressive ones.

At another level the psychiatric research and clinical work of Cloninger (2004) has led him to the conclusion that individuals have the potential for either peaceful or violent behavior; a world view of connectedness (or cooperativeness) promotes peace, whereas separateness promotes violence. Furthermore, connectedness appears to be natural in the absence of abuse and defective development (see also Chapter 19, this volume). People are normally happy and content when they are cooperative (connected) but show hostility when they are alone and alienated.

We are not trying to ignore the role of aggression and competition in understanding primate and human social interactions. Our perspective, however, is that affiliation, cooperation, and social tolerance associated with long-term mutual benefits form the core of social group-living. Our earliest ancestors lived in a world populated by large, fearsome predators. Strong indications from the fossil record and living primate species led to the conclusion that hominins were regularly hunted and required social organization that promoted inconspicuous behaviors, minimal internal conflicts, and coordinated vigilance (Hart and Sussman, 2005, 2009; Treves and Palmqvist, 2007). What would have been the best strategy to avoid being eaten—conspicuous, violent interpersonal conflicts, or high levels of cooperation and reciprocity to facilitate as inconspicuous a presence as possible?

Is "Man the Hunter" and associated human violence the norm or the exception? Alternatively, is "Man the Hunted"—and the necessity for cooperation and altruism leading to human well-being—a more realistic view of the origin and nature of human sociality than the old paradigm of "Man the Hunter"? These questions lead us to ponder how new scientific theories or paradigms get accepted or, on the other hand, ignored? Unfortunately, the answer to this question may turn out to be much more political than scientific. In 1962, Kuhn wrote a classic book, *The Structure of Scientific Revolution*. In it he argued that scientists examine the evidence related to their questions and come up with the most parsimonious explanation that fits the data and techniques currently available at the time. However, the evidence is also filtered through a scientist's own background and theoretical orientation by his or her world view and cultural milieu. Changing currently popular, engrained paradigms—those that have become "conventional wisdom," like the "Man the Hunter theory"—is very difficult especially if the theory also fits standard cultural views of the world. Scientists, like most people, are generally conservative in their ability to adopt new paradigms.

Once a paradigm becomes established within a scientific community, most practitioners become technicians working within the parameters of the theory but rarely questioning the validity of the theory itself. In fact even questioning the theory is often thought of as unscientific because the new theory and the old are incompatible and the internal logic of each paradigm differs. Proponents of each paradigm are often talking past one another—speaking a different language. As expressed by Strum when she was trying to get primatologists to accept her observations that aggression was not as pervasive or important an influence on the evolution of baboon behavior as had been previously thought: “In science, according to Kuhn, ideas do not change simply because new facts win out over outmoded ones. Many more social, cultural and historical variables make up the complete picture. Since the facts can’t speak for themselves, it is their human advocates who win or lose the day” (2001:164).

So, yes, science is an accumulation of better and better evidence to fit a theory . . . or of finding that the old and new evidence is better accommodated by a completely new theory. And, in the end, even with new evidence and a better way of explaining it, ultimately, the politics of science must take its course. It is up to the audience to weigh the evidence. Discrepancies among the theories and the evidence must be evaluated. Once these discrepancies are seen to be overwhelming, the new paradigm will be accepted in favor of the old.

Science is not always truth. Science is just the best way to answer a particular question given the available evidence and technology at a particular time and place. At this time and place, we believe “Man the Hunted” as a paradigm of early human evolution best fits the currently available evidence.

There is little doubt that modern humans, particularly those in Western cultures, think of themselves as the dominant form of life on earth, and we seldom question whether that view also held true for our species’ distant past (or even for the present, outside of urban areas). Is “Man the Hunter” a cultural construction of the West? Belief in a sinful, violent ancestor does fit nicely with Christian views of original sin and the necessity to be saved from our own awful, yet natural, desires. Other religions do not necessarily emphasize the ancient savage in the human past; indeed, many modern-day hunter-gatherers who lived as part of nature until recent times, hold supernatural beliefs in which humans are a part of the web of life, not superior creatures who dominate or ravage nature and each other.

Think of our ancestors as prey, and you put a different face on our past. The shift forces us to see that for most of our evolutionary existence, instead of being violent or predaceous, we needed to live in groups (like most other primates) and work together to avoid predators. Thus, an urge to cooperate can clearly be seen as a functional tool rather than a Pollyannaish nicety, and deadly competition among individuals or nations may be highly aberrant behavior, not hard-wired survival techniques. Our earliest evolutionary history as a prey suggests that we should be able to take our ancestral tool kit of sociality, cooperation, interdependency, and mutual protection and use it to make a brighter future for ourselves and our planet.

We evolved as a mainly plant-eating species that also ate some animal protein collected opportunistically. But this latter activity did not make us a predator or a scavenger. We hunted but were not *hunters,* and we may have scavenged but were not *scavengers*. We are neither naturally aggressive hunters and killers nor always kind and loving. Humans have the capacity to be both. It is what we learn and our life experiences, our world view, and our culture that have the greatest influence on our behavior, even how we react to stress. That is exactly why it is necessary to comprehend that we have not inherited a “propensity” to kill derived from our hunting past. We are no more born to be hunters than to be gardeners. We are no more inherent killers than we are angels. We are, for the most part, what we learn to be.

## References

Alderton, D. 1991. *Crocodiles and Alligators of the World*. Facts on File, New York.

Angier, N. 1999. Illuminating how bodies are built for sociality. In: *The Biological Basis of Human Behavior: A Critical Review*, R. Sussman (ed.). Prentice Hall, Upper Saddle River, NJ, pp. 350–352.

Angier, N. 2002. Wired by evolution to get along. *The New York Times Large Type Weekly*, 7/29-8/4, p. 24.

Ardrey, R. 1961. *African Genesis: A Personal Investigation into the Animal Origins and Nature of Man*. Atheneum, New York. 1963 reprint, Dell, New York.

Associated Press (AP). 2005. Were human ancestors hunted by birds? Science MSNBC.com. http://www.msnbc.msn.com/id/10819471/from/ET/

Bahn, P. 2005. Cannibalism or ritual dismemberment. In: *The Cambridge Encyclopedia of Human Evolution*, S. Jones, R. Martin, and D. Pilbeam (eds.). Cambridge University Press, Cambridge, p. 330.

Bailey, R. 1993. The behavioral ecology of Efe pygmy men. *University of Michigan Anthropological Papers* 86. Museum of Anthropology, Ann Arbor.

Bekoff, M. and J. Pierce. 2009. *Wild Justice: The Moral Lives of Animals.* University of Chicago Press, Chicago.

Berger, L. and R. Clarke. 1995. Eagle involvement in accumulation of the Taung child fauna. *Journal of Human Evolution* 29:275–299.

Bezanson, M., P. Garber, J. Rutherford, and A. Cleveland. (2002) Patterns of subgrouping, social affiliation and social networks in Nicaraguan mantled howler monkeys (*Alouatta palliata*). *American Journal of Physical Anthropology*, Supplement 34:44.

Blumenshine, R. 1988. An experimental model of the timing of hominid and carnivore influence on archaeological bone assemblages. *Journal of Archaeological Science* 15:483–502.

Blumenshine, R. 1995. Percussion marks, tooth marks and experimental determinations of the timing of hominid and carnivore access to long bones at FLK Zinjanthropus, Olduvai Gorge, Tanzania. *Journal of Human Evolution* 29:21–51.

Blurton Jones, N. 1993. The lives of hunter-gatherer children: Effects of parental behavior and parental reproductive strategy. In: *Juvenile Primates: Life History, Development and Behavior*, M. Pereira and L. Fairbanks (eds.). Oxford University Press, Oxford, pp. 309–326.

Blurton Jones, N., K. Hawkes, and J. O'Connell. 1989. Modeling and measuring the costs of children in two foraging societies. In: *Comparative Socioecology: The Behavioral Ecology of Humans and Other Mammals*, V. Standen and R. Foley (eds.). Oxford University Press, Oxford, pp. 367–390.

Boaz, N. and R. Ciochon. 2001. The scavenging of "Peking Man." *Natural History* 110(2):46–51.

Boaz, N., R. Ciochon, Q. Xu, and J. Liu. 2000. Large mammalian carnivores as a taphonomic factor in the bone accumulation at Zhoukoudian. *Acta Anthropologica Sinica* (Suppl.) 19:224–234.

Boaz, N., R. Ciochon, Q. Xu, and J. Liu. 2003. Taphonomy of Zhoukoudian Homo erectus: Locality 1 as a hyaenid den [unpublished manuscript].

Boesch, C. 1991. The effects of leopard predation on grouping patterns in forest chimpanzees. *Behaviour* 117(3–4):220–242.

Boesch, C. and H. Boesch-Achermann. 2000. *The Chimpanzees of the Taï Forest: Behavioural Ecology and Evolution*. Oxford University Press, Oxford.

Boesch C., C. Bolé, N. Eckhardt, and H. Boesch. 2010. Altruism in forest chimpanzees: The case of adoption. PLoS ONE 5(1):e8901. doi:10.1371/journal.pone.0008901.

Borja, C., M. Garcia-Pacheco, E. Olivares, G. Scheuenstuhl, and J. Lowenstein. 1997. Immunospecificity of albumin detected in 1.6 million-year-old fossils from Venta Micena in Orce, Granada, Spain. *American Journal of Physical Anthropology* 103(4):433–441.

Brain, C. 1981. *The Hunters or the Hunted?* University of Chicago Press, Chicago.

Bunn, H. 1981. Archaeological evidence for meat eating by Plio-Pleistocene hominids from Koobi Fora and Olduvai Gorge. *Nature* 291:574–677.

Carter, S. (ed.). 1999. *Hormones, Brain and Behavior: Integrative Neuroendocrinology of Affiliation*. MIT Press, Boston, MA.

Carter, S. and B. Cushing. 2004. Proximate mechanisms regulating sociality and social monogamy in the context of evolution. In: *Origins and Nature of Sociality*, R. Sussman and A. Chapman (eds.). Aldine de Gruyter, New York, pp. 99–121.

Cloninger, C. 2004. *Feeling Good: The Science of Well-Being.* Oxford University Press, Oxford.

Clutton-Brock, T. 2002. Breeding together: Kin selection and mutualism in cooperative vertebrates. *Science* 296:69–72.

Dart, R. 1953. The predatory transition from ape to man. *International Anthropological and Linguistic Review* 1:201–217.

Darwin, C. 1874. *The Descent of Man*, Revised Edition. The Henneberry Company, Chicago.

Deacon, H. and J. Deacon. 1999. *Human Beginnings in South Africa: Uncovering the Secrets of the Stone Age*. AltaMira Press, Walnut Creek, CA.

DeVault, T., O. Rhodes, and J. Shivik. 2003. Scavenging by vertebrates: Behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos* 102(2):225–234.

de Waal, F. 2006. *Primates and Philosophers: How Morality Evolved*. Princeton University Press, Princeton, NJ.

Domico, T. 1988. *Bears of the World*. Facts on File, New York.

Dominguez-Rodrigo, M. 1997. Meat-eating by early hominids at the FLK Zinjanthropus Site, Olduvai Gorge (Tanzania): An experimental approach using cut mark data. *Journal of Human Evolution* 33:669–690.

Dominguez-Rodrigo, M. 1999. Distinguishing between apples and oranges: The application of modern cut mark studies to the Plio-Pleistocene (a reply to Monahan). *Journal of Human Evolution* 37:793–800.

Fay, J., R. Carroll, J. Kerbis Peterhans, and D. Harris. 1995. Leopard attack on and consumption of gorillas in the Central African Republic. *Journal of Human Evolution* 29(1):93–99.

Ferris, C., C. Snowdon, J. King, T. Duong, T. Ziegler, K. Ugurbil, R. Ludwig, N. Schultz-Darken, Z. Wu, D. Olson, J. Sullivan, P. Tannenbaum, and J. Vaughan. 2001. Functional imaging of brain activity in conscious monkeys responding to sexually arousing cues. *Neuroreport* 12(10):2231–2236.

Ferris, C., C. Snowdon, J. King, J. Sullivan, T. Ziegler, D. Olson, N. Schultz-Darken, P. Tannenbaum, R. Ludwig, Z. Wu, A. Einspanier, J. Vaughan, and T. Duong. 2004. Activation of neural pathways associated with sexual arousal in non-human primates. *Journal of Magnetic Resonance Imaging* 19:168–175.

Fourrier, M., R. Sussman, R. Kippen, and G. Childs. 2008. Demographic modeling of a predator-prey system and its implication for the Gombe red colobus (*Procolobus badius*) population. *International Journal of Primatology* 29:497–508.

Fox, M. 2004. Was pre-human a failed "experiment?" Fossil hints at violent death 900,000 years ago. Science MSNBC.com. http://www.msnbc.msn.com/id/5343787/

Fry, D. 2006. *The Human Potential for Peace: An Anthropological Challenge to Assumptions about War and Violence*. Oxford University Press, New York.

Gore, R. 2002. New find: The first pioneer? *National Geographic* 8/02 [unnumbered addition to issue].

Goren-Inbar, N., N. Alperson, M. Kislev, O. Simchoni, Y. Melamed, A. Ben-Nun, and E. Werker. 2004. Evidence of hominin control of fire at Gesher Benot Ya'aqov, Israel. *Science* 304: 725–727.

Hart, D. 2000. *Primates as prey: Ecological, morphological, and behavioral relationships between primate species and their predators.* Ph.D. dissertation, Washington University, St. Louis, MO.

Hart, D. and R. Sussman. 2005. *Man the Hunted: Primates, Predators, and Human Evolution*. Westview Press, Boulder, CO.

Hart, D. and R. Sussman. 2009. *Man the Hunted: Primates, Predators, and Human Evolution*, Expanded Edition. Westview Press, Boulder, CO.

Harvard University Press Online Catalog. Advertisement for *A View to a Death in the Morning: Hunting and Nature through History* by Matt Cartmill (1993). http://www.hup.harvard.edu/catalog/CARVIE.html

Hauser, M. 2006. *Moral Minds: How Nature Designed Our Universal Sense of Right and Wrong.* Harper Collins, New York.

Hawkes, K., J. O'Connell, and N. Blurton Jones. 1995. Hadza children's foraging: Juveniles' dependency, social arrangements and mobility among hunter-gatherers. *Current Anthropology* 36:688–700.

Hayden, B. 1981. Subsistence and ecological adaptations of modern hunter/gatherers. In: *Omnivorous Primates: Gathering and Hunting in Human Evolution*, R. Harding and G. Teleki (eds.). Columbia University Press, New York, pp. 344–421.

Hladik, C. 1977. Chimpanzees of Gabon and chimpanzees of Gombe: Some comparative data on the diet. In: *Primate Ecology: Studies of the Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes*, T. Clutton-Brock (ed.). Academic, New York, pp. 481–501.

Hladik, C., D. Chivers, and P. Pasquet. 1999. On diet and gut size in non-human primates and humans: Is there a relationship to brain size? *Current Anthropology* 40(5):695–697.

James, S. 1989. Hominid use of fire in the lower and middle Pleistocene. *Current Anthropology* 30(1):1–26.

Kirsch, P., C. Esslinger, Q. Chen, D. Mier, S. Lis, S. Siddhanti, H. Gruppe, V. Mattey, B. Gallhofer, A. Meyer-Lindenberg. 2005. Oxytocin modulates neural circuitry for social cognition and fear in humans. *Journal of Neuroscience* 25:11489–11493.

Klein, L. 2004. *Women and Men in World Cultures*. McGraw Hill, Boston, MA.

Klein, R. 1999. *The Human Career: Human Biological and Cultural Origins*, Second Edition. University of Chicago Press, Chicago.

Klein, R. and B. Edgar. 2002. *The Dawn of Human Culture*. Wiley, New York.

Kosfeld, M., M. Heinrichs, P. Zak, U. Fischbacher, E. Fehr. 2005. Oxytocin increases trust in humans. *Nature* 435:673–676.

Kruuk, H. 2002. *Hunter and Hunted: Relationships between Carnivores and People*. Cambridge University Press, Cambridge.

Kuhn, T. 1962. *The Structure of Scientific Revolutions*. Chicago University Press, Chicago.

Lazaro-Perea, C., M. de Fátima Arruda, and C. Snowdon. 2004. Grooming as a reward? Social function of grooming between females in cooperatively breeding marmosets. *Animal Behaviour* 67:627–636.

Lupo, K. and J. O'Connell. 2002. Cut and tooth mark distributions on large animal bones: Ethnoarchaeological data form the Hadza and their implications for current ideas about early human carnivory. *Journal of Archaeological Science* 29:85–109.

Macdonald, D. 1984. *The Encyclopedia of Mammals*. Facts on File, New York.

Marlowe, F. 2005. Hunter-gatherers and human evolution. *Evolutionary Anthropology* 14:54–67.

McDougal, C. 1991. Man-eaters. In: *Great Cats: Majestic Creatures of the Wild*, J. Seidensticker and S. Lumpkin (eds.). Rodale Press, Emmaus, PA, pp. 204–211.

McGraw, W., C. Cooke, and S. Shultz. 2006. Primate remains from African crowned eagle (*Stephanoaetus coronatus*) nests in Ivory Coast's Tai Forest: Implications for primate predation and early hominid taphonomy in South Africa. *American Journal of Physical Anthropology* 131(2):151–165.

Milton, K. and M. Demment. 1989. Features of meat digestion by captive chimpanzees (*Pan troglodytes*). *American Journal of Physical Anthropology* 18:45–52.

Monge, J. and A. Mann. 2007. Paleodemography of extinct hominin populations. In: *Handbook of Paleoanthropology: Principles, Methods, and Approaches*, Vol. I, W. Henke and I. Tattersall (eds.). Springer, Berlin, pp. 673–700.

Mosquera Martínez, M. 1998. Differential raw material use in the Middle Pleistocene of Spain. Evidence from Sierra de Atapuerca, Torralba, Ambrona and Aridos. *Cambridge Archaeological Journal* 8(1):15–28.

Munger, N. 1971. Aggression and violence in man. *Munger Africana Library Notes* 9, 24pp.

Nowak, R. 1991. *Walker's Mammals of the World, Sixth Edition* – Vol. II. Johns Hopkins University Press, Baltimore, MD.

Potts, R. and P. Shipman. 1981. Cutmarks made by stone tools on bones from Olduvai Gorge. *Nature* 291:577–580.

Ragir, S., M. Rosenberg, and P. Tierno. 2000. Gut morphology and the avoidance of carrion among chimpanzees, baboons, and early hominids. *Journal of Anthropological Research* 56(4): 477–512.

Rilling, J. 2008. Neuroscientific approaches and applications within anthropology. *Yearbook Physical Anthropology* 51:2–32.

Rilling, J., A. Glenn, M. Jairam, G. Pagnoni, D. Goldsmith, H. Effenbein, S. Lilienfeld. 2007. Neural correlates of social cooperation and non-cooperation as a function of psychopathy. *Biological Psychiatry* 61:1260–1271.

Rilling, J., D. Gutman, T. Zeh, G. Pagnoni, G. Berns, and D. Kilts. 2002. A neural basis for social cooperation. *Neuron* 35:395–405.

Senut, B. 2001. Fast Breaking Comments. Essential Science Indicators Special Topics. December 2001. http://www.esi-topics.com/fbp/comments/december-01-Brigitte-Senut.html

Sept, J. 1994. Beyond bones: Archaeological sites, early hominid subsistence, and the costs and benefits of exploiting wild plant foods in East African riverine landscapes. *Journal of Human Evolution* 27:295–320.

Silk, J. 2002. Using the "F"-word in primatology. *Behaviour* 139:421–446.

Silk, J., S. Alberts, and J. Altmann. 2003. Social bonds of female baboons enhance infant survival. *Science* 302:1231–1234.

Small, L. 2005. Our adaptable ancestors: Recent discoveries of skull fragments and tools testify to the resourcefulness of early humans. *Smithsonian*, February 2005, p. 12.

Snowdon, C. 2003. Affiliative processes and male primate social behavior. Paper presented at the Annual Meeting of the American Anthropological Association, Chicago, IL, November 2003.

Snowdon, C. and K. Cronin. 2007. Cooperative breeders do cooperate. *Behavioural Processes* 76:138–141.

Snowdon, C., T. Ziegler, and R. Almond. 2006. Affiliative hormones in primates: Cause or consequence of positive behavior? Paper presented at the Annual Meeting of the American Association for the Advancement of Science, St. Louis, MO, February 2006.

Speth, J. 2010. *The Paleoanthropology and Archaeology of Big-Game Hunting: Protein, Fat, or Politics? (Interdisciplinary Contributions to Archaeology).* Springer, New York.

Strum, S. 2001. *Almost Human: A Journey into the World of Baboons*. University of Chicago Press, Chicago.

Sussman, R. and P. Garber. 2004. Rethinking sociality: Cooperation and aggression among primates. In: *The Origin and Nature of Sociality*, R. Sussman and A. Chapman (eds.). Aldine de Gruyter, New York, pp. 161–190.

Sussman, R. and P. Garber. 2011. Cooperation, collective action, and competition in primate social interactions. In: *Primates in Perspective*, 2nd Edition, C.J. Campbell, A. Fuentes, K.C. Mackinnon, S.K. Bearder, and R.S.M. Stumpf (eds.). Oxford University Press, New York, pp. 587–599.

Tanaka, J. 1976. Subsistence ecology of Central Kalahari San. In: *Kalahari Hunter-Gatherers: Studies of the !Kung San and Their Neighbors*, R. Lee and I. De Vore (eds.). Harvard University Press, Cambridge, MA, pp. 98–119.

Taylor, S., L. Cousino, B. Klein, T. Gruenewals, R. Gurung, and J. Updegraff. 2000. Biobehavioral responses to stress in females: Tend-and-befriend, not fight-or-flight. *Psychological Review* 107:411–429.

Teaford, M. and P. Ungar. 2000. Diet and the evolution of the earliest human ancestors. *Proceedings of the National Academy of Science* 97(25): 13,506–13,511.

Treves, A. and P. Palmqvist. 2007. Reconstructing hominin interactions with mammalian carnivores (6.0–1.8 ma). In: *Primate Anti-Predator Strategies*, S. Gursky and K. Nekaris (eds.). Springer, New York, pp. 355–381.

Trinkaus, E. 2000. Hard times among the Neanderthals. In: *Annual Editions: Physical Anthropology 00/01*, E. Angeloni (ed.). Dushkin McGraw-Hill, Guilford, CT, pp. 131–135.

Tsukahara, T. 1993. Lions eat chimpanzees: The first evidence of predation by lions on wild chimpanzees. *American Journal of Primatology* 29(1):1–11.

Uprety, A. 1998. Killers on the prowl. *The Week* 8/2/98.

Vincent, A. 1985. Plant foods in savanna environments: A preliminary report of tubers eaten by the Hadza of northern Tanzania. *World Archaeology* 17:1–14.

Watts, D. 2002. Reciprocity and interchange in the social relationships of wild male chimpanzees. *Behaviour* 139:343–370.

Weiss, K. and A. Buchanan. 2009. *The Mermaid's Tale: Four Billion Years of Cooperation in the making of Living Things.* Harvard University Press, Cambridge.

WoldeGabriel, G., T. White, G. Suwa, P. Renne, J. de Heinzelin, W. Hart, and G. Heiken. 1994. *Nature* 371:330–333.

Wong, K. 2003. Stranger in a new land. *Scientific American* 289(5):74–83.

Young, L., A. Murphy Young, E. Hammock. 2005. Anatomy and neurochemistry of the pair bond. *Journal of Comparative Neurology* 493:51–57.

# Chapter 4
# Born to Cooperate? Altruism as Exaptation and the Evolution of Human Sociality

**Telmo Pievani**

## Introduction

In recent papers (e.g. Wilson and Wilson, 2007), it has been confirmed that the two standard solutions for the apparent paradox of the evolution of altruism and pro-social behaviours – 'kin selection', which leaves unsolved the question of population structure, and 'group selection' – can indeed be consistent with one other. The result is a possible explanation of the ambiguity between deeply entrenched attitudes to cooperation inside social groups and organized hostility among them (Bowles, 2008). Nevertheless, these models seem to undervalue the potential effects of 'multilevel' evolution and both notions remain strongly engaged with gene-centred interpretations of evolutionary dynamics – which lose their explanatory power when applied to group-living species that show unconditioned forms of altruism and pro-social feeling, especially when cultural evolution enters the process. In order to avoid 'cultural discontinuity' hypotheses at the other extreme, I emphasize the importance of 'functional cooptation', or 'exaptation' (Gould and Vrba, 1982; Gould, 2002) in arriving at a more satisfying explanation of the origins of free or reciprocal unselfishness, in group-living animals and in culture-bearing species.

## Individuals or Tribes? A Pluralistic Darwinian Heritage

While the theory of evolution was developing in his private notes, between 1836 and 1842, Charles Darwin discovered the logic of the selective process and modified his perspective on the 'transmutation' of species, which he had previously viewed as an abrupt transition between discrete entities that were physically and geographically isolated. After incorporating 'Malthusian' ideas into his theory in September of 1838, he no longer saw change in species as 'per saltum' but as a gradual

---

T. Pievani (✉)
Department of Human Sciences, University of Milan II, Milan, Italy
e-mail: telmo.pievani@gmail.com

R.W. Sussman, C.R. Cloninger (eds.), *Origins of Altruism and Cooperation*,
Developments in Primatology: Progress and Prospects 36, DOI 10.1007/978-1-4419-9520-9_4,

accumulation of 'infinitesimal' changes in populations of organisms exposed to selective environmental pressures:

> Three principles will account for all:
>
> 1) Grandchildren like grandfathers;
> 2) Tendency to small change, especially with physical change
> 3) Great fertility in proportion to support of parents (Notebook E, p. 58 of the original; see Barrett et al., 1987, p. 412).

In order to implement this 'tendency to small change' in the struggle for existence, tiny infinitesimal advantages are enough:

> Seeing the beautiful seed of a Bull Rush, I thought, surely no 'fortuitous' growth could have produced these innumerable seeds. Yet if a seed were produced with infinitesimal advantage it would have better chance of being propagated and so on (Notebook E, p. 137 of the original, see the edition quoted above p. 436).

Thus the language itself was changing in Darwin's writings at that time, drifting towards a competitive and rigorous logic of selection in environments where there was limited supply (here a passage dated March 12th 1839):

> It is difficult to believe in the dreadful but quiet war of organic beings, going on the peaceful woods and smiling fields (Notebook E, p. 114 of the original, see edition quoted above, p. 429).

It is still evident that the explanatory power of natural selection derives from the fact that it is a demographic, statistical, ecological mechanism involving individuals in populations. The process is without foresight, absolute perfection, and design. But in its explanatory power there also lies a weakness, because to be effective, natural selection has two significant requirements: a strict generational continuity in population lineages and an immediate individual advantage, however slight, that can slowly enhance the frequency of a variant in a population. No interaction between different species is possible:

> Natural selection cannot possibly produce any modification in a species exclusively for the good of another species; though throughout nature one species incessantly takes advantage of, and profits by, the structures of others. . . . If it could be proved that any part of the structure of any one species had been formed for the exclusive good of another species, it would annihilate my theory, for such could not have been produced through natural selection. (*On the Origin of Species*, sixth edition 1872, Chap. 6, p. 162, www.darwinonline.edu)

Darwin's risky prediction ('if it could be proved that. . .') is that natural selection promotes only individual advantage:

> Natural selection will never produce in a being any structure more injurious than beneficial to that being, for natural selection acts solely by and for the good of each. . . . If a fair balance be struck between the good and evil caused by each part, each will be found on the whole advantageous. (ibid., pp. 162–163)

But it is equally evident that animal, and especially human, behaviours are frequently unselfish, occasionally threatening the life of the individual, and cooperation is widely recognized as a powerful evolutionary strategy.[1] Following Darwin, when they are fixed in populations and well established, such behaviours can be easily understood in the light of natural selection, with concurrent individual and group advantages, as in cases of cooperation in hunting, mutualism, or defensive alliance. But it is more difficult, both theoretically and historically, to explain the origin of purely altruistic behaviours, because they simultaneously produce a disadvantage for the altruist and an indirect advantage for the selfish, who exploit the actions of the altruists without costs to themselves. So we must ask the following questions: what triggers unselfish behaviours? Why do egotists not prevail immediately, forestalling any 'experiment' of social cooperation and reciprocity? Let us listen to Darwin again, here discussing the case of the evolution of sterile castes in ants and bees:

> Hence I can see no great difficulty in any character becoming correlated with the sterile condition of certain members of insect-communities: the difficulty lies in understanding how such correlated modifications of structure could have been slowly accumulated by natural selection. (ibid., Chap. 8, p. 230)

This paradox seems to need solution at several levels. A logic of individuals is no longer enough:

> This difficulty, though appearing insuperable, is lessened, or, as I believe, disappears, when it is remembered that selection may be applied to the family, as well as to the individual, and may thus gain the desired end. (p. 230)

But how, precisely, can selection be applied to families or the group? Darwin's central dependence here is upon the concept of 'instinct', developing through natural selection from the very simple to the highly complex. Darwin is saying that the foundation of moral qualities and sociality lies in social instincts, including the family ties, love, and emotions of sympathy. In his concluding remarks to *The Descent of Man*, Darwin writes that 'Animals endowed with the social instincts take pleasure in one another's company, warn one another of danger, defend and aid one another in many ways'. Nevertheless, 'these instincts do not extend to all the individuals of the species, but only to those of the same community. As they are highly beneficial to the species, they have in all probability been acquired through natural selection'. (p. 610, on-line edition).

A benefit for the species is taken for granted, but nothing is said about how such behaviours originated in the first cooperators: 'Social animals are impelled partly by a wish to aid the members of their community in a general manner but more commonly to perform certain definite actions'. Rapidly, Darwin's discussion about sociality moves on to the human species, which has few or no special instincts about sociality (which is rooted anyway in the greatest-happiness principle and

---

[1] In the XIX century debate about the priority of the common ancestorship and the degree of relatedness between man and gorillas and between man and chimpanzees, Darwin – in this case against the opinion of T.H. Huxley – argued that chimpanzees, rather than gorillas, would have probably been closer to humans because of their more developed feelings of sympathy and love, the instincts of cooperation at the base of human sociality as well. See *The Descent of Man*, first part.

in emotive sympathy, 'strengthened by exercise or habit'), and which can express desires by words and reasoning power, no longer constrained by blind instinctive impulses but influenced by the praise or blame of one's fellows: 'and then the self-regarding virtues come within the scope of public opinion, and receive praise, and their opposites blame'. (p. 611)

Quite surprisingly, Darwin eventually finds adaptive power in sociality, not between individuals but between groups and human 'tribes':

> It must not be forgotten that although a high standard of morality gives but a slight or no advantage to each individual man and his children over the other men of the same tribe, yet that an advancement in the standard of morality and an increase in the number of well-endowed men will certainly give an immense advantage to one tribe over another. (p. 166, on line edition)

Tribes of altruists are much stronger in the struggle for life, so this is natural selection after all:

> There can be no doubt that a tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity, obedience, courage, and sympathy, were always ready to give aid to each other and to sacrifice themselves for the common good, would be victorious over most other tribes; and this would be natural selection. (ibid.)

In the end, when human instinctual sociality evolves in 'the highest part of man's nature', the struggle for existence, and natural selection, lose their agency:

> The moral qualities are advanced, either directly or indirectly, much more through the effects of habit, the reasoning powers, instruction, religion, &c., than through natural selection. (p. 618)

In sum, for the purposes of this chapter, we can represent Darwin's legacy by citing the following three points:

(1) He presents a conceptual frame for the evolutionary explanation of unselfish behaviours and sociality through a plurality of integrated factors and patterns, including standard natural selection among individuals, natural selection between families or 'tribes', and later habits of learning and culture.
(2) Altruism is selective in origin; it is a good strategy for groups or tribes against others; In this way, Darwin attributes to altruism a substantially 'defensive' function; but, if this is true, altruism and cooperation *inside* the community would necessarily have their counterpart in hostility towards *outsiders.*
(3) The evolution of the 'highest part of man's nature' suggests that the reasoning power of humans can deny one side or the other of the paradoxical human ambiguity between high cooperation and of warfare, and it also suggests that in the human cultural and symbolic niches, previous adaptations can assume completely new functions.

Yet, the origin of unselfish behaviours in individual organisms, and the relationships between individual and group benefit, still needs clarification.

## The Hardening of a Genetic Cost–Benefit Paradigm and the Unresolved Theme of Population Structure

With the ‘genetical theory of natural selection’ (Fisher, 1930) and the study of the genetic components of animal behaviour (Mayr, 1961; Tinbergen, 1963), the paradox of altruism assumed a new, more radical aspect, due to the fact that – in the mathematical and quantitative models of population genetics – the fitness of the individual precedes, and prevails over, any incidental advantages of species, families or tribes. If generous individuals neglect their direct interests, and thus have a lower reproductive fitness while the egoists on the contrary give up nothing, why are unselfish behaviours tolerated by natural selection?

Even if altruism is satisfying for the individual, it should be overwhelmed generation by generation, ultimately leaving no traces.[2] Altruism thus seems really improbable from a strongly selective and individual point of view, as well as from a gradualist and functionalist one. Nevertheless, we know that altruism, cooperation and sociality are widely diffused and successful evolutionary strategies’, and in many species, humans included, we see clear neurological and hormonal traits that reinforce pro-social behaviours.

But the mere presence today of physiological conditions enabling cooperation (‘proximate causes’) tells only half the story. We need also to understand the evolutionary ‘remote causes’ of the emergence of these behaviours (Mayr, 1961; Sterelny and Griffiths, 1999). In the history of biological and ethological thought of the twentieth Century, the following two main answers were provided:

(a) The paradox does not actually exist because altruism is not an evolutionary reality: it is an indirect and sophisticated kind of selfishness, and there are in fact no pure acts of altruism in nature.
(b) The paradox is a trade-off: altruism is an evolutionary reality, but it is also consistent, at a different level, with the basic selfish evolutionary logic of neo-Darwinism.

As we embark on the twenty-first century, a third solution is being crystallized, aiming not at the paradox itself, but at the background theoretical conditions that lie behind it.

The framework for the first solution recalls the work of J. B. S. Haldane, Ronald A. Fisher and Sewall Wright. In 1930, Fisher noted that a gene for a trait that is disadvantageous for the individual but useful for the group (such as a bad taste of an insect against its predators) could evolve only in populations where many others have the same gene for being disgusting. Otherwise, the sacrifice of the individual would be useless. This is possible in groups of organisms both closely related

---

[2] “If natural selection followed the classical models exclusively, species would not show any behaviour more positively social than the coming together of the sexes and the parental cares” (Hamilton, 1996, p. 31).

to each other and gregarious. The gene of the insect eaten will diffuse copies of itself through the survival of the others. But the problem of the ‘internal overthrow’ remains unsolved: a gene for the direct defence of the individual against predators would be much more effective, no matter what the fate of the others.

Haldane (1932) proposed a model of diffusion of unselfish genes where the lower reproductive fitness of the altruist is balanced by advantages given conferred by the presence of a high proportion of altruists in a small population. According to Haldane and Wright, the accumulation of a random mutation in a small number of individuals with a high level of inbreeding could allow the allele conferring altruism to spread rapidly, despite being detrimental to individual reproductive fitness. However, this advantage might still be subverted by a subgroup of aggressive egotists with a double advantage to their strategy. At that point, altruism and cooperation could survive only through a ‘trick’ whereby the population splits into different isolated groups, some composed by egoists and some not, with the second ones having a selective advantage over the first ones (Wright, 1945; see also Wilson and Sober, 1994).

In 1955, Haldane added another possible reason for the evolution of apparently unselfish genes: he calculated costs and benefits of altruistic acts in a population where all members are closely related. If selfishness acts in favour of relatives, then the genetic fitness (not the reproductive fitness) of the altruist could increase because the individual loses its genes but enhances the genes shared with relatives. A brilliant solution at a first glance: altruism is useful if the individual saves more than two sons, or four nephews, or eight cousins, and so on. However, since animals cannot measure their kinships, natural selection favours these behaviours only in small populations of individuals that are all closely related. Altruism is a kind of indirect genetic egotism (Haldane, 1955).

William D. Hamilton formalized this model of exclusive individual advantage in 1962 and 1964, including a possible solution for the initial diffusion of the ‘gene for altruism’ in populations of egotists, in order to explain eusociality in social hymenopterans. The central idea is that altruistic behaviour is a good strategy for the individual whenever group members around are closely genetically related, apart from their behaviours. If they are related sufficiently to altruistic me, then they will surely have alleles for altruism, so my altruism will have an ‘inclusive fitness effect’ on others in my social environment, and, as a result, the alleles for altruism will spread. The individual confers its fitness on relatives, producing a greater ‘inclusive fitness’ (that is, the contribution to the part of alleles shared with others, a measure of the fitness of relatives)[3]: but if the social environment is in fact predominantly composed by egotists, my altruistic genotype will be rapidly ‘diluted’. In Hamilton’s view, Haldane’s condition of small populations is no longer necessary.

If an individual gains an increment in individual fitness, and the sum of the effects on members of the social group is positive as well, we have mutualism. If the subject

---

[3] Inclusive fitness is not the sum of the direct individual fitness and the fitness of relatives (Grafen, 1982).

gains in fitness without affecting the fitness of others, we have selfishness between relatives or non-kin. Altruism is possible, on the other hand, only if the inclusive fitness is decisively higher than the contingent loss of individual fitness. Natural selection acts on animal behaviour accounting for the presence of relatives: they bear my genes, so it is a good strategy for me to be unselfish towards them ('kin selection' to use the terminology of John Maynard Smith in 1964). Altruism would be an unconscious calculation of individual genetic interests,[4] but the possibility of explaining it without a consideration of the population structure of a species (e.g. in its division into many little isolated populations, as proposed by Wright) remains controversial.

It is possible to distinguish the following three clear methodological and epistemological assumptions of this approach:

(1) Individual reproductive interest has priority with respect to ecological survival ('interactors' are just means for the maximization of the interests of 'replicators').
(2) From the Darwinian organism, we move to the gene and genetic lineages as the central units of selection (relatives are bearers of percentages of shared alleles according to a correlation of kinship).
(3) The logic of evolution follows a genetic instrumental and economical rationality based on cost/benefit.

## Genes in Conflict or 'Parochial Altruism'?

When John Maynard Smith (1964, 1976) refuted the strong version of 'intergroup selection' in the evolution of social systems proposed in 1963 by Vero C. Wynne-Edwards, introducing the term 'kin selection' in the process, an interesting weak version of 'group selection' entered the debate and refreshed the old Darwinian intuition. According to the 'group selection' hypothesis, a gene advantageous for the group could succeed even if it were disadvantageous for the individual. A population of altruists has an independent higher fitness, and the internal growth of selfish subgroups is counterbalanced by the expansion of the group due to unselfishness. Let us see how.

Wynne-Edwards' ethological and biogeographical studies led him to believe that social animals are able to check both the dimensions and the ecological impact of their group. They manage the distribution of territories and control the density of population, maintaining its environmental sustainability like a homeostatic system. Since each group is a small society competing with others, organisms are not programmed for maximizing their individual interests but the interests of their society (Wynne-Edwards, 1986).

---

[4] Edward O. Wilson dates his "paradigm shift" towards Hamilton's approach at the spring of 1965 (Wilson, 1994, pp. 319–320).

This ‘strong’ version of group selection, based on spontaneous mechanisms of self-regulation that damages the interests of individuals, presented both theoretical and experimental problems, as Maynard Smith soon remarked. Study of the ‘regulation of numbers’ in biological populations had a long history, beginning with the Malthusian influence on Darwin’s idea of ‘struggle for existence’, and passing through Carr-Saunders’ ‘principle of optimal number’ (1922). And while in the Darwinian tradition the solution for the overgrowth of populations is natural selection between individuals, in Wynne-Edwards it is the sacrifice of individuals due to the capacity of self-control of the group.

However, Maynard Smith, and later Hamilton, easily showed how the behaviours advantageous for society cited by Wynne-Edwards could be traced back to the effects, in terms of costs–benefits, of standard natural selection between individuals – and even of balances between aggressive behaviours. No ‘laws of the group’, or sacrifices for the group, were needed. According to Maynard Smith, strategies of aggression/expansion vs. sociality/regulation are mixed up in any population (or even individual) at any one time, in an ongoing dynamic equilibrium depending on the frequency of one strategy with respect to the other. There is a plurality of ‘evolutionary stable strategies’, with a weaving of variables playing their role in animal behaviours; but in the end ‘genes are always in conflict’, through the different strategies of their bearers, even inside genomes and between parents and offspring.

Nevertheless, even if we do not need group selection to explain the natural management of resources and territories in biological populations, Maynard Smith noted that altruism remained the big issue to explain from the point of view of the maximization of individual performances. So, in his artificial ‘mouse of the haystacks’ model, he stressed a kind of kin selection where many competing groups of altruists and egotists (able to recognize themselves as separate) are involved in the evolution of apparent unselfishness, as in Sewall Wright’s idea of a species composed by many little isolated populations, and in George and Doris Williams’ model of altruism (1957) where a marginal consideration is given to competition between groups of donors and of non-donors.

Yet, as Elliott Sober and David Sloan Wilson noted in *Unto Others* (1998), it seems that some focus on ‘groups’ as independent entities are needed, even in models of social behaviour like those of Wright, Haldane, Williams and Maynard Smith.[5] Competitions between groups of cooperators and of egotists produce a differential survival (of groups and therefore of individuals). Groups where unselfishness is dominant are more efficient, united and stronger against enemies. In Hamilton’s later models, when competition between groups is diminishing, the frequency of alleles disadvantageous for individuals tends to be reduced: altruism

---

[5] Most of them, and Hamilton specifically, were nevertheless suspicious about the possibility that such ecological systems could really exist, maintaining a high degree (but not too high) of isolation, a low degree of migrations and flows of individuals between groups, high variability between groups, therefore strong systems of recognition and separation between egoists and altruists: features not necessarily adaptive and eventually an handicap for the range of choice of partners, degree of inbreeding, etc. So, the role of group selection remains hypothetical (Hamilton, 1996).

needs a degree of competition between groups. We could name this kind of process a ‘weak version’ of group selection because it does not need a problematic self-discipline among animals as Wynne-Edwards’ model requires. With respect to the three methodological and epistemological assumptions proposed at the end of point 2, the weak version of group selection does not either refuse or confute any of them. In all cases, social qualities depend on the success of some genes that individuals or groups bear.

But what is interesting in this model from the point of view of the philosophy of biology is that altruism seems founded on conflict between groups, and the exclusion of outsiders. As in Darwin’ tribes, the ultimate selective criterion is efficiency in the struggle for existence among groups. Quite evidently, both kin selection and the soft version of group selection, attempting to explain sociality by natural selection (at different levels), assume that conflict and warfare among humans are the complementary expression of underlying behaviours toward strangers and non-relatives.

As Samuel Bowles (2008) pointed out in *Nature*, presenting the results of his simulations of game theory, conflict is ‘altruism’s midwife’: ‘Generosity and solidarity towards one’s own may have emerged only in combination with hostility towards outsiders’; in other words, this crucial ambiguity is historically rooted in human sociality, much more than happens in other primates. When they occur separately altruism and parochialism produce selective disadvantages; but they could have acted synergistically in human evolution, at the level of selection between groups competing for resources, to confer better reproductive fitness (especially in periods of intense environmental stress) upon groups with the most ‘parochial altruists’.

## Toward Humans: Something Breaks the Logic

As a result of these considerations we might say that when we try to explain the biology of sociality we find an unexpected theoretical continuity between models based on inclusive fitness and on group selection. This was the later aim of Hamilton himself when, adopting the mathematical notation proposed by George Price in 1975, he advanced an allegedly integrated model for selection involving both selfish benefit and, given some special conditions in the structure of population, selection between groups. In the second case, the model showed how altruism might evolve. Similarly, Edward O. Wilson, father of sociobiology (Wilson, 1975), and his colleague David Sloan Wilson proposed a theory where selection acts at ‘multiple levels’ and upon different ‘units’ (Wilson and Wilson, 2007). Apart from the proclaimed ‘conversion’ of the influential E. O. Wilson to group selection, there are no new ideas here (Lewontin, 1970; Keller, 1999; Gould and Lloyd, 1999; Okasha, 2006) and the paper does not deliver quite what it promises. Instead, it is a manifesto for the diffuse role of group selection in evolution. It distinguishes between ‘intrademic selection’ (inside the same population) and ‘trait-group selection’ (the evolution of the traits in a group) but without distinguishing between individual and social advantage or specifying how the two might interact. A simple individual–group dualism thus pervades the paper, despite the ‘multilevel’ theory promised in its title. Just as Hamilton considered inclusive fitness a more general model that includes group selection as a special case, Wilson and Wilson seem to incorporate kin selection as a special case of group selection. The difference lies in the explanatory ‘weight’ given to lower levels by Hamilton and to higher ones by Wilson and Wilson: it is not a matter of alternative and incompatible explanations. So leaving aside ‘strong’ versions of selection based purely on ‘selfish genes’, available hypotheses concerning the central role of cooperation and altruism in primate and human life are reduced to competition arguments, at different levels of selection.

Yet it would be much more interesting to understand the relationship between the ‘two selective forces’ of Hamilton. Are they coherent or antagonistic? Does group selection apply only to weak altruism (or cooperation, where the unselfish act has some social compensation via reciprocity) or also to strong and free altruism (when donor has no advantage at all, in a free and unconditioned act of generosity)? What degree of genetic correlation inside a group is needed for group selection? What about unselfishness in larger groups of non-relatives? What about free altruism without any reciprocity perceptible by the individual? What about acts of empathy and altruism between members of different species? What about altruism in species with social learning and cultural evolution? None of these questions is properly broached by the Wilson and Wilson approach.

At this point in many contemporary papers, even in strongly theoretical contributions such as Bowles (2008) and in those involving strongly biological hypotheses about social behaviours in animals, we typically read a ritual recitation about a theoretical ‘gap’. Usually the arguments are as follows: biology in humans is not fate; we are cultural animals; there is no linear genetic determination of complex social behaviours such as altruism; human plasticity has no equivalent; interactions between genes, individuals and cultures have completely different qualitative patterns; instincts are much less compulsory in human species; we are free to choose our social behaviours following a multiplicity of developmental, cultural and educational factors.

Of course, there is a lot of truth in these considerations, and this is the context in which an updated and non-simplistic evolutionary biology of sociality is desperately needed. Today’s primates are not our direct ancestors but cousins of different degrees, and millions of years of separate evolution in heterogeneous ecological niches make our natural histories divergent. Clearly we are special: we not only have ideas of altruism and justice and the rational dream of universal human rights but also the possibility of being freely evil without any advantage (the non-adaptive ‘spite’ strategy in Hamilton: damaging others without any advantage to the damager, something similar to stupidity for free). Nevertheless, a simple argument of ‘discontinuity’ does little to help us explain the unusual human condition. Human beings are both hugely different from other primates and show interesting behavioural analogies or even homologies with them (Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 2005), but continuities should be discernible even considering the uniqueness of our species.

So, beyond reductionist notions of 'imperialist' colonization by genetic benefits (Dupré, 2001), we need some bridges to approach our status as a cultural animal. It is one thing to say that our animal instincts, or emotional attitudes, or cognitive limits, are 'vestigia' of a deep and distant evolutionary past; it is entirely another to claim that natural 'precursors' were already present but were at different times co-opted for new uses in new ecological niches. In the first case, our evolutionary nature is seen as passive inertia; in the other it appears as a still-active constraint, one that we should be aware of even if it is now useless or has been co-opted for different functions. This, surely is where we will find those bridges.

Firstly, we can look for bridges in recent experimental approaches. The package of kin selection plus sexual selection plus 'tit-for-tat' cooperation plus punishment for free riders might be a good place to start explaining (with some case-by-case reservations) such things as eusociality in insects, opportunistic cooperation (for hunting), mutualism, parasitism, commensalism, reciprocal altruism between non-relatives and other classic convergences of reciprocal genetic 'interest'. But what about the origins (not only the usefulness) of endosymbiosis, indirect reciprocity, sexual behaviours without reproductive interest, free altruism among unrelated strangers, cooperation without reciprocity, even between different species? Something here breaks the selective logic of the exchange, and it needs a satisfying evolutionary explanation because such cases are being documented in nature with increasing frequency.

The function of widespread cooperation as defence against predators, instead for the promotion of more coordinated and aggressive hunting, is one of the bridges between the social behaviours seen among living primates and the hypothetical social behaviours in groups of our hominid ancestors (Hart and Sussman, 2009). The range of behaviours that does not conform with models of mere kin selection is expanding (Clutton-Brock, 2002). While in some cases still debated, empirical clues are accumulating from behavioural comparisons that social animals empathetically react to the emotions of others (De Waal, 2006, 2008). We know cases of repulsion at the suffering of others, leading to self-sacrifice even where individual advantage in such suffering can be seen, and there are cases too of inter-specific empathy. Tomasello et al. have, for example, documented cases of spontaneous altruism and unconditioned assistance in chimps (Warneken et al., 2007). Since 1996 (de Waal, 2007), we have seen consolation of the defeated after conflict, and altruism toward strangers. Seyfarth and Cheney (1984) in vervets, and de Waal (1997) in chimps, have documented gratitude for grooming, implying reciprocal altruism and relational memory. Brosnan and de Waal (2003) have even hypothesized a sense of justice, or at least a reaction against inequity in exchanges without expectation of reward, in capuchin monkeys. According to Marc Bekoff and Jessica Pierce (2009), animals of a wide range of social-living species show clear signs of emotive and 'moral' intelligence in a set of behaviours including fairness, trust, reciprocity and a 'wild justice'.

Such cases impressively remind us of Darwin's anecdotes, in *The Descent of Man*, about acts of altruistic heroism in little monkeys and baboons, which he saw as deeply rooted evolutionary bases of our moral qualities and sociality. Nevertheless, so far the argument still seems based on a shifting of explanatory weight: at one end of the spectrum envisaged by the 'competitive paradigm', cooperation and altruism are the widespread norm of behaviour in primate and human life, while at the other end, violence and aggressiveness are tolerated exceptions. But does this truly change our evolutionary hypotheses about the nature of social life? If it does not, then maybe we need something more than experimental bridges. We need new theoretical bridges, resting on an 'extended theory of evolution' in progress (Pigliucci and Kaplan, 2006; Pigliucci and Müller, 2010).

Indeed, it is fair to suppose in all these cases that the assumed immediate individual benefit of the cooperative behaviour (e.g. reducing stress, promoting social conformity) must coincide with an evolutionary benefit for the group. This also applies to the origin of the behaviour concerned, as it must to all coordinated behaviours and alliance formations for an immediate end: collective actions are a low-cost behavior, and this offers an evolutionary insight about the beginning of any behavioral trait.

Thus it is the logic itself of our evolutionary explanations that needs to be extended: this is not only a matter of 'interactors' belonging to genetic pools but also a matter of the economy of survival, immediate physical benefits, responses to contingent conditions in the surrounding ecological systems, the ability to learn new behaviours, phenotypic and behavioural plasticity and the flexibility of social patterns of interactions – all of them macro-evolutionary independent factors in a hierarchy of evolutionary levels (Eldredge, 1985, 1995, 1999; Gould, 2002).

## Unselfish Behaviour as Exaptation in Group-Living Animals: Why Hypotheses Based on Cooperation and Altruism are Not Completely Reducible to Competition Arguments

So far we have developed mostly a theoretical bridge, dealing with the 'adaptationist' posture of many evolutionary explanations of human behaviours and sociality. One of the major difficulties in selectionist reasoning lies in the need to justify the adaptive value of intermediate structures: what can you do with half an eye or with incipient mimicry? Darwin had already sensed that there could not be a 'teleological deployment' of an organism towards perfection in the construction of its organs. In the chapter of sixth edition of the *Origin* dedicated to 'difficulties' with the theory of evolution, he advanced the hypothesis of the functional shift: a rough model of an eye is not used to see with but for a 'pre-adaptive' function that is later modified. An incipient wing, an early form of mimicry or parts of the organism selected for a certain ancestral function could then have been 're-adapted' opportunistically for new functions. Something similar could happen in the evolution of animal behaviours, like in Darwin's hypothesis of parental and filial affections 'extended' to pro-social general feelings.

The Darwinian intuition – which later faded into the background because of the strict adaptationist posture at the core of the 'evolutionary synthesis' – was that a continuity of morphological transformation by natural selection did not necessarily correspond to a progressive continuity in function. Natural selection frequently results in 'contrivances', and sometimes in oddities because it uses the available material that carries historical and 'architectural' (structural) constraints. In a seminal essay of 1982, palaeontologists Stephen J. Gould and Elisabeth S. Vrba described the ensemble of currently useful characteristics as 'aptations', allowing for the identification of subsets of characteristics that were shaped for one specific reason yet available to selection for another function in different circumstances (Gould and Vrba, 1982; Gould, 1993). The hypothesis was that not all cases of similar structure should be considered as 'adaptation for' one specific function. Rather, we should speak of 'exaptation' (apted 'from' the structure) in all those cases where there is co-optation, for new functions, of structures employed in the past for something else.

Exaptation is thus the 'effect' (in the sense of Williams, 1966) of something evolved for other reasons and does not lead to the negation of adaptation as an evolutionary reality. Rather, it redefines and integrates the concept of adaptation. Feathers, used today (though not always) for flying, were initially selected for purposes of thermoregulation or sexual selection. Evolutionary outcomes appear in this perspective as the unforeseeable results of secondary and sub-optimal adaptations: the product of an opportunistic tinkering often due to trade-offs between genetic and ontogenetic constraints and environmental possibilities. The present perceived adaptive reason of a structure or behaviour does not imply that the structure concerned has been built selectively for that use: an organ's *current usefulness* and its *historical origin* should be seen as possibly separate; to infer the second from the first could often be a mistake.

More importantly with exaptation we understand that natural selection is not a force freely acting on organisms but a force acting in a context of constraints. Furthermore, the available material used by natural selection might have had a functional origin (as in pre-adapted structures or vestigia, standard Darwinian processes) but not necessarily; it could also have had a structural, neutral, non-selective or non-adaptive origin (as in Gould's metaphor of architectural 'spandrels'; see Gould, 2002).[6] The disjunctive rationality of some modern biology, habitually separating inside from outside, organism from environment, activity from passivity, replicators from interactors, seems to be checkmated by the development of a kind of evolutionary approach in which natural history appears like co-evolution amongst organisms and environments (Odling-Smee et al., 2003): a weaving of interactions among plastic systems, an opportunistic and creative tinkering reorganizing available materials.

---

[6] The explanatory role of the processes of exaptation is growing in recent literature of many evolutionary fields. Pre-adaptations and spandrels could be involved in the evolution of language according to Hauser, Chomsky and Fitch (2002), and more recently according to Lieberman (2006). Even some of the most important current faculties of the human brain, like reading, seem to be functional cooptations of evolutionarily older brain circuits, as in the interesting evolutionary reconstruction proposed by Stanislas Dehaene (2009).

Apart from other epistemological and experimental weaknesses (Buller, 2005; Richardson, 2007), this seems the major focus of dissatisfaction over the 'just so stories' of evolutionary psychology, the heir presumptive, with some non-crucial differences, of sociobiology. Criticism of the adaptationist programme, anticipated in an essay by Gould and Richard Lewontin more than 30 years ago (Gould and Lewontin, 1979), has focused on two epistemological proposals: (1) to demonstrate that a pan-adaptive problem-solving approach cannot be imputed to Darwin and (2) to outline an 'extended taxonomy' of adaptive phenomena, in which the general class of evolutionary innovations (*aptations*) includes neutral introductions (by genetic drift), *exaptation*s and standard *adaptations*.

What is most interesting today is that, while adaptationist explanations are waning in general evolutionary biology because of their frustratingly limited explanatory power, they are still adopted, and publicized by the mass media, in a ubiquitous 'pop evolutionary psychology'. The evolution of human sociality thus seems to be the last territory where a 'stereotyped Darwinism' reigns almost undisputed. This approach almost invariably involves the following: division of the object of study into discrete traits, the assumption of a linear association between each trait and one genetic codification, a speculative reconstruction of adaptive stories starting in mythical and stable 'ancestral adaptive environments' and the strong preference for a competitive paradigm of interpretation of any evolutionary phenomenon.

In 1986, in a second paper about exaptation, Gould and Vrba extended the idea of functional cooptation to 'spandrels' that pass through the different levels of an evolutionary 'hierarchy' composed of genes, organisms and groups: a trait recognized at one level could become an exaptation or indirect 'effect' at another level (cross-level spandrels; see Vrba and Gould, 1986). A random mutation at the level of the genes becomes an exaptation at the level of organism. Adaptations at the level of organisms could have consequences on the capability of a species to evolve or to resist extinction. This concept of exaptation is now crucial in Evolutionary Developmental Biology (Evo-Devo), for understanding the functional cooptation of regulatory genes, the role of epigenetic processes and the different utilization and regulation of the same structural information (Jacob, 1981), and is also extensively used in the field of human evolution as well (Tattersall, 1998, 2002; Pievani 2003a, b; Pievani and Serrelli, 2011).

Furthermore, with exaptation major transitions, for example in human behaviours, do not imply either discontinuities or hypotheses about cultural evolution as something completely new and disobedient of biological interests (as in the case of the 'just so memetic stories', where memes start an independent and divergent evolutionary path). What we call the Palaeolithic 'Revolution' might well have been a crucial event of exaptation of mental and linguistic faculties, potentially already present and triggered by an ecological opportunity or a cultural advancement (Tattersall, 1998, 2002). A new process of 'niche construction' began, ultimately leading toward our unusual symbolic and cognitive niche, and many abilities of our brain are clearly 'exapted'. In this way, our current behaviours could have *originated* as collateral effects of ancestral adaptive constraints but then sporadically exapted for new functions – even in radically new frames of selective or cultural pressures.

We should, then, explore the possibility that human cooperation and free altruism could have had ancient natural precursors (not vestigia) in such characteristics as empathy, refusal of someone else's suffering, reciprocity. They could then have been retained by various hominid precursors as predator-protection mechanisms, in tribes of gatherers who were frequently victims of predators. Subsequently, this deeply rooted attitude was exapted in several different ways: firstly in the transition of later species of genus *Homo* to better articulated practices of organized hunting; then in the Palaeolithic transition to cognitively modern humans. Here we see the exaptation of altruism and human sociality from a defensive adaptation to a successful model of social organization with division of the work and new forms of exploitation of ecosystems (including big-game hunting). Though repeatedly exapted, these behaviours maintained their relationship with their natural precursors, which is why in various non-human animals we see echoes of them, and they appear to peep out as emotional and apparently instinctual attitudes in current cultural contexts that have nothing to do with its evolutionary history.

With exaptation, we also better understand a neglected claim by Darwin that could be crucial for the understanding of the evolution of altruism and cooperation. That is natural selection does not aim at perfection or optimization but at contingent survival. It tinkers with structural constraints of the moment, as a bricoleur more than an engineer. Even the optimal use of resources in an ecosystem and the best exploitation of evolutionary potential are not necessary results of natural selection: something that is also clearly true for our ambiguous and contradictory behaviours of former preyed-upon and predators at the same time. The exaptive idea is that the selective criterion of greater efficiency in the struggle for existence between groups was not the ultimate stimulus for the way we are but quite possibly the initial one. In the evolution of social animals, the effects of competition among individuals, constrained by an instinctive solidarity towards one's own, and suspicion towards strangers, have gradually receded in importance even as competition among groups has become more intense.

This provided evolutionary advantage for cooperators. Practices that suppressed the stress of direct conflicts inside the group (avoidance, toleration, negotiation, and so on) evolved, while individuals shared growing levels of reproductive (and cultural) success with other members of the same group. With social protections against exploitation by egotist free-riders, altruism became not only a possible social strategy but also an advantageous one, both inside the group and against other groups. Cultural evolution, language and learning radically renewed our social niches, and the legacy of this ambiguous disposition, both inside the group and among them, was 'exapted' for completely new functions.

There are, then, three interesting theoretical advantages[7] to an 'exaptive' hypothesis about the evolution of cooperation in animals and humans and are as follows:

---

[7] Criticisms about the alleged irrelevant role of exaptation, or its reducibility to normal adaptation – advanced among others by Dawkins (1986) and Dennett (1995) – seem solved in Arnold (1994) and Gould (2002).

1. It does not see a conflict between selection for the individual survival or genetic benefit and the benefit of the group; this is consistent with both standard natural selection and the weak version of group selection: an adaptation, or a neutral non-aptation, at the individual level could become an exaptation at the group level (Gould's 'cross-level spandrels', 2002).
2. It is consistent with a 'hierarchical' or 'multilevel' theory of evolution, where a plurality of factors, organized in two inclusive hierarchies, genetic and ecological, interact both inside each hierarchy and between hierarchies (as in Niles Eldredge's 'sloshing bucket model', Eldredge, 1999). Frequently, as in helping strategies among birds, cases of evident altruism do not match the calculations of kin selection because changing ecological constraints are the chief determinants: ecological survival and genealogical interests must interact and find trade-offs as two independent and inter-dependent logics (Vrba and Eldredge, 1984; Eldredge and Grene, 1992). According to the 'effect hypothesis' proposed by palaeontologist Elisabeth Vrba, an adaptive trait at a lower level could have an alternative 'effect' at a higher level (Vrba, 1983).
3. A series of multiple exaptations could explain the transition between a previously prevailing biological niche (now showing its weaker influences under the skin) and the currently prevailing cultural and symbolic niche in human evolution. This series would have involved trade-offs between opposite behaviours, leading to the current behavioural ambiguities so familiar in human beings. We no longer need a radical discontinuity between our biology and our culture.

This series of advantages has the potential to lead to a truly productive debate among the proponents of three methodological and epistemological assumptions at the end of point 2. This debate can take place in the context of an extended and pluralistic, although still Darwinian, theory of evolution. The multifactorial and integrated approach involved brings together, in a viable and testable way, genealogical, ecological and cultural logics that are not reducible to standard arguments based on competition. This allows us to approach the problem of human behavioural origins without having to adopt 'universal laws' for evolution (as in the universal strong Darwinian 'algorithm'), but instead by seeking at evolutionary law-like 'patterns', that are repeated schemes of regular events (Eldredge, 1999).

## A Final Philosophical Caveat: Avoiding a 'Cooperative Evolutionary Psychology'

Altruism and selfishness both seem equally 'natural', intelligible, products of an evolutionary process. What is more, given the results of human evolution today, they seem both natural and cultural in the same way. They are cultural through nature (a series of exaptations) and natural through culture (in our symbolic niche). But it is clear that emotionally we react poorly to selfishness (at least in others) for its ethical consequences.[8] We do not like to consider that altruism is an advanced form of egotism and that there are no evolutionary foundations for solidarity and reciprocity. In twentieth-century debates about kin selection and group selection, this ethical side of the controversy could not remain hidden, implicit or otherwise. An excessively naturalistic and deterministic approach to human social behaviour seems to threaten the bases of personal responsibility, with the result that a possible ‘biology of generosity’ sounds very attractive.

But the eagerness to preserve a ‘natural’ foundation for the ethics of solidarity could be badly misleading. We saw that even group selection – and the idea that altruism is a real evolutionary possibility rather than an indirect form of selfishness – could have ethically unpleasant consequences: parochialism inside the group and aggressiveness against others in a competitive system. Though for impeccable ethical reasons we might wish to refute a selfishness-oriented paradigm for human behaviour, this would be mistaken – even if we kept firmly in mind that cooperation and altruism are at the core of primate and human life. The ‘exaptive’ interpretation adopted here could avoid this emotional dimension by emphasizing a very different point: the ultimate criterion should be explanatory power, not the possible ethical consequences. Let us look a bit more closely at this final caveat.

Thomas Henry Huxley, ‘Darwin’s bulldog’, was probably wrong to think entirely dualistically in his very effective metaphor for human emergence of the gardener taming the wilderness. He saw that there is a conflict between the gladiatorial biological aspects of the unheeding evolutionary process, ‘red in tooth and claw’, from which we derive and the recently acquired exquisite moral faculties of the educated man. But hewing more closely to Darwin himself, we know that there are strong natural precursors to the attributes of the modern human mind. Morality is an evolved trait, but we also have the power not only to understand biology but also to deny it. Biology is a way to illuminate both the past and the present of our condition within a ‘liberalized’ or ‘pluralistic’ interpretation of naturalism (De Caro and Macarthur, 2004). And understanding our evolutionary history might help us to improve our peaceful and social behaviours, based on our knowledge of the enabling conditions for human sociality.

If we discover that, for the greater part of our evolutionary history, the defence of ourselves and of our families from predators, and not the contrary, has been the main driver of our survival; that sociality and cooperation have had a function connected to avoid predators, and not to the glorious aim of hunting and dominating environments, we will have to change the major paradigm that has dominated our views of our essential selves from the earliest days of paleoanthropology. This paradigm concerns not only the origins of humans as physical beings but also the origins of human mind, most especially in terms of atavistic fears and remaining instincts (Hart and Sussman, 2009). This theoretical change has a *pars destruens*: It enables us to see

---

[8] Williams and Williams (1957), from the point of view of an evolutionary biology of social behaviour based on the exclusive interest of Darwinian selfish individuals, proposed for this reason to use more neutral categories like “donors” and “non donors”.

the fallacy embedded in many of the adaptationist, competitive and gene-centred stereotypes of evolutionary psychology. But it has a much more important *pars construens*: Through its lens, we better understand human evolution, in terms of a plurality of levels and units of selection and in terms of adaptations and exaptations.

Nevertheless, nature is not a norm, even if the norm is cooperation. If we state that we should cooperate because it is more natural to do so, then we are likely to undervalue the multilevel nature of the evolution of human behaviours. Searching in nature for what we ethically hope to find, and replacing a competitive-selfish model with its opposite one just because it is more edifying, is a recipe for misunderstanding the scientific data. In Europe, an influential movement of theologians and philosophers nowadays fashionably disputes the scientific solidity of the neo-Darwinian theory of evolution, asserting that we are moving towards a new, alternative theory based on cooperation, self-organization, complexity and symbiosis. Following this trend, one would be tempted to construct an opposite 'cooperative evolutionary psychology'. But this would leave us vulnerable to the same epistemological fallacies I have already deplored in contemporary 'pop evolutionary psychology'. Reversing competitive evolutionary psychology to its opposite is not enough: we need to oppose its seductive theoretical assumptions.

The 'Man the Hunted' paradigm is 'positive', with respect to the opposite 'Man the Predator' notion, because it offers much more effective and realistic evolutionary explanations (Hart and Sussman, 2009). Without denying that humans are extremely able in warfare, it removes the idea that egotism is natural and cooperation a cultural epiphenomenon. It also eliminates the concept that cooperation and sociality are marginal contingencies that may be explained merely as anomalies tolerated by an alleged 'universal Darwinian algorithm'. And it does away with the idea of a supposed evolutionary determinism of selfishness, frequently used as a support for conservative and class-conscious ways of putting questions in sociological researches and biased questionnaires of evolutionary psychology (Dupré, 2001).

In sum, the approach based on the concept of 'Man the Hunted' opens the possibility that sociality is not only deeply rooted in our entire evolutionary history – genealogical and ecological, natural and cultural, multileveled and 'exaptive' – but has also been a crucial, independent factor for the definition of human species identity. We are born to cooperate as well as to be human.

## References

Arnold, E.N. (1994) Investigating the origins of performance advantage: adaptation, exaptation and lineage effects. In *Phylogenetics and Ecology* (Eggleton P, Vane-Wright R, eds.). pp. 123–168. London, Academic Press.

Barrett, P.H., P.J. Gautrey, S. Herbert, D. Kohn, S. Smith (eds.). (1987) *Charles Darwin's Notebooks – 1836–1844*, British Museum Natural History, Cornell University Press, Ithaca, New York.

Bekoff, M., J. Pierce (2009) *Wild Justice. The Moral Lives of Animals*, The University of Chicago Press, Chicago.

Bowles, S. (2008) Conflict: Altruism's midwife. *Nature*, 456, 326–327.

Boyd, R., P.J. Richerson (2005) *Not by Genes Alone: How Culture Transformed Human Evolution*, The University of Chicago Press, Chicago.

Brosnan, S.F., F.B.M. de Waal (2003) Monkeys reject unequal pay. *Nature*, 425, 297–299.

Buller, D.J. (2005) *Adapting Minds. Evolutionary Psychology and the Persistent Quest for Human Nature*, The MIT Press, Cambridge, MA.

Carr-Saunders, A.M. (1922) *The Population Problem. A Study in Human Evolution*, Clarendon Press, Oxford.

Cavalli-Sforza, L.L., M. Feldman (1981) *Cultural Transmission and Evolution*, Princeton University Press, Princeton, NJ.

Clutton-Brock, T. (2002) Breeding together: Kin Selection and mutualism in cooperative vertebrates. *Science*, 296, 69–72.

Darwin, C., (1836–1882) *The Complete Work on line*, University of Cambridge, UK www.darwinonline.edu

Dawkins, R. (1986) *The Blind Watchmaker*, Longman, London.

De Caro, M., D. Macarthur (eds.). (2004) *Naturalism in Question*, Harvard University Press, Cambridge, MA.

Dehaene, S. (2009) *Reading in the Brain. The Science and Evolution of a Human Invention*, Penguin Viking, New York.

Dennett, D. (1995) *Darwin Dangerous Idea*, Simon and Schuster, New York.

de Waal, F.B.M. (1997) The chimpanzee's service economy: Food for grooming. *Evolution and Human Behavior*, 18, 375–386.

de Waal, F.B.M. (2006) *Primates and Philosophers*, Princeton University Press, Princeton, NJ.

de Waal, F.B.M. (2007) With a little help from a friend. *PLoS Biology*, 5(7), 190.

de Waal, F.B.M. (2008) Putting altruism back into altruism. *Annual Review of Psychology*, 59, 279–300.

Dupré, J. (2001) *Human Nature and the Limits of Science*, Oxford University Press, Oxford.

Eldredge, N. (1985) *Unfinished Synthesis. Biological Hierarchies and Modern Evolutionary Thought*, Columbia University Press, New York.

Eldredge, N. (1995) *Reinventing Darwin*, Wiley, New York.

Eldredge, N. (1999) *The Pattern of Evolution*, Freeman and C., New York.

Eldredge, N., M. Grene (1992) *Interactions. The Biological Context of Social Systems*, Columbia University Press, New York.

Fisher, R.A. (1930) *The Genetical Theory of Natural Selection*, ed. 1958, Dover Publications, New York.

Gould S.J. (1980) *The Panda's Thumb*, Norton and C., New York.

Gould, S.J. (1993) *Eight Little Piggies*, Norton and C., New York.

Gould, S.J. (2002) *The Structure of Evolutionary Theory*, Belknap-Harvard University Press, Cambridge, MA.

Gould, S.J., E. Lloyd (1999) Individuality and adaptation across levels of selection. *PNAS*, 96, 11904–11909.

Gould, S.J., E.S. Vrba (1982) Exaptation, a missing term in the science of form. *Paleobiology*, 8(1), 4–15.

Gould, S.J., R.C. Lewontin (1979) The spandrels of San Marco and the Panglossian Paradigm. A critique of the adaptationist program. *Proceedings of the Royal Society of London*, 205, 581–598.

Grafen, A. (1982) How not to measure inclusive fitness. *Nature*, 298, 425–426.

Haldane, J.B.S. (1932) *The Causes of Evolution*, ed. 1990, Princeton University Press, Princeton, NJ.

Haldane, J.B.S. (1955) Population genetics. *New Biology*, 18, 34–51.

Hamilton, W.D. (1963) The evolution of altruistic behaviour. *The American Naturalist*, 97, 354–356, now also in Hamilton, 1996.

Hamilton, W.D. (1964) The genetical evolution of social behaviour, Part I. *Journal of Theoretical Biology*, 7, 1–16.

Hamilton, W.D. (1970) Selfish and spiteful behaviour in an evolutionary model. *Nature*, 228, 1218–1220, now also in Hamilton, 1996.

Hamilton, W.D. (1996) *Narrow Roads of Gene Land. Evolution of Social Behaviour*, W.H. Freeman, New York.

Hart, D., R.W. Sussman (2009) *Man the Hunted. Primates, Predators, and Human Evolution*, expanded edition, Westview Press, Boulder, CO.

Hauser, M.D., N. Chomsky, W.T. Fitch (2002) The faculty of language: What is it, who has it, and how did it evolve? *Science*, 298, 1569–1579.

Jacob, F. (1981) *Les jeux des possibles*, Seuil, Paris.

Keller, L. (ed.) (1999) *Levels of Selection in Evolution*, Princeton University Press, Princeton, NJ.

Lewontin, R.C. (1970) The units of selection. *Annual Review of Ecology and Systematics*, 1, 1–18.

Lewontin, R.C. (1998) Survival of the nicest? Review, 'Unto Others'. *The New York Review of Books*, Oct. 22nd, pp. 59–63.

Lieberman, P. (2006) *Toward an Evolutionary Biology of Language*, The Belknap Press of Harvard University Press, Cambridge, MA.

Maynard Smith, J. (1964) Group selection and kin selection. *Nature*, 201, 1145–1146.

Maynard Smith, J. (1976) Group selection. *Quarterly Review of Biology*, 51, 277–283.

Mayr, E. (1961) Cause and effect in biology. *Science*, 134, 1501–1506.

Odling-Smee, F.J., K.N. Laland, M.W. Feldman (2003) *Niche Construction. The Neglected Process in Evolution*, Princeton University Press, Princeton, NJ.

Okasha, S. (2006) *Evolution and the Levels of Selection*, Oxford University Press, Oxford.

Pievani, T. (2003a) Rhapsodic evolution: Essay on exaptation and evolutionary pluralism. *World Futures*, 59(2), 63–81.

Pievani, T. (2003b) The contingent subject. A radical theory of emergence in developmental processes. *Journal of European Psychoanalysis*, 17, 35–78.

Pievani, T., E. Serrelli (2011) Exaptation in human evolution: how to test adaptive vs exaptive evolutionary hypotheses. *Journal of Anthropological Sciences*, June 2011, in press.

Pigliucci, M., G.B. Müller (2010) *Evolution: the Extended Synthesis*, MIT Press, Cambridge, MA.

Pigliucci, M., J. Kaplan (2006) *Making Sense of Evolution*, The University of Chicago Press, Chicago.

Richardson, R.C. (2007) *Evolutionary Psychology as Maladapted Psychology*, The MIT Press, Cambridge, MA.

Seyfarth, R.M., D. Cheney (1984) Grooming, alliances and reciprocal altruism in vervet monkeys. *Nature*, 308, 541–443.

Sober, E., D.S. Wilson (1998) *Unto Others. The Evolution and Psychology of Unselfish Behaviour*, Harvard University Press, Cambirdge, MA.

Sterelny, K., P. Griffiths (1999) *Sex and Death. An Introduction to Philosophy of Biology*, The University of Chicago Press, Chicago.

Tattersall, I. (1998) *Becoming Human: Evolution and Human Uniqueness*, Harcourt Brace, New York.

Tattersall, I. (2002) *The Monkey in the Mirror. Essays on the Science of What Makes Us Human*, Harcourt, New York.

Tinbergen, N. (1963) On aims and methods of ethology. *Zeitschrift fir Tierpsychologie*, 20, 410–433.

Vrba, E.S. (1983) Macroevolutionary trends: New perspectives on the roles of adaptation and incidental effect. *Science*, 221(22), 387–389.

Vrba, E.S., N. Eldredge (1984) Individuals, hierarchies and processes: Towards a more complete evolutionary theory. *Paleobiology*, 10, 146–171.

Vrba, E.S., S.J. Gould (1986) The hierarchical expansion of sorting and selection: Sorting and selection cannot be equated. *Paleobiology*, 12(2), 217–228.

Warneken, F., B. Hare, A.P. Melis, D. Hanus, M. Tomasello (2007) Spontaneous altruism by chimpanzees and young children. *PLoS Biology*, 5(7), 184.

Williams, G.C. (1966) *Adaptation and Natural Selection*, Princeton University Press, Princeton, NJ.

Williams, G.C., D.C. Williams (1957) A theory of group selection. *PNAS*, 72, 143–146.

Wilson, D.S., E. Sober (1994) Reintroducing group selection to the human behavioural science. *Behavioural and Brain Sciences*, 4(17), 585–654.

Wilson, D.S., E.O. Wilson (2007) Rethinking the theoretical foundation of sociobiology. *Quarterly Review of Biology*, 4(82), 327–348.

Wilson, E.O. (1975) *Sociobiology. The New Synthesis*, Harvard University Press, Cambridge, MA.

Wilson, E.O. (1994) *Naturalist*, Island Press, Washington, DC.

Wright, S. (1945) Tempo and mode in evolution. A critical review. *Ecology*, 26, 415–419.

Wynne-Edwards, V.C. (1963) Intergroup Selection in the evolution of social systems. *Nature*, 200, 623–626.

Wynne-Edwards, V.C. (1986) *Evolution through Group Selection*, Blackwell Scientific, Oxford.

# Chapter 5
# The Phylogenesis of Human Personality: Identifying the Precursors of Cooperation, Altruism, and Well-Being

**C. Robert Cloninger and Sita Kedia**

## Introduction

Human beings have a natural potential for love and altruism that is expressed when they are functioning in a healthy way. Prosocial behavior is a prominent aspect of health and happiness in human beings, which is characteristic of integrated states of physical, mental, social, and spiritual well-being (Cloninger and Zohar, 2010). From a neuropsychiatric perspective, selfish and uncooperative behaviors are signs of mental dysfunction because they are strongly associated with life dissatisfaction and ill health (Cloninger, 2004). From an evolutionary perspective, antisocial behavior in human beings is the unregulated expression of primitive impulses because it is a consequence of the failure of the human capacity for apperception of unity (Cloninger, 2009).

Because humans retain both primitive and higher cognitive functions, people are capable of either terrifying violence and cruelty (Virkkunen et al., 2007) or peaceful kindness and altruism (Moll et al., 2006). Cooperation or violence may be expressed by different people in the same situation or by the same person in different situations (Fleeson, 2004). Whether people act violently or kindly depends on complex influences on their past personality development, their immediate situation, and their values and aspirations for the future (Cloninger and Svrakic, 1997; Fleeson, 2004).

In order to understand the development and regulation of prosocial and antisocial behavior in individuals, it is essential to understand the complex evolutionary development of cooperation in human beings. A rigorous understanding of personality, like everything else in biology, makes no sense except in the light of evolution (Dobzhansky, 1973). The unity of personality within a person and its diversity among people can only be understood when considered from the perspectives of both ontogeny (Cloninger, 2003) and phylogeny (Cloninger and Gilligan, 1987; Cloninger, 1994).

---

C.R. Cloninger (✉)
Department of Psychiatry, Center for Psychobiology of Personality, Washington University School of Medicine, St. Louis, MO 63110, USA
e-mail: clon@wustl.edu

R.W. Sussman, C.R. Cloninger (eds.), *Origins of Altruism and Cooperation*,
Developments in Primatology: Progress and Prospects 36, DOI 10.1007/978-1-4419-9520-9_5,

Personality is defined as the way people learn, but as simple as that sounds, the processes by which living organisms learn involve complex adaptive systems. The self-organizing unity of an individual's personality must ultimately be understood in its full context, which includes awareness of its sexual, material, emotional, intellectual, and spiritual aspects (Cloninger, 2004). There is widespread agreement among cognitive scientists and psychobiologists that personality is (i) a complex set of abilities or adaptive functions, and (ii) the functions crucial for information processing involve multiple steps including the initial perception of sensory inputs, conceptual processing of percepts, and intuitive synthesis of perceptual and conceptual phenomena in self-aware consciousness, and (iii) that apperception (i.e., the contextual spatio-temporal processing of perceptions in self-awareness) is episodic, intuitive, preverbal, and synthetic. Most neuroscience assumes that there is a universal structure of human brain functions that has a distinct evolutionary history. However, much uncertainty remains about how to specify the complex set of functions that comprise human adaptation, but, as I will describe here, accumulating evidence about human phylogeny may finally fill that gap (Cloninger, 2009).

Abilities that emerge at one point in phylogeny are often co-opted later for more general functions that expand awareness within this hierarchy. For example, complex functional abilities like language have many precursors that emerge before the syntactical functions of modern human language—among them the ability to communicate through expressive gestures, emotional vocalizations, and meaningful signs (Christiansen and Kirby, 2003; Hauser et al., 2002; Pollick and de Waal, 2007; Weiss and Newport, 2006). Hence, modern language is like "a new machine built out of old parts" (Bates and MacWhinney, 1989). Similarly, many animals can cooperate in diverse ways, but there are diverse physical, emotional, intellectual, and transcendental abilities that are needed before altruism (i.e., the intentional practice of disinterested and selfless concern for the well-being of others) is possible.

## The Triune Human Brain

From the evolutionary perspective of comparative neuroanatomy, the human brain is "triune," that is, one whole with three distinct components. MacLean distinguished these components as the "reptilian" brain, the old mammalian brain, and the new mammalian brain of primates (MacLean, 1985). A closely related, but not identical, distinction is between the components of the human brain that regulate the three major systems of learning and memory: behavioral conditioning, semantic learning, and episodic or self-aware learning (Cloninger, 2004, 2009; Tulving, 1987). These perspectives are based on recognition of fully developed brain systems for behavioral conditioning in reptiles and birds, followed by more complex mental processing with differentiation of the neocortex in the forebrain of mammals, and self-awareness in human beings (Cloninger, 2009). These three major systems of learning and memory have distinct properties and can be dissociated experimentally by specific brain lesions (Tulving, 1987, 2001, 2002).

Self-aware consciousness has an objective biological basis and produces observable phenomena, such as autobiographical memories, about which predictions can be made and tested (Levine, 2004; Tulving, 1987, 2002). Self-aware memory matures at about 4 years of age in human children, and it is only after this that human children show much cognitive advantage in development when compared to chimps (Povinelli, 2000; Povinelli and Giambrone, 2001; Tulving, 2001).

## What Evolutionary Transitions Led to Humans?

Elsewhere I have described in detail the timeline of major transitions in brain system structure and function in human evolution (Cloninger, 2009). Here I will only briefly review this and summarize key information in Table 5.1.

All life forms share DNA and its associated cellular apparatus as the mechanism of genetic inheritance going back to the emergence of the first life forms on earth 4 billion years ago. The ancestral lineage leading to humans includes the first eukaryotes, craniates, and amniotes, thereby leading to the common ancestor shared by squamates and mammals. Among mammals, the line probably continues from the earliest non-placental mammals to ancestral tree shrews and then to the proto-primates called plesiadapiforms (see Table 5.1).

Mating behavior is the first brain function to come under neocortical control in mammals, as is colorfully displayed by Echidnas (Rismiller, 1999). During the mating season, echidnas form a train of three to four males (sometimes 2–11) following a single female. The female produces a pheromone that attracts the males. They walk nose to tail in queue for up to 6 weeks before mating. Males may lose up to 25% of their body mass while pursuing the female. Echidnas are highly versatile in mating either above or below ground, indicating intentional regulation of a strong sex drive by the somatosensory (touch) neocortex (Proske et al., 1998; Proske and Gregory, 2003; Kaas, 2008).

The tree shrews are small placental mammals that are known from around 125–65 mya during the Cretaceous when flowering plants were beginning to diversify and dinosaurs were still the dominant land animals. The common ancestor of tree shrews, colugos, and primates diverged before 65 mya from other orders of placental mammals (Murphy et al., 2001; Springer et al., 2003). Modern tree shrews are solitary foragers in pair territories marked by scent (Kawamichi and Kawamichi, 1979; Emmons, 2000). Tree shrews must spend most of their time foraging in order to consume enough arboreal insects to survive (Emmons, 2000). Their young develop rapidly to begin their own solitary foraging. Understanding the behavior of tree shrews is important because, as remote ancestors of all primates, the behavior of ancestral tree shrews can serve as homologues of the functions common to all placental mammals, such as the basic drives for sex and food. In particular, tree shrews provide a model of the common neurobiological mechanisms that produce anxiety, aggression, craving and sensitization to drugs of abuse when confronted by intruders who would compete in foraging for the limited nutrients in their territory

**Table 5.1** Overview of the evolution of major brain functions in human evolution

**Clade 0: Craniates (ancestor of hagfish—505 mya)**

*Emergent Functions*: Animals with skulls, all associated with emergence of the neural crest for development of central nervous system. Also all have ectodermal placodes for development of paired organs for smell, hearing, and vision in the head.

*Emergent Structures*: Neural crest derivatives—skull, brain with five components, and cranial nerves 1–10 (except for eye muscle nerves 3,4,6 which may have been secondarily lost by hagfish). All have peripheral nervous systems, endocrine tissues, in addition to paired organs for smell, hearing, and vision in head. Neuropeptides have important regulatory functions in all craniates (Holmgren and Jensen, 2001) as well as in early invertebrates (Strand, 1999).

**Clade 1a: Early Vertebrates (ancestor of fish, amphibia—480 mya)**

*Emergent Functions*: Fish and amphibia show well-developed associative conditioning. Whole genome duplicated. Amphibia still reproduce in water.

*Emergent Structures*: Fish have a bony vertebral column, fins for locomotion in water, scales, and a two-chambered heart. Fins are adapted for walking on land in lung fish and amphibia. Cranial nerves for eyes (3,4,6) are present typically (Janvier, 1997). Unlike higher vertebrates, the earliest vertebrates (i.e., lampreys) have no myelin sheaths around nerves, so neural responses are slow. In fish and amphibia, cerebral hemispheres are small and mostly concerned with smell. Amphibians were the first vertebrates to develop vocalization, making sounds with their mouth closed. The midbrain is the dominant association center that regulates both sensory input and motor output in fish and amphibians. Midbrain receives nervous input from throughout the body and sends extensive output to other parts of the brain and spinal cord. Midbrain has two large optic lobes for processing visual information. Cerebrum and thalamus in the small forebrain receive sensory input but have no feedback to or control of midbrain.

**Clade 1b: Early Amniotes (ancestor of reptiles and birds—315 mya)**

*Emergent Functions*: Adaptations for tetrapods to live and reproduce on land, breathing oxygen, and amnion to protect developing fetus.

*Emergent Structures*: The hypothalamus in the basal forebrain is enlarged in amniotes compared to anamniotes. The brain of squamates is centrally regulated by the hypothalamus without thalamo-cortical feedback to or control of hypothalamus. The dorsal cortex of squamates is a single layer of pyramidal neurons with connections with the thalamus (Bruce and Neary, 1995; Nieuwenhuys, 1994). The thalamus receives much sensory input and is larger than the midbrain in amniotes. In birds, forebrain control of vision becomes important and smell unimportant, much as it does in primates.

Table 5.1 (continued)

**Clade 2a: Early Mammals (ancestor of non-placental mammals—220 mya)**

*Emergent Functions*: All mammals are warm-blooded, have skin with hair and glands, including milk-producing glands to feed young. The behavior of early mammals is concerned with intentional control of basic impulses of life preservation, such as mating and eating.

*Emergent Structures*: Neocortex emerges with five to six layers as the dominant association center for sensory input and motor output, allowing cortical control of bodily functions integrated by the midbrain of fish and amphibians, including sex, diet, and movement, in a way directed primarily for life preservation. All special senses are represented neocortically, but most of neocortex processes touch with no separate motor areas. Neocortex is the dominant association center for control of sensory input and motor output in all mammals but is not differentiated into sensory and motor regions in non-placental mammals. Hence intention and action are not well-differentiated in non-placental mammals.

**Clade 2b: Placental Mammals (ancestor of tree shrews—125–65 mya)**

*Emergent Functions*: Specialized genital openings and placenta so tree shrews can bear live young. Young develop quickly and require little maternal care, so they can spend most of their time foraging for insects in trees. They have well-developed distance senses and skill in grasping insects but limited ability to digest fruits. They have greater ability to regulate cravings, such as desire for sex or food, than monotremes, and do not reproduce when there is inadequate supply of nutrients for childbearing (Emmons, 2000). Anxiety and impulsive aggression may result when frustrated or threatened by intruders into their territory, which threatens their source of food and self-preservation.

*Emergent Structures*: Somatosensory, motor, and pre-motor areas are differentiated in neocortex of tree shrews. About 20 distinct cortical regions have been identified compared to over 200 in human beings (Kaas, 2008).

**Clade 3a: Proto-primates (ancestor of plesiadapiforms—65–55 mya)**

*Emergent Functions*: Enhanced physical agility to grasp food and digest fruit, and provide extended maternal care of young compared to tree shrews. Eyes still laterally directed.

*Emergent Structures*: Only fossils are extant, but fossils and functions suggest similarity to strepsirhines except eyes are not forward-directed.

**Table 5.1** (continued)

| |
|---|
| **Clade 3b: Strepsirhines (ancestor of lemurs, lorises, bushbabies—47 mya)** |
| *Emergent Functions*: Nocturnal solitary foragers with skill in finding and selecting food. Brain size varies with foraging complexity, flexibility of diet and activity patterns, not social variables. Extensive maternal care provided to young. Teeth are distinctive for highly variable diets of primates. |
| *Emergent Structures*: Taste is processed in primary gustatory cortex prior to hypothalamus and amygdala (frontal operculum and insula) (Verhagen et al., 2004). Eye–hand coordination facilitated by greater topical ordering of inputs to nuclei for hand and foot and expansion of parietal association cortex. Ventromedial hypothalamus has many oxytocin receptors, allowing regulation of feeding behavior in favor of reproductive role. Social bonding and maternal care are regulated by olfactory cues, mediated by oxytocin binding in amygdala, nucleus accumbens, and the olfactory bulb that facilitate preference bonds and scent recognition (Broad et al., 2006). Differentiation of dorsal posterior insular cortex (DPIC) supports awareness of the affective aspects of sensation (Craig, 2005). |
| **Clade 4a: Haplorhines (ancestor of tarsiers and monkeys—40 mya)** |
| *Emergent Functions*: Modern tarsiers are nocturnal or crepuscular in activity but have specializations for day-time activity (fovea and absence of light-reflecting tapetum lucidum in their eyes). Monkeys are diurnal and social with increased metabolic rate able to support larger body and brain. In order to take advantage of warmth and light of day-time activity in a cooling climate, there was increased reliance on visual information accessible at a distance, rather than chemosensory input, even in simians of small size (Broad et al., 2006; Ross, 2000; Ross and Kirk, 2007). Anthropoids have enhanced emotional awareness from adaptation to diurnality, which fostered development of enduring social relationships. Much time in social activities of large groups provides protection from visual predation. Monkeys show cooperative behaviors such as prosocial giving (de Waal et al., 2008) and noncooperation with inequity (Brosnan and De Waal, 2003; Brosnan et al., 2006). |
| *Emergent Structures*: Prefrontal cortex (mainly orbital and medial PFC) expands and projects directly to hypothalamus, thalamus, septum, basal amygdala, and striatum, allowing neocortical control of functions regulated by hypothalamus in basal forebrain of squamates. Olfactory links to social reward centers in amygdala and nucleus accumbens are largely, but not entirely, replaced by PFC inputs concerned with multisensory integration, emotion regulation, and motor sequence planning (Broad et al., 2006). Central integration of sensory and motor functions in the limbic forebrain (hypothalamus and interconnected portions of prefrontal cortex) allows affective regulation of behavior and social interactions. Mirror neuron system appears in monkeys, allowing mirroring of observed behaviors by neurons in speech motor area (BA 44, posterior inferior frontal gyrus), ventral premotor area (VPA), and IPL (BA 40) (Rizzolatti and Craighero, 2004). The VPA supports action understanding and imitation, a precursor to language. In monkeys, multi-modal affective information is also relayed to the middle insular cortex, which has extensive reciprocal connections with the amygdala and hypothalamus, so it is well-positioned for the regulation of sensuality. |

**Table 5.1** (continued)

**Clade 4b: Apes (ancestor of lesser and greater apes—16–4 mya)**

*Emergent Functions*: Highly social, warm emotional expression and affectivity, flexible dominance hierarchies, imitation learning, and proto-cultural transmission of traditions and local conventions (Bonnie et al., 2007; Whiten et al., 2007). Australopithecines emerged about 4 mya and developed skilled bipedal walking (Agnew et al., 1996).

*Emergent Structures*: Somatosensory processing becomes serial and less parallel for greater depth of processing. Differentiation of parietal association cortex for integration of visual, auditory, and somatosensory information. Great apes and humans, and not other primates, have Von Economo Neurons that allow reciprocal connections of AIC and ACC. Mirror neurons are also present in great apes in Broca’s area (BA 44) and IPL. Also in great apes there is differentiation of the anterior insular cortex (AIC) for enhanced emotional awareness, which supports the communication of social emotions in great apes (Craig, 2009).

**Clade 5a: Hominids (ancestor of *H. ergaster*, 1.9–0.8 mya)**

*Emergent Functions*: Precision grip for making stone tools, omnivorous with reduced size of post-canine teeth, group-living gatherers with some planning, and/or hunting in social groups to obtain essential nutrients for increasing brain size. This is described as early “mimetic” or “intellectual” culture in which there are executive skills for non-emotional problem-solving and long-term planning according to a mental template (Donald, 1991; Cloninger, 2009). *H. habilis* had enlarged brain of about 640 cc (about half of modern *H. sapiens* 1350 average) (Conroy et al., 1998), smaller back teeth and jaw muscles for chewing (Rak, 1985; Rak et al., 2007), and hemispheric asymmetry like later hominids (Corballis, 2003), but postcranial skeleton similar to australopithecines (Wood and Collard, 1999). *H. ergaster* had an enlarged brain (about 800 cc), reduced arm length with arm/leg proportions like modern humans, forward projection of external nose, narrow pelvis, barrel chest, and reduced sexual dimorphism compared to australopiths and possibly *H. habilis* (Klein, 2009). They were able to emigrate out of Africa and were ancestors of all later species of *Homo*, so they are likely to have been the first largely hairless hominids and developed dark skin replacing the pale skin under the fur of apes and earlier hominids. The external nose and naked dark skin provided adaptation to hot arid climate and seasonal rainfall that occurred at the time of their emergence (Klein, 2009).

*Emergent Structures*: Hemispheric asymmetry is observed in *Homo* and some australopithecines, particularly around the lateral sulcus in regions related to language in modern humans (Corballis, 2003, 2009b; Deacon, 1997; Eccles, 1989). Fossils only but enlarged frontal opercular area and IPL, suggesting emergence of executive planning and representation based on cross-modal transformation of tactile, auditory, and visual information. PFC inputs to brain reward centers allow meaning and purposeful planning to organize social relationships and solve physical problems using a non-syntactical protolanguage of mime, vocalization, and metaphoric understanding (Broad et al., 2006; Bickerton, 2010; Pinker, 2010) and/or segmentation of loud calls (Geissmann, 2002). The frontal opercular and ventral premotor area support action understanding and imitation, which are characteristic of an early “mimetic” culture with a longer working memory than observed in great apes (Corballis, 2009a; Deacon, 1997).

**Table 5.1** (continued)

**Clade 5b/6: Pre-modern hominids of Middle Pleistocene (780–126 kya)**

*Emergent Functions*: Development of gatherer–hunter culture of middle Pleistocene with evidence of executive intellectual abilities (i.e., objective/non-emotional problem-solving and long-term planning), such as refined tools with local stylistic traditions, domestication of fire, organized group hunting, cooperative division of labor, sharing, trade, prolonged care for young and disabled, and possibly taboo, as well as construction of temporary shelters and widespread migration in social groups (McBrearty and Brooks, 2000; Goren-Inbar et al., 2000; Tattersall, 2008a). There was a cooperative social structure with cultural transmission of skills and traditions in hunting and tool-making, but communication was probably by gesture and meaningful sounds involving observation of body language, action understanding, and imitation without a syntactical language involving conceptual shifts in time and viewpoint. There is no direct evidence for or against modern language or self-awareness in pre-modern hominids except that no pre-modern hominids competed successfully for survival with modern *Homo sapiens*, who are the only primates who do have the capacity for autobiographical narrative and flexible viewpoint shifting as observed in modern syntactical language. The only known advantage of modern humans over Neandertals and other pre-modern hominids of the Middle Pleistocene is their self-awareness, which is necessary for the syntactical functions of modern language and music, such as perception of harmony and temporal viewpoint. Because of lack of detail about brain networks and lack of certainty about the functional capacities of particular hominids, it is unclear whether all hominids existing during the Middle Pleistocene should be grouped together or if Neandertals or possibly other pre-modern hominids should represent a sixth clade.

*Emergent Structures*: Only fossils are extant, but findings indicate cross-modal symbolic ability with prominent development of IPL (BA 39/40) and emergence of brain default network that supports daydreaming, holistic attention, and subconscious problem-solving. Default brain network includes neo-neocortical regions as subsystems in the ventral medial PFC, dorsal medial PFC, IPL, posterior cingulate/retrosplenial cortex, and hippocampal formation and related entorhinal and parahippocampal cortex (Buckner et al., 2008; Raichle et al., 2001).

**Clade 7: Modern *Homo sapiens* (about 150 kya to present)**

*Emergent Functions*: Early “mythic” culture (7a) of *H. sapiens* involves evidence of self-awareness suggested by ritual burials with grave-goods and ornamentation and probably spoken syntactical language suggested by prehistoric oral traditions in cosmogenic and heroic myths. By 35 kya, there is strong evidence of a “theoretic” culture (7b) with self-aware consciousness allowing uniquely human development of art, science, and spirituality, including symbolic representation of lunar cycles. There was still a hunter–gatherer culture until near the end of the Ice Age about 11–10 kya when there were founding of permanent cities with agriculture of domesticated grains and domestication of animals.

*Emergent Structures*: The face of *H. sapiens* is distinguished from earlier hominids by absence of thick brow and by presence of a chin due to small size of structures for mastication (Rak et al., 2002). Auto-noetic awareness depends on a distributed fronto-temporo-parietal network with encoding via hippocampus (Levine, 2004). The same brain regions are most recently differentiated in evolution and are late to myelinate. The whole neocortex becomes a functional whole by linking all association areas through projections of visual system, Once developed in children after 4 years of age, anterior and medial prefrontal cortex is activated in support of egalitarianism (Fehr et al., 2008), charitable donation (Moll et al., 2006), spontaneous musical improvisation (Limb and Braun, 2008), and syntactical functions for shifting viewpoints in dialog and perception of harmony in musical sequences (Schellenberg et al., 2005).

Adapted with permission, Cloninger, 2009, Center for Well-Being

(McEwen, 2000; Toates, 2001) (see Table 5.1). Hence tree shrews are a model for the root causes of aggression in human beings when there is failure of the regulatory mechanisms that evolved later to promote cooperation in primates.

Only one arboreal species of tree shrew can survive in the same area because of the limited number of arboreal insects, so they are aggressive for sake of self-preservation in craving to obtain what they need for survival. They develop anxiety with impaired spatial memory when stressed by a dominant intruder to their territory (Kawamichi and Kawamichi, 1979; Magarinos et al., 1996; McEwen, 2000). Consequently, adaptive radiation from the primitive tree shrew involved expansion to diurnal and terrestrial niches in more derived tree shrews (*Tupai*) (Emmons, 2000).

The common ancestor of tree shrews and primate-like mammals are thought to be like the pentail tree shrew in being strictly nocturnal, arboreal, and having only rudimentary capacity for obtaining and digesting fruits. To be able to exploit the availability of fruits in flowering trees more fully, ancestors of primates needed hands for grasping fruit in terminal branches, teeth adapted for eating fruit, and a more complex digestive system with a slower transit time compared to ancestral tree shrews and pentails (Emmons, 2000).

The primate-like mammals called Plesiadapiforms, like *Carpolestes simpsoni*, are known from 65 to 55 mya in the Paleocene epoch of North America and Eurasia. They had a grasping foot like primates, including an opposable toe and a nail rather than a claw. It could probably grasp with its hands as well. As a result, it was well-adapted to move in the terminal branches of fruit-bearing trees that flourished at that time (Sussman, 1991; Sargis, 2002; Bloch et al., 2007). Other proto-primates, like *Purgatorius ceratops*, were also small, arboreal, and nocturnal, like ancestral tree shrews, but were better adapted for consuming fruit and nuts, as indicated by their primate-like teeth, shorter snouts, and adaptations for grasping. Unlike ancestral tree shrews, proto-primates were omnivorous, consuming fruits, nuts, seeds, leaf buds, insects, and small vertebrates (Biknevicius, 1986). Visually guided reaching and grabbing with the forelimb tended to replace grasping with the mouth, requiring eye–hand coordination, as observed in true primates.

Among primates, the line to human beings continues through ancestors in common with lower primates (i.e., suborder *Strepsirhini*, characterized by their wet noses, including lemurs, lorises, and bushbabies) and later with higher primates (i.e., suborder *Haplorhini* with simple dry noses, including tarsiers, monkeys, and apes) (Fleagle, 1999; Springer et al., 2003). The members of the primate suborder Strepsirhini are remarkably varied in their characteristics. The ancestral Strepsirhini (i.e., ancestral adapiform or earliest lemur) was the earliest true primate, which is known from fossils dated to the early Eocene (56–50 mya) or perhaps slightly earlier based on phylogenetic analyses (Kay et al., 1997, 2004). Like ancestral tree shrews and plesiadapiforms, they were nocturnal and arboreal with wet noses (Fleagle, 1999; Kay et al., 1997). A prominent behavioral breakthrough from plesiadapiforms to strepsirhines is superior adaptation for grasping and leaping for feeding and locomotion in trees (Szalay and Delson, 2001). The superior grasping and leaping abilities were accompanied by only minor skeletal changes, such as a grasping pollex and hallux (probably already present in plesiadapiforms) and changes in the articulation of bones in the arm. However, the superior grasping–leaping ability coevolved with great dietary flexibility in ancestral primates (Chivers and Hladik, 1980; Chivers, 1998).

Despite the benefits of their improved physical agility and their ability to digest fruits and seeds well, strepsirhines are still constrained by the need for energy conservation. For example, many of the traits of lemurs in Madagascar are either adaptations to conserve energy (e.g., low basal metabolic rate, torpor, sperm competition, small group size, and seasonal breeding) or to maximize the efficiency of use of scarce resources in a harsh and unpredictable environment (e.g., the ability to alternate activity between day and night, territoriality, female dominance, fibrous diet, weaning synchrony) (Wright, 1999). Gestation and lactation are periods of high expenditure of energy, so they are limited to seasons when nutrients like fruits are relatively abundant (Meyers and Wright, 1993).

Strepsirhine characteristics were originally associated with solitary activity at night in trees, but are often still retained in strepsirhine lines that successfully adapted to other habitats and social organizations. For example, lemurs include species that are solitary, pair-living, or group-living (Kappeler, 1997). The nocturnal strepsirhines are usually solitary, and the pair-living strepsirhines are usually at least partly active at night. Diurnal species, like the ring-tailed lemur, are group-living (Kappeler, 1997; Sussman, 2003). Despite this variability in habitat and social organization, all strepsirhines are typified by characteristics that distinguish them from anthropoid primates. The typical strepsirhine features include a highly developed sense of smell, specialized scent glands for non-visual communication, protruding snout, prominent whiskers, a dental comb from lower incisors and canines, large and mobile external ears, a postorbital bar, and forward-directed eyes with binocular vision and tapetum lucidum (which reflects light back toward the pupil and makes eyes visible in the dark). Strepsirhines have a simple (epitheliochorial) placenta, and they lack the capacity for year-round reproduction conferred by the menstrual cycle of haplorhines (Chivers, 1998). Their upper lip is attached to their gums by a membrane, thereby limiting facial expression. The regulation of social and parental relationships in strepsirhines depends on individual recognition by olfactory cues (Broad et al., 2006).

The ancestral strepsirhines were nocturnal and solitary (Kappeler, 1997; Overdorff, 1998; Jolly, 1998; Hilgartner et al., 2008), presumably because of the continued reliance of social organization on close contact for olfactory cues and hormonal regulation by the hypothalamus in strepsirhines, rather than emotional processing of visual information and integration of multisensory information at a distance in the prefrontal cortex in anthropoids (Broad et al., 2006). With no competition with anthropoid primates on Madagascar, lemurs were able to diversify in many ecological niches, including gregarious species that are active during the day (i.e., either diurnal or cathemeral). Gregarious lemurs differ from anthropoid primates in several social, demographic, morphological and ecological features (van Schaik and Kappeler, 2010). They lack sexual dimorphism in canine and body size. They live in groups with equal adult sex ratios (pairs or larger groups). In most species of lemurs, females dominate males and have brief and often synchronized estruses. Gregarious lemurs illustrate a pathway to social organization in which the strepsirhine social groups are based on pair-bonding with breeding pairs of adults at the core of the social structure and additional individuals serving to bolster an essentially pair-bonded relationship that facilitates reproductive success (Shultz and Dunbar, 2007; van Schaik and Kappeler, 2010). Social interactions between male and female lemurs help to initiate ovarian cycles and behavioral estrus (Whitten and Brockman, 2001). However, gregarious lemurs differ clearly from gregarious anthropoid primates: most species of pair-living lemurs are at least partly nocturnal and do not provide direct paternal care for young dependents (Kappeler, 1997). A qualitatively distinct second pathway to bonded social systems involves extending the maternal-infant attachment into adulthood and to other members of a social group as conciliatory caretakers of one another for protection from predators, as typically occurs in anthropoid primates (Broad et al., 2006; Dunbar and Shultz, 2007; Shultz and Dunbar, 2007). The human nuclear family emerges much later along with reduced sexual dimorphism, pair-bonding, and specialized roles for both parents in child care in *Homo ergaster* and its descendents (Klein, 2009).

Tarsiers have mixed features of both strepsirhines and anthropoids (see Table 5.1). They are classified with anthropoids on the basis of their dry nose, cranial morphology, and specialization for day-time activity, but behaviorally they are closer to strepsirhines in their nocturnality, solitary foraging, seasonal breeding, and reliance on scent marking for social communication. Like nocturnal strepsirhines (i.e., lorises, bushbabies, pottos, and some lemurs), the solitary activity of tarsiers suggests that they do not form emotional attachments like those of anthropoid primates (Mineka and Suomi, 1978; Suomi, 1984; Weaver and de Waal, 2002).

By the end of the Eocene, there was a climatic upheaval with temperatures cooling during which the early anthropoids emerged and many strepsirhine species became extinct. Tarsiers survive only on several islands in Southeast Asia. The transition from nocturnality to diurnality has been considered to be the key adaptive shift that occurred at the base of the tarsier-anthropoid transition (Kay et al., 1997). The early anthropoids were small, diurnal, arboreal insectivore–frugivores with unfused mandibular symphyses, small brains, and either dichromatic or trichromatic vision (Kay et al., 1997). The early anthropoids adopted locomotor patterns with more arboreal quadrupedalism and less leaping. The fundamental importance of diurnality during the cooling temperatures of the Eocene-Oligocene transition is shown by the extensive anthropoid adaptations for diurnal visual acuity in comparison to their nocturnal ancestors who became extinct except in isolated island habitats (Ross, 2000; Ross and Kirk, 2007). Distinctive adaptations of the anthropoid visual system for diurnality include highly convergent orbits, small corneal diameter and posterior nodal distance, high concentration of cones and ganglion cells, and extreme magnification of foveal regions of the visual field in the visual cortex (Ross, 2000; Ross and Kirk, 2007).

Monkeys and apes are typically diurnal and active in social groups most of the time (Sussman, 2003; Sussman and Chapman, 2004). Like tarsiers, monkeys have non-reflective eyes and binocular vision. In contrast to prosimians (i.e., strepsirhines and tarsiers), monkeys have a reduced snout and less reliance on smell for communication, a free upper lip allowing for more expressive faces, usually one offspring with extended maternal care, delayed sexual maturity and an extended life span. The olfactory input to limbic areas concerned with social reward, such as amygdala and nucleus accumbens, is replaced in monkeys and apes by prefrontal neocortical inputs concerned with multimodal sensory integration, emotional regulation, and planning (Broad et al., 2006). These changes allow greater social regulation of aggression and conflict in anthropoids than in prosimians. Compared to prosimians, the social interactions of anthropoids became less dependent on olfaction as a result of the combination of enhanced diurnal visual acuity, facial mobility, and related sensory changes facilitating emotional intimacy and attachment (Broad et al., 2006). The evolution of larger brains, symphyseal fusion, and definitive trichromacy occurred later in anthropoid evolution (Ross, 2000).

Mentally, chimps show learning abilities comparable to a 2- or 3-year-old modern human child (Suddendorf and Whiten, 2001) but not the capacity for self-aware recollection that develops in 3–4-year-old human children (Povinelli, 2000; Povinelli and Dunphy-Lelii, 2001; Povinelli and Giambrone, 2001). For example, chimpanzees have excellent visual-motor hand coordination and learn to make stick tools from opportune plants to fish out termites from their mounds for eating, and their status in social groups varies according to which of their friends and family are present (Donald, 1991; Preston and De Waal, 2002; van Lawick-Goodall, 1967). They can identify themselves in a mirror and can plan how to obtain food that is out of reach by using what is in their environment instrumentally, as demonstrated in the early “insight” experiments of Wolfgang Kohler (Donald, 1991). Chimps have also been taught to communicate with gestures like sign language. They can be trained to produce two- to four-word sentences, but they do not spontaneously develop symbolic language or have a capacity for syntactic functions beyond simple two-word order rules or to fully describe what they evidently know about the environment (Donald, 1991; Povinelli, 2000). Chimps can be trained to use signs for dozens of things to obtain food rewards but they do not display evidence of any recollection of internal memories in self-aware consciousness, such as shifts in viewpoint about things that are out of sight (Suddendorf et al., 2009).

The great apes can show warm emotional expressions and affectivity, including ventral hugging, but do not do not spontaneously provide food to other group members, which suggests that they lack a capacity for perception of unity needed for a concept of fairness or egalitarianism. Prosocial giving is well-documented in monkeys, particularly when there is social affiliation and the distribution of rewards are equitable (Brosnan and De Waal, 2003; Brosnan et al., 2006; de Waal, 2008; de Waal et al., 2008; Preston and De Waal, 2002). In contrast, anthropoids act selfishly when the possible recipient is out of sight or the distribution of rewards cannot be equitable (de Waal et al., 2008). The social behavior of monkeys and apes is usually docile in natural free-ranging habitats (Sussman and Chapman, 2004), but aggressive competition, threat displays, and violence increase in monkeys and apes in response to social strangers, violation of territorial space with increasing population density, and frustration over restricted access to food and other cravings (Southwick, 1967). The affective quality of anthropoid social behavior is not based on an instinct for either peace or violence; rather it is an adaptive function or tool for emotional competition, social negotiation, and conflict resolution (de Waal, 2000).

The sociality of anthropoid primates can be characterized in terms of its tendency toward "reconciliation" after emotional conflicts. For example, after a fight, chimps often engage in mouth-to-mouth kissing and embraces. Other anthropoid primates reconcile by sexual intercourse, clasping the other's hips, grooming, grunting, and holding hands (de Waal, 2000). Responsiveness to long-distance cues in anthropoid primates facilitates close emotional relationships among triads and larger groups of individuals, so that a third party, such as a high-ranking group leader, can intervene to help pacify and resolve conflicts among members of the social group (de Waal, 1996, 2000; Parr et al., 1997). Affective reconciliation is an important function in anthropoid primates because their survival depends substantially on social cooperation. Consequently, conflict resolution is advantageous to promote fitness and to reduce emotional distress. Monkeys and apes show emotional hypersensitivity with the display of a wide range of prosocial and antisocial behaviors by the same individual depending on the social context rather than a drive for either prosocial or antisocial behavior (de Waal, 2000). Even aggressive monkeys, such as rhesus macaques, can learn conciliatory behaviors as a result of their need for conflict resolution (de Waal, 1996, 2000). Such social learning in anthropoid primates also allows proto-cultural transmission of traditions in courting, foraging, food preparation, and grooming (Kawai, 1965; de Waal, 1999; Whiten et al., 2007).

Among the hominoids, the line to modern humans continues through the first ancestors of Australopiths to members of genus *Homo*. The details of the lineage are intensively debated, but the functional and structural changes are fairly clear even when the precise transitional forms remain uncertain. The earliest hominids lived in what are now the African countries of Chad (*Sahelanthropus*), Ethiopia (*Ardipithecus*), and Kenya (*Orrorin*) around 6.5–4.4 million years ago (Tattersall, 2008b; White et al., 2009). The earliest striding bipedal ape (*Australopithecus anamensis*) is known in Kenya 4.2 mya, and is regarded as ancestral to *Australopithecus afarensis* and *A. garhi* (Kimbel et al., 2006; White et al., 2006; Shreeve, 2010). The australopiths lived at the forest edge and surrounding woodlands in Africa at a time when the dry climate and increasing seasonality were breaking up the forests (Tattersall, 2008a). Despite being bipedal and having a wide environmental niche throughout Africa, they still had small ape-like brains. For example, the endocranial volume of *A. garhi* was about 450 cc (Shreeve, 2010). Australopithecines also retained ape-like body proportions with relatively short legs, narrow shoulders, conical thoraxes, flaring pelves, and long arms for millions of years without developing more modern human features. Bipedal australopiths differed from hominids that emerged later in their ape-like brains and bodies and in their lack of innovation.

*Homo habilis* is usually classified as the earliest species in the genus *Homo* on the basis of the average brain volume being greater than 600 cc and prominent development in cranial endocasts of brain regions corresponding to Broca's area (BA 44) and the inferior parietal cortex (BA 39/40) in the left, but not the right, hemisphere. However, these asymmetric fronto-parietal prominences are almost certainly related to increasing facility in control of the free hands of bipedal habilines, not speech. In extant apes, Broca's area is an area controlling sequences of movements of the hand and is not involved at all in speech or vocalizations (Passingham, 1981). Damage to Broca's area in nonhuman primates has no effect on the rate or acoustic qualities of vocalization and does not impair social communication (Jurgens, 1982; Kirzinger and Jurgens, 1982). Anthropoid vocalization is sometimes called "limbic language" or "emotional language" because monkey calls are expressed in response to the anterior cingulate cortex (ACC) and amygdala acting on brainstem centers such as the periaqueductal gray area (PAG). The ACC is only necessary for the volitional initiation of vocalization and not for spontaneous vocalization in emotional situations, such as spontaneous monkey calls or human pain groans (Jurgens, 1982, 1983, 2009; Jurgens et al., 1982; Kirzinger and Jurgens, 1982). Accordingly, Broca's area began to regulate vocalization by programming the premotor area's control of the oral and laryngeal musculature for expressive speech early in the hominid lineage, perhaps as early as habilines (Corballis, 2003).

Nevertheless, there is no angular gyrus in anthropoid primates like that in the inferior parietal lobe (IPL) of modern humans (Geschwind, 1965a, b). The parietal lobe of modern humans has a larger size and globular shape that are unlike that of any pre-modern hominid (Bruner et al., 2003; Bruner, 2004; Bruner and Holloway, 2010), so it is likely that *Homo sapiens* was the first hominid with syntactical language, which depends on the angular gyrus in the inferior parietal lobe as part of a distributed frontal-temporal-parietal network supporting self-awareness (Levine, 2004). Other features unique to human beings emerging along with syntactical language are related to the capacities to perceive unity and to shift perspective within that unity (e.g., between self and other viewpoints, between expected and unexpected viewpoints, and across time and place). For example, humor in humans is often based on incongruity (which involves a shift between expected and unexpected viewpoints at the "punch-line") (Taber et al., 2007; D'Argembeau et al., 2007). Altruism in humans is based on feeling engagement and compassion for others (involving shifts between self and other viewpoints) (Moll et al., 2006). The uniquely human functions of self-awareness, perspective taking, humor about incongruity, improvisation (i.e., automatic and fluid inventiveness without intellectual effort or deliberation), altruism, and crucial features of syntactical language (like viewpoint aspect, which involves perspective taking) all depend on the activation of the anterior prefrontal cortex (BA 10) along with other components of the self-aware learning system (Moll et al., 2006; D'Argembeau et al., 2007; Limb and Braun, 2008). The anterior prefrontal cortex of modern human beings (BA 10) is unique in its functions and connectivity; no homologous brain area is present in any extant nonhuman primates (Ongur and Price, 2000). The angular gyrus (BA 39) in the IPC is also unique to modern humans and plays a key interpretive role in language reception and humor detection (Geschwind, 1965a, b; Moran et al., 2004),

There is consensus that there was a qualitative shift in skeletal organization and a general increase in the size of the brain and body of hominids between australopithecines and *H. ergaster* (Hawks et al., 2000). *H. ergaster* had long limbs and femoral-pelvic articulation that was well suited for long-distance walking, providing advantages for hunting and gathering (Lordkipanidze et al., 2007; Pontzer et al., 2010; Rightmire, 2009). They also had an enlarged brain (about 800 cc), reduced arm length with arm/leg proportions like modern humans, forward projection of external nose, narrow pelvis, barrel chest, and reduced sexual dimorphism compared to australopiths and possibly *H. habilis* (Klein, 2009). They were able to emigrate out of Africa and were ancestors of all later species of *Homo*, so they are likely to have been the first largely hairless hominids and developed dark skin replacing the pale skin under the fur of apes and earlier hominids. The external nose and naked dark skin provided adaptation to hot arid climate and seasonal rainfall that occurred at the time of their emergence (Klein, 2009).

Hominids are likely to have had advanced forms of social communication and reenactment using on mime, gesture, and emotional vocalization ("appeal") because of the enlargement of their left fronto-parietal neocortex (Corballis, 2003, 2009a, b), but syntactical language is probably unique to modern human beings, as previously discussed (Donald, 1991; Mithen, 1998; Suddendorf et al., 2009; Tattersall, 2009).

The hominids of the Middle Pleistocene had larger prefrontal cortices than earlier hominids (Bruner et al., 2003; Bruner, 2004; Bruner and Holloway, 2010), and they also had more advanced executive abilities, including problem-solving and long-term planning with a mental template, such as mode 3 tool-making ("prepared cores"), domestication of fire, and construction of shelters by the Middle Pleistocene (McBrearty and Brooks, 2000; Tattersall, 2008a). Planning, preparation, and problem solving really involve more than mime and imitation. Long-term planning and preparation to solve problems involves the executive cognitive functions dependent on the prefrontal cortex, which are better described as intellectual abilities. Therefore, we suggest the term "meaning" as an appropriate way to describe the emergent cognitive ability of pre-modern human beings. Meaning refers to the process of non-emotional communication that conveys implicit or explicit significance or purpose in a non-emotional way, which is present to a limited degree even in the early hominids. Meaning is the process of objective communication of understanding and significance, which involves at least the basic use of symbols but not necessarily language with syntax.

The human capacity for music and language may have evolved from both the loud calls and the ability to sing found in apes, and therefore they are expected to be present in hominids with increasing development of Broca's area, the auditory association area (i.e., superior temporal gyrus), and the inferior parietal lobule (Corballis, 2003; Masataka, 2007; Vaneechoutte and Skoyles, 1998). This view does not conflict with the importance of cortical control of gesture in the development of language because both gesture and vocalization begin to be regulated by Broca's area in the frontal cortex of hominids (Corballis, 2003). Monkeys and apes show volitional initiation of phonation, as well as learning of the acoustic qualities of their vocalizations, which is mediated by the anterior cingulate cortex (Jurgens et al., 1982; Jurgens, 2009; Kirzinger and Jurgens, 1982; Masataka, 2007). Although prosimians and monkeys do not produce any multisyllabic utterances (Passingham, 1981), apes produce loud calls and singing of pure tones, stereotyped phrases, and biphasic notes like an 8-month-old human infant (Masataka, 2007).

Nevertheless, the nature of the protolanguage of pre-modern hominids is unknown. The segmentation of song by means of greater working memory and volitional control than is observed in apes produce speech in which the emotional aspect of vocalization becomes less salient than its semantic aspect. However, segmentation of singing produces a hominid protolanguage with little or no syntax, much as is seen in the well-articulated babbling of a 9-month-old human infant or perhaps an 18-month old human child with a vocabulary of 5–20 nouns (Masataka, 2007). By 2 years of age, a modern human child often has a vocabulary of 150–300 words that can be used in noun–verb sentences along with some appropriate use of pronouns and prepositions. The development of further syntactical functions of modern human language and music, like aspect (i.e., viewpoint shifting) and harmony (i.e., knowing what sounds pleasing), depends on the emergence of self-awareness (Schellenberg et al., 2005; Smith, 1997), which does not begin to mature until modern human children begin to be able to recall their past after 3–4 years of age. Viewpoint shifting allows modern humans to shift their contextual focus and to switch in self-aware consciousness from analytical and intuitive modes of reasoning, giving modern people the potential to be inventive and creative (Cloninger, 2004; Gabora, 2004, 2008). The emergence of self-aware consciousness in *H. sapiens* is likely to explain the rapid divergence in learning ability of modern human children from apes after 3 years of age, as well as the complete displacement of pre-modern hominids by modern humans.

## The Development of Hominid Cultures

The cultural development of spoken language was associated with an increase in the size and shape of the inferior parietal cortex in *H. sapiens* that is not observed in pre-modern hominids based on detailed morphometric analyses of available brain endocasts of extinct and modern hominids (Bruner et al., 2003; Bruner, 2004; Bruner and Holloway, 2010). There was a correlated increase in left fronto-parietal cortex in early hominids, but there is a novel change in size and shape of the parietal cortex in modern humans not seen in any pre-modern hominid. The function of the fronto-parietal areas for eye–hand coordination, understanding of gesture, and social communication is likely to have served as a precursor for the development of these areas as expressive and receptive modules for syntactical language in modern humans.

The first crude stone tools are known from 2.5 to 2.0 mya in Africa, indicating that the earliest toolmakers had the bodily proportions of an australopithecine (Tattersall, 2008a, b). Early hominid toolmakers not only knew how to make tools but also planned ahead. Their long-term planning is documented by evidence that they carried the right kinds of rocks for miles before making them into tools, and once made they carried the tools in anticipation of using them to butcher carcasses when needed. In contrast, chimpanzees make and use stick tools with materials that do not require long-term planning about things that are out of sight (Povinelli, 2000). The reduced sexual dimorphism and narrowing of the pelvis in *H. ergaster* led to the emergence of the human nuclear family structure with pair-bonding, cooperative and specialized roles of both parents in supporting the family and its children, and a taboo against public sex unlike anything observed in monkeys or apes (Klein, 2009).

*Homo heidelbergensis* appeared in Ethiopia around 0.6 mya and in Europe around 0.5 mya. Unlike *H. sapiens*, Heidelberg man had no chin and had a thick brow ridge composed of vermiculated bone. The increased brain and body size of *H. ergaster* and later hominids like *H. heidelbergensis, Homo erectus, Homo neanderthalensis*, and *H. sapiens* required a new way of obtaining nutrients to support the greater energy consumption of a larger body and brain, particularly dietary fats from hunting and later from fishing (Bartzokis, 2004; Eaton et al., 1997). There is evidence of the acquisition of meat and marrow by hominids at least by the middle Pleistocene 0.8 mya (Rabinovich et al., 2008) and perhaps as early as the Pliocene 2.5 mya (de Heinzelin et al., 1999). Much as in modern human societies, the hunting of big game by early humans may have been motivated in part by a desire to show off as well as for nutrition. The social prestige of hunting by male hominids is partly related to its importance for reproductive success and health of hunter–gatherer groups. Although women may provide most of the food most of the time in hunter–gatherer societies (Marlowe, 2005), provisioning by men is also crucial for reproduction, particularly when women are unable to forage near the time of child-delivery (Marlowe, 2003). Provisioning of food by men frequently benefits the whole hunter–gather group because large quantities of food are cooperatively shared when intermittently available (Mace and Sear, 2005).

The importance of prestige from hunting is evidenced by protein comprising only a small portion of the diet of extant hunter–gatherers most of the time and the ability of hominids to survive without meat by acquiring essential nutrients from plants alone, as is done by modern vegetarians (Speth, 1991). Nevertheless, the actual nutritional value of hunting by omnivorous hominids is indicated by clear evidence of the systematic butchering of the whole carcasses of deer by hominids around 0.8 mya in the Levant using technologies originating earlier in Africa (Goren-Inbar et al., 2000; McBrearty and Brooks, 2000; Rabinovich et al., 2008). The planned use of Acheulian handaxes and possible planned use of fire by hominids are known from about 1.5 mya in Africa (McBrearty and Brooks, 2000). Later such planned use of tools and fire spread by human movement along the migratory corridor in the rift valley connecting Africa with Eurasia during the early Middle Pleistocene (Goren-Inbar et al., 2000). In depth planning of tool use, controlled use of fire using flint, systematic butchering of the whole carcasses of deer, preparation of nuts and grains with hammers and cooking, and formalized conceptualization of the spatial organization of living space are well documented at Gesher Benot Ya'aqov (i.e., "bridge of the daughters of Jacob") on the river Jordan just south of Lake Galilee in Israel around 750–800 kya, which is well before the emergence of anatomically modern humans (Goren-Inbar et al., 2000, 2002, 2004, 2008; Rabinovich et al., 2008; Alperson-Afil et al., 2009; Sharon et al., 2010). The controlled use of fire and planned organization of ways of processing large game, nuts, and wild seeds of barley and grapes indicates a well-organized hunter–gatherer culture by 790 kya in pre-modern hominids (Goren-Inbar et al., 2004).

Still later there is archeological evidence of further spread of hunter–gatherer technologies to Europe. Wooden spears dating from about 400 kya were preserved in a peat bog in Schoeningen, Germany along with cut-marked animal bones and flint artifacts. Huts with hearths constructed by *H. Heidelbergensis* are also known from 400 kya at Terra Amata in southern France.

Even later, pre-modern and modern hominids both existed at the same time and had contact with one another, as shown by the evolution of divergent strains of head lice (Reed et al., 2004). Around 80 kya pre-modern hominids were competent hunters and fishers who planned their settlement choices around the seasonal availability of game and fish, such as the spawning of large catfish rich in omega-3 fatty acids at the beginning of the rainy season in the rift valley (McBrearty and Brooks, 2000). The skills of pre-modern hominids in obtaining of an abundant source of preformed omega-3 fatty acids from fish available from lakes and ocean sources appear to have been important as a means of supporting the expansion of the pre-modern hominid brain with nutrients essential for the more extensive and prolonged myelination of the modern human brain (Crawford et al., 1999; Bartzokis, 2004; Cunnane et al., 2007). Thus pre-modern hominids showed in-depth conceptual planning in their making and use of stone tools, spears for hunting, systematic butchering of big game, domestication of fire, the building of shelters, organization of living spaces, and flexible utilization of seasonal resources throughout the Pleistocene (1.6–0.1 mya), which are executive cognitive skills unknown in non-hominids (Tattersall, 2008a, b). The capacity for planning allowed pre-modern hominids to exploit the flexibility inherent in their generalized digestive system to adapt to a wide range of habitats and external conditions beyond their control, utilizing plants, game, or fish according to whatever was available. Evidence for what happened to be abundant when modern hominids emerged is indicated by nutrients that are essential for modern humans, such as plant and animal sources of omega-3 fatty acids, such as rift valley catfish, for healthy brain development and functioning (Crawford et al., 1999; Cunnane et al., 2007). The influence of an abundant contextual source of omega-3 fatty acids in the transition from pre-modern to modern human brain structure can be understood as an example of context-driven actualization of potential in evolution (Gabora, 2006). The influence of dietary context on evolution provides an example of the pervasive importance of cooperative interactions in ecology and development rather than selfish competition between individuals within social groups or competition between socio-cultural groups (Weiss and Buchanan, 2009).

The executive cognitive skills and social life of early hominids were distinct from both apes and modern *H. sapiens*. The prefrontal cortex (PFC) serves as the senior executive system in hominids. In modern human beings, the PFC's executive functions include working memory (dorsolateral PFC, BA 11/46), evaluation of internal stimuli (medial PFC, BA 8/9), long-term planning for a main goal while problem solving and carrying out multiple intermediate tasks (anterior PFC, frontal poles, BA 10) (Bengtsson et al., 2009; Burgess et al., 2000; Fuster, 2000; Passingham et al., 2010; Rowe et al., 2007). Hence the emergence of evidence for long-term planning and problem solving in pre-modern hominids suggests that the development of the prefrontal cortex had an important role in pre-modern hominid development. The hypothesis of prefrontal development in pre-modern hominids is supported directly by the increasing height and width of the frontal cortex in the anterior part of hominid endocasts, which largely accounts for the increasing total brain in the pre-modern hominid lineages (Bruner et al., 2003; Bruner, 2004; Bruner and Holloway, 2010).

The development of the prefrontal cortex of hominids allowed improvements in motor planning and control of manual gestures, which are important precursors for the later development of vocal control and syntactical language (Corballis, 2003, 2009a). By the Middle Pleistocene (781–126 kya), there is direct evidence of hominids hunting large mammals and indirect evidence of their social cooperation, division of labor, and sharing of food (McBrearty and Brooks, 2000; Goren-Inbar et al., 2002; Rabinovich et al., 2008; Sharon et al., 2010). The divergence of body lice from head lice between 83 and 170 kya in Africa suggests that closely tailored clothing were produced and worn by hominids at that time (Toups et al., 2010). Adult men and women organized and divided their labor in a cooperative manner in a hunter–gatherer culture (Zihlman, 1997; Marlowe, 2005). The greater size and strength of men and the child-bearing ability of women led to gender-based division of labor with both genders playing complementary and essential roles. The adult women and children often gathered most of the food, and men provided defense from predators and some hunting (Marlowe, 2005). Given difficulties in traveling when pregnant and the short-life span at the time, women are likely to have maintained a temporary home base where young, weak, and sick could be nursed. The bands of nomadic hunter–gatherers may have included 15–30 or so individuals. Adaptations for bipedalism meant that the bipedal hominid foot could no longer grasp the hair of the mother, so the mother had to hold infants actively. With narrower pelvis and larger brains, much of the development of hominid infants occurred after birth, leading to a need for extended child care (Klein, 2009). Hominid children had prolonged periods of dependence on parental care for food, safety, and education. Artisans could develop expertise in tool-making for hunters (McBrearty and Brooks, 2000), and food could be processed and prepared by others in temporary camps or settlements (Goren-Inbar et al., 2002, 2008; Rabinovich et al., 2008; Sharon et al., 2010). The division of labor was needed to care for the young while providing a stable food supply and food preparation and storage for a cooperative group of several adults and their dependents. *H. ergaster* and its descendents were able to migrate widely throughout Eurasia during the middle and late Pleistocene. To do so, they needed a way to survive injuries that would have precluded their keeping up with a mobile hunting or gathering troop. Consequently, pre-modern hominid social groups maintained temporary camps as a relatively secure home base with a formal conceptualization of living space with specialized areas for tool-making, food preparation, cooking, and sleeping, as is documented at Gesher Benot Ya’aqov in the Levant around 0.8 mya (Alperson-Afil et al., 2009) and earlier around 1.5 mya in Africa (McBrearty and Brooks, 2000). Such home bases provided for pregnant women, children, and the infirm as a conceptualized extension of the anthropoid mother–infant attachment pattern in which a secure home base is fundamental (Mineka and Suomi, 1978; Bowlby, 1983). The home base changed sprained ankles and fevers from fatal events to minor ailments, allowing hominids to migrate more safely to areas without prior immunity to local diseases than could apes. Chimps also hunt in cooperative groups that share meat with one another, but the sharing of meat is reciprocal among hunters as an aspect of male social bonding during times of food abundance and not for nutrition or sexual reproduction (Mitani and Watts, 1999, 2001; Mitani et al., 2000).

Hence, the cooperative sharing and division of labor in hominids involved a greater degree of long-term planning, intellectual awareness, and social organization than the emotion-based reconciliation and social cooperation observed in monkeys and apes (de Waal, 1996, 2000). The intellectual basis of cooperation in humans meant that conflicts between social groups can be better reconciled than in monkeys and apes, whereas emotion-based reconciliation based on social affiliation and prestige are effective *within* social groups but not *between* them (Southwick, 2000).

The division of labor between men and women for food acquisition, child care, and defense is likely to have motivated customs that culturally reinforced sexual and emotional predispositions that favor exogamy and the incest taboo in Pleistocene hominids. All group-living primates and some other social mammals avoid mating with familiar relatives and non-relatives with which they live in close conditions (Lumsden and Wilson, 1980). Among nomadic hunter–gatherers, children were often nursed and reared together in close domestic conditions that involve cooperative interactions among both parents, grandparents, and other members of the group (Mace and Sear, 2005). Such domestic familiarity during childhood predisposes modern humans to express a strong aversion to sexual intercourse with familiar people later in life, even when customs and social pressures actually favor it (e.g., marriage among children reared communally in kibbutzim) (Lumsden and Wilson, 1980). The incest taboo is in part culturally constructed in hominids, even though it depends on emotional disinterest or aversion to breeding with co-resident kin, as well as on social dependency for status (Chapais, 2008). Social status in anthropoid primates depends substantially on the ability to recruit social support by means of alliances with both kin and non-kin (Chapais, 1988, 1995; de Waal, 2000). However, taboos are defined as customs and cultural expectations that create concern for the cultural meaning that others in one's social group give to particular behaviors. The meaning-based nature of taboo in hominids is illustrated by the taboo against public sex, which does not occur in apes but is likely to have emerged along with reduced sexual dimorphism and pair-bonding that led to the emergence of the human nuclear family in *H. ergaster* and all its later descendents (Wade, 2006). Such culturally defined meaning may be biologically arbitrary or even unnatural (e.g., fashion designers suggesting women should be ultrathin anorexics and that it is shameful for women to be well-fed and reproductively fit) (Brinch et al., 1988; Gendall et al., 1998). Thus culturally constructed taboos give both form and force to social norms about what behaviors are likely to elicit social support or exclusion (Krill and Platek, 2009).

Likewise, there was strong norm-favoring for peaceful negotiation that made fighting within the group and war with other groups rare, as is the case among extant nomadic hunter–gatherers (Fry, 2009). Cooperation between neighboring bands of hunter–gatherers would be favored by exchange of mates among neighboring bands, thereby reducing fighting over territorial borders (Chapais, 1995). Cooperativeness in women would also have favored their survival for reproduction, which may contribute to the fact that women are substantially higher than men in the heritable personality trait of cooperativeness (Cloninger, 1995). Likewise, communication between groups of long-distance trading partners would have facilitated exchange of mates, as well as the exchange of locally rare materials (McBrearty and Brooks, 2000). A custom of exogamy is suggested by the fairly frequent occurrence in the Middle Pleistocene of hominids who had mixtures of robust and gracile morphological features (Tianyuan and Etler, 1992). The existence of a taboo against public sex during the Pleistocene cannot be proven, but the intellectual capacities that made such customs possible and the social conditions that made them advantageous arose at that time.

Hence it is likely that a hunter–gatherer culture with cooperative division of labor, trade, sharing, norm-favoring, and taboo arose in pre-sapiens hominids before the emergence of a "mythic" culture with totemism, animism, or a concept of the sacred (Donald, 1991; McBrearty and Brooks, 2000; Marlowe, 2003, 2005; Mace and Sear, 2005). Mythical, self-transcendent, or spiritual thinking requires a capacity for autobiographical narrative, whereas taboo is a more instinctive aspect of intellectual understanding of what is prohibited that may have arisen along with other norm-favoring customs. Cultural norm-favoring is a strong component of social cooperation in modern humans (Cloninger and Svrakic, 1997) and reproductively advantageous (Mace and Sear, 2005; Chapais, 2008).

It is noteworthy that the hunter–gatherer culture of pre-sapiens hominids was characterized by the accumulation of mechanisms for cooperation that facilitated coping with the increasing size and complexity of social organization. Such predisposition for cooperation makes it possible for human beings to be healthy and reproductively fit when functioning coherently (as in states of calm allowing perception of unity). On the other hand, people also have predispositions toward violence when reacting for the sake of physical survival (as in states of fear or hunger promoting perception of separateness reminiscent of a tree shrew threatened by an intruder). The conditions of a hunter–gatherer society favored a combination of both self-directedness and cooperativeness in hominids, with some bias toward assertiveness in men and cooperativeness in women for survival and reproductive success.

Skill in walking and social cooperation facilitated the widespread migration of hominids long before the emergence of any evidence of theoretical thinking characteristic of syntactical language or scientific understanding of natural phenomena in terms of uniform laws. The migration of hominids from Africa to Europe and Asia occurred in successive waves of migration at 1.8–1.6 mya, 1 mya, 500 kya, and 70–40 kya (Tattersall, 2008b). The first two waves of emigration by *H. ergaster* led to the emergence of *H. erectus* in Asia. The adaptive radiation of hominids in Europe following the emergence of *H. heidelbergensis* around 500 kya in Africa led to the emergence of *H. neanderthalensis*. The emigration of anatomically modern hominids out of Africa around 50 kya led to the worldwide spread of modern *H. sapiens* and the eventual extinction of other hominids (Krause et al., 2010; Ian Tattersall, 2008b). The DNA of Neandertals differs equally from all groups of modern humans, supporting the hypothesis that modern humans emerged as part of an adaptive radiation of hominids in Africa independent of the radiation of hominids leading to Neandertals in Europe (Ovchinnikov et al., 2000).

Neandertals functioned in small bands of 15–30 individuals that roamed from one campsite to another when local resources were exhausted. They were highly flexible and able to survive the numerous climatic changes that occurred between their emergence around 200,000 years ago and their extinction 27,000 year ago. They had large brains, ranging from 1200 to 1740 cc in volume compared to the modern human range of about 1000–2000 cc (Tattersall, 2008b). Neandertals appear to have sometimes scavenged meat and at other times to have used ambush-hunting techniques, resulting in frequent skeletal fractures (Trinkaus and Zimmerman, 2005). Neandertals showed their capacity for planning by controlled use of fire, and beginning about 50,000 year ago invented the tradition of burying their dead occasionally and in simple ways without the grave artifacts characteristic of later Cro-Magnon burials (Tattersall, 2008b). There is evidence at Shandigar cave in northern Iraq of Neandertals surviving to advanced age despite severe handicaps (like a useless arm), suggesting social cooperation with empathy for others (Tattersall, 2008b).

Anatomically modern humans appeared outside Africa for the first time about 90,000 ago. The Cro-magnons became widespread and produced impressive artifacts that indicate a new kind of awareness that allowed the development of art, science, and spirituality. Geometrically incised ochre tablets were created in South Africa 75,000 years ago. The earliest known cave paintings, musical instruments, figurines, and notations were created by Cro-magnons in Europe around 34,000 years ago at the beginning of the Upper Paleolithic period. Cro-magnons buried their dead with body ornamentation and grave goods beginning about 28,000 years ago. Shortly afterwards, Neandertals became extinct, and Cro-magnons flourished to achieve the unusual distinction of being the single hominid species in existence (Tattersall, 2008a, b).

## What Brain Structures Emerged Coincident with the Functional Changes?

Ecological shifts elicited adaptive changes in brain structure and function, as detailed elsewhere (Cloninger, 2009). The emergent brain structures and functions for the lineage of craniates leading to human beings, detailed in Table 5.1, will be briefly summarized to provide an overview of the major transitions in the central integration of brain functions from the midbrain in early vertebrates, the hypothalamus in reptiles, and the neocortex in mammals.

In early vertebrates (i.e., anamniotes, including fish and amphibia), the midbrain is the dominant association center for integration of sensory input and regulation of motor output, including large optic lobes for processing visual input (Darling, 2010). The forebrain (including cortex dorsally, hypothalamus, and basal ganglia ventrally) of anamniotes receives sensory input, particularly about smell, but exerts no feedback control of sensory integration or motor output by the midbrain. The hypothalamic–pituitary axis of anamniotes does regulate endocrine functions, much as in amniotes (Goos, 1978). The basal ganglia of anamniotes have few cells and receive little if any cortical input or dopaminergic input from the ventral tegmental area (VTA) of the midbrain (Reiner et al., 1998). In contrast, in all amniotes (reptiles, birds, and mammals) the basal ganglia are neuron-rich and receive extensive cortical input and dopaminergic input from the midbrain, thereby allowing amniotes to learn and execute a more sophisticated repertoire of behaviors and movements on land than do anamniotes in water (Reiner et al., 1998; Reiner, 2002). It seems likely that the common ancestor of amniotes developed greater forebrain organization of both the dorsal cortex and basal ganglia because the organization of the basal ganglia of early vertebrates is less elaborate than that of amniotes. In particular, cortical-striatal-cortical loops (i.e., feedback connections between cortex and basal ganglia) are present in all amniotes and are lacking in all earlier vertebrates (Reiner, 2002).

The clade of amniotes are divided into two sub-clades: *Sauris* (i.e, reptiles and birds) and *Mammalia*. The last common ancestor of sauropsids (i.e., lizard-like reptiles and birds) and synapsids (i.e., mammal-like reptiles and mammals) lived in the late Cretaceous period around 320 mya. Within the sub-clade *Sauris*, lizards and snakes are grouped together in the order *Squamata*. In squamates and other reptiles, the central regulation of brain function is invariably organized in the hypothalamus of the basal forebrain (Bruce and Neary, 1995; Nieuwenhuys, 1994). Sensory information is first processed in the basal forebrain of lizard-like animals before being relayed to their thalamus and dorsal cortex. Like earlier vertebrates, the dorsal cortex and thalamus of lizard-like animals receive sensory input, but do not reciprocate with output that could modulate the hypothalamus (Butler and Cotterill, 2006; Nieuwenhuys, 1994).

Hence squamates and their ancestors are probably limited to the experience of mental images in the present, which is called "primary" or "perceptual" consciousness (Butler and Cotterill, 2006). In squamates, the hypothalamus in the basal forebrain is the dominant association center that integrates external and internal sensory inputs and regulates motor output (Bruce and Neary, 1995; Nieuwenhuys, 1994). In contrast, both mammals and birds have developed forebrain systems that permit higher level control of the hypothalamus by thalamic and cortical structures, although mammals and birds do so with structures that are only partly homologous (Butler and Cotterill, 2006). The dorsal cortex of early mammals was differentiated into a multilayered neocortex, and there is a progressive series of transitions in brain function along the ancestral lineage from synapsids to human beings whereby neocortex took control of central regulatory functions from the hypothalamus (Cloninger, 2009).

Like mammals, the dorsal cortex of birds developed forebrain structures that are not found in lizard-like reptiles and that are comparable in function to that of mammalian neocortex, including functional counterparts to mammalian prefrontal cortex (Butler and Cotterill, 2006; Jarvis et al., 2005; Reiner et al., 2004). Unlike their ancestors (i.e., fish, amphibians, and reptiles), birds have cortical-striatal-cortical loops like the prefrontal-striatal-prefrontal loops that regulate movement and emotion in anthropoid primates (Levy and Dubois, 2006).

Compared to reptiles, both mammals and birds have high brain–body ratios, forebrains with a relatively large volume of non-limbic cortex, and multiple cortical association areas that process multi-sensory input and support executive planning of movement (Butler and Cotterill, 2006). However, birds lack the multilayered neocortical architecture of all mammals, as well as the claustrum and the highly stratified organization of afferent innervation observed in therian mammals. The supervisory thalamic-cortical circuits of birds support functions that have sometimes been claimed to be unique capacities of mammals or humans, such as working memory, number sense, episodic memory in scrub jays and pigeons, complex vocalization and communication abilities in songbirds and parrots, use of available twigs as tools to obtain food in New Caledonian crows, and the capacity for deception by jays and ravens (Butler and Cotterill, 2006). However, birds lack self-awareness comparable to that of modern human beings. No single region on the avian brain has been shown to be homologous to mammalian prefrontal cortex, but there are regions that play analogous roles to prefrontal cortex in the complex cognitive functions displayed by birds and not by reptiles or amphibians (Butler and Cotterill, 2006).

The homologies and functional analogies between mammalian and avian thalamo-cortical structures and functions are examples of independent evolution of similar higher level cognitive functions beyond perceptual consciousness of the present moment. Here I will follow only along the human lineage without any claim that the abilities that develop are unique to that lineage.

The five major transitions in brain structure and function in mammals are summarized in Table 5.2. In early mammals and tree shrews, the major neocortical function is facultative control of mating, which is reflexive in squamates (Emmons, 2000; Wersinger and Baum, 1997). Primary somatosensory cortex is clearly developed in tree shrews (clade designated here as 2b), but there is little or no differentiation of sensory neocortex from motor neocortex (Kaas, 2006, 2008).

Compared to tree shrews, strepsirhines have greater motoric agility (e.g., adaptation for grasping and leaping) (Bloch et al., 2007; Szalay and Delson, 2001), greater dietary flexibility (Chivers and Hladik, 1980; Hladik et al., 1999), more maternal care of young (Broad et al., 2006), and more time spent in allogrooming (Emery and Amaral, 2002; Emmons, 2000; Moynihan, 2006). These functions involve regulation of material things like acquisition of food and related activities of daily living. Unlike rodents, in primates there is no direct path from the brainstem taste areas like the Nucleus of the Solitary Tract to the hypothalamus and amygdala. Information about taste in primates, in contrast, reaches the amygdala and orbitofrontal cortex from the primary taste cortex, which is in the frontal operculum and insula (Verhagen et al., 2004).

**Table 5.2** Cladistic staging of evolution of the functional components of self-aware consciousness in human beings: five basic transitions from the common ancestor of squamates and mammals to modern human beings

| Transitional clades | Emergent brain structural networks | Major function (voluntary) | Component functions |
|---|---|---|---|
| Early mammals | Somatosensory neocortex regulating bodily functions of midbrain for sex and survival | Mating (i.e., rudimentary intentionality influencing whether to copulate and reproduce conditional on success in foraging for adequate nutrient resources) | Sex drive<br>Foraging |
| Proto-primates and early primates | Differentiation of sensory and motor neocortex; neocortex regulating taste; social relations controlled by smell | Physicality (i.e., preferences regarding taste of food, enhanced physical agility for grasping, and capacity for digestion of fruits) | Rhythmicity<br>Agility<br>Discrimination |
| Anthropoids | Prefrontal cortex regulating hypothalamic functions of the limbic system (Semendeferi et al., 2001); PFC inputs replaces olfactory inputs regulating brain reward centers, facilitating emotion regulation (Smith et al., 2001; Broad et al., 2006); Von Economo neurons in AIC/ACC allowing rapid coordination of emotional preferences and behavior (Craig, 2008); mirror neuron system enhancing eye–hand coordination and emotional regulation of gesture, vocalization, and social interaction (Corballis, 2003; Rizzolatti and Craighero, 2004) | Emotionality (i.e., emotional regulation of individual behavior and social relationships leading to individual and social traditions, as well as awareness and expression of subjective feelings in gestures and vocalizations) | Receptivity<br>Closeness<br>Reconciliation<br>Tradition |

**Table 5.2** (continued)

| Transitional clades | Emergent brain structural networks | Major function (voluntary) | Component functions |
|---|---|---|---|
| Early Homo | Fronto-parietal perceptual-motor praxis system permits refined tool-making (Stout et al., 2000, 2008). Linkage of prefrontal cortex and auditory association cortex regulates cross-modal representation for meaningful and purposeful planning in solving social and physical problems (Pinker, 2010); coupling of terminal associative neo-neocortical regions in brain default network regulates attention and daydreaming; the communication of pre-modern hominids is probably based on coordination of gesture and vocalization with its meaning expressed by rudimentary cross-modal representation and interpreted by metaphoric understanding of action and sound production with greater involvement of the enlarged prefrontal cortex in hominids (Bruner, 2004) compared to anthropoids that have volitional initiation of vocalization regulated by the ACC and interpreted by the superior temporal gyrus and inferior parietal cortex (Hauser, 1997; Rauschecker and Tian, 2000; Hauser et al., 2002; Corballis, 2003) | Meaning (i.e., the process of reasoning and understanding objectively, which allows executive non-emotional problem-, long-term planning, and cooperation according to a mental template. Communication is by body language and volitional initiation of vocalization, but not with syntactical language, scientific notation, or abstract art. Hence meaning is a rudimentary and concrete form of symbolic learning and episodic memory that allows asking what, where, when, who, and how, but not abstract theoretical questions about why or what if. Accordingly it favors tradition and imitation, rather than symbolic invention. Hence pre-modern hominid intellect allows the proposal of plans, problem-solving with learning set formation (i.e., inter-set improvement in performance in subjects given discriminations involving different pairs of stimuli), elaboration of methods of implementation, evocation of feelings, and interpretation of the meaning of concrete cross-modal representations. Such long-term planning and problem solving is observed in hominids (e.g., mode 3 tool making, building shelters, domestication of fire), and similar | Taboo<br>Metaphor<br>Empathy<br>Judgment<br>Subliminal |

**Table 5.2** (continued)

| Transitional clades | Emergent brain structural networks | Major function (voluntary) | Component functions |
|---|---|---|---|
| | | operation with shorter working memory capacity is seen in apes and cetaceans (Macphail, 1982; Gaskin, 1982). However, such planning, problem-solving, and interpretation do not involve self-awareness, theoretical abstraction, or flexibility in shifting one's viewpoint in time or attitude because there is little or no capacity for mental time travel or theoretical creativity to ask "what if" or why except in special states of calm passive fixation like rituals) | |
| Modern *Homo sapiens* | Auto-noetic system unifying fronto-parieto-temporal neo-neocortical association areas (linked by visual projection system) (Levine, 2004; Tulving, 1987). Parietal cortex of modern humans is more rounded in shape and larger in volume than in pre-modern hominids (Bruner, 2004; Bruner and Holloway, 2010). | Apperception of unity (i.e., self-awareness of omni-sensory information as aspects of coherent and transcendental whole in which the components are interdependent and inseparable, as in the perception of harmony in music, awareness of the continuity of the self in personal narratives over time and place, and need for fairness in social relationships, compassion and altruistic concern for the weak or disadvantaged, and sometimes perception of universally uniform scientific laws and/or a universal unity of being) | Harmony<br>Sublimation<br>Aesthetics<br>Science<br>Awareness of unity |

Adapted with permission, Cloninger, 2009, Center for Well-Being

## What is the Functional Architecture of Human Brain Functions?

Before continuing with a description of the evolution of brain functions in anthropoids, it is essential to describe the method of summarizing information about the phylogeny of brain functions. Without a systematic way of organizing information, patterns in evolution can be difficult to recognize. An outline of my proposed model of the functional architecture of human beings is given in Table 5.3 as a matrix of functional abilities that emerged in mammalian evolution.

Each of the proposed functional labels has been defined psychologically and described in terms of comparative neuroanatomy and behavior. This information will be published elsewhere because of space limitations here. The reality of human evolution is a bushy nonlinear dynamic system as a whole (Wright, 1982; Tattersall, 2008a), but by following only the ancestral lineage leading to humans, it is adequate as a first approximation to describe the local process as a linear sequence of steps. The matrix given in Table 5.3 describes the functional organization of information processing by brain circuitry as it emerges in phylogeny from lizard-like animals to modern human beings. The matrix of functions represents the homologous modular structure of the human brain, which is comprised of domain- or situation-specific functions organized in terms of information processing systems with nested sub-systems and sub-subsystems (Cole and Schneider, 2007; Mithen, 1998). These brain modules are functionally dissociable but highly interactive, like components of a quantum field (Eccles, 1989; Pribram, 1993). The theoretical specification of a general functional model in this way is designed to allow predictions and interpretations of data from paleontology and anthropology that are ambiguous when taken one fossil or one extant animal at a time.

What we present must be considered as a working model to be tested, corrected, and refined. Such synthesis of data from psychology, cognitive neuroscience, and phylogeny offers a way for anthropologists and psychobiologists to begin to make adequate tests and interpretations of the wealth of data available about the evolution of brain functions.

We want to emphasize the importance of the matrix structure: a nested matrix structure is essential in order to take into account the holographic and modular nature of human consciousness and brain functions (Pribram, 1993; Cloninger, 2009). The matrix structure has crucial dividends because it requires a systematic approach and also suggests a testable mechanism for cladogenesis based on precursor functions that become generalized at transitions in response to adaptive challenges and natural selection, as described in subsequent tables. The strongest evidence for the matrix structure is the consistent evidence for the same brain system to regulate converse functions (i.e., functions that are the reverse of one another in the sense of involving the same elements but with the direction of effects transposed). For example, handicraft, such as planning how to build stone tools, is the material aspect of intellectual functioning (designated as 5–3, as explained in the next paragraph), whereas its converse function, gesture, is communicating by means of parts of the body (designated as 3–5). The same lateral prefrontal network regulates planning of motor sequences in both handicraft and gestural expression (Koechlin et al., 2000; Passingham et al., 2010). Such symmetries reveal a matrix

**Table 5.3** Functional architecture of human beings as it emerges from **core functions** (in bold) and other precursor functions in mammalian evolution[a]

| Plane | Sexual sub-plane—2 | Material sub-plane—3 | Emotional sub-plane—4 | Intellectual sub-plane—5 | Spiritual sub-plane—7 |
|---|---|---|---|---|---|
| 7—Spiritual | Moderation [7] | Spontaneity [7] | Altruism [7] | Dialog [7] | **Unity [7]** |
| 5—Intellectual | Planning [5] | Handicraft [5] | Rapport [5] | **Meaning [5]** | Diplomacy [7] |
| 4—Emotional | Intimacy [4] | Motive [4] | **Mood [4]** | Appeal [5] | Humor [7] |
| 3—Material | Parenting [3] | **Physicality [3]** | Sensibility [4] | Gesture [5] | Charity [7] |
| 2—Sexual | **Mating [2]** | Gratification [3] | Sensuality [4] | Community [5] | Egalitarianism [7] |

[a] The clade in which functions emerge are indicated in brackets [ ]. The labels of sub-planes given here describe examples of functions that emerge or are qualitatively enhanced in a stepwise function along the evolutionary lineage of clades leading to human beings, represented here as an expanding matrix of functions. The only aspect of dialog discussed here is syntactical language

Adapted with permission, Cloninger, 2009, Center for Well-Being

pattern that helps to recognize the same causal processes as they are reflected in converse or transposed situations.

The sequence of emergence of function involves the emergence of precursor functions within a matrix prior to each major transition. For example, in early mammals (stage 2a involving sexuality of the common ancestor of monotremes, marsupials, and tree shrews), the most basic function regulated by neocortex is mating (designated as functional sub-plane 2–2 in which the first number specifies the plane and the second number specifies the sub-plane). Then in tree shrews (stage 2b) there is emergence of an enhanced ability to restrain sexual activity intentionally for other functions like feeding by neocortical regulation of the ventromedial hypothalamius (VMH). Tree shrews spend most of their time foraging and do not reproduce unless they obtain sufficient nutrients for childbearing.

The emergence of neocortical modulation of taste in early primates was coincident with new adaptive functions regulating gratification (sub-plane 2–3, material aspects of sexuality) and parenting (sub-plane 3–2, sexual aspects of materiality). Precursors of emotionality emerge in strepsirhines (i.e., stage 3b) including enhanced sensory discrimination, enhanced maternal care, and preference bonding, which are late emotional aspects of sub-planes 3–3, 3–2, and 2–3, respectively. Accordingly, each stage is divided into an early phase that is followed by a late phase in which there are precursors that provide a foundation for future major transitions.

## Brain Development in Anthropoid Primates

Strepsirhines have well-differentiated sensory and motor neocortical areas in contrast to tree shrews. Detailed studies of galagos revealed several changes in brain structure that support enhanced motor agility with advanced grasping and leaping adaptations compared to tree shrews (Kaas, 2006, 2008). The findings include greater topographical ordering of sensory input for the hands and feet, premotor and supplementary motor areas, at least two motor areas in cingulate cortex, and feedback circuits among prefrontal cortex, premotor cortex, and primary motor cortex. In addition, strepsirhines have an enlarged posterior parietal cortex for processing visual, auditory, and somatosensory information to form and relay instructions about hand and eye movements to premotor areas.

In anthropoids there is emergence of emotionality with patterns of mood regulation, intimacy, motive, sensuality, and sensibility (see Table 5.3) that are similar to human affectivity, as noted by Darwin, Bowlby, and others (Preston and De Waal, 2002; Sussman and Chapman, 2004). Related brain changes include the development of prefrontal cortex for regulation of emotional functions (Semendeferi et al., 2001), a distinctive system for interoceptive processing of sensual aspects of touch (Craig, 2004, 2005, 2009), and the emergence of the mirror neuron system to provide rapid functional coordination of frontal and parietal cortical areas (Rizzolatti and Craighero, 2004). The orbital prefrontal network regulates the sensory awareness of the affective qualities of stimuli, and the medial prefrontal network organizes emotional expression along with other visceral functions (Ongur and Price, 2000).

The medial prefrontal cortex operates as a component of a brain circuit that first emerges in anthropoids, called the “default mode network” (Raichle et al., 2001; Rilling et al., 2007; Buckner et al., 2008). It is called the default mode because it is most active in states of restful calm. The medial prefrontal network, but not the orbital network, expands and differentiates in a multi-step progression of size and number of areas and functions in the transition from anthropoid to human (Ongur and Price, 2000). The expansion and differentiation of the medial PFC and the default mode network are implicated in the stepwise progression from medial prefrontal regulation of emotionality in simians to that of symbolism in pre-modern humans and the perception of unity in modern humans (Cloninger, 2009).

Apes represent the transitional group in which precursor functions emerge that serve as a foundation for the emergence of intellectual learning (i.e., “meaning” with objective problem solving and long-term planning) in early humans. The precursor functions for meaning observed in apes include intergroup proto-cultural variation in traditions for courting, foraging, tool-use, food preparation, and grooming styles (aspects of 4–3, motive) (Kawai, 1965; Whiten et al., 2007; Bonnie et al., 2007) along with enhanced observational learning involving imitation (Beck, 1974) and secondary representation including mirror self-recognition (see 4–3) (de Waal, 1996; de Waal et al., 2005), reconciliation after fights (de Waal, 2000), melodious loud calls (aspects of 3–4, sensibility) (Geissmann, 2002), daydreaming (an aspect of 4–2, intimacy), and the ability to recognize when others may not see what they intend to do (de Waal, 2008), such as mating with a receptive partner when out of sight of the dominant male (an aspect of 2–4, sensuality). Monkeys do show some observational learning, as in for using tools and other skills and traditions (Beck, 1973a, b), but such learning in apes is more frequent and involves learning arbitrary proto-cultural conventions independent of conditioning to obtain rewards (Beck, 1974; de Waal, 1999; Bonnie et al., 2007). These precursor functions emerged as useful abilities in cooperative group foraging in anthropoid primates (Deacon, 1997), thereby setting the stage for the emergence of language and other unique aspects of modern human cognition later in evolution (Tattersall, 2004).

In early hominids (i.e., members of the genus *Homo*), there is emergence of neocortical regions with several unique functional properties, which has been called “neo-neocortex” (Eccles, 1989). In addition to being late to emerge in evolution, neo-neocortex is also late to myelinate in modern humans and has delayed dendritic and synaptic developments when compared to the “old” neocortex present in the sensory, motor, and emotional systems of non-hominids. When lesions of neo-neocortical areas occur in young people, especially before puberty, neo-neocortical development is able to compensate functionally by reallocating functions to intact areas. The protracted development of these “terminal zones” of associative neocortex is regulated by oligodendrocytes, which continue to differentiate into myelin-producing cells late into the fifth decade of life (Bartzokis, 2004). The unique metabolic demands of producing and maintaining the myelination of the expanded hominid neocortex created an increased demand for essential nutrients from fishing and the brains of game in hominids as sources of dietary fats, such as omega-3 fatty acids (Eaton et al., 1997; Crawford et al., 1999; Cunnane et al., 2007). The nutrient and metabolic demands of neo-neocortex also resulted in the vulnerability of unique human cognitive functions to Alzheimer's dementia and other uniquely human brain dysfunctions (Bartzokis, 2004).

The emergence of neo-neocortex is documented in early hominids by evidence of cerebral asymmetry in brain endocasts and of right-handedness in the clockwise rotation of stone cores during flaking by 1.8 mya in Africa (Toth, 1985; Holloway, 2009). In modern humans, there is marked lateralization of the functions of neo-neocortex in the two cerebral hemispheres. The right neo-neocortex carries out geometrical and spatial processing, and processing of music, prosody, holistic images, and synthesis over time, whereas the left neo-neocortex processes conceptual similarities and analysis of details over time algorithmically (Sperry, 1982).

The regions of neo-neocortex that function asymmetrically are terminal association areas, which include the polar and medial prefrontal cortex, inferior temporal cortex, and inferior parietal cortex, and other regions that are jointly activated through the Default Mode Network (DMN). The rudimentary core of the DMN was already present in anthropoids (Buckner et al., 2008), in which it regulates emotionality (Drevets et al., 2008; Price and Drevets, 2010). In hominids, its functional capacity expanded with emergence of neo-neocortex for intellectual functions that are activated when hominids are in a state of calm (e.g., eyes closed resting) or passive alertness (e.g., passive visual fixation), as when meditating, in reverie, or in fantasy (Raichle et al., 2001; Rilling et al., 2007; Travis et al., 2010). Later in evolution, the functions of neo-neocortical regions expanded into a proactive functional fronto-temporo-parietal circuit serving autobiographical memory and self-aware consciousness in modern *H. sapiens* (Levine, 2004), rather than being functionally active mainly at rest in pre-modern hominids (Raichle et al., 2001; Rilling et al., 2007; Buckner et al., 2008). The potential for greater cognitive flexibility and creativity of modern human thinking under stressful conditions provided an adaptive advantage that may explain the extinction of all other hominid species after the emergence of modern *H. sapiens*. Hence the evolution of neocortex in hominids involves not just quantitative growth in size, but a succession of two qualitative functional shifts marked by the emergence of cerebral asymmetry in pre-modern hominids and of self-awareness in modern humans.

Symbolic activity like symbol-based cognitive control and other executive functions are possible with the neo-neocortical enhancement of the anthropoid Brain Default Network in hominids, which allowed first-person perspective taking and daydreaming, as when a person is letting his or her mind freely wander about inner thoughts and feelings (Buckner et al., 2008; Raichle et al., 2001; Rilling et al., 2007). Meaning builds on the emotion-regulating functions needed for cooperative group foraging in anthropoids (Deacon, 1997). For example, *H. erectus* showed executive skills and craftsmanship in the making of refined tools in their Acheulian culture (Stout et al., 2000, 2008). These symbolic functions depend on processing in the inferior parietal lobule (IPL), which is a convergence area for touch, hearing, and vision, allowing cross-modal transformations important for symbolism and language (Deacon, 1997; Eccles, 1989; McGeoch et al., 2007). In modern humans, the angular gyrus (BA 39) of the IPL in particular has an important role in the comprehension of metaphor and allegory (Ramachandran, 2005). The core functions of meaning or basic hominid symbolism involve cross-modal transformation, such as capacities for taboo, metaphor, empathy, and intellectual problem solving (Cloninger, 2009).

In modern human beings, the evolution of functional connectivity among all the regions of neo-neocortex allows self-awareness and the transcendental apperception of unity. For example, the emotional aspects of the perception of unity involve the unique modern hominid perception of unity that can be described as "humanism". Humanism is composed of feelings of engagement and altruism. Such humanistic engagement and altruism have been investigated in studies of child development and of brain imaging while adults make voluntary charitable donations as a personal sacrifice. Modern human children are selfish at age 3–4 before their brain network for self-awareness begins to mature, but then develop altruistic attitudes by the ages of 5–7 years (Fehr and Rockenbach, 2004; de Quervain et al., 2004; Fehr et al., 2008). Altruism, as measured by costly donations to humanitarian causes, was strongly associated with activation of anterior prefrontal cortex (BA 10/11/32). The subgenual cingulate (BA 25) was also activated by altruistically motivated decisions and not by monetary rewards (Moll et al., 2006). The activation of the frontal poles (BA 10) during altruistic acts by humans is noteworthy because there is no brain region homologous to the human frontal polar cortex (BA10) in monkeys (Ongur and Price, 2000).

Pre-modern hominids such as Neandertals and ancient *H. sapiens* represent the transitional group in which precursor functions emerge that serve as a foundation for the emergence of self-aware consciousness in modern human beings. The precursor functions for self-aware consciousness involve activation of neo-neocortex in restful states by means of the Default Mode Network, such as passive visual fixation or ritualized burying of the dead by Neandertals and ancient *H. sapiens*.

Finally, modern human beings have the potential for stable self-aware perception of a sense of unity in all aspects of life, manifest by emergent capacities for harmony, sublimation, aesthetics, science, spirituality, humor, and inventiveness (Cloninger, 2004). These integrative abilities give modern human beings their potential in art, science, and spirituality, which sometimes lead to transcendent joy about beauty, truth, or goodness (Mithen, 1996; Cloninger, 2004). The self-aware perception of unity is fundamental for art, science, and spirituality. Modern human art involves aesthetic qualities beyond the artistic craftsmanship observed in pre-modern hominids. With modern aesthetic sensibility, art has become the creative search for the awareness of beauty by an integrated representation and organization of diverse parts that make up a harmonious whole (Merriam-Webster, 2003). Science is the search for knowledge of general truth by systematic theorem-like study of the operation of uniform laws to explain and predict particular events that comprise a coherent model of space and time within the universe (Merriam-Webster, 2003). Science is described as "theorem-like" or hypothetical and deductive (i.e., If…, then….) because it is a search for specific conditions that predict particular consequences, which depends on an understanding of the relationships of parts to one another in a whole. Likewise, spirituality with the capacity for transcendence observed in modern humanity involves the search for personal knowledge of what is divine or good by self-awareness of the universal unity of being, particularly including what is beyond transient individual existence (Cloninger, 2007). As a result of the transcendental unity of apperception (Kant, 1781), modern human beings have the extraordinary Promethean potential to plan for the future while consciously recollecting the lessons of their past, which is variously called foresight, "pure reason" (Kant, 1797), "conscious time-binding" (Stebbins, 1982), or "mental time travel" (Suddendorf et al., 2009; Tulving, 2001).

Such integrated awareness of unity in art, science, and spirituality is supported by the auto-noetic system of learning and memory (Tulving, 2001, 2002). Such self-aware consciousness allows a person to travel in space and time in their recollection of episodic events, which is essential for self-awareness of a person's own life narrative. Such autobiographical or holistic thinking involves a distributed fronto-temporo-parietal network (Levine, 2004) in which memory is encoded by the left MPFC and hippocampus and is retrieved by the right MPFC (Tulving and Lepage, 2001; Tulving, 2002). Essentially the visual projection system connects regions of neo-neocortex in all tertiary association cortices so that the brain can function as a coherent whole. Whereas in pre-modern hominids, the terminal association areas of neo-neocortex can be transiently engaged in states of calm passive alertness, these areas can be stably coupled in self-awareness even under stressful conditions in modern human beings.

Modern human language with syntax is an important example of the functions that emerge with the perception of unity. The abilities that depend on the perception of unity emerge along with the ability to shift temporal perspective, as well as the ability to recollect one's personal past after age 4 years. In linguistics, viewpoint aspect is the temporal organization of situations (e.g., events or states) and temporal perspective (Smith, 1997). In music, harmony is the simultaneous combination of notes into chords and the sequential temporal ordering of chords (i.e., chord progressions). Human children normally have implicit knowledge and ability to perceive the syntactic functions that typify harmony in music and viewpoint aspect in language by age 6 or 7 years with no special musical or linguistic training. In other words, they know what sounds good (i.e., consonant) and what sounds bad (i.e., dissonant) (Schellenberg et al., 2005). Syntactic functions, such as the perception of harmony or the ability to appreciate shifts in viewpoint aspect (McColgan and McCormack, 2008), depend on the perception of unity, which is the core function of the self-aware consciousness system. Self-awareness begins to mature after age 4 years and is fairly well developed by age 7 years in most children at the same time that harmony (Schellenberg et al., 2005), the theorem-like understanding of grammatical rules (including rules for representation of contextual perspective, such as tense and viewpoint aspect) (Crain, 2005; Lind and Bowler, 2008), and preferences for egalitarianism (Fehr et al., 2008) emerge. The dependence of syntactical and grammatical functions on the self-aware consciousness system suggests that the meta-perceptual functions required for modern language emerged for the first time in modern humans.

The perception of unity permits the personal integration of values, thoughts, and actions. Despite the capacity of modern human beings for integration, there are substantial differences between individuals in the development of their self-awareness, humor, creativity, and well-being (Cloninger, 2004).

## Implications for the Anthropology of Cooperation

The complex phylogeny of human functional abilities presents both opportunities and challenges for both anthropologists and psychobiologists. Such core functions never operate in isolation because adaptation involves the whole person, not separate organs or functions. Accordingly, the emergence of a new functional ability leads to interactions with all the individual's other abilities. Detailed observational studies are needed in other mammalian species in order to distinguish the functional abilities that are possible with the brain structures of those species. For example, dogs do not have the type of slow-conducting sensory nerves that allows anthropoids to distinguish the affective quality of what is pleasant versus unpleasant. They can experience pain and pleasure, but do not have the nervous system that allows processing of affective valence in the same way as anthropoid primates (Craig, 2004, 2009). People can observe the behavioral expressions and responses of dogs and may empathically project what another human being would feel if they showed the same expressions and behavioral responses. However, dogs simply cannot have the same affective experience that human beings can imagine they might be having.

As a result, we must be careful in deconstructing the components of cooperation and suggesting what other species can or cannot experience. For example, it is essential that we distinguish between altruism and the social affiliation seen in anthropoids. I would reserve the word "altruism" for an attitude that is only possible in an animal that has the capacity for self-transcendence, which requires identification with what is beyond the existence of the individual. Altruism is an expression of self-awareness that emerges for the first time in modern human beings along with self-aware consciousness and the capacity for sublimation. Altruism depends on brain structures that are only present in human beings and not in nonhuman primates. Altruism emerges in human beings along with other aspects of the perception of unity, such as science, art, and spirituality. Hence animals without self-awareness and a capacity for self-transcendence are incapable of altruism as defined here. Even chimpanzees do not have the capacity for self-transcendence, as indicated by abilities like "mental time travel" (Povinelli, 2000; Rilling et al., 2007; Suddendorf and Whiten, 2001; Tulving, 2001). Of course the word altruism can be used for other cooperative behaviors, but then what word can we use to distinguish "the intentional practice of disinterested and selfless concern for the well-being of others" from other kinds of cooperation seen in strepsirhines or the cooperation seen in haplorhines? Even in modern human children, altruistic thinking, as commonly defined (i.e., selfless concern for the welfare of others) only emerges between 4 and 7 years of age along with the maturation of self-aware consciousness and the capacity for theory of mind (Fehr et al., 2008).

My point is that we need to use our knowledge of phylogeny and comparative neuroanatomy to develop a systematic terminology with practical definitions and descriptions of the terms so that we do not anthropomorphize our interpretations of behavior in other species. Communication and understanding are compromised when people attribute functions like intimacy to species that have no brain capacity for emotionality, taboo or culture to species that have no capacity for symbolization, or altruism to species that have no capacity for self-awareness. Likewise debates about whether human beings are either prosocial or antisocial only serve to polarize and confuse discussion when the reality is that human beings are capable of peace and violence under different conditions. We all have the primitive functions of an "inner tree shrew" within us, which may be expressed when we fail to utilize the higher cognitive functions of human self-awareness that allow the perception of unity even under stressful conditions, like when we are hungry, frustrated, or threatened. The pretense that we can make theory-free observations is naïve, and an understanding of brain-behavior relationships requires a theory that integrates neurobiology and behavior in their joint evolutionary context. As Kant said, "intuitions without concepts are blind, and concepts without intuitions are empty (Kant, 1781)." Unless we have clear concepts of functional abilities in terms of the mode of information processing and the situational context, then our observations are blind and cannot lead to real understanding.

## References

Agnew N, Demas M, Leakey MD (1996). The laetoli footprints. *Science* 271: 1651–1652.

Alperson-Afil N, Sharon G, Kislev M, Melamed Y, Zohar I, Ashkenazi S, Rabinovich R, Biton R, Werker E, Hartman G, Feibel C, Goren-Inbar N (2009). Spatial organization of hominin activities at gesher benot ya'aqov, israel. *Science* 326: 1677–1680.

Bartzokis G (2004). Age-related myelin breakdown: A developmental model of cognitive decline and alzheimer's disease. *Neurobiol Aging* 25: 5–18; author reply 49–62.

Bates E, MacWhinney B (1989). Functionalism and the competitive model. In *The crosslinguistic study of sentence processing* (MacWhinney B, Bates E, eds.). pp. 3–73. Cambridge, Cambridge University Press.

Beck BB (1973a). Cooperative tool use by captive hamadryas baboons. *Science* 182: 594–597.

Beck BB (1973b). Observation learning of tool use by captive guinea baboons (papio papio). *Am J Phys Anthropol* 38: 579–582.

Beck BB (1974). Baboons, chimpanzees, and tools. *J Hum Evol* 3: 509–516.

Bengtsson SL, Haynes JD, Sakai K, Buckley MJ, Passingham RE (2009). The representation of abstract task rules in the human prefrontal cortex. *Cereb Cortex* 19: 1929–1936.

Bickerton D (2010). *Adam's tongue: How humans made language*. New York, Hill and Wang.

Biknevicius AR (1986). Dental function and diet in the carpolestidae (primates, plesiadapiformes). *Am J Phys Anthropol* 71: 157–171.

Bloch JI, Silcox MT, Boyer DM, Sargis EJ (2007). New paleocene skeletons and the relationship of plesiadapiforms to crown-clade primates. *Proc Natl Acad Sci USA* 104: 1159–1164.

Bonnie KE, Horner V, Whiten A, de Waal FB (2007). Spread of arbitrary conventions among chimpanzees: A controlled experiment. *Proc Biol Sci* 274: 367–372.

Bowlby J (1983). *Attachment*. New York, Basic Books.

Brinch M, Isager T, Tolstrup K (1988). Anorexia nervosa and motherhood: Reproduction pattern and mothering behavior of 50 women. *Acta Psychiatr Scand* 77: 611–617.

Broad KD, Curley JP, Keverne EB (2006). Mother-infant bonding and the evolution of mammalian social relationships. *Philos Trans R Soc Lond B Biol Sci* 361: 2199–2214.

Brosnan SF, De Waal FB (2003). Monkeys reject unequal pay. *Nature* 425: 297–299.

Brosnan SF, Freeman C, De Waal FB (2006). Partner's behavior, not reward distribution, determines success in an unequal cooperative task in capuchin monkeys. *Am J Primatol* 68: 713–724.

Bruce LL, Neary TJ (1995). Afferent projections to the ventromedial hypothalamic nucleus in a lizard, gekko gecko. *Brain Behav Evol* 46: 14–29.

Bruner E (2004). Geometric morphometrics and paleoneurology: Brain shape evolution in the genus homo. *J Hum Evol* 47: 279–303.

Bruner E, Holloway RL (2010). A bivariate approach to the widening of the frontal lobes in the genus homo. *J Hum Evol* 58: 138–146.

Bruner E, Manzi G, Arsuaga JL (2003). Encephalization and allometric trajectories in the genus homo: Evidence from the neandertal and modern lineages. *Proc Natl Acad Sci USA* 100: 15335–15340.

Buckner RL, Andrews-Hanna JR, Schacter DL (2008). The brain's default network: Anatomy, function, and relevance to disease. *Ann N Y Acad Sci* 1124: 1–38.

Burgess PW, Veitch E, de Lacy Costello A, Shallice T (2000). The cognitive and neuroanatomical correlates of multitasking. *Neuropsychologia* 38: 848–863.

Butler AB, Cotterill RM (2006). Mammalian and avian neuroanatomy and the question of consciousness in birds. *Biol Bull* 211: 106–127.

Chapais B (1988). Rank maintenance in female japanese macaques: Experimental evidence for social dependency. *Behavior* 104: 41–59.

Chapais B (1995). Alliances as a means of competition in primates: Evolutionary, developmental, and cognitive aspects. *Am J Phys Anthropol* 38: 115–136.

Chapais B (2008). *Primeval kinship: How pair-bonding gave birth to human society*. Cambridge, MA, Harvard University Press.

Chivers DJ (1998). Measuring food intake in wild animals: Primates. *Proc Nutr Soc* 57: 321–332.

Chivers DJ, Hladik CM (1980). Morphology of the gastrointestinal tract in primates: Comparisons with other mammals in relation to diet. *J Morphol* 166: 337–386.

Christiansen MH, Kirby S (2003). *Language evolution*. New York, Oxford University Press.

Cloninger CR (1994). The genetic structure of personality and learning: A phylogenetic model. *Clin Genet* 46: 124–137.

Cloninger CR (1995). The psychobiological regulation of social cooperation. *Nat Med* 1: 623–625.

Cloninger CR (2003). Completing the psychobiological architecture of human personality development: Temperament, character, and coherence. In *Understanding human development: Dialogues with lifespan psychology* (Staudinger UM, Lindenberger UER, eds.). pp. 159–182. London, Kluwer Academic Publishers.

Cloninger CR (2004). *Feeling good: The science of well-being*. New York, Oxford University Press.

Cloninger CR (2007). Spirituality and the science of feeling good. *South Med J* 100: 740–743.

Cloninger CR (2009). The evolution of human brain functions: The functional structure of human consciousness. *Aust N Z J Psychiatr* 43: 994–1006.

Cloninger CR, Gilligan SB (1987). Neurogenetic mechanisms of learning: A phylogenetic perspective. *J Psychiatr Res* 21: 457–472.

Cloninger CR, Svrakic DM (1997). Integrative psychobiological approach to psychiatric assessment and treatment. *Psychiatry* 60: 120–141.

Cloninger CR, Zohar AH (2011). Personality and the perception of health and happiness. *J Affect Disord* 128: 24–32.

Cole MW, Schneider W (2007). The cognitive control network: Integrated cortical regions with dissociable functions. *Neuroimage* 37: 343–360.

Conroy GC, Weber GW, Seidler H, Tobias PV, Kane A, Brunsden B (1998). Endocranial capacity in an early hominid cranium from sterkfontein, South Africa. *Science* 280: 1730–1731.

Corballis MC (2003). From mouth to hand: Gesture, speech, and the evolution of right-handedness. *Behav Brain Sci* 26: 199–208; discussion 208–160.

Corballis MC (2009a). Language as gesture. *Hum Mov Sci* 28: 556–565.

Corballis MC (2009b). The evolution and genetics of cerebral asymmetry. *Philos Trans R Soc Lond B Biol Sci* 364: 867–879.

Craig AD (2004). Human feelings: Why are some more aware than others? *Trends Cogn Sci* 8: 239–241.

Craig AD (2005). Forebrain emotional asymmetry: A neuroanatomical basis? *Trends Cogn Sci* 9: 566–571.

Craig AD (2008). Interoception and emotion: A neuroanatomical perspective. In *Handbook of emotions* (Lewis M, Haviland-Jones JM, Barrett LF, eds.). pp. 272–290. New York, Guilford Press.

Craig AD (2009). How do you feel – now? The anterior insula and human awareness. *Nat Rev Neurosci* 10: 59–70.

Crain WC (2005). *Theories of development: Concepts and applications*. Englewood Cliffs, NJ, Prentice Hall.

Crawford MA, Bloom M, Broadhurst CL, Schmidt WF, Cunnane SC, Galli C, Gehbremeskel K, Linseisen F, Lloyd-Smith J, Parkington J (1999). Evidence for the unique function of docosahexaenoic acid during the evolution of the modern hominid brain. *Lipids* 34(Suppl): S39–47.

Cunnane SC, Plourde M, Stewart K, Crawford MA (2007). Docosahexaenoic acid and shore-based diets in hominin encephalization: A rebuttal. *Am J Hum Biol* 19: 578–581.

D'Argembeau A, Ruby P, Collette F, Degueldre C, Balteau E, Luxen A, Maquet P, Salmon E (2007). Distinct regions of the medial prefrontal cortex are associated with self-referential processing and perspective taking. *J Cogn Neurosci* 19: 935–944.

Darling D (2010). Vertebrate nervous system. Internet Encyclopedia of Science, vol. 5 at http://www.daviddarling.info/encyclopedia/V/vertebrate_nervous_system.html, Downloaded May 10, 2010.

Deacon TW (1997). *The symbolic species: The co-evolution of language and the brain*. New York, W.W. Norton and Company.

de Heinzelin J, Clark JD, White T, Hart W, Renne P, WoldeGabriel G, Beyene Y, Vrba E (1999). Environment and behavior of 2.5-million-year-old bouri hominids. *Science* 284: 625–629.

de Quervain DJ, Fischbacher U, Treyer V, Schellhammer M, Schnyder U, Buck A, Fehr E (2004). The neural basis of altruistic punishment. *Science* 305: 1254–1258.

de Waal FB (1996). Macaque social culture: Development and perpetuation of affiliative networks. *J Comp Psychol* 110: 147–154.

de Waal FB (1999). Cultural primatology comes of age. *Nature* 399: 635–636.

de Waal FB (2000). Primates – a natural heritage of conflict resolution. *Science* 289: 586–590.

de Waal FB, Dindo M, Freeman CA, Hall MJ (2005). The monkey in the mirror: Hardly a stranger. *Proc Natl Acad Sci USA* 102: 11140–11147.

de Waal FB, Leimgruber K, Greenberg AR (2008). Giving is self-rewarding for monkeys. *Proc Natl Acad Sci USA* 105: 13685–13689.

de Waal FBM (2008). The thief in the mirror. *PLoS Biol* 6: 1621–1622.

Dobzhansky T (1973). Nothing in biology makes sense except in the light of evolution. *Am Biol Teacher* 35: 125–129.

Donald M (1991). *Origins of the modern mind: Three stages in the evolution of culture and cognition*. Cambridge, MA, Harvard University Press.

Drevets WC, Price JL, Furey ML (2008). Brain structural and functional abnormalities in mood disorders: Implications for neurocircuitry models of depression. *Brain Struct Funct* 213: 93–118.

Dunbar RI, Shultz S (2007). Evolution in the social brain. *Science* 317: 1344–1347.

Eaton SB, Eaton SB, 3rd, Konner MJ (1997). Paleolithic nutrition revisited: A twelve-year retrospective on its nature and implications. *Eur J Clin Nutr* 51: 207–216.

Eccles JC (1989). *Evolution of the brain: Creation of the self*. London, Routledge.

Emery NJ, Amaral DG (2002). The role of the amygdala in primate social cognition. In *Cognitive neuroscience of emotion* (Lane RD, Nadel L, eds.). pp. 156–191. New York, Oxford University Press.

Emmons LH (2000). *Tupai: A field study of bornean treeshrews*. Berkeley, CA, University of California Press.

Fehr E, Bernhard H, Rockenbach B (2008). Egalitarianism in young children. *Nature* 454: 1079–1083.

Fehr E, Rockenbach B (2004). Human altruism: Economic, neural, and evolutionary perspectives. *Curr Opin Neurobiol* 14: 784–790.

Fleagle JG (1999). *Primate adaptation and evolution*. New York, Academic Press.

Fleeson W (2004). Moving personality beyond the person-situation debate. *Curr Directions Psychol Sci* 13: 83–87.

Fry DP (2009). *Beyond war: The human potential for peace*. New York, Oxford University Press.

Fuster JM (2000). Prefrontal neurons in networks of executive memory. *Brain Res Bull* 52: 331–336.

Gabora L (2004). Ideas are not replicators but minds are. *Biol Philos* 19: 127–143.

Gabora L (2006). Self-other organization: Why early life did not evolve through natural selection. *J Theor Biol* 241: 443–450.

Gabora L (2008). The cultural evolution of socially situated cognition. *Cogn Syst Res* 9: 104–114.

Gaskin DE (1982). *The ecology of whales and dolphins*. London, Honeymoon.

Geissmann T (2002). Duet-splitting and the evolution of gibbon songs. *Biol Rev Camb Philos Soc* 77: 57–76.

Gendall KA, Joyce PR, Sullivan PF, Bulik CM (1998). Personality and dimensions of dietary restraint. *Int J Eat Disord* 24: 371–379.

Geschwind N (1965a). Disconnexion syndromes in animals and man. I. *Brain* 88: 237–294.

Geschwind N (1965b). Disconnexion syndromes in animals and man. Ii. *Brain* 88: 585–644.

Goos HJT (1978). Hypophysiotropic centers in the brain of amphibians and fish. *Am Zoologist* 18: 401–410.

Goren-Inbar N, Alperson N, Kislev ME, Simchoni O, Melamed Y, Ben-Nun A, Werker E (2004). Evidence of hominin control of fire at gesher benot ya'aqov, israel. *Science* 304: 725–727.

Goren-Inbar N, Feibel CS, Verosub KL, Melamed Y, Kislev ME, Tchernov E, Saragusti I (2000). Pleistocene milestones on the out-of-africa corridor at gesher benot ya'aqov, israel. *Science* 289: 944–947.

Goren-Inbar N, Sharon G, Alperson-Afil N, Laschiver I (2008). The acheulean massive scrapers of gesher benot ya'aqov-a product of the biface chaine operatoire. *J Hum Evol* 55: 702–712.

Goren-Inbar N, Sharon G, Melamed Y, Kislev M (2002). Nuts, nut cracking, and pitted stones at gesher benot ya'aqov, israel. *Proc Natl Acad Sci USA* 99: 2455–2460.

Hauser MD (1997). *The evolution of communication*. Cambridge, MA, MIT Press.

Hauser MD, Chomsky N, Fitch WT (2002). The faculty of language: What is it, who has it, and how did it evolve? *Science* 298: 1569–1579.

Hawks J, Hunley K, Lee SH, Wolpoff M (2000). Population bottlenecks and pleistocene human evolution. *Mol Biol Evol* 17: 2–22.

Hilgartner R, Zinner D, Kappeler PM (2008). Life history traits and parental care in lepilemur ruficaudatus. *Am J Primatol* 70: 2–11.

Hladik CM, Chivers DJ, Pasquet P (1999). On diet and gut size in non-human primates and humans: Is there a relationship to brain size? *Curr Anthropol* 40: 695–697.

Holloway RL (2009). Brain fossils: Endocasts. In *Encyclopedia of neuroscience* (Squire LR, ed.). pp. 353–361. New York, Elsevier.

Holmgren S, Jensen J (2001). Evolution of vertebrate neuropeptides. *Brain Res Bull* 55: 723–735.

Janvier P (1997). Craniata: Animals with skulls. In *The Tree of Life Web Project*, http://tolweb.org/Craniata/14826/1997.01.01. Downloaded July 1, 2009.

Jarvis ED, Gunturkun O, Bruce L, Csillag A, Karten H, Kuenzel W, Medina L, Paxinos G, Perkel DJ, Shimizu T, Striedter G, Wild JM, Ball GF, Dugas-Ford J, Durand SE, Hough GE, Husband S, Kubikova L, Lee DW, Mello CV, Powers A, Siang C, Smulders TV, Wada K, White SA, Yamamoto K, Yu J, Reiner A, Butler AB (2005). Avian brains and a new understanding of vertebrate brain evolution. *Nat Rev Neurosci* 6: 151–159.

Jolly A (1998). Pair-bonding, female aggression and the evolution of lemur societies. *Folia Primatol (Basel)* 69(Suppl 1): 1–13.

Jurgens U (1982). Amygdalar vocalization pathways in the squirrel monkey. *Brain Res* 241: 189–196.

Jurgens U (1983). Afferent fibers to the cingular vocalization region in the squirrel monkey. *Exp Neurol* 80: 395–409.

Jurgens U (2009). The neural control of vocalization in mammals: A review. *J Voice* 23: 1–10.

Kaas JH (2006). Evolution of the neocortex. *Curr Biol* 16: R910–914.

Kaas JH (2008). The evolution of the complex sensory and motor systems of the human brain. *Brain Res Bull* 75: 384–390.

Kant I (1781). *Critique of pure reason*. New York, The Modern Library.

Kant I (1797). *Anthropology from a pragmatic point of view*. Carbondale, IL, Southern Illinois University Press.

Kappeler PM (1997). Determinants of primate social organization: Comparative evidence and new insights from malagasy lemurs. *Biol Rev Camb Philos Soc* 72: 111–151.

Kawai M (1965). On the newly-acquired pre-cultural behavior of the natural troop of japanese monkeys on koshima islet. *Primates* 6: 1–30.

Kawamichi T, Kawamichi M (1979). Spatial organization and territory of tree shrews (tupaia glis). *Animal Behav* 27: 381–393.

Kay RF, Ross C, Williams BA (1997). Anthropoid origins. *Science* 275: 797–804.

Kay RF, Williams BA, Ross CF, Takai M, Shigehara N (2004). Anthropoid origins: A phylogenetic analysis. In *Anthropoid origins: New visions* (Ross CF, Kay RF, eds.). pp. 91–135. New York, Kluwer Academic/Plenum Publishers.

Kimbel WH, Lockwood CA, Ward CV, Leakey MG, Rak Y, Johanson DC (2006). Was australopithecus anamensis ancestral to a. Afarensis? A case of anagenesis in the hominin fossil record. *J Hum Evol* 51: 134–152.

Kirzinger A, Jurgens U (1982). Cortical lesion effects and vocalization in the squirrel monkey. *Brain Res* 233: 299–315.

Klein RG (2009). *The human career: Human biological and cultural origins*. Chicago, University of Chicago Press.

Koechlin E, Corrado G, Pietrini P, Grafman J (2000). Dissociating the role of the medial and lateral anterior prefrontal cortex in human planning. *Proc Natl Acad Sci USA* 97: 7651–7656.

Krause J, Fu Q, Good JM, Viola B, Shunkov MV, Derevianko AP, Paabo S (2010). The complete mitochondrial DNA genome of an unknown hominin from southern siberia. *Nature* 464: 894–897.

Krill A, Platek SM (2009). In-group and out-group membership mediates anterior cingulate activation to social exclusion. *Front Evol Neurosci* 1: 1.

Levine B (2004). Autobiographical memory and the self in time: Brain lesion effects, functional neuroanatomy, and lifespan development. *Brain Cogn* 55: 54–68.

Levy R, Dubois B (2006). Apathy and the functional anatomy of the prefrontal cortex-basal ganglia circuits. *Cereb Cortex* 16: 916–928.

Limb CJ, Braun AR (2008). Neural substrates of spontaneous musical performance: An fmri study of jazz improvisation. *PLoS One* 3: e1679.

Lind S, Bowler D (2008). Episodic memory and autonoetic consciousness in autism specrum disorders: The roles of self-awareness, representation abilities, and temporal cognition. In *Memory in autism: Theory and evidence* (Boucher JM, Bowler DM, eds.). pp. 166–187. Cambridge, UK, Cambridge University Press.

Lordkipanidze D, Jashashvili T, Vekua A, Ponce de Leon MS, Zollikofer CP, Rightmire GP, Pontzer H, Ferring R, Oms O, Tappen M, Bukhsianidze M, Agusti J, Kahlke R, Kiladze G, Martinez-Navarro B, Mouskhelishvili A, Nioradze M, Rook L (2007). Postcranial evidence from early homo from dmanisi, georgia. *Nature* 449: 305–310.

Lumsden CJ, Wilson EO (1980). Gene-culture translation in the avoidance of sibling incest. *Proc Natl Acad Sci USA* 77: 6248–6250.

Mace R, Sear R (2005). Are humans cooperative breeders? In *Grandmotherhood: The evolutionary significance of the second half of female life* (Voland E, Chasiotis A, Schiefenhovel W, eds.). pp. 143–159. Piscataway, NJ, Rutgers University Press.

MacLean PD (1985). Evolutionary psychiatry and the triune brain. *Psychol Med* 15: 219–221.

Macphail EM (1982). *Brain and intelligence in vertebrates*. Oxford, Clarendon Press.

Magarinos AM, McEwen BS, Flugge G, Fuchs E (1996). Chronic psychosocial stress causes apical dendritic atrophy of hippocampal ca3 pyramidal neurons in subordinate tree shrews. *J Neurosci* 16: 3534–3540.

Marlowe FW (2003). A critical period for provisioning by hadza men: Implications for pair bonding. *Evol Hum Behav* 24.

Marlowe FW (2005). Hunter-gatherers and human evolution. *Evol Anthropol* 14: 54–678.

Masataka N (2007). Music, evolution and language. *Dev Sci* 10: 35–39.

McBrearty S, Brooks AS (2000). The revolution that wasn't: A new interpretation of the origin of modern human behavior. *J Hum Evol* 39: 453–563.

McColgan KL, McCormack T (2008). Searching and planning: Young children's reasoning about past and future event sequences. *Child Dev* 79: 1477–1497.

McEwen BS (2000). The neurobiology of stress: From serendipity to clinical relevance. *Brain Res* 886: 172–189.

McGeoch PD, Brang D, Ramachandran VS (2007). Apraxia, metaphor and mirror neurons. *Med Hypotheses* 69: 1165–1168.

Merriam-Webster (2003). *Collegiate dictionary*. New York, Wiley.

Meyers DM, Wright PC (1993). Resource tracking: Food availability and propithecus seasonal reproduction. In *Lemur social systems and their ecological basis* (Kappeler PM, Ganzhorn JU, eds.). pp. 179–192. New York, Plenum Press.

Mineka S, Suomi SJ (1978). Social separation in monkeys. *Psychol Bull* 85: 1376–1400.

Mitani JC, Watts DP (1999). Demographic influences on the hunting behavior of chimpanzees. *Am J Phys Anthropol* 109: 439–454.

Mitani JC, Watts DP (2001). Why do chimpanzees hunt and share meat? *Animal Behavior* 61: 915–924.

Mitani JC, Merriwether DA, Zhang C (2000). Male affiliation, cooperation and kinship in wild chimpanzees. *Anim Behav* 59: 885–893.

Mithen S (1996). *The prehistory of the mind: The cognitive origins of art, religion and science*. London, Thames and Hudson.

Mithen S (1998). From domain specific to generalized intelligence: A cognitive interpretation of the middle/upper paleolithic transition. In *Reader in archeological theory: Post-processual and cognitive approaches* (Whitley DS, ed.). pp. 137–156. New York, Routledge.

Moll J, Krueger F, Zahn R, Pardini M, de Oliveira-Souza R, Grafman J (2006). Human fronto-mesolimbic networks guide decisions about charitable donation. *Proc Natl Acad Sci USA* 103: 15623–15628.

Moran JM, Wig GS, Adams RB, Jr., Janata P, Kelley WM (2004). Neural correlates of humor detection and appreciation. *Neuroimage* 21: 1055–1060.

Moynihan (2006). Comparative aspects of communication in new world primates. In *Primate ethology* (Morris D, Bruce D, eds.). pp. 236–266. Piscataway, NJ, Aldine Transaction.

Murphy WJ, Eizirik E, Johnson WE, Zhang YP, Ryder OA, O'Brien SJ (2001). Molecular phylogenetics and the origins of placental mammals. *Nature* 409: 614–618.

Nieuwenhuys R (1994). The neocortex. An overview of its evolutionary development, structural organization and synaptology. *Anat Embryol (Berl)* 190: 307–337.

Ongur D, Price JL (2000). The organization of networks within the orbital and medial prefrontal cortex of rats, monkeys and humans. *Cereb Cortex* 10: 206–219.

Ovchinnikov IV, Gotherstrom A, Romanova GP, Kharitonov VM, Liden K, Goodwin W (2000). Molecular analysis of neanderthal DNA from the northern caucasus. *Nature* 404: 490–493.

Overdorff DJ (1998). Are eulemur species pair-bonded? Social organization and mating strategies in eulemur fulvus rufus from 1988–1995 in southeast madagascar. *Am J Phys Anthropol* 105: 153–166.

Parr LA, Matheson MD, Bernstein IS, De waal FBM (1997). Grooming down the hierarchy: Allogrooming in captive brown capuchin monkeys, cebus apella. *Anim Behav* 54: 361–367.

Passingham RE (1981). Broca's area and the origins of human vocal skill. *Philos Trans R Soc Lond B Biol Sci* 292: 167–175.

Passingham RE, Bengtsson SL, Lau HC (2010). Medial frontal cortex: From self-generated action to reflection on one's own performance. *Trends Cogn Sci* 14: 16–21.

Pinker S (2010). Colloquium paper: The cognitive niche: Coevolution of intelligence, sociality, and language. *Proc Natl Acad Sci USA* 107(Suppl 2): 8993–8999.

Pollick AS, de Waal FB (2007). Ape gestures and language evolution. *Proc Natl Acad Sci USA* 104: 8184–8189.

Pontzer H, Rolian C, Rightmire GP, Jashashvili T, Ponce de Leon MS, Lordkipanidze D, Zollikofer CP (2010). Locomotor anatomy and biomechanics of the dmanisi hominins. *J Hum Evol*.

Povinelli DJ (2000). *Folk physics for apes: The chimpanzee's theory of how the world works*. New York, Oxford University Press.

Povinelli DJ, Dunphy-Lelii S (2001). Do chimpanzees seek explanations? Preliminary comparative investigations. *Can J Exp Psychol* 55: 185–193.

Povinelli DJ, Giambrone S (2001). Reasoning about beliefs: A human specialization? *Child Dev* 72: 691–695.

Preston SD, De Waal FB (2002). The communication of emotions and the possibility of empathy in animals. In *Altruism and altruistic love* (Post SG, ed.). pp. 284–308. New York, Oxford University Press.

Pribram K (ed.) (1993). *Rethinking neural networks: Quantum fields and biological data*. Hillsdale, NY, Lawrence Erlbaum.

Price JL, Drevets WC (2010). Neurocircuitry of mood disorders. *Neuropsychopharmacology* 35: 192–216.

Proske U, Gregory E (2003). Electrolocation in the platypus – some speculations. *Comp Biochem Physiol A Mol Integr Physiol* 136: 821–825.

Proske U, Gregory JE, Iggo A (1998). Sensory receptors in monotremes. *Philos Trans R Soc Lond B Biol Sci* 353: 1187–1198.

Rabinovich R, Gaudzinski-Windheuser S, Goren-Inbar N (2008). Systematic butchering of fallow deer (dama) at the early middle pleistocene acheulian site of gesher benot ya'aqov (israel). *J Hum Evol* 54: 134–149.

Raichle ME, MacLeod AM, Snyder AZ, Powers WJ, Gusnard DA, Shulman GL (2001). A default mode of brain function. *Proc Natl Acad Sci USA* 98: 676–682.

Rak Y (1985). Australopithecine taxonomy and phylogeny in light of facial morphology. *Am J Phys Anthropol* 66: 281–287.

Rak Y, Ginzburg A, Geffen E (2002). Does homo neanderthalensis play a role in modern human ancestry? The mandibular evidence. *Am J Phys Anthropol* 119: 199–204.

Rak Y, Ginzburg A, Geffen E (2007). Gorilla-like anatomy on australopithecus afarensis mandibles suggests au. Afarensis link to robust australopiths. *Proc Natl Acad Sci USA* 104: 6568–6572.

Ramachandran VS (2005). *A brief tour of consciousness*. Upper Saddle River, NJ, Pi Press.

Rauschecker JP, Tian B (2000). Mechanisms and streams for processing of "What" And "Where" In auditory cortex. *Proc Natl Acad Sci USA* 97: 11800–11806.

Reed DL, Smith VS, Hammond SL, Rogers AR, Clayton DH (2004). Genetic analysis of lice supports direct contact between modern and archaic humans. *PLoS Biol* 2: e340.

Reiner A (2002). Functional circuitry of the avian basal ganglia: Implications for basal ganglia organization in stem amniotes. *Brain Res Bull* 57: 513–528.

Reiner A, Medina L, Veenman CL (1998). Structural and functional evolution of the basal ganglia in vertebrates. *Brain Res Brain Res Rev* 28: 235–285.

Reiner A, Perkel DJ, Bruce LL, Butler AB, Csillag A, Kuenzel W, Medina L, Paxinos G, Shimizu T, Striedter G, Wild M, Ball GF, Durand S, Gunturkun O, Lee DW, Mello CV, Powers A, White SA, Hough G, Kubikova L, Smulders TV, Wada K, Dugas-Ford J, Husband S, Yamamoto K, Yu J, Siang C, Jarvis ED (2004). Revised nomenclature for avian telencephalon and some related brainstem nuclei. *J Comp Neurol* 473: 377–414.

Rightmire GP (2009). Out of africa: Modern human origins special feature: Middle and later pleistocene hominins in africa and southwest asia. *Proc Natl Acad Sci USA* 106: 16046–16050.

Rilling JK, Barks SK, Parr LA, Preuss TM, Faber TL, Pagnoni G, Bremner JD, Votaw JR (2007). A comparison of resting-state brain activity in humans and chimpanzees. *Proc Natl Acad Sci USA* 104: 17146–17151.

Rismiller PD (1999). *The echidna – Australia's enigma*. Westport, CT, Hugh Lauter Levin Associates.

Rizzolatti G, Craighero L (2004). The mirror-neuron system. *Annu Rev Neurosci* 27: 169–192.

Ross CF (2000). Into the light: The origin of anthropoidea. *Annu Rev Antjhropol* 29: 147–194.

Ross CF, Kirk EC (2007). Evolution of eye size and shape in primates. *J Hum Evol* 52: 294–313.

Rowe JB, Sakai K, Lund TE, Ramsoy T, Christensen MS, Baare WF, Paulson OB, Passingham RE (2007). Is the prefrontal cortex necessary for establishing cognitive sets? *J Neurosci* 27: 13303–13310.

Sargis EJ (2002). Paleontology. Primate origins nailed. *Science* 298: 1564–1565.

Schellenberg EG, Bigand E, Poulin-Charronnat B, Garnier C, Stevens C (2005). Children's implicit knowledge of harmony in western music. *Dev Sci* 8: 551–566.

Semendeferi K, Armstrong E, Schleicher A, Zilles K, Van Hoesen GW (2001). Prefrontal cortex in humans and apes: A comparative study of area 10. *Am J Phys Anthropol* 114: 224–241.

Sharon G, Alperson-Afil N, Goren-Inbar N (2010). Cultural conservatism and variability in the acheulian sequence of gesher benot ya'aqov. *J Hum Evol*.

Shreeve J (2010). The evolutionary road. In National Geographic (Chris J, ed.). pp. 34–67. Washington, DC, National Geographic Society.

Shultz S, Dunbar RI (2007). The evolution of the social brain: Anthropoid primates contrast with other vertebrates. *Proc Biol Sci* 274: 2429–2436.

Smith CS (1997). *The parameter of aspect*. Dordrecht, The Netherlands, Kluwer.

Smith TD, Siegel MI, Bhatnagar KP (2001). Reappraisal of the vomeronasal system of catarrhine primates: Ontogeny, morphology, functionality, and persisting questions. *Anat Rec* 265: 176–192.

Southwick CH (1967). An experimental study of intragroup agonistic behavior in rhesus monkeys (macaca mulatta). *Behaviour* 28: 182–209.

Southwick CH (2000). Conflict and resolution in primates – all too human? *Science* 290: 1095–1097.

Sperry R (1982). Some effects of disconnecting the cerebral hemispheres. *Science* 217: 1223–1226.

Speth JD (1991). Protein selection and avoidance strategies of contemporary and ancestral foragers: Unresolved issues. *Philos Trans R Soc Lond B Biol Sci* 334: 265–269; discussion 269–270.

Springer MS, Murphy WJ, Eizirik E, O'Brien SJ (2003). Placental mammal diversification and the cretaceous-tertiary boundary. *Proc Natl Acad Sci USA* 100: 1056–1061.

Stebbins GL (1982). *Darwin to DNA, molecules to humanity*. New York, Freeman.

Stout D, Toth N, Schick K, Chaminade T (2008). Neural correlates of early stone age tool-making: Technology, language, and cognition in human evolution. *Phils Trans R Soc London B Biol Sci* 363: 1939–1949.

Stout D, Toth N, Schick K, Stout J, Hutchins L (2000). Stone tool-making and brain activation: Pet studies. *J Archaeological Science* 27: 1215–1223.

Strand FL (1999). *Neuropeptides: Regulators of physiological processes*. Cambridge, MA, MIT Press.

Suddendorf T, Addis DR, Corballis MC (2009). Mental time travel and the shaping of the human mind. *Philos Trans R Soc Lond B Biol Sci* 364: 1317–1324.

Suddendorf T, Whiten A (2001). Mental evolution and development: Evidence for secondary representation in children, great apes, and other animals. *Psychol Bull* 127: 629–650.

Suomi SJ (1984). The development of affect in rhesus monkeys. In *The psychobiology of affective development* (Fox NA, Davidson RJ, eds.). pp. 119–160. Hillsdale, NJ, Lawrence Erlbaum Associates.

Sussman RW (1991). Primate origins and the evolution of angiosperms. *Am J Primatol* 23: 209–223.

Sussman RW (2003). *Primate ecology and social structure, vol. 1: Lorises, lemurs and tarsiers*. Needham Heights, MA, Pearson Custom Publishing.

Sussman RW, Chapman AR (eds.) (2004). *The origins and nature of sociality*. New York, Aldine de Gruyter.

Szalay FS, Delson E (2001). *Evolutionary history of the primates*. New York, Academic.

Taber KH, Redden M, Hurley RA (2007). Functional anatomy of humor: Positive affect and chronic mental illness. *J Neuropsychiatr Clin Neurosci* 19: 358–362.

Tattersall I (2004). The dual origin of modern humanity. *Coll Antropol* 28(Suppl 2): 77–85.

Tattersall I (2008a). An evolutionary framework for the acquisition of symbolic cognition by homo sapiens. *Comp Cogn Behav Rev* 3: 99–114.

Tattersall I (2008b). *The world from beginnings to 4000 bce*. New York, Oxford University Press.

Tattersall I (2009). Out of africa: Modern human origins special feature: Human origins: Out of africa. *Proc Natl Acad Sci USA* 106: 16018–16021.

Tianyuan L, Etler DA (1992). New middle pleistocene hominid crania from yunxian in china. *Nature* 357: 404–407.

Toates F (2001). Multiple factors controlling behavior: Implications for stress and welfare. In *The biology of animal stress: Basic principles and implications for welfare* (Moberg GP, Mench JA, eds.). pp. 199–226. New York, CABI Publishing.

Toth N (1985). Archeological evidence for preferential right-handedness in the lower and middle pleistocene, and its possible implications. *J Hum Evol* 14: 607–614.

Toups MA, Kitchen A, Light JE, Reed DL (2010). Origin of clothing lice indicates early clothing use by anatomically modern humans in africa. *Mol Biol Evol*.

Travis F, Haaga DA, Hagelin J, Tanner M, Arenander A, Nidich S, Gaylord-King C, Grosswald S, Rainforth M, Schneider RH (2010). A self-referential default brain state: Patterns of coherence, power, and eloreta sources during eyes-closed rest and transcendental meditation practice. *Cogn Process* 11: 21–30.

Trinkaus E, Zimmerman MR (2005). Trauma among the shanidar neandertals. *Am J Phys Anthropol* 57: 61–76.

Tulving E (1987). Multiple memory systems and consciousness. *Hum Neurobiol* 6: 67–80.

Tulving E (2001). Episodic memory and common sense: How far apart? *Philos Trans R Soc Lond B Biol Sci* 356: 1505–1515.

Tulving E (2002). Episodic memory: From mind to brain. *Annu Rev Psychol* 53: 1–25.

Tulving E, Lepage M (2001). Where in the brain is the awareness of one's past? In *Memory, brain, and belief* (Schacter DL, Scarry E, eds.). pp. 208–227. Cambridge, MA, Harvard University Press.

van Lawick-Goodall, J. (1967). *My Friends: The Wild Chimpanzees*. Washington, D.C., National Geographic Society.

Vaneechoutte M, Skoyles JR (1998). The memetic origin of language: Modern humans as musical primates. *Journal of Memetics: Evolutionary Models of Information Transmission* 2: 84–117.

van Schaik CP, Kappeler PM (2010). The social systems of gregarious lemurs: Lack of convergence with anthropoids due to evolutionary disequilibrium? *Ethol Sociobiol* 102: 915–941.

Verhagen JV, Kadohisa M, Rolls ET (2004). Primate insular/opercular taste cortex: Neuronal representations of the viscosity, fat texture, grittiness, temperature, and taste of foods. *J Neurophysiol* 92: 1685–1699.

Virkkunen M, Rissanen A, Naukkarinen H, Franssila-Kallunki A, Linnoila M, Tiihonen J (2007). Energy substrate metabolism among habitually violent alcoholic offenders having antisocial personality disorder. *Psychiatr Res* 150: 287–295.

Wade N (2006). *Before the dawn: Recovering the lost history of our ancestors*. New York, Penguin Books.

Weaver A, de Waal FB (2002). An index of relationship quality based on attachment theory. *J Comp Psychol* 116: 93–106.

Weiss KM, Buchanan AV (2009). The cooperative genome: Organisms as social contracts. *Int J Dev Biol* 53: 753–763.

Weiss DJ, Newport EL (2006). Mechanisms underlying language acquisition: Benefits from a comparative approach. *Infancy* 9: 241–257.

Wersinger SR, Baum MJ (1997). Sexually dimorphic processing of somatosensory and chemosensory inputs to forebrain luteinizing hormone-releasing hormone neurons in mated ferrets. *Endocrinology* 138: 1121–1129.

White TD, Asfaw B, Beyene Y, Haile-Selassie Y, Lovejoy CO, Suwa G, WoldeGabriel G (2009). Ardipithecus ramidus and the paleobiology of early hominids. *Science* 326: 75–86.

White TD, WoldeGabriel G, Asfaw B, Ambrose S, Beyene Y, Bernor RL, Boisserie JR, Currie B, Gilbert H, Haile-Selassie Y, Hart WK, Hlusko LJ, Howell FC, Kono RT, Lehmann T, Louchart A, Lovejoy CO, Renne PR, Saegusa H, Vrba ES, Wesselman H, Suwa G (2006). Asa issie, aramis and the origin of australopithecus. *Nature* 440: 883–889.

Whiten A, Spiteri A, Horner V, Bonnie KE, Lambeth SP, Schapiro SJ, de Waal FB (2007). Transmission of multiple traditions within and between chimpanzee groups. *Curr Biol* 17: 1038–1043.

Whitten PL, Brockman DK (2001). Strepsirrhine reproductive ecology. In *Reproductive ecology and human evolution* (Ellison PT, ed.). pp. 321–350. New York, Aldine de Gruyter.

Wood B, Collard M (1999). The human genus. *Science* 284: 65–71.

Wright PC (1999). Lemur traits and madagascar ecology: Coping with an island environment. *Am J Phys Anthropol* Suppl 29: 31–72.

Wright S (1982). The shifting balance theory and macroevolution. *Annu Rev Genet* 16: 1–19.

Zihlman A (1997). The paleolithic glass ceiling: Women in human evolution. In *Women in human evolution* (Hager L, ed.). pp. 91–113. London, Routledge.

# Part II
# Altruism and Cooperation Among Nonhuman Primates

# Chapter 6
# Cooperation and the Evolution of Social Living: Moving Beyond the Constraints and Implications of Misleading Dogma: Introduction Part II

**Marc Bekoff**

> *"Evolution has produced a mind that evolves toward an appreciation of the vastness of our collective design, and emotions that enable us to enact these loftier notions. We are wired for good." (Dacher Keltner, 2009. p. 269)*

The chapters in this section offer fascinating insights into the social behavior and social organization of various primates. They emphasize the importance of long-term fieldwork on identified individuals for learning about the evolution and ecology of social behavior. As such, these essays are extremely valuable not only because they review current information but also because they go beyond mere paradigm and often lazy-thinking about the factors that influence group-living in free-ranging animals. To wit, and in the spirit of the other chapters in this forward-looking and very important book, the authors show that cooperation even among non-kin is very important in structuring the social organization of different species living in different environments. They emphasize that cooperation has not merely evolved to reduce aggression or as a reaction to competition but serves a significant, perhaps a leading role, in the evolution of social behavior and social organization. To simply put it, cooperation is *normal* behavior.

Across species, individuals have a need to belong to a group and this drives the evolution of cooperative group-living. The same can be said of humans. A number of recent books have been concerned with the importance and prevalence of human cooperation, goodness, and empathy. These include Dacher Keltner's *Born To be Good*, Jeremy Rifkin's *The Empathic Civilization* (2010), Frans de Waal's *The Age of Empathy* (2009), and *The Compassionate Instinct* (Keltner et al., 2010). It is important to correct the misleading "nature red in tooth and claw" views that dominate the literature and diminish cooperation and empathy to sideshows in the evolution of sociality (Bekoff, 2007, 2010; Bekoff and Pierce, 2009). Sheratt and Wilkinson (2009) see cooperation as being one of ten "big questions in ecology and evolution." It is safe to say that Charles Darwin (1871/2004) would also

---

M. Bekoff (✉)
Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO, USA
e-mail: marc.bekoff@gmail.com

R.W. Sussman, C.R. Cloninger (eds.), *Origins of Altruism and Cooperation*,
Developments in Primatology: Progress and Prospects 36, DOI 10.1007/978-1-4419-9520-9_6,

agree about the importance of cooperation in the evolution of group-living. Darwin would not have been the least surprised if he knew what we have discovered in the past decade or so about the emotional and moral intelligence in animals (Keltner, 2009; Bekoff, 2010). He believed that animals, like humans, could be moral beings. Darwin suggested that human morality is continuous with similar social behavior in other animals and he paid special attention to the capacity for sympathy, which he believed was evidenced in a large numbers of animals.

While we still have a lot to learn about cooperation in free-ranging animals, the chapters in this section provide a strong springboard for future research and for reassessing existing data in light of a paradigm shift that gives more attention to cooperation. While research on captive animals can provide important information on social behavior when field observations are difficult or impossible, unnatural social conditions (groups do not reflect the composition of natural groups in terms of the number of individuals present or age/sex ratios and the lack of opportunity for dispersal or integration of new members) and the atypical physical settings (small cages, individuals cannot hunt or do not have to defend themselves, territories, or food) in which animals are kept often preclude gathering relevant information on the importance of cooperation (Bekoff, 2010).

A brief summary of the chapters in this section reveals fascinating new information that challenges the current *zeitgeist*. Katherine MacKinnon and Agustin Fuentes note the importance of cooperation and altruism in the evolution of social complexity and social niche construction, and discuss the resurgence of group selection even among people who previously argued that it was not a factor in the evolution of social behavior (see also Bekoff and Pierce, 2009). They also discuss recent research on inequity aversion that shows that an individual's ability to sense and expect fairness in social interactions is also important for cooperative group-living. Individuals do not like being treated unfairly and will not do what is needed to maintain group cohesion if they sense inequity (Bekoff and Pierce, 2009).

Paul Garber and Martin Kowalewski discuss the importance of collective action and male affiliation in howler monkeys based on their field observations in Argentina. They note "there is a growing body of evidence that increased fitness benefits accrue to individual males and females that reside in a functioning, cooperative, stable, and affiliative group." It is important that we get out of the rut of giving cooperation and fairness secondary roles in the evolution of cohesive and smoothly functioning social groups. Garber and Kowalewski show that "resident males are highly tolerant of each other across a range of contexts including feeding, foraging, resting, and mating. It is likely that tolerance is achieved over time and through individual experience during frequent and predictable social interactions." Concerning the importance of group stability mentioned above, they also note that in another study of howler monkeys "males who were co-residents in the same group for over four years were more likely to engage in collective action . . ." compared to resident males who had not lived together for as long. Further, they conclude, "many forms of cooperative behavior among both kin and non-kin may be explained in terms of the mutual and reciprocal benefits that individuals receive maintaining coordinated, strong, and predictable social bonds that enhance group cohesion." It is possible that individuals who live together learn what to expect from other individuals in different situations and develop theories of behavior and theories of mind about group members with whom they are very familiar. In my own fieldwork on coyotes living in the Grand Teton National Park (Bekoff and Wells, 1986), individuals were labeled as being fair or unfair players and were avoided by other group members based on how they were classified (Bekoff and Pierce, 2009). As a result of being avoided and not developing strong social bonds, coyotes who played unfairly tended to leave their group and suffer higher mortality—fairness was related to fitness.

Fieldwork on many species has shown that there is considerable plasticity in social behavior, a trait that is not always apparent in work on captive animals. Based on her long-term fieldwork on wild northern muriquis in Brazil, Karen Strier discovered that there is a good deal of within-species flexibility and that these primates "live in an unusually egalitarian society in which males are philopatric and the majority of females disperse from their natal groups prior to the onset of puberty." Strier's conclusion is one that we should all take to heart: "Local conditions can favor cooperation or competition at different times in an individual's lifetime. The ability to move between cooperative and competitive modes, and social plasticity in general, may be the underlying adaptation of primate evolution."

In our fieldwork on coyotes, we also noted that speaking about "the typical coyote" is misleading because of considerable within-species variability, a point made by Karen Strier and also by Mary Pavelka in her discussion of social cohesion in black howler monkeys. Following up on the work of renowned ethologist Robert Hinde who argued that "each relationship is a set in a nexus of other relationships, which mutually affect each other" with the social group "constituted by those relationships," Pavelka argues that the various social relationships among individuals hold the group together and are the mechanism of cohesion. Pavelka discovered that black howler monkeys engage in very few social interactions and have no visible social relationships, but they live in perhaps "the most cohesive of primate societies." How is this so? Pavelka argues that there are two possible alternative mechanisms "for social cohesion in species such as black howlers in which intragroup social interaction and opportunities for reciprocity and altruism are rare: behavioral synchrony and intergroup encounters." She observed that in more than 85% of scan samples, all group members were engaged in the same activity (inactive, forage, travel, social). Pavelka also argues that intergroup encounters consisting of howling bouts with adjacent groups might also be important for group cohesion. Social and cultural anthropologists have championed the "common foe" hypothesis as an important mechanism favoring sociality. However, Pavelka also notes that there are no "winners" or "losers" in these intergroup bouts and they "may have more in common with sporting events than with warfare in humans." Thus, competition over resources does not drive the bouts, and a major effect is to develop and maintain close social bonds within a group. This is a fascinating and novel suggestion that needs further comparative study.

## Some Ideas for Future Comparative Research

*Working toward a shared vocabulary:* While we know more than we often realize about the central role of cooperation in the evolution of sociality, more data are needed and researchers in different disciplines have to agree about what they are writing about. Thus, we need a shared vocabulary, an idea I have been working on with my colleague and coauthor of *Wild Justice*, Jessica Pierce. The main reason we need a shared language for studying the evolution and expression of cooperation is that we need to be able to cross disciplinary boundaries and build bridges among different fields of study. The interest of researchers from diverse disciplines is what makes the study of cooperation so exciting and challenging. Some of the terms on which we might focus include cooperation, altruism, empathy, sympathy, justice, reciprocity, selfishness, moral emotions, moral cognition, intelligence, and morality. As it is, many of these terms have no shared meaning, and for example, philosophers and biologists tend to them quite differently (Bekoff and Pierce, 2009).

In terms of challenging presuppositions in science and philosophy (in addition to challenging the central tenet that cooperation is only a by-product of competition) Pierce and I also note that scientists and others should avoid looking for a linear, sequential view of the evolution of cooperative/altruistic/moral behaviors. Just as complex brains and cognition have evolved from simpler brains multiple times and independently, so perhaps have cooperative behaviors.

*We need to go beyond primates*: In order to understand the evolution of cooperation and other prosocial behavior patterns, we need to consider animals other than nonhuman primates, a point we stress in *Wild Justice*. For example, we know that mice show empathy and rats can be kind to one another (http://www.plosbiology.org/article/info:doi/10.1371/journal.pbio.0050196). We began *Wild Justice* with these examples that clearly show how cooperation, empathy, and compassion can be found in diverse species:

> A teenage female elephant nursing an injured leg is knocked over by a rambunctious, hormone-laden teenage male. An older female sees this happen, chases the male away, and goes back to the younger female and touches her sore leg with her trunk. Eleven elephants rescue a group of captive antelope in KwaZula-Natal; the matriarch undoes all of the latches on the gates of the enclosure with her trunk and lets the gate swing open so the antelope can escape. A rat in a cage refuses to push a lever for food when it sees that another rat receives an electric shock as a result. A male Diana monkey who has learned to insert a token into a slot to obtain food helps a female who can't get the hang of the trick, inserting the token for her and allowing her to eat the food reward. A female fruit-eating bat helps an unrelated female give birth by showing her how to hang in the proper way. A cat named Libby leads her elderly, deaf, and blind dog friend, Cashew, away from obstacles and to food. In a group of chimpanzees at the Arnhem Zoo in The Netherlands individuals punish other chimpanzees who are late for dinner because no one eats until everyone's present. A large male dog wants to play with a younger and more submissive male. The big male invites his younger partner to play and restrains himself, biting his younger companion gently and allowing him to bite gently in return. Do these examples show that animals display moral behavior, that they can be compassionate? Yes they do.

So, in the future it is essential that researchers studying the evolution of social behavior in different species talk with one another and not think that the animals they study are unique. Sure Darwin's ideas about evolutionary continuity mandate such a comparative approach to the questions at hand.

## Social Play in Mammals

My long-term research on social play behavior points to the importance of not only studying animals other than nonhuman primates but also focusing on a behavior that many mammals perform but one that has not been factored into discussions of the evolution of cooperation, although it is a natural fit (Bekoff and Pierce, 2009; http://chronicle.com/article/Moral-in-ToothClaw/48800/; http://www.scientificamerican.com/article.cfm?id=the-ethical-dog). One of the clearest places to see how specific social rules apply is in animal play. Play has been extensively studied in social canids (members of the dog family) like wolves, coyotes, and domestic dogs; so it is a good example to use to examine the mechanisms of fair play (Bekoff, 1975, 1977, 1995).

Although play is fun, it is also a serious business. When animals play, they are constantly working to understand and follow the rules and to communicate their intentions to play fairly. They fine-tune their behavior on the run, carefully monitoring the behavior of their play partners and paying close attention to infractions of the agreed-upon rules. Four basic aspects of fair play in animals are as follows: ask first, be honest, follow the rules, and admit you are wrong. When the rules of play are violated, and when fairness breaks down, so does play.

When dogs and other animals play, they use actions like biting, mounting, and body-slamming one another, which are also used in other contexts, like fighting or mating. Because those actions can be easily misinterpreted, it is important for animals to clearly state what they want and what they expect.

In canids an action called a "bow" is used to ask others to play. When performing a bow, an animal crouches on his or her forelimbs. He or she will sometimes bark, wag the tail wildly, and have an eager look. So that the invitation to play is not confusing, bows are highly stereotyped and show little variation. Play bows are honest signals, a sign of trust. Research shows that animals who violate that trust are often ostracized, suggesting that violation of the rules of play is maladaptive and can disrupt the efficient functioning of the group. For example, among dogs, coyotes, and wolves, individuals who do not play fairly find that their invitations to play are ignored or that they are simply avoided by other group members. Long-term field research on coyotes living in the Grand Teton National Park, near Jackson, Wyoming, shows that coyotes who do not play fairly often leave their pack because they do not form strong social bonds. Such loners suffer higher mortality than those who remain with others.

Animals engage in two activities that help create an equal and fair playing field: self-handicapping and role-reversing. Self-handicapping (or "play inhibition") occurs when individuals perform behavior patterns that might compromise them outside of play. For example, coyotes will inhibit the intensity of their bites, thus abiding by the rules and helping to maintain the play mood. The fur of young coyotes is very thin, and intense bites are painful and cause high-pitched squeals. In adult wolves, a bite can generate as much as 1,500 pounds of pressure per square inch, so there is a good reason to inhibit its force. Role-reversing happens when a dominant animal performs an action during play that would not normally occur during real aggression. For example, a dominant wolf would not roll over on his back during fighting, making himself more vulnerable to attack, but would do so while playing.

Play can sometimes get out of hand for animals, just as it does for human beings. When play gets too rough, canids keep things under control by using bows to apologize. For example, a bow might communicate something like, "Sorry I bit you so hard—I did not mean it, so let us continue playing." For play to continue, it is important for individuals to forgive the animal who violated the rules. Once again there are species differences among young canids. Highly aggressive young coyotes bow significantly more frequently than dogs or wolves before and after delivering bites that could be misinterpreted.

The social dynamics of play require that players agree to play and not to eat one another or fight or try to mate. When there is a violation of those expectations, others react to the lack of fairness. For example, young coyotes and wolves react negatively to unfair play by ending the encounter or avoiding those who ask them to play and then do not follow the rules. Cheaters have a harder time finding play partners.

It is just a step from play to morality. Researchers who study child's play have discovered that basic rules of fairness guide play and that egalitarian instincts emerge very early in childhood. Indeed, while playing, children learn, as do other young animals, that there are right and wrong ways to play and that transgressions of fairness have social consequences, like being ostracized. The lessons children learn particularly about fairness are also the foundation of fairness among adults.

The parallels between human and animal play, and the shared capacity to cooperate and to understand and behave according to rules of right and wrong conduct, are striking. They lead us to believe that animals are morally intelligent. Morality has evolved in many species, and unique features of human morality, like the use of language to articulate and enforce social norms, are simply modifications of broadly evolved behavioral patterns specific to our species.

The study of animal play thus offers an invitation to move beyond philosophical and scientific dogma and to take seriously the possibility that morality exists in many animal societies. A broad and expanding study of animal morality will allow us to learn more about the social behaviors that make animal societies so successful and so fascinating, and it will also encourage us to reexamine assumptions about human moral behavior. That study is in its infancy, but we hope to see ethologists, neuroscientists, biologists, philosophers, and theologians work together to explore the implications of this new science. Already, research on animal morality is blossoming, and if we can break free of theoretical prejudice, we may come to better understand ourselves and the other animals with whom we share this planet.

## The Compassion Footprint and the Jen Ratio: The Bigger, Challenging, and Real Picture

*We are born to be good*: My work on the notion of the "compassion footprint" developed in *The Animal Manifesto* (see also Bekoff, 2008) and that of Dacher Keltner's ideas about the Jen ratio overlap in many different ways and are related to the "big picture" that emerges from these and other essays in this book. Keltner and I agree we will learn a lot about the evolution of cooperation, goodness, fitness, and compassion by going beyond humans and paying attention to how other animals negotiate their social interactions. In many instances, one could substitute the word "animal" where Keltner wrote about humans in *Born To be Good*, and "humans" where Marc wrote about animals (recognizing of course that we are all members of the animal kingdom and should be proud of that commonality) in *The Animal Manifesto*. Keltner uses the Confucian concept of *Jen*, which refers to "kindness, humanity, and reverence" to discuss our "good nature" and offers the concept of the *Jen* ratio to "look at the relative balance of good and uplifting versus bad and cynical in life."

Basically, the Jen ratio is the balance of good and bad in one's life and as the value of one's Jen ratio increases so does the humanity and meaningfulness in their life. The Jen ratio can be likened to a ratio between one's compassion footprint and their carbon footprint. One's compassion footprint is composed of the kindness and respect she or he adds to the world by doing things to protect animals or not doing certain things that harm them, whereas one's carbon footprint can be viewed as something "bad" in the world. As we expand our compassion footprint and reduce our carbon footprint, we increase global Jen. We can perhaps look at the analyses done by Robert Sussman et al. (2005) to operationalize the Jen ratio and the compassion footprint.

Keltner and I argue it is in our nature to be cooperative, good, kind, and fair. We know it feels good to be nice. We are often filled with warm feelings when we cooperate. Neural imaging research on humans by James Rilling (Chapter 17, this volume) shows that mutual cooperation is associated with activation of the brain's reward-processing centers, the dopamine system. Our brain releases dopamine when we cooperate, giving us instant pleasurable feedback and reinforcing the behavior. This is significant research for it posits that being nice is rewarding in social interactions and might in itself be a stimulus fostering cooperation and fairness.

Is it rational to argue for inherent goodness? Renowned biologist and writer Matt Ridley convincingly shows that there are reasons to be a rational optimist despite global negativity. In his book *The Rational Optimist* (2010) Ridley argues that we can get out of the messes we have created because people are kinder and fairer than most believe. Mass media hype concentrates on our battles and the negativity we bring to the world, and on occasion notes our goodness and kindness, usually tagged on to the end of news broadcast.

People often criticize the idea that nonhuman and human animals are basically good by looking at the data collected on competition and aggression in animals. Surely, humans and other animals can be mean to one another. And yes, Jane

Goodall (1986) did observe what could be construed as warlike behavior when a group of male chimpanzees systematically hunted down and killed individuals in another group. However, Goodall only observed this once in 50 years of research.

In *Beyond Revenge* psychologist Michael McCullough (2008) writes, "After many years of believing that chimpanzees were mostly peace-loving and docile . . . naturalists began to publish case after case in which chimpanzees from one community went out of their way to seek out the members of other chimpanzee communities, and then to maim and kill them." But available data are actually quite slim because of small sample sizes and a good deal of variability among different communities of chimpanzees. To wit, in their review of comparative rates of violence in chimpanzees and humans Harvard anthropologist and chimpanzee expert Richard Wrangham et al. (2006) note, "the relatively small sample size and great variation among sites renders imprecise any estimate of violence-related mortality rates for chimpanzees as a species."

What do the data tell us? After carefully analyzing the social interactions of various primate species, primatologists Robert Sussman and his colleagues came to the conclusion that the vast majority of social interactions are affiliative rather than agonistic or divisive. Grooming and bouts of play predominate the social scene, with only an occasional fight or threat of aggression. In prosimians, the most ancestral of existing primates, an average of 93.2% of social interactions are affiliative. In New World monkeys who live in the tropical forests of southern Mexico and Central and South America, 86.1% of interactions are affiliative, and likewise, for Old World monkeys who live in South and East Asia, the Middle east, Africa, and Gibraltar, 84.8% are affiliative. Unpublished data for gorillas show that 95.7% of their social interactions are affiliative. After about 25 years of research on chimpanzees, Jane Goodall noted in her book *The Chimpanzees of Gombe* ". . . it is easy to get the impression that chimpanzees are more aggressive than they really are. In actuality, peaceful interactions are far more frequent than aggressive ones; mild threatening gestures are more common than vigorous ones; threats per se occur much more often than fights; and serious, wounding fights are very rare compared to brief, relatively mild ones." These do not appear to be animals whose social lives are defined mainly by conflict. It is not really a dog-eat-dog world because dogs do not eat other dogs.

So, while human and nonhuman animals can be nasty, they are predominantly good (http://greatergood.berkeley.edu/article/item/expanding_our_compassion_footprint/), and we should keep this in mind when we interact with friends and strangers. When one dismissingly says, "Oh, you are acting like an animal" the correct response would be "Thanks for the complement."

The challenges for the future are not only to get people to think about our goodness but also to act on it and do things that expand our compassion footprint and increase our Jen ratio. If we believe we are inherently good, then it will be easier to be proactively compassionate for the greater good.

The essays in this section and in the book as a whole will help us correct the false message that has been put out concerning the behavior of nonhuman animals and will allow for the development of models that have realistic assumptions. We need to put out the message that is emerging from comparative research that emphasizes the importance of cooperation, one that will have wide-ranging implications for how we view other animals and ourselves. Nature "red in tooth and claw" runs counter to what we are rapidly learning about human and other animals.

## References

Bekoff, M. 1975. The communication of play intention: Are play signals functional? *Semiotica*, 15, 231–239.

Bekoff, M. 1977. Social communication in canids: Evidence for the evolution of a stereotyped mammalian display. *Science* 197, 1097–1099.

Bekoff, M. 1995. Play signals as punctuation: The structure of social play in canids. *Behaviour*, 132, 419–429.

Bekoff, M. 2007. *The Emotional Lives of Animals*. Novato, CA: New world Library.

Bekoff, M. 2008. Increasing our compassion footprint: Some reflections on the treatment of animals. *Zygon (Journal of Religion and Science)* 43, 771–781.

Bekoff, M. 2010. *The Animal Manifesto: Six Reasons for Expanding Our Compassion Footprint.* Novato, CA: New world Library.

Bekoff, M., J. Pierce. 2009. *Wild Justice: The Moral Lives of Animals*. Chicago, IL: University of Chicago Press.

Bekoff, M., M.C. Wells. 1986. Social behavior and ecology of coyotes. *Advances in the Study of Behavior* 16, 251–338.

Darwin, C. 1871/2004. *The Descent of Man and Selection in Relation to Sex*. New York: Penguin Classics.

de Waal, F. 2009. *The Age of Empathy*. New York: Harmony.

Goodall, J. 1986. *The Chimpanzees of Gombe*. Cambridge, MA: Harvard University Press.

Keltner, D. 2009. *Born to be Good*. New York: W. W. North & Company.

Keltner, D., J. Marsh, J.A. Smith (eds.). 2010. *The Compassionate Instinct*. New York: W. W, Norton & Company.

McCullough, M.C. 2008. *Beyond Revenge: The Evolution of the Forgiveness Instinct*. San Francisco, CA: Jossey-Bass

Ridley, M. 2010. *The Rational Optimist.* New York: Harper.

Rifkin, J. 2010. *The Empathic Civilization: The Race to Global Consciousness in a World in Crisis.* New York: Tarcher.

Sheratt, T.N., D.M. Wilkinson. 2009. *Big Questions in Ecology and Evolution*. New York: Oxford University Press.

Sussman, R.W., P.A. Garber, J.M. Cheverud. 2005. Importance of cooperation and affiliation in the evolution of primate sociality. *American Journal of Physical Anthropology* 128, 84–97.

Wrangham, R.W., M. Wilson, M. Muller. 2006. Comparative rates of violence in chimpanzees and humans. *Primates* 47, 14–26.

# Chapter 7
# Primates, Niche Construction, and Social Complexity: The Roles of Social Cooperation and Altruism

**Katherine C. MacKinnon and Agustín Fuentes**

The explication of altruistic behavior in primates remains complex. Gregarious, socially complex primates are characterized by a diverse array of social behavior patterns with seemingly altruistic behavior being relatively commonplace. Human societies are a form of primate society but with much higher levels of social complexity and extremely high levels of cooperative and apparently altruistic behavior. It is likely that there are elements of primate (at least anthropoid) sociality that act as baseline for subsequent expansion and elaboration during human evolution. Can understanding patterns and contexts of primate social complexity and cooperation help us understand human altruism? In this chapter we have two primary objectives: to examine three nonhuman primate genera to show how social cooperation, social bonding, and niche construction can affect our understandings of altruism and to illustrate where we think that such nonhuman primate information is a good model for humans and where it is not.

## Theoretical and Historical Underpinnings

Although some argue that true altruism cannot occur (e.g., Trivers, 1971; Dugatkin, 2006), we believe it can and will use as a baseline for this chapter the assumption that it is possible that some organisms do exhibit truly altruistic behavior. However, altruism, strictly defined as acts that have a net loss of evolutionary fitness to the actor but a net gain in fitness to the receiver, does not make sense if organisms benefit by maximizing their own fitness as per basic assumptions in much current evolutionary behavioral theory. Therefore, one challenge to anyone attempting to examine altruism in a neo-Darwinian context is a theoretical justification for why it might occur. Let us briefly summarize the salient positions on this point to date.

---

K.C. MacKinnon (✉)
Department of Sociology and Criminal Justice, Center for International Studies,
St. Louis University, St. Louis, MO 63103, USA
e-mail: ackinn@slu.edu

R.W. Sussman, C.R. Cloninger (eds.), *Origins of Altruism and Cooperation*,
Developments in Primatology: Progress and Prospects 36, DOI 10.1007/978-1-4419-9520-9_7,

Darwin saw social animals as, at least partially, structurally altruistic; "impelled partly by a wish to aid members of their community in a general manner, but more commonly to perform certain definite actions" (*Descent of Man*, p. 913). Wallace saw altruistic and sympathetic behavior toward one's fellow humans as a core adaptive pattern and competition between human groups as an essential factor in the evolution of human behavior and cognitive capabilities (Richards, 1987). Spencer noted that humans vary in their behavioral proclivities and moral senses (which he divided into selfish instinct and sentiment of sympathy). He proposed altruistic behavior as core to human evolutionary success. Spencer described two ways in which altruism could arise and become a dominant behavioral characteristic. Unlike Darwin and Wallace, Spencer saw the individual expression of altruism as having a selfish motivation. He said that as humans relate to the misery of others (engage in a sympathetic response) they act to alleviate others' suffering in order to avoid their own (Principles of Psychology, 1855, 1872). Spencer also allowed for a form of altruism that can arise through a series of reciprocally beneficial acts between individuals and then be "selected" for if these exchanges resulted in increased fitness for the participants (The Principles of Ethics, 1893). Spencer did agree with Darwin and Wallace that within-group altruism could arise via selection. He argued that this type of altruism could arise via competition between groups, those having more altruists most likely doing better over all than those with too few altruists. In fact, he went as far as to suggest that the functional adaptation by such groups to social conditions would allow those groups to reduce the impact that challenges of the environment (natural selection) placed upon them. This perspective was even cited by the cooperation advocate Petr Kropotkin as evidence in support of his perspectives on the hyper-cooperative adaptation in humans (Richards, 1987). In short, the "founding fathers" of evolutionary theory held that altruism was a core feature of social animals, especially humans, and emerged out of either selfish intent or between-group competition. This theme has been echoed ever since, but the puzzle of a mechanism for such behavior was not elaborated by these early theoreticians.

The evolutionary biologist Lee Dugatkin wrote "Eventually biology did solve the puzzle of blood kinship and altruism in the form of a mathematical equation developed by a shy, brilliant evolutionary biologist named William D. Hamilton" (Dugatkin, 2006). This "solution" was the concept of "kin selection" and its corollary: reciprocal altruism. For many theorists these hypotheses laid to rest that the conundrum of altruism is social animals.

Kin selection, the behavioral favoring of your close genetic relatives (Hamilton, 1964), was proposed by William Hamilton to explain the dilemma posed by altruism. While Darwin, Wallace, Spencer invoked a form of group selection, natural selection acting at the level of intergroup competition, to explain why altruism occurs, the theoretical work in genetics and evolutionary theory through the middle of the 20th century produced a negative view of group selection (Williams, 1966). The focus of selection shifted solely to the individual. Kin selection offers a simple equation predicting when an individual organism might behave in a manner that looks altruistic: $r \times b > c$, with $r =$ genetic relatedness between the actor and receiver of the behavior, $b =$ the fitness benefit to the receiver, and $c =$ the fitness cost to the actor. If the individual who receives the benefit from a behavior that has fitness costs to the actor is a relative, then a certain percentage of the actor's genotype (depending on the degree of relatedness) also benefits from the action. Relatedness is then calculated as a simple percentage given a sexual reproducing system. Each offspring is assumed to share 50% of the unique genetic component of each parent, while an uncle or aunt is then related at 25% to an actor. Here genetic investment decreases as "relatives" become more distant (genotypically) from the individual. Because close kin share much of their genotype, we would expect behaviors among them to be seemingly altruistic, as they frequently appear. This simple equation, and its assumptions about genetic systems, forms an integral core to the current paradigm dominating the understanding of altruistic behavior.

Robert Trivers published "the evolution of reciprocal altruism" in 1971 drawing on ideas of Darwin, Spencer, and Hamilton, and proposing a set of mathematical models with a series of predictive assumptions which he termed "reciprocal altruism." The reciprocal altruism model states that unrelated organisms can enter into relationships that can be characterized as fitness value exchanges. Using a simplistic genetic system as a model (like Hamilton), Trivers presents a mathematical equation for the relationship between an actor and a recipient in a series of reciprocal exchanges using a prisoner's dilemma style "payoff matrix." The core of the hypothesis revolves around the frequency and symmetry of potentially altruistic situations. There are three main conditions that are relevant in the potential selection for reciprocal altruism. First, that there be many opportunities for altruistic action during the lifetime of the actors. Second, that a given actor repeatedly interacts with the same small set of individuals. And third, that pairs of altruists are exposed "symmetrically" to altruistic opportunities so that over time two such actors are able to render roughly equivalent benefits to each other while incurring roughly compatible costs. These three conditions set the stage for the selection of a reciprocal altruistic system. Some biological parameters that affect the form of the system include length of lifetime (chances of reciprocal altruism rise with longevity), dispersal pattern (low dispersal rate also favors reciprocal altruism), and degree of mutual independence (group-living animals are more reliant on one another more frequently than solitary ones). Other important biological factors include presence and type of parental care, dominance hierarchy structure, and aid in combat. Trivers predicted that if the three primary conditions are met and the biological parameters set favorable conditions, then reciprocal altruism will evolve as an adaptation in that population. This set of ideas is especially important as it had substantial influence on theoreticians since the 1970s and forms a main basis for models of animal and human behavior in many hypotheses. Recently, Trivers (2006) has argued (following deWaal and Brosnan, 2006) that nonhuman primates who practice reciprocal altruism (capuchins and chimpanzees in his example) develop a sense of aversion to inequity which can be seen as a basal sense of "fairness."

Challenging the four-decade-long aversion to group selection, Wilson and Sober (1994), Sober and Wilson (1998), and more recently Wilson and Wilson (2007), have proposed the insertion of multilevel selection as a core factor in understanding behavior that appears altruistic (especially for humans). The basic concept is that the evolution of behavior can result from selection focusing at multiple levels: the genic, the individual, and the group. In this conceptualization extensive interaction within and between groups produces a context wherein multilevel selection can result in widespread cooperative patterns. That is, selection at the group level can favor groups that have a larger number of individuals who behave altruistically (within group) over those that have fewer such individuals. This in turn can have effects on the local gene pool shifting genotypic frequencies in accord with these intergroup, or local population, level interactions and the selective environments/landscapes they create. This allows for such behavior to emerge without having relied on either kin selection or reciprocal altruism, although both of those might also be at play within groups. A version of this perspective is also promulgated by Richerson and Boyd (2005) to explain high levels of cooperation within human groups and the concomitant competition between such groups. It is worth noting that Darwin, Wallace, Spencer, and E.O. Wilson all proposed some form of this within-group cooperation/altruism model as core to their views on human evolution (Fuentes, 2009). Many past and current theorists see these intragroup versus intergroup relationships as being major players in the augmentation of social complexity with altruistic reciprocity playing a major role for the within-group dynamics and between-group contest evolutionary success.

Thinking about the selective landscapes that such groups and populations inhabit, the concept of "niche construction" takes on particular relevance. Building on work of Richard Lewontin (1983), Ernst Mayr (1963), Conrad Waddington (1959), and taking from the "extended phenotype" concept of Richard Dawkins (1982), F. John Odling-Smee, Kevin Laland, and Marcus Feldman (2003) proposed "niche construction" as a significant evolutionary force. Niche construction is the modification by organisms of the functional relationship between themselves and their environment through an active change of one of the factors of that environment. "Through niche construction organisms not only influence the nature of their world, but also in part determine the selection pressures to which they and their descendants are exposed, and they do so in a non-random manner" (Day et al., 2003). As organisms respond to environmental selective pressures which are themselves modified by the organisms, a feedback mechanism is created, and such feedback loops can fundamentally alter the outcome of evolutionary scenarios. This mutual mutability of organism and environment is a core consideration for primate species whose primary selective environments exist as complex social networks. Flack et al. (2006) argue for a form of social niche construction in primates where social networks constitute the essential social resources in gregarious primate societies. They posit that "The structure of such networks plays a critical role in infant survivorship, emergence and spread of cooperative behavior, social learning and cultural traditions." If this is the case and social interactions impact these networks, it could be argued that social complexity, reciprocity, and even altruistic behavior could be active agents in primate niche construction and major factors in their evolutionary trajectories (see also Fuentes et al., 2010).

## Social Cooperation and Reciprocity: Can It Be Altruism?

There is little debate that strong social attachments are *necessary* for primate survival. Social bonding and the manipulation of those bonds are characteristic of all gregarious primate societies: complex sociality is a core primate adaptation (Silk, 2007). Such relationships are traditionally examined via analyses of hierarchies, cooperative alliances, and long social histories among individuals. As such, understanding social cooperation is a major element in primate studies. Cooperation can be most generally defined as social interactions that have costs to an actor and benefits to other conspecifics, and as Peter Kappeler and Carel van Schaik recently put it "Cooperative behavior is the hallmark of the primate order" (Kappeler and van Schaik, 2006).

The concepts of cooperation and altruism are closely related. However, while it is commonplace to argue that forms of social cooperation characterize many primate societies, we still have a great deal to investigate in regards to specific patterns of reciprocity and the possibility that altruism, outside of reciprocal exchanges, occurs. Reciprocity is frequently measured by analyzing coalitionary behavior, directionality/symmetry of grooming, food sharing, social association patterns, and direct cooperation in task solving. deWaal and Brosnan (2006) suggest that we can envision primate reciprocity along a continuum that ranges from Triver's strong reciprocal altruism at one end to a reciprocity reflecting simple social symmetries at the other. They lay out three specific types of reciprocity: symmetry based, attitudinal based, and calculated. In symmetrical reciprocity, there is no "score keeping," there is a strong mutuality of interactions, and a "strong aversion to major, lasting imbalances in incoming and outgoing benefits" (deWaal and Brosnan, 2006). One could argue that indeed, given the loose and general assessment of symmetry in exchanges, this level of reciprocity may simply be altruism as a byproduct of a social complexity that maximizes close social bonding amongst individuals within a group (between non-kin). The second level of reciprocity, attitudinal based, reflects a mild tit-for-tat strategy wherein individuals who generally have positive and predictive relationships will invest in one another without close tabs on recouping investments. deWaal and Bosnan refer to this as the "if you are nice, I will be nice" principle where the level of reciprocity is based on simple assessments of recent interactions between individuals. The final level, calculated reciprocity, is a full-blown Triver's style reciprocal altruism which involves relatively extensive individual "score keeping" and the potential punishment of cheaters. If this continuum accurately reflects the range of reciprocity, then the possibility exists that reciprocity and altruism are behaviors that share a common origin and are differentiated by the types, contexts, and patterns of relationships between individuals. This, however, does not leave room for altruism occurring outside of familiar social partners in the nonhuman primates. Might this be a distinct difference between humans and other primates?

At this point in the discussion, it is worth briefly discussing an alternative approach to understanding cooperation: biological markets. Introduced nearly two decades ago (Noe et al., 1991), the concept of biological markets as an analytical tool has gained substantial popularity amongst primatologists (Barrett and Henzi, 2006). The basal assumptions of this paradigm match those of free market capitalist systems: (1) individuals control resources or can provide services—these are commodities that can be socially exchanged, (2) trading partners are chosen from the social context via a mechanism of outbidding competition, maximizing social profit, and (3) supple and demand determine the bartering value of the "commodities" exchanged. In other words, cooperative interactions such as coalitionary support and grooming are seen as commodities that can be traded on an open market with market forces (social contexts) driving the value of the commodities. This approach differs to an extent form the models of kin selection and reciprocal altruism in that it sees the interchange between individual variation and group contexts as creating the market driving differentiation of value in the "commodities." This results in an expectation of a good deal of individual flexibility in behavioral response across contexts and time when cooperating (dependent on the "market" conditions at the moment of exchange). However, under this rubric, there is no category for altruism as market models inherently assume all transactions as having a value, and while actors may not try to maximize, they do try to profit. Thus transactions are a profit, a loss, or an equitable transfer, but no models including an option for "non-tax deductable charitable donation" (altruism in this system) are recognized. Our perspective on the biological market model is that it constrains analysis by limiting the types of questions one can ask and by resting on assumptions of limited good, costs, and profit taking that stem from a specific human paradigmatic world view and not necessarily the organic world.

## Social and Ecological Niche Construction and Hyper-Sociality as Primate Heritage: The Social Mind, the Primate Mind and the Cultural Mind

All members of the primate order are characterized by complex interactions between their central nervous system (CNS) and the social/physical environments in which they live (sensorimotor pathways). In particular, information crucial to primate survival is disseminated primarily through *social networks*. The physiological and social correlates of this mandate are an extended period of infant development and brain maturation, which allows for the acquisition of species-appropriate skill sets and knowledge. Initiated during this period and extending for the life of the individual, primates participate in a complex practice of social niche construction (see Flack et al., 2006; Fuentes, 2009, 2011). One can envision that social complexity itself acts as a niche-constructing tool causing the interface between individuals within a group, individuals with their environment, and conspecifics groups within that local population to be seen best as a mutually mutable process. The social and biotic/abiotic ecologies are then modified by social behavior which is in turn affected by the pressures of those same social and abiotic/biotic environments.

Primates are characterized by a specific type of "social intelligence" (Dunbar and Shultz, 2007) such that "distinctive aspects of primate cognition evolved mainly in response to the especially challenging demands of a complex social life of constant competition and cooperation with others in the social group" (Herrmann et al., 2007; Silk, 2007) in addition to the external ecological pressures. There could therefore be a ratcheting up of this social complexity in anthropoids, which is increased in hominoids and exponentially enhanced in hominins. One might envision a scenario wherein the basal complex sociality of mammals is enhanced in primates, and primates then use their social networks/contexts as a tool to meet and modify the demands of the environment (the selective landscape). As the local environments are being modified, selection pressures alter changing the selective landscapes for the primate populations. Increased cognitive complexity in the hominoids facilitates a faster or more intensive utilization of the social bonds and relationships as tools to meet ecological challenges. This increased cooperation and reciprocity becomes a central component of behavioral repertoires and is constantly engaging the social and biotic ecologies in feedback scenarios resulting in niche construction and concomitant shifting/modification of selective landscapes. As broad and complex social behavioral complexes (reliant on extensive cooperation) become commonplace in the hominins, true altruism (actions engaging in a cost for self with other's benefit) arises as an emergent property of the system. Because of the extensive cooperation and the generally intensive reciprocity in hominins/humans, multiple instances of altruism can be experienced across the lifetimes of individuals without effectively

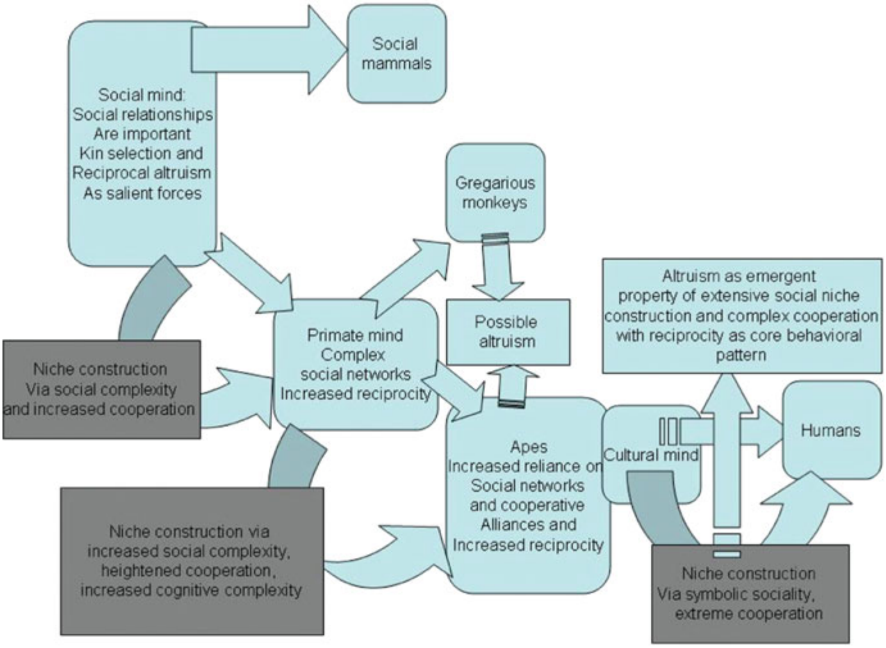


**Fig. 7.1** A model for the relationship between social complexity, niche construction and the possible emergence of altruism in primates and humans

negative fitness costs. No individuals are uniformly altruistic but altruistic acts can appear, even commonly, and not be selected against within the populations. Here altruistic action emerges as a by-product of the physiological and behavioral adaptations required to effectively negotiate high level and complex social networks where coalitions, multi-party social negotiations, and reciprocity are the primary avenues for social and reproductive success (see Fig. 7.1) (see also de Waal, 1996; Hauser, 2006; Tomasello, 2009).

If this model is accurate, we should be able to look to anthropoid primates, especially those known for very complex coalitionary behavior, broad geographic range and behavioral plasticity, and see the basal components of this system. If these baselines occur, we benefit from their study and the comparative analyses of human and other primate systems specifically in our attempts to understand the mechanisms and evolution of behavioral systems that can produce altruistic acts.

## Case Studies: *Macaca, Cebus, Pan, and Homo*

### *The Genus Macaca*

Macaque monkeys (members of the genus *Macaca*) are among the most widespread of any primate genus. The genus *Macaca* underwent a radiation in the Plio-Pleistocene, about 2 million years ago, similar to that of the genus *Homo* at the same time. The macaques spread across much of Asia and into central Eurasia and even northern Africa. Macaques have encountered many diverse habitats. As a result, they reflect responses to a broader range of environmental pressures than nearly any other nonhuman primate group. There are about 19 macaque species, but they tend to cluster into a few major species groups. Macaques are generalists in their feeding patterns, preferring fruit but eating a wide variety of foodstuffs, including leaves, insects, and occasionally vertebrates. They are full quadrupeds and frequently arboreal; however, most macaque species also use the ground for foraging and distance locomotion.

The majority of macaques live in multi-female/multi-male groups that can number from 10 to more than 100 individuals. There are usually more adult females than adult males in these groups, and social activity revolves around clusters of related females (Thierry, 2011). Males tend to leave their natal groups and seek out other groups to join. Females, on the other hand, are philopatric, and thus surrounded by their female relatives throughout their lives. Female macaques spend a great deal of time and energy associating and interacting with their maternal kin. A few adult males do associate with these matrifocal units, but most males are relatively solitary, remaining on the outskirts of the groups and occasionally interacting with females and other males. Subadult males may be seen together in small subgroups that have varying cohesion. An explanation for these social differences between males and females can be found in the dispersal and dominance patterns of macaque societies. Although there is a range of dominance patterns, from very strict linear (“despotic”) dominance systems to relaxed, “egalitarian” ones, macaque grouping and overall social patterns are surprisingly cohesive but are characterized by a wider range of behavioral variation across individuals (Thierry, 2011).

For female macaques, the main arena of social interactions involves female maternal kin. Depending on the size of the overall macaque group, there are usually from two to six matrifocal units within it. The dominant matrifocal units are usually able to displace the others from prime food sources, sleeping sites, and other preferred resources. This is partly because the dominant matrifocal units are also the largest. With more individuals in a cluster, they have a better chance of intimidating or outcompeting other, smaller clusters of individuals. However, although there is strength in numbers, individuals are not always dominant on their own. Macaque females rely heavily on alliances with female relatives to gain access to resources and win competitions. There are also dominance relationships within matrifocal groups. Generally, a prime-age female (about 8–12 years old) holds the highest rank within such clusters, with youngest daughters inheriting their mother's rank.

Males have linear dominance relationships that can change rapidly. Due to their dispersal patterns, males cannot rely on kin to assist them in conflicts and need to form associations with other males and females in order to negotiate dominance disputes. High-ranked males often form coalitions with other males to acquire/defend social position and gain access to preferred resources. There are many ways for males to attain a high dominance rank. Some males are extremely aggressive and use fighting and conflict to move up the dominance hierarchy. Fighting in male macaques can result in substantial injuries; however, it is not clear how often these injuries result in deaths. Other males use association with females to form coalitions to create strong social bonds with other individuals. These males participate in much grooming and other social interactions with females and young, even including holding infants. Overall most male ranks are fragile, and males may spend anywhere from a few months to many years at high rank (Bercovitch and Huffman, 1999).

For the macaques then, kin–kin interactions and non-kin intra- and intersexual coalition formation and competition are the keystone components of their social networks. Following Flack et al. (2006), we can envision the potential for social niche construction, as individuals in macaque groups negotiate these social networks modifying their boundaries and internal landscapes in the context of changing demographic and, potentially, ecological variables. For males, the social networks need to be learned anew when moving between groups, and for females these networks are layered with intra and inter-matrifocal group relationships providing the primary social landscapes. Because nearest neighbors and most frequent interaction partners for females are often relatives, kin selection has been invoked to explain a majority of alliance and coalitionary actions by female macaques.

Adult female–adult male coalitions are rarely kin based and thus reflect possible circumstances for reciprocal altruism to occur. Such intersexual relationships could also be seen as intersexual cooperation and competition with differential payoffs to participants dependant on social skill, experience, and context. The proximate social benefits of macaque intersexual cooperation could be different for males and females. Females may receive active male assistance in dominance contests (improving their access to contested resources), while males might be receiving social benefits such as increased grooming and social interactions. Both sexes may receive reproductive benefits and suffer reproductive costs from such alliances. Manipulation of the social networks can alter the selective landscapes (in terms of both social and reproductive parameters) changing the pressures and payoffs for all involved (social niche construction). For adult males, associations with larger or more dominant matrifocal groups might offer increased mating opportunities and an overall greater level of social interaction potentially ameliorating social stress emerging from male–male competition. However, one does see aggregations of young males who play together and spend large amounts of time in social activities such as grooming. In these cases reciprocal altruism or mutualism might be invoked to explain these social and temporally variable associations, but one could also as easily invoke a simple benefit of access to social partners. In this case, if costs are moderate or negligible in regards to overall reproductive success, we could see potentially altruistic acts emerge out of simply a high density of prosocial relationships amongst young males without any significant impact on fitness. This is also the case with large matrifocial groups wherein some females might be distantly related but extremely familiar and frequent social partners to others. In such cases, we might also expect to see possible altruism on occasion as fitness costs for such actions would be negligible, but the pattern of prosocial behavior within the whole group would be high. Obviously, we would not expect to see frequent high-cost altruistic acts in any of these cases, but one can envision in these macaque social networks many opportunities for actors to engage in small costs that benefit others with no social or physical negative repercussions.

## *The Genus Cebus*

The genus *Cebus* traditionally consists of four species: *C. apella, C. albifrons, C. olivaceus* (formerly *C. nigrivittatus*), and *C. capucinus*, with the recently discovered *C. Kaapori* often included as a fifth species (Queiroz, 1992). There are more than 30 subspecies recognized (Ford and Hobbs, 1996). More recently, some have argued for three subspecies of *C. apella* to be listed as distinct species (e.g., Groves, 2001; Rylands et al., 2000; and see Jack, 2011 and Fragaszy et al., 2004 for reviews). All of these monkeys can be classified generally as arboreal, diurnal, medium-sized primates with robust bodies and semi-prehensile tails. The better known species are commonly divided into two morphological groups, “tufted” (*C. apella*) and “nontufted” (*C. albifrons, C. olivaceus,* and *C. capucinus*), based on the degree of erect hairs on either side of the crown (Hershkovitz, 1949; Napier and Napier, 1985). The primary differences between the four species are coat color, coat pattern, and geographical range (Freese and Oppenheimer, 1981). They all are somewhat similar in diet and behavior. Capuchin monkeys are found throughout Central and South America. *C. capucinus* ranges from Honduras to the northwestern part of Ecuador (Rowe, 1996) and is the only *Cebus* species that occurs in Central America. The other three species are found primarily in the Orinoco and Amazon River basins of South America and have varying levels of sympatry. *C. apella* has the most extensive range of any New World monkey and occurs throughout most of Amazonia, the

Brazilian coastal forests, and northern Argentina. On the genus level, only *Alouatta* has a more extensive range overall among Platyrrhines (Sussman, 2000).

All four capuchin species are moderately sexually dimorphic and live in large multi-male, multi-female social groups of 4–36 individuals (Freese and Oppenheimer, 1981; Fedigan and Jack, 2001). Average group sizes differ slightly: *C. capucinus* with 16.4 members, *C. albifrons* with 19.8, *C. apella* with 18, and *C. olivaceus* with 21 (Fragaszy et al., 2004). All species show linear dominance hierarchies, with an alpha male and alpha female; however, it is often difficult to determine specific individual rankings lower than beta in wild groups.

Capuchin monkeys are highly adaptable and occupy a wide array of habitat types (lowland rain forest, cloud forest, tropical dry forest, living in proximity to humans, etc). They are quite omnivorous, using a range of foods such as insects, fruits, and vertebrate prey (Chapman and Fedigan, 1990; Panger et al., 2002; Fragaszy et al., 2004). Capuchins are described as manipulative and extractive foragers: they can exploit hard-to-obtain and hard-to-process resources including larvae from embedded substrates, hard-shelled fruits and nuts, and fast-moving vertebrate prey such as squirrels, tree rats, birds, and lizards (Fedigan, 1990; Rose, 1997; Panger et al., 2002; O'Malley and Fedigan, 2005; MacKinnon, 2006). Consequently, they have been characterized as eating foods that "fight back". The documented studies of tool/object use in *Cebus* (see Panger, 1998 for definitions, and Panger, 2007 for review; but see Garber and Brown, 2002) describe how palm nuts are repeatedly pounded against another surface until opened (Izawa and Mizuno, 1977; Struhsaker and Leland, 1977; Anderson, 1990; Visalberghi et al., 2007, 2008), how marine oysters are opened by the use of stones and other oysters (Fernandez, 1991; Parker and Gibson, 1977), and how sticks are used to groom wounds or to contact a potentially dangerous object (Boinski, 1988; Cooper and Harlow, 1961; Richie and Fragaszy, 1989; Visalberghi, 1990; Westergaard and Fragaszy, 1987). This combination of manipulative skills and an opportunistic feeding strategy allow the highly adaptive *Cebus* species to exploit different habitats and diets. Juvenile capuchins are skilled foragers from a young age and exploit many of the same foods as adults (MacKinnon, 2006). Capuchins forage in a social context, and while there is much debate about whether capuchins can truly imitate (e.g., Visalberghi and Fragaszy, 1990, 2002; Visalberghi and Limongelli, 1996; Custance et al., 1999; Visalberghi and Addessi, 2003), young animals do intensely observe the behavior of others around them. Therefore, varying group compositions and extended periods of juvenility might allow differing opportunities for observational learning (Whiten, 1989; Custance et al., 1999).

Capuchin physical development is slow compared to other New World monkey species, and the major life history stages occur later when contrasted to similar-sized primates (Fragaszy, 1990; Robinson and Janson, 1987). For example, an adult female *Cebus capucinus* in the wild first gives birth around age seven (Fedigan and Rose, 1995; Fragaszy et al., 2004; Fedigan, pers. comm. and pers. obs). Males at age 7–10 years are still considered subadult but are on the threshold of adult status and are already engaged in sexual mountings with adult females.

Adult capuchins have an unusually large brain for their body size and have well-developed cerebellum, neocortex, and dorsal thalamus areas (Bauchot, 1982;

Passingham, 1973). The sensory and motor cortices that control the hand and the visual cortex are particularly enlarged (Clark, 1960). Such enlargement provides the skills needed for complex manipulative abilities and the construction of object relationships (Gibson, 1990). Thus, capuchins may need a longer period of development for brain growth and cognitive functioning associated with learning their foraging and social behavior repertoires. Among primates, capuchins are especially altricial at birth (Fragaszy et al., 2004). They acquire postural control, prehension and locomotion later than squirrel monkeys, to which they are most closely related, and even later than some Old World monkey species (e.g., baboons and macaques) (Fragaszy, 1990; Bezanson, 2006). Skeletal development is not completed until after the sixth year of life (Jungers and Fleagle, 1980).

As capuchins' immatures develop, certain individuals are preferred for play bouts, foraging partners, grooming partners, and carriers (see Sherrow and MacKinnon, 2011). The juvenile stage is especially important for developing and maintaining early formative relationships: play is common, strong bonds among peers develop, and preferential relationships with certain older animals are formed. As juveniles grow into adolescents, they will begin the transition to either assuming an adult role in the natal group, if female, or transferring out, if male. During this time, they may show an increase in conflict with adult members, rougher and more boisterous play sessions, and an increase in allomothering by females.

Capuchins are a male-transfer species. Even after an individual leaves its birth group, occasional encounters may occur between him and members of his former group. He may leave and return many times or may be followed by a younger juvenile to a neighboring group (Jack, 2003). Parallel dispersal occurs in *C. capucinus* and lasts through multiple migration events (Jack and Fedigan, 2004a, b). Females may occasionally transfer, although it is rare by comparison. Intergroup encounters are common in some areas (e.g., see Jack, 2001 for information on Santa Rosa National Park, Costa Rica), and there is a high likelihood that not all individuals in these groups are strangers to each other. Adult females may have dispersed offspring and siblings in neighboring groups, males may have mothers and siblings, juveniles may have siblings, and adult males have been documented making "visits" to a neighboring group for short periods of time. Male reunion displays have been documented not only among males within a group who are separated for brief amounts of time (captive data for *C. apella*: Phillips and Goodchild, 2005; Matheson et al., 1996; Phillips et al., 1994) but also among males in different groups during intergroup encounters (Jack, 2007; pers. obs.).

Across the *Cebus* species, males and females generally show egalitarian relationships and are characterized as affiliative, with little physical aggression occurring between the sexes. The alpha female usually ranks directly below the alpha male but can dominate over all other males; in several species female coalitions form and can displace the alpha male in context-specific circumstances (Fragaszy et al., 2004). Kinship is an important factor in female–female relationships, although it may not be as important a factor as in cercopithecines. While the overall characteristics of female social relationships are generally consistent across groups and species, male capuchins show extensive variation in their relationships with each other—ranging from despotic to highly cooperative and affiliative. Such diversity reflects behavioral plasticity in these primates and may be based on shifting ecological (resource abundance/defense) and social (kinship/familiarity) pressures (Janson, 1986).

Mating behavior in *Cebus* is best known in two of the four main species: *C. apella* and *C. capucinus* and is highlighted by elaborately coordinated complex courtship displays that can last for hours (Carosi and Visalberghi, 2002; Jack, 2011). Both conceptive and nonconceptive mating occurs throughout the year, and these behaviors appear to have been co-opted in social exchanges of dominance, affiliation, and perhaps reconciliation (Manson et al., 1997).

As with macaques, interactions based on biological kin, as well as non-kin intra- and intersexual coalition formation and competition are evident components of capuchin social systems (Perry, 1996, 1997, 1998). Because males typically transfer out, social relationships need to be reestablished within their new groups, however many times they switch groups in their lifetimes. Yet, there is evidence that males may also exhibit extended networks of relationships among neighboring groups (see Jack and Fedigan, 2004a, b). Female capuchins who stay in their birth group—and live upwards of 20–30 years in the wild—have a dense constellation of intragroup social networks to keep track of and maintain over the course in their lifetimes. Primates that are highly plastic and variable in their behaviors, and that live in large, multi-male multi-female social groups, have an intricate web of social relationships to remember. Each relationship has its own particular history of positive and negative reinforcements, possible kinship and relatedness factors, and ongoing dynamics. Thus, a form of social niche construction (see Flack et al., 2006) is likely in this genus, given their longevity and complex social landscapes with multiple changing variables.

Capuchins appear to be able to sense fairness in reward/trade situations and value equitable behavior in cooperative situations over rewards in certain tasks (Brosnan and de Waal, 2003, 2004a, b; Brosnan et al., 2006). They are also quite intent on grooming sick/injured individuals of varying rank and are distressed when group members die (MacKinnon, pers. obs.). Thus, they may be astute at empathizing with others' emotional states in varying social contexts—a precondition for altruistic acts. *Cebus* and hominoids share many behavioral and morphological convergences. Given that, do capuchins exhibit any of the core comparison facets (see Table 7.1) for a basal potential for altruism? Recent work on social conventions/traditions in the genus suggests they do. Complex coalitionary behavior exists across the *Cebus* species, with frequent and sustained behavioral exchanges between individuals. For example, males and females generally show egalitarian relationships and are characterized as affiliative, with little physical aggression. Dyadic and triadic interactions occur between and within the sexes; male capuchins in particular show extensive variation in their relationships with each other, ranging from despotic to highly cooperative and affiliative. Extensive visual monitoring and communication (postural, vocal, tactile, visual), grooming, solicited assistance during conflicts, and long bouts of being in contact and/or proximity with others in the group are just some of the daily components of capuchin repertoires. The genus also occupies a broad geographic range, having adaptive success in a diverse array of environments (tropical dry forest, primary rain forest, and living in close proximity to humans).

**Table 7.1** Core comparison facets for target primate groups in order to examine basal potential for altruism

| Facet | Complex coalitionary behavior | Broad geographic range | Behavioral plasticity | Extended period of socially mediated learning |
|---|---|---|---|---|
| Importance | A basal assumption underlying the potential for altruistic behavior is the occurrence of frequent and sustained behavioral exchanges between individuals | Broad geographic distribution of a primate group across diverse eco-types/habitats indicates a level of adaptive success representing some ability to ameliorate diverse ecological pressures, possibly niche construction | If we are trying to model the potential emergence of complex and flexible behavior patterns, then one assumes that there must be a strong underlying malleability in the basal neurological and physiological infrastructure for behavioral action | In order to acquire the social skills and apparent "theory of mind" necessary for interpreting others' complex actions, presumed intentions, and emotional states, a prolonged period of learning in a social context is required |

They exhibit a high level of behavioral plasticity. For example, in an examination of cross-site differences in foraging behavior in *C. capucinus*, long-term data from three Costa Rican field sites (geographically close and ecologically similar) identified 30% of shared food items that were processed differently (Panger et al., 2002). Also, in a study that involved a 19,000-hour combined data set (13 social groups, four study sites in Costa Rica, over a 13-year period), several social traditions were identified according to outlined criteria. It is hypothesized that capuchins use these group- or clique-specific social conventions to test the quality of their social relationships (Perry et al., 2003a).

Finally, the genus *Cebus* displays an extended period of socially mediated learning. Evidence suggests that they may need a longer period of development compared to many primate species for brain growth and cognitive functioning associated with learning their foraging and social behavior repertoires. Given the above, it seems plausible that the genus *Cebus* possesses the fundamental and underlying socio-cognitive architecture for basal altruism. . .at least potentially. Living in large complex groups/networks, composed of long-lived, cognitively sophisticated, and behaviorally plastic individuals capable of modifying their social repertoires and histories, positions capuchins well within the range of primate trends discussed here; including the genus *Cebus* in this context provides a Platyrrhine extension to considering social cooperation and (potential) altruism as components of niche construction and social complexity across primates.

## *Genus Pan*

There are two species of chimpanzee: *Pan troglodytes* and *Pan paniscus*, frequently called the bonobo, found across central Africa (Stumpf, 2011). All members of the genus *Pan* are heavily frugivorous (fruit-eating) and their lives are substantially affected by seasonality and fruit abundance. Both species of chimpanzees live in multi-female/multi-male communities ranging in size from 20 to more than 150 individuals. All these individuals are rarely, if ever, in the same location at the same time, however. Chimpanzee communities are characterized by a *fission–fusion* social pattern, meaning that individuals spend their time in various subgroups, which have variable compositions across space and time. Both species are characterized by female dispersal and male philopatry, although there is some female philopatry in at least a few eastern chimpanzee populations (Stumpf, 2011).

Subgroups generally consist of mixtures of age and sex classes. Mother–offspring subgroups are made up of an adult female and her dependent offspring (usually a youngster under 7 years of age). Multi-female subgroups consist of multiple adult females and their offspring. Subgroups made up of clusters of related individuals consist of females and their offspring, some of whom may be adult or at least independent of the mother. All-male subgroups are made up of multiple adult and sometimes subadult (teenage) males. Heterosexual subgroups consist of adult males and females and frequently young individuals. Consort pairs are two adult individuals (usually one male and one female) who separate themselves from other individuals in the community and spend a good deal of time mating. Finally, individual chimpanzees occasionally move around the range of their community by themselves.

In *P. troglodytes*, males are, on average, dominant over females; however, both males and females compete with others of their sex and establish hierarchical ranks (Stumpf, 2011). Males attain high rank by forming alliances and coalitions with other males (frequently those of similar ages) and by using spectacular displays and other intimidation tactics, including serious fighting, to manipulate other members of their community into ceding access to favored resources. Male competition for rank can result in serious injuries and occasionally death. Some males attain rank through extreme aggression and maintain that behavior once they are high ranking. Others appear to rely heavily on coalition partners and mutual grooming and social bonding to achieve and maintain dominance status. For females, dominance is associated with substantially improved access to food sources and high infant survivorship (especially in east African populations). High-ranking females tend to have a large number of offspring in the group, and occasionally mother–daughter pairs act together to achieve or maintain high rank. Females do achieve dominance via aggressive displays and occasionally fighting, but they do not do so as frequently or intensely as males. In east African *P. troglodytes,* both males and females who are high ranking gain access to favored food sources and social partners and therefore have increased reproductive success. In West African forms, rank does not always result in increased reproductive success (Boesch et al., 2002; Stumpf, 2011).

In *P. paniscus*, dominance contests, dominance relationships, and the overall tenor of rank are different than in *P. troglodytes*. In this species, females are generally dominant to males and put on substantial dominance displays in which they drag tree braches or other objects behind them (White, 1996; Furuichi, 1997). However, dominance interactions rarely result in serious fighting. Rather, many of the dominance interactions and other conflicts in this species are resolved via genital–genital rubbing and other sociosexual behavior (Kano, 1992; Parish, 1996). Male bonobos also have an intrasexual dominance hierarchy, but they are seldom dominant over females. A male's rank is frequently tied to that of his mother. Males do compete with one another aggressively at times, but compared with *P. troglodytes*, bonobos show lower overall rates of aggression (Furuichi and Ihobe, 1994).

Although females disperse in both species, strong bonds between unrelated females are common in *P. paniscus* and fairly rare in *P. troglodytes* (Parish, 1996; Stanford, 1998; Kano, 1992). This difference may have to do with the differences in dominance systems and in the way that community members treat recent migrants in the two species.

Both species of the genus *Pan* hunt and eat other mammals, but *P. troglodytes* does so more frequently than *P. paniscus*. Hunting appears to coincide with times of fruit abundance, suggesting that meat may not be merely a nutritional supplement. Although females hunt in both species, it is an activity performed predominantly by males in *P. troglodytes*. Populations of *P. troglodytes* in western Africa hunt in a more coordinated manner than those in eastern Africa (Boesch et al., 2006; Stanford, 1998). Hunting success rates seem to be related to the size of the subgroup doing the hunting, with larger parties being more successful. When kills are made, the meat is frequently shared among a few individuals, usually the coalition partners and allies of the successful hunter. Occasionally, if the kill is made by a low-ranking individual, then a high-ranking male may steal the kill and not share any with the actual hunter. Interestingly, infanticide (killing of infants) and cannibalism are both reported for *P. troglodytes*. There are cases in which adult females and males have captured, killed, and eaten infants from their own community and from females of neighboring communities. When an infant is killed and consumed, it is treated very much like a colobus monkey that has been hunted and captured.

In populations of *P. troglodytes* in eastern Africa, researchers have reported incidents of intercommunity conflict that resulted in deaths. "Border patrols," or groups of males moving along the communities' geographic boundaries, are reported for most, but not all, populations of chimpanzees. It has been hypothesized that these "patrols" are subgroups of males searching for small subgroups or lone individuals from neighboring communities. Occasionally, when these subgroups encounter individuals from another community, they attack as a mob. It is hypothesized that these attacks are an effort to increase the community's access to desired resources and that chimpanzees strategically assess the relative "power" of their neighbors in attempts to increase their ranges (Stumpf, 2011; Wilson and Wrangham, 2003).

### *Genus Homo*

*Homo sapiens* are found distributed across nearly all habitable areas on the planet. The species exhibits a startling high degree of morphological variation while simultaneously demonstrating relatively little inter-populational genetic variation (Fuentes, 2006; Long et al., 2009, Relethford, 2009). Humans live in mixed sex groups ranging from less than 50 individuals to many thousands of individuals in areas where they have undertaken substantial ecological engineering (villages, urban zones etc.). Human behavioral, dietary, and social plasticity exceeds all other living animals. Patterns of intergroup transfer, mating, alliances and coalitions within and between groups, social hierarchies, politico-economic systems and all manner of social structures vary in human societies across the globe. Humans are amongst the slowest developing primates, with extensive social learning core to a complex ontogenetic sequence involving linguistic and symbolic as well and more general behavioral instruction. Tool use and manufacture along with extensive extra-somatic manipulation of the environment is standard for all human groups with massive niche alteration and construction ongoing throughout our evolutionary history and more recently and regularly at an accelerated pace across local, regional, and global levels.

## Primate Trends and Human Patterns: Overlap, Differences, and Evolutionary Implications

The above taxonomic examples highlight important facets of social complexity and map to our notions of social niche construction and social networks. Specifically, complex coalitionary behavior, inhabiting a broad geographical range, high levels of behavioral plasticity, and an extended period of socially mediated learning are all malleable and can change rapidly from one generation to the next (or stay in stasis). Being able to accommodate such potential change underscores the adaptive advantage of social networks in terms of functioning as a niche construction *mechanism* (see Fuentes et al., 2010).

Humans are primates, yet we display a wide array of significant differences, especially at the level of social complexity and relative frequency of altruistic behavior (or at least apparently altruistic behavior). How can we envision the derivation of the modern human system in line with the phylogenetic connections to other primates?

The earliest human ancestors existed in multi-adult groups with a relatively high degree of social complexity, patterns of social bonding between individuals within the group, and a level of inter-individual cooperation and competition at least equal to that found in ape and monkey societies. Individuals exhibited substantial behavioral flexibility, at least as much as the modern apes, and a repertoire of vocal and gestural communication, but not language. Rudimentary tool use and manipulation of the environment was present as was sexual dimorphism in size, with males being larger than females resulting in some differences in behavioral roles between males and females. However, specific patterns of dominance relationships between individuals are not clear. These earliest human ancestors shared with their primate cousins specific type of "social intelligence" (Dunbar and Shultz, 2007). Humans stand apart via the *vast amount* of information that is disseminated socially through space *and* time (via spoken/written language characterized by abstraction and symbolism). In the relatively brief period of evolution for the genus *Homo*, we have been able to dramatically alter/manipulate myriad environments (affecting our survival on a populational level via predator avoidance, better food acquisition, cultural complexity, increased infant survivorship, and overall group health) in a short amount of time (Fuentes et al., 2010). We are also characterized by the most extended period of infant dependency and development in our order, including a protracted period of brain maturation. It has been suggested that an extension of the primate social intelligence hypothesis to reflect the fact that humans are "ultra-social" would be useful, resulting in what some have called the cultural intelligence hypothesis (Herrmann et al., 2007). So, where all primates have evolved social-cognitive skills for cooperating and competing with group/community members, humans have also evolved skills for establishing distinct cultural groups, with different physical and symbolic markers (social institutions, artifacts, language, etc). While primates transmit many behaviors socially (see Whiten et al., 1999; Panger et al., 2002; Perry et al., 2003a, b; Preutz and Bertolani, 2007, and van Schaik et al., 2003), their species-typical cognition does not require participation in specific cultural interactions in the same way as it does in humans (Tomasello, 1999). Only humans have a *species-specific* set of social-cognitive skills (that emerges early in ontogeny) for participating and exchanging knowledge in cultural groups (see Herrmann et al., 2007). [However, as Boesch (2007) points out, most claims of human cognitive uniqueness are based on comparisons of White middle class Westerner humans (*H. sapiens*) with captive chimpanzees (*P. troglodytes*).] Thus, the extent to which our biological and cultural traits are intertwined and embedded in our species' evolutionary history is unique among primate taxa.

In summary, the potential for altruism—or even just the basal proclivity toward an altruistic ability—is likely present in many primate lineages and potentially reflects a gradient of the "cultural mind as niche construction" concept. We have attempted to highlight here the plasticity and resulting adaptability in each of the four genera and propose that bonding and cooperation play a significant role in social niche construction among primates.

## References

Anderson, J. R. (1990). Use of objects as hammers to open nuts by capuchin monkeys (*Cebus apella*). *Folia Primatol. 54*, 138–145.

Barrett, L. & Henzi, S. (2006). Monkeys, markets and minds: Biological markets and primate sociality. In P. M. Kappeler & C. P. van Schaik (eds.), *Cooperation in primates and humans* (pp. 209–232). New York: Springer.

Bauchot, R. (1982). Brain organization and taxonomic relationships in Insectivora and Primates. In Armstrong, E. (ed.), *Primate brain evolution* (pp. 163–174). New York: Plenum Press.

Bercovitch, F. B. & Huffman, M. A. (1999). The macaques. In P. Dolhinow & A. Fuentes (eds.), *The nonhuman primates* (pp. 77–85). Mountain View, CA: Mayfield Publishing.

Bezanson, M. (2006). Leap, bridge or ride? Ontogenetic influences on positional behavior in *Cebus* and *Alouatta*. In A. Estrada, P. A. Garber, M. S. M. Pavelka, & L. Luecke (eds.), *New perspectives in the study of mesoamerican primates: Distribution, ecology, behavior, and conservation* (pp. 333–348). New York: Springer.

Boesch, C. (2007). What makes us human (*Homo sapiens*)? The challenge of cognitive cross-species comparison. *J. Comp. Psychol. 121(3)*, 227–240.

Boesch, C., Gone Bi, Z. B., Anderson, D. & Stahl, D. (2006). Food choice in Tai chimpanzees: Are cultural differences present? In G. Hohmann, M. M. Robbins, & C. Boesch (eds.), *Feeding ecology in apes and other primates: Ecological, physical and behavioral aspects* (pp. 183–201). New York: Cambridge University Press.

Boesch, C., Hohmann, G. & Marchant, L. (eds.). (2002). *Behavioral diversity in chimpanzees and bonobos*. New York: Cambridge University Press.

Boinski, S. (1988). Use of a club by a wild white-faced capuchin (*Cebus capucinus*) to attack a venomous snake (*Bothrops asper*). *Am. J. Primatol. 14(2)*, 177–179.

Brosnan, S. F. & de Waal, F. B. M. (2003). Monkeys reject unequal pay. *Nature 425(6955)*, 297–299.

Brosnan, S. F. & de Waal, F. B. M. (2004a). A concept of value during experimental exchange in brown capuchin monkeys, *Cebus apella*. *Folia Primatol*. *75(5)*, 317–330.

Brosnan, S. F. & de Waal, F. B. M. (2004b). Socially learned preferences for differentially rewarded tokens in the brown capuchin monkey (*Cebus apella*). *J. Comp. Psych. 118(2)*, 133–139.

Brosnan, S. F., Freeman, C. & de Waal, F. B. (2006). Partner′s behavior, not reward distribution, determines success in an unequal cooperative task in capuchin monkeys. *Am. J. Primatol. 68(7)*, 713–724.

Carosi, M. & Visalberghi, E. (2002). Analysis of tufted capuchin (*Cebus apella*) courtship and sexual behavior repertoire: Changes throughout the female cycle and female interindividual differences. *Am. J. Phys. Anthropol. 118(1)*, 11–24.

Chapman, C. A. & Fedigan, L. M. (1990). Dietary differences between neighboring *Cebus capucinus* groups: Local traditions, food availability or responses to food profitability? *Folia Primatol. 54*, 177–186.

Clark, W. E. Le Gros (1960). *The antecedents of man.* Chicago: Quadrangle Books.

Cooper, L. R. & Harlow, H. F. (1961). Note on a cebus monkey's use of a stick as a weapon. *Psychol. Rep. 8*, 418.

Custance, D., Whiten, A. & Fredman, T. (1999). Social learning of an artificial fruit task in capuchin monkeys (*Cebus apella*). *J. Comp. Psychol. 113(1)*, 13–23.

Darwin, C. (1871). *The descent of man and selection in relation to sex.* London: John Murray.

Dawkins, R. (1976). *The selfish gene*. Oxford: Oxford University Press.

Dawkins, R. (1982). *The extended phenotype*. Oxford: Oxford University Press.

Day, R. L., Laland, K. & Odling-Sme, J. (2003). Rethinking adaptation: the niche construction perspective. *Perspect. Biol. Med. 46(1)*, 80–95.

de Waal, F. B. M. (1996). *Good natured*. Cambridge, MA: Harvard University Press.

deWaal, F. B. M. & Brosnan, S. F. (2006). Simple and complex reciprocity in primates. In P. M. Kappeler & C. P. van Schaik (eds.), *Cooperation in primates and humans: Mechanisms and evolutions* (pp. 85–105). New York: Springer.

Dugatkin, L. A. (2006). *The altruism equation: Seven scientists search for the origins of goodness*. Princeton, NJ: Princeton University Press.

Dunbar, R. I. & Shultz, S. (2007). Evolution in the social brain. *Science 317(5843)*, 1344–1347.

Fedigan, L. M. (1990). Vertebrate predation in *Cebus capucinus*: Meat-eating in a neotropical monkey. *Folia Primatol. 54*, 196–205.

Fedigan, L. M. & Jack, K. (2001). Neotropical primates in a regenerating Costa Rican dry forest: A comparison of howler and capuchin population patterns. *Int. J. Primatol. 22(5)*, 689–713.

Fedigan, L. M. & Rose, L. M. (1995). Interbirth interval variation in three sympatric species of neotropical monkey. *Am. J. Primatol. 37(1)*, 9–24.

Fernandez, M. E. B. (1991). Tool use and predation of oysters (*Crassostrea rhizophorae*) by the tufted capuchin, *Cebus apella apella*, in brackish water mangrove swamp. *Primates 32(4)*, 529–531.

Flack, J. C., Girvan, M., de Waal, F. B. M. & Krakauer, D. C. (2006). Policing stabilizes construction of social niches in primates. *Nature 439*, 426–429.

Ford, S. M. & Hobbs, D. G. (1996). Speices definition and differentiation as seen in the postcranial skeleton of *Cebus*. In M. A. Norconk, A. L. Rosenberger, & P. A. Garber (eds.), *Adaptive radiations of neotropical primates* (pp. 229–249 and 540–541). New York: Plenum Press.

Fragaszy, D. M. (1990). Early behavioral development in capuchins (*Cebus*). *Folia Primatol. 54*, 119–128.

Fragaszy, D. M., Fedigan, L. M. & Visalberghi, E. (2004). *The complete capuchin: The biology of the genus Cebus*. New York: Cambridge University Press.

Freese, C. H. & Oppenheimer, J. R. (1981). The capuchin monkeys, genus *Cebus*. In A. F. Coimbra-Filho & R. A. Mittermeier (eds.), *Ecology and behavior of neotropical primates, Vol. I* (pp. 331–400). Rio de Janeiro: Academia Brasiliera de Ciencias.

Fuentes, A. (2006). Human culture and monkey behavior: Assessing the contexts of potential pathogen transmission between macaques and humans. *Am. J. Primatol. 68(9)*, 880–96.

Fuentes, A. (2009). Re-situating Anthropological approaches to the evolution of human behavior. *Anthropol. Today 25(3)*, 12–17.

Fuentes, A. (2011). Social systems and socioecology: Understanding the evolution of primate behavior. In C. Campbell, A. Fuentes. K. C. MacKinnon, S. Bearder, & R. Stumpf (eds.), *Primates in perspective, 2nd edition* (pp. 500–511). New York: Oxford University Press.

Fuentes, A., Wyczalkowski, M. & MacKinnon, K. C. (2010). Niche Construction through cooperation: A nonlinear dynamics contribution to modeling facets of the evolutionary history in the genus *Homo. Curr. Anthropol. 51(3)*, 435–444.

Furuichi, T. (1997). Agonistic interactions and matrifocal dominance rank of wild bonobos (*Pan paniscus*) at Wamba. *Int. J. Primatol. 18(6)*, 855–875.

Furuichi, T. & Ihobe, H. (1994). Variation in male relationships in bonobos and chimpanzees. *Behaviour 130(3–4)*, 211–228.

Garber, P. A. & Brown, E. (2002). Experimental field study of tool use in wild capuchins (*Cebus capucinus*): Learning by association or insight? *Am. J. Phys. Anthropol. Suppl 34*, 74–75.

Gibson, K. R. (1990). New perspectives on instincts and intelligence: Brain size and the emergence of hierarchical mental constructional skills. In S. T. Parker & K. R. Gibson (eds.), *"Language" and intelligence in monkeys and apes: Comparative developmental perspectives* (pp. 97–128). Cambridge: Cambridge University Press.

Groves, C. P. (2001). *Primate taxonomy*. Washington, DC: Smithsonian Institution Press.

Hamilton (1964). The genetical evolution of social behavior. Parts I and II. *J. Theor. Biol. 7*, 1–52.

Hauser, M. (2006). *Moral minds: How nature designed our universal sense of right and wrong*. New York: Harper Collin Publishers.

Herrmann, E., Call, J., Hernandez-Lloreda, M. V., Hare, B. & Tomasello, M. (2007). Humans have evolved specialized skills of social cognition: the cultural intelligence hypothesis. *Science 317*, 1360–1366.

Hershkovitz, P. (1949). Mammals of northern Colombia. Preliminary report No. 4: Monkeys (primates), with taxonomic revisions of some forms. *Proc. U.S. Natl. Museum 98*, 323–427.

Izawa, K. & Mizuno, A. (1977). Palm-fruit cracking behavior of wild black-capped capuchin (*Cebus apella*). *Primates 18*, 773–792.

Jack, K. (2003). Explaining variation in affiliative relationships among male white-faced capuchins (*Cebus capucinus*). *Folia Primatol. 74(1)*, 1–16.

Jack, K. (2011). The Cebines: Toward an explanation of variable social structure. In C. Campbell, A. Fuentes. K. C. MacKinnon, S. Bearder, & R. Stumpf (eds.), *Primates in perspective, 2nd edition* (pp. 108–122). New York: Oxford University Press.

Jack, K. M. (2001). Effect of male emigration on the vigilance behavior of coresident males in white-faced capuchins (*Cebus capucinus*). *Int. J. Primatol. 22*, 715–732.

Jack, K. M. & Fedigan, L. (2004a). Male dispersal patterns in white-faced capuchins, *Cebus capucinus*. Part 1: Patterns and causes of natal emigration. *Anim. Behav. 67(4)*, 761–769.

Jack, K. M. & Fedigan, L. (2004b). Male dispersal patterns in white-faced capuchins, *Cebus capucinus*. Part 2: Patterns and causes of secondary dispersal. *Anim. Behav. 67(4)*, 771–782.

Janson, C. H. (1986). Capuchin counterpoint. *Nat. Hist. 2/86*, 45–53.

Jungers, W. & Fleagle, J. (1980). Postnatal growth allometry of the extremities in *Cebus albifrons* and *Cebus apella*: A longitudinal and comparative study. *Am. J. Phys. Anthropol. 53*, 471–478.

Kano, T. (1992). *The last ape: Pygmy chimpanzee behavior and ecology*. Stanford: Stanford University Press.

Kappeler, P. M. & van Schaik, C. P. (2006). Infanticide risk and the evolution of male-female association in primates. *Proc. Biol. Sci. 264(1388)*, 1687–1694.

Kropotkin, P. (1914). *Mutual aid: A factor of evolution*. Porter Sargent Publishers, New edition (June 1976).

Lewontin, R. (1983). Gene, organism and environment. In D. S. Bendall (ed.), *Evolution from molecules to men*. Cambridge: Cambridge University Press.

Long, J. C., Li, J. & Healey, M. E. (2009). Human DNA sequences, more variation and less race. *Am. J. Phys. Anthropol. 139(1)*, 23–34.

MacKinnon, K. C. (2006). Food choice by juvenile capuchin monkeys (*Cebus capucinus*) in a tropical dry forest. In: A. Estrada, M. Pavelka, P. Garber, & L. Luecke (eds.), *New perspectives in the study of mesoamerican primates: Distribution, ecology, behavior, and conservation* (pp. 349–366). New York: Springer.

Manson, J. H., Perry, S. & Parish, A. R. (1997). Nonconceptive behavior in bonobos and capuchins. *Int. J. Primatol. 18*, 767–786.

Matheson, M. D., Johnson, J. S. & Feuerstein, J. (1996). Male reunion displays in tufted capuchin monkeys (*Cebus apella*). *Am. J. Primatol. 40(2)*, 183–188.

Mayr, E. (1963). *Animal speciation and evolution.* Cambridge, MA: Harvard University Press.

Napier, J. R. & Napier, P. H. (1985). *The natural history of the primates.* London: British Museum (Natural History).

Noe, R., van Schaik, C. P. & van Hooff, J. A. R. A. M. (1991). The market effect: An explanation for pay-off asymmetries among collaborating animals. *Ethology 87(1–2)*, 97–118.

Odling-Smee, F. J., Laland, K. N. & Feldman, M. W. (2003). *Niche construction: The neglected process in evolution*. Monographs in Population Biology 37. Princeton, NJ: Princeton University Press.

O'Malley, R. C. & Fedigan, L. M. (2005). Evaluating social influences on food-processing behavior in white-faced capuchins (*Cebus capucinus*). *Am. J. Phys. Anthropol. 127(4)*, 481–491.

Panger, M. (1998). Object-use in free-ranging white-faced capuchins (*Cebus capucinus*) in Costa Rica. *Am. J. Phys. Anthropol. 106(3)*, 311–321.

Panger, M. (2007). Tool use and cognition in primates. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, M. Panger, & S. K. Bearder (eds.), *Primates in perspective, 1st edition* (pp. 665–676). New York: Oxford University Press.

Panger, M., Perry, S., Rose, L. M., Gros-Louis, J., Vogel, E., MacKinnon, K. C. & Baker, M. (2002). Cross-site differences in foraging behavior of white-faced capuchins (*Cebus capucinus*). *Am. J. Phys. Anthropol. 119*, 52–66.

Parish, A. R. (1996). Female relationships in bonobos (*Pan paniscus*): Evidence for bonding, cooperation, and female dominance in a male-philopatric species. *Hum. Nat. 7(1)*, 61–96.

Parker, S. & Gibson, K. (1977). Object manipulation, tool use, and sensorimotor intelligence as feeding adaptations in *Cebus* monkeys and great apes. *J. Hum. Evol. 6*, 623–641.

Passingham, R. E. (1973). Anatomical differences between the neocortex of man and other primates. *Brain Beh. Evol. 7*, 337–359.

Perry, S. (1996). Female-female social relationships in wild white-faced capuchin monkeys, *Cebus capucinus*. *Am. J. Primatol. 40(2)*, 167–182.

Perry, S. (1997). Male-female social relationships in wild white-faced capuchins (*Cebus capucinus*). *Behaviour 134*, 477–510.

Perry, S. (1998). Male-male social relationships in wild white-faced capuchins (*Cebus capucinus*). *Behaviour 135*, 139–172.

Perry, S., Baker, M. Fedigan, L. M. Gros-Louis, J., Jack, K., MacKinnon, K. C., Manson, J. H., Panger, M., Pyle, K. & Rose, L. M. (2003a). Social conventions in wild white-faced capuchins: Evidence for traditions in a neotropical primate. *Curr. Anthropol. 44(2)*, 241–268.

Perry, S., Panger, M., Rose, L., Baker, M., Gros-Louis, J., Jack, K., MacKinnon, K. C., Manson, J. H., Fedigan, L. & Pyle, K. (2003b). Traditions in wild white-faced capuchin monkeys. In D. M. Fragaszy & S. Perry (eds.), *The biology of traditions: Models and evidence* (pp. 391–425). Cambridge: Cambridge University Press.

Phillips, K. A., Bernstein, I. S., Dettmer, E. L., Devermann, H. & Powers, M. (1994). Sexual behavior in brown capuchins (*Cebus apella*). *Int. J. Primatol. 15(6)*, 907–917.

Phillips, K. A. & Shauver Goodchild, L. M. (2005). Reunion displays in captive male brown capuchins (*Cebus apella*). *Primates 46(2)*, 121–125.

Preutz, J. D. & Bertolani, P. (2007). Savanna chimpanzees, *Pan troglodytes verus*, hunt with tools. *Curr. Biol. 17(5)*, 412–417.

Queiroz, H. L. (1992). A new species of capuchin monkey, genus *Cebus* Erxleben, 1777 (Cebidae: Primates) from eastern Brazilian Amazonia. *Goeldiana Zoologia 15*, 1–13.

Relethford, J. H. (2009). Race and global patterns in phenotypic variation. *Am. J. Phys. Anthropol. 139(1)*, 16–23.

Richards, R. (1987). *Darwin and the emergence of evolutionary theories of mind and behavior*. Chicago, IL: University of Chicago Press.

Richerson, P. J. & Robert, B. (2005). *Not by genes alone: How culture transformed human evolution*. Chicago, IL: The University of Chicago Press.

Richie, B. & Fragaszy, D. M. (1989). A capuchin monkey (*Cebus apella*) uses tools on her infant's wound. *Am. J. Primatol. 16*, 345–348.

Robinson, J. G. & Janson, C. H. (1987). Capuchins, squirrel monkeys, and Atelines: Socioecological convergence with old world primates. In B. B. Smuts, D. L., Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (eds.), *Primate societies* (pp. 69–82). Chicago: University of Chicago Press.

Rose, L. M. (1997). Vertebrate predation and food-sharing in *Cebus* and *Pan*. *Int. J. Primatol. 18(5)*, 727–765.

Rowe, R. (1996). *The pictorial guide to the living primates*. East Hampton, NY: Pogonias Press.

Rylands, A. B., Schneider, H., Langguth, A., Mittermeier, R. A., Groves, C. P. & Rodriguez-Luna, E. (2000). An assessment of the diversity of New World primates. *Neotropical Primates 8(2)*, 61–93.

Sherrow, H. M. and MacKinnon, K. C. (2011). Juvenile and adolescent primates: The application of life history theory. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, R. Stumpf, & S. K. Bearder (eds.), *Primates in perspective, 2nd edition* (pp. 455–464). New York: Oxford University Press.

Silk, J. B. (2007). Social component of fitness in primate groups. *Science 317*, 1347–1351.

Sober, E. & Wilson, D. S. (1998). *Do unto others: The evolution and psychology of unselfish behavior*. Cambridge, MA: Harvard University Press.

Spencer, H. (1855). *Principles of psychology*. London: Longman, Brown, Green and Longmans.

Spencer, H. (1872). *Principles of psychology* (2nd edn.). London: Williams and Norgate.

Spencer, H. (1893). The inadequacy of natural selection. *Contemp. Rev. 63*, 152–166, 439–456.

Stanford, C. B. (1998). The social behavior of chimpanzees and bonobos: Empirical evidence and shifting assumptions. *Curr. Anthropol. 39(4)*, 399–420.

Struhsaker, T. T. & Leland, L. (1977). Palmnut smashing by *Cebus a. apella* in Colombia. *Biotropica 9*, 124–126.

Stumpf, R. M. (2011). Chimpanzees and bonobos: Inter- and intraspecies diversity. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, R. Stumpf, & S. K. Bearder (eds.), *Primates in Perspective, 2nd edition* (pp. 340–456). New York: Oxford University Press.

Sussman, R. W. (1999). *The biological basis of human behavior: A critical review*. Upper Saddle River, NJ: Prentice Hall.

Sussman, R. W. (2000). *Primate ecology and social structure. Vol. 2: New world monkeys*. Heights, MA: Pearson Custom Publishing.

Thierry, B. (2011). The macaques: A double-layered social organization. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, R. Stumpf, & S. K. Bearder (eds.), *Primates in perspective, 2nd edition* (pp. 229–241). New York: Oxford University Press.

Tomasello, M. (1999). The human adaptation for culture. *Ann. R. Anthropol. 28*, 509–529.

Tomasello, M. (2009). *Why we cooperate*. Cambridge, MA: MIT Press.

Trivers, R. (1971). The evolution of reciprocal altruism. *Q. Rev. Biol. 46(10)*, 35–57.

Trivers, R. (2006). Reciprocal altruism: 30 years later. In P. M. Kappeler & C. P. van Schaik (eds.), *Cooperation in primates and humans* (pp. 67–83). New York: Springer.

van Schaik, C. P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C. D., Singleton, I., Suzuki, A., Utami, S. S. & Merrill, M. (2003). Orangutan cultures and the evolution of material culture. *Science 299(5603)*, 102–105.

Visalberghi, E. (1990). Tool use in *Cebus*. *Folia Primatol. 54*, 146–154.

Visalberghi, E. & Addessi, E. (2003). Food for thought: Social learning about food in feeding capuchin monkeys. In D. M. Fragaszy & S. Perry (eds.), *The biology of traditions* (pp. 187–212). Cambridge: Cambridge University Press.

Visalberghi, E. & Fragaszy, D. M. (1990). Do monkeys ape? In S. T. Parker & K. R. Gibson (eds.), *"Language" and intelligence in monkeys and apes: Comparative developmental perspectives* (pp. 247–273). Cambridge: Cambridge University Press.

Visalberghi, E. & Fragaszy, D. M. (2002). Do monkeys ape? Ten years after. In K. Dautenhahn & C. L. Nehaniv (eds.), *Imitation in animals and artifacts* (pp. 471–479). Cambridge, MA: MIT Press.

Visalberghi, E., Fragaszy, D., Ottoni, E., Izar, P., de Oliveira, M. G., & Andrade, F. R. D. (2007). Characteristics of hammer stones and anvils used by wild bearded capuchin monkeys (*Cebus libidinosus*) to crack open palm nuts. *Am. J. Phys. Anthropol. 132(3)*, 426–444.

Visalberghi, E. & Limongelli, L. (1996). Action and understanding: Tool use revisited through the mind of capuchin monkeys. In A. Russon, K. Bard, & S. Parker (eds.), *Reaching into thought: The minds of the great apes* (pp. 57–79). Cambridge: Cambridge University Press.

Visalberghi, E., Sabbatini, G., Spagnoletti, N., Andrade, F. R. D., Ottoni, E., Izar, P. & Fragaszy, D. (2008). Physical properties of palm fruits processed with tools by wild bearded capuchins (*Cebus libidinosus*). *Am. J. Primatol. 70(9)*, 884–891.

Waddington, C. H. (1959). Canalization of development and genetic assimilation of acquired characters. *Nature 183*, 1654–1655.

Westergaard, G. C. & Fragaszy, D. M. (1987). The manufacture and use of tools by capuchin monkeys (*Cebus apella*). *J. Comp. Psych. 101*, 159–168.

White, F. J. (1996). Comparative socio-ecology of *Pan paniscus*. In W. C. McGrew, L. F. Marchant, T. Nishida (eds.), *Great ape societies* (pp. 29–41). Cambridge: Cambridge University Press.

Whiten, A. (1989). Transmission mechanisms in primate cultural evolution. *Trends Ecol. Evol. 4(3)*, 61–62.

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W., & Boesch, C. (1999). Cultures in chimpanzees. *Nature 399(6737)*, 682–685.

Williams, G. C. (1966). *Adaptation and natural selection: A critique of some current evolutionary thought.* Princeton, NJ: Princeton University Press.

Wilson, D. S. & Sober, E. (1994). Reintroducing group selection to the human behavioral sciences. *Behavioral and Brain Sciences 17(4)*, 585–608.

Wilson, D. S. & Wilson, E. O. (2007). Rethinking the theoretical foundation of sociobiology. *Q. Rev. Biol. 82*(4), 327–348.

Wilson, M. L., & Wrangham, R. W. (2003). Intergroup relations in chimpanzees. Intergroup relations in chimpanzees. *Ann. R. Anthropol. 32*, 363–392.

# Chapter 8
# Collective Action and Male Affiliation in Howler Monkeys (*Alouatta caraya*)

**Paul A. Garber and Martin K. Kowalewski**

## Introduction

> "Primates differ from many other animal lineages in that they show rather good evidence of cooperation, especially in long-term relationships" (van Schaik and Kappeler, 2006: 13).

Traditional models of primate socioecology highlight female within-group feeding competition and aggression over limited food resources as a primary driver of primate social interactions. In this regard, several authors have argued that within-group feeding competition is a pervasive cost of social group-living and that individuals should live in groups that are small enough to avoid the costs of aggression at feeding sites and large enough to benefit from predator detection and reduced infanticide risk (Janson, 1988; van Schaik, 1989; Isbell, 1991; Sterck et al., 1997; Chapman and Chapman, 2000; Crockett and Janson, 2000; Kappeler and van Schaik, 2002). These models (ecological constraints, socioecological, intersexual selection, infanticide) also focus on aggression among males, both within-group and between-group over access to reproductive partners, and male sexual coercion of females as major determinants of female mating patterns (Henzi and Barrett, 2003; Pradhan and van Schaik, 2008; Boyko and Marshall, 2009; Clarke et al., 2009; Kitchen et al., 2009). Certainly within-group dominance relationships and social hierarchies offer critical insight into the behavior of individuals residing in the same group. However, Thierry (2008: 93) has recently argued that the traditional socioecological model "now impedes the development of new lines of thought and that the time has come to ask where the Emperor's clothes are." Given a series of recent books and articles on the benefits to individuals of cooperative behavior (Dugatkin, 2002; Clutton-Brock, 2002; Mitani et al., 2002; Sussman and Chapman, 2004; Sussman et al., 2005; Chapais, 2006; van Schaik and Kappeler, 2006; Kitchen and Beehner, 2007; Sussman and Garber, 2007, 2011), there is a growing body of evidence that increased fitness benefits accrue to individual males and females

---

P.A. Garber (✉)
Department of Anthropology, University of Illinois, Urbana, IL 61801, USA
e-mail: p-garber@illinois.edu

R.W. Sussman, C.R. Cloninger (eds.), *Origins of Altruism and Cooperation*,
Developments in Primatology: Progress and Prospects 36, DOI 10.1007/978-1-4419-9520-9_8,

that reside in a functioning, cooperative, stable, and affiliative social group. Many species of primates live in social groups composed of multiple adult males and females. Although changes in group size and composition commonly occur, sets of related and unrelated individuals may remain together in a group for periods of months, years, and in some cases for decades (Sussman and Garber, 2007, 2011). Group-living requires that individuals form predictable social relationships, explore a common set of resources, defend a common range, and develop affiliative and cooperative social bonds. We define cooperation as "joint action [by two or more individuals] for mutual benefit" (Gilby and Wrangham, 2008).

Animals living in social groups commonly confront what has been described as the "collective action problem." The collective action problem represents an economic model of social interactions designed to "investigate how the distribution of benefits within groups motivates individual action" (Nunn, 2000: 192). The model examines and describes the costs and benefits to individuals of joint or coordinated action (alliance formation, cooperation, resource, mate, group, or predator defense), as well as the costs and benefits to those group members who act as "free-riders" or receive the immediate benefits of successful group action, but by not joining the action incur none of the costs. For example, many primate species reside in multimale–multi-female groups in which some or all resident adult males act collectively to exclude neighboring or extragroup males from entering the group (Nunn, 2000; Cooper et al., 2004; Garber, 1988; Kitchen et al., 2004; Kitchen and Beehner, 2007). It has been argued that under conditions in which the benefits to free-riders are high (continued access to feeding sites and mating partners), and the costs are low (minimal social sanctions or retaliation), a collective action problem may arise resulting in a breakdown of cooperative behavior as additional individuals adopt a free-rider strategy (Nunn, 2000; Cooper et al., 2004). However, asymmetrical benefits of social group-living are common in many primate species (Jack and Fedigan, 2007; van Noordwijk and van Schaik, 1999; van Schaik, 1989; Noe et al., 1991; Cooper et al., 2004; Kitchen et al., 2004; Kitchen and Beehner, 2007), and even in the absence of direct coercion or aggressive retribution targeting free-riders, it is unlikely that individuals who fail to engage in cooperative behavior gain greater long-term benefits than individuals who actively participate, especially in cases in which the number of collective actors increases the success of the action (Kitchen and Beehner, 2007). Moreover, dominant individuals may benefit from the presence of subordinate group members who only occasionally engage in collective action, if their presence or their actions serve to deescalate encounters with neighboring groups or lone intruders (Kitchen et al., 2004). Finally, models of male collective action argue that kinship, length of male–male associations, and the degree of within-group reproductive skew represent critical factors in understanding the nature of male cooperative behavior (Nunn and Lewis, 2001; Kitchen et al., 2004).

In this chapter, we present data based on a 21-month field investigation of within-group social tolerance, cooperation, collective action, and mating strategies of male black and gold howler (*Alouatta caraya*) monkeys in Argentina. New World monkeys differ from Old World monkeys in several important ways including (1) limited sexual dimorphism in body size (Garber and Estrada, 2009), (2) an adult female to adult male sex ratio in established groups that more closely approaches 1:1 (adult sex ratios in OWM are highly biased toward females (Jack and Fedigan, 2007), (3) a greater prevalence of bisexual dispersal or female-biased dispersal (Strier, 1994), (4) lower levels of direct male sexual coercion of females (van Schaik et al., 2004), (5) generally greater levels of within-group male intrasexual tolerance and affiliation (Garber and Kowalewski, in press), and (6) less frequent takeovers and eviction of an alpha males by invading extragroup males (Sterck and van Hooff, 2000). We argue that models of primate socioecology based on within-group reproductive and feeding competition derived from studies of Old World primates fail to adequately explain within-group male affiliation, mating strategies, and collective action in many taxa of New World primates (Strier, 1994).

## *Alouatta caraya*

*Alouatta caraya* is a sexually dichromatic species of howler monkey that exploits a range of forest types including gallery forests, flooded forests, subtropical forests, seasonal semideciduous fragmented forests, and less seasonal forests on island ecosystems throughout northern Argentina, southern Brazil, eastern Bolivia, and Paraguay (Brown and Zunino, 1994; Bravo and Sallenave, 2003; Kowalewski and Zunino, 2004). Black and gold howlers commonly form multi-male and multi-female social groups of 8–20 individuals and are characterized by female mating promiscuity and collective male territory and mate defense (Kowalewski, 2007). In *A. caraya*, as in *A. palliata* (but to a much smaller degree in *A. pigra*, van Belle et al., 2009; *A. seniculus*, Agoramoorthy and Hsu, 2000, and *A. guariba*, Sousa Fialho and Setz, 2007), females solicit copulations and mate with multiple resident and neighboring adult males during fertile and non-fertile periods (Wang and Milton, 2003; Kowalewski, 2007). In *A. caraya*, resident males appear to be extremely tolerant of the social and mating activities of other resident males but highly aggressive to nonresident males that attempt to enter the group or copulate with resident females (Kowalewski, 2007). As in other howler species, both male and female *A. caraya* are reported to disperse from their natal group. The result of bisexual dispersal (Di Fiore and Campbell, 2007) is that individuals are likely to spend most or part of their adult lives in social groups with non-relatives (but see Pope, 2000 for evidence of paired migration and kin bonds in red howlers, *Alouatta seniculus*). Given the presence of stable multi-male social groups and a pattern of female mating promiscuity, we explore how resident adult male black and gold howlers confront the collective action problem of shared group and mate defense (Nunn, 2000) and examine the role of between-group factors in strengthening within-group social bonds among resident adult males. We argue that affiliative behaviors and social bonds that characterize resident adult males are reinforced across a range of social and ecological contexts, and offer important insights into the individual benefits that adult male's receive through their collective actions.

## Methods

Data on the behavior and ecology of two groups of black and gold howlers were collected over the course of 21 months (December 2003–November 2004) on Isla Brasilera near the confluence of the Paraná and Paraguay rivers in northern Argentina (27°20′S and 58°40′W). The island represents an area of 292 ha without permanent human settlement and is covered by continuous flooded forest and temporary lagoons. At least 35 groups of black and gold howler monkeys (*A. caraya*) naturally inhabit the island (Pave, pers. comm.). The climate is subtropical with an average annual temperature of 21.6°C and an average annual rainfall of 1,200 mm. A more complete description of the site is provided elsewhere (Kowalewski and Zunino, 2004, Kowalewski, 2007).

Over 1,465 h of behavioral data were collected on two neighboring groups of black and gold howler monkeys. Individuals in each group were followed from sunrise to dusk for 5 days a month. Group X contained nine members including three to four adult males and three to four adult females (group size changed during the study). Group G contained 11–12 individuals including four adult males and four adult females. All adults in our study groups were marked with anklets and ear tags to insure accurate identification. We recorded the social interactions between individuals in our two study groups, as well as their interactions with three neighboring groups (Group E, Group M, and Group LR) and one solitary male who had emigrated from Group G in 2002 (Oklander, 2007). The population density of howlers on Isla Brasilera is 348 ind/km$^2$. This is considerably higher than the density (104 ind/km$^2$) reported for populations living in nearby anthropogenically altered mainland forests (Kowalewski and Zunino, 2004; Zunino et al., 2007).

### *Behavioral Data Collection*

Scan sampling data (Altmann, 1974) were collected by dividing each hour into six 10-min periods. Data were collected at 2-min intervals during each 10-min period. This was accomplished by having three trained researchers recording the behavior, location, diet, activity, and nearest neighbor of all group members. Thus, we obtained six data points per group member per hour or a total of 35,160 individual activity records for Group X and 39,555 individual activity records for Group G. Our goal was to obtain information on all group members throughout the day and to track the coordinated activities and social interactions of the entire group. In this way, we are confident that we observed and recorded all social interactions between individuals of the study group and between residents and individuals from neighboring groups. All observers were trained together for a period of 15–20 days prior to data collection in order to maximize accuracy and inter-observer reliability. This study was part of larger study on social behavior and affiliative relationships in *A. caraya*.

## *Association Indices*

In order to examine evidence of male intrasexual social bonds and alliances, we calculated two indices of association. The first was based on patterns of spatial association and nearest neighbor preferences. We assumed that individuals who were each other's nearest neighbors and spatially separated by a distance of $\leq 2$ m comprised a strong affiliative dyad. The distance of 2 m represents a distance of approximately 2–3 howler arm lengths. Crockett and Eisenberg (1987) have suggested that spatial association is a strong measure of partner preference in howlers. Our second measure of affiliation was based on grooming relationships and the frequency of grooming bouts exchanged by individual males.

Using the scan samples, we calculated a Twice Weight Index of Association for each pair of individuals in each group (Cairns and Schwager, 1987; Dias and Rodriguez Luna, 2006). This index of association is expressed as follows:

$$\mathrm{I_{AB}} = \#\mathrm{AB}/(\#\mathrm{A} + \#\mathrm{B} - \#\ \mathrm{AB})$$

$\mathrm{I_{AB}}$: dyadic association index of two individuals A and B
#AB: Number of scan samples in which A and B appeared together
# A: Number of scan samples in which A was present but B was not
# B: Number of scan samples in which B was present but A was not

The Twice Weight Index reduces the likelihood of overestimating the association frequencies between dyads because it includes information both on the presence of two individuals in the same subgroup as well as the absence of one of these individuals from a subgroup. Following Dias and Rodriguez Luna (2006), the dyadic association indices were transformed into a relative measurement of association (Newton-Fisher, 1999) using the following formula:

$$\mathrm{Z_{AB}} = (\mathrm{I_{AB}} - \mathrm{I})/\mathrm{s}$$

where,

$\mathrm{Z_{AB}}$: dyadic association strength (deviations from the indices of all dyads are outweighed by mean association levels across all dyads)
I: mean association index across all dyads
s: standard deviation of the sample

Association indices vary from 0 (never a given conspecific's nearest neighbor) to 1 (always that conspecific's nearest neighbor). To test if the individuals associated more with certain individuals than expected by chance, we used a permutation test based on Monte Carlo procedures included in the software SOCPROG2.3 (http://myweb.dal.ca/hwhitehe/social.htm). The test compares the original association indices against a series of results obtained by random permutations of the original data set. We ran 20,000 permutations. At that number of iterations the *p* values were stabilized.

### Grooming Interactions

Using scan samples, we also calculated an index of association based on grooming for every pair of individuals in each group. Grooming was scored when an individual (groomer) was cleaning and/or inspecting the fur of another individual (receiver) using his mouth and/or hands. The index used is similar to the Simple Ratio Index (Cairns and Schwager, 1987), with frequencies of both grooming bouts given and grooming bouts received. It was calculated as follows:

$$\mathrm{IG}_{\mathrm{AB}} = \#\mathrm{AB}/(\#\mathrm{A} + \#\mathrm{B})$$

$\mathrm{IG}_{\mathrm{AB}}$: Index of grooming interactions
#AB: Number of grooming interactions with AB
# A: Total number of grooming interactions for individual A
# B: Total number of grooming interactions for individual B

This index varies from 0 (no interactions between a potential dyad) to 1 (all interactions were between these two individuals). To test if the individuals groomed certain individuals more frequently than expected by chance, we ran a permutation analysis using the SOCPROG software as in the previous analysis. We present the intensity and direction of these interactions using sociograms constructed through SOCPROG software.

### Intergroup Encounters

An intergroup encounter was scored when two groups were within 50 m of each other and in visual contact. We considered that two encounters with the same group during the same day represented different encounters if either of the groups was involved in an encounter with a third group or the two original groups were separated by a distance of more than 100 m for more than 3 h between encounters, and that during this interval, individuals were engaged in normal activities such as feeding or resting. For each encounter, we recorded the identity of the groups involved, duration, and location.

### Mating Behavior

A copulation was scored when we observed a mounting, intromission, and a thrusting sequence (Jones, 1985; Strier, 1997). Serial copulations were scored as a single copulatory event, if they occurred in rapid sequence or during the same resting period. Female sexual receptivity was determined by their sexual activity. A female was considered sexually active on a given day if she was observed copulating.

We considered her to remain in a sexually active state until a period of greater than 2 days had elapsed during which she was not observed to copulate. Data from other studies indicate that black and gold howler females conceive during a 3–4-day ovulatory period (Di Fiore and Campbell, 2007). Across several howler species, gestation is consistently reported to be between 180 and 194 days (Colillas and Coppo, 1986; Glander, 1980; Crockett and Sekulic, 1982; Shoemaker, 1979; Kowalewski and Zunino, 2004—although one study reported a variation of 152–195 days [Calegaro-Marques and Bicca-Marques, 1993]).

We were able to determine the date of birth for each infant born in our study group within 1–4 days (Kowalewski and Garber, 2010). Assuming an average gestation length of 180 ± 7 days, we counted back to identify the likely period of conception and pregnancy for all group females. We considered a female to be potentially fertile and ovulating (PFO), if she was observed copulating during periods when she was not pregnant or lactating, including the 2-week period during which she was likely to have conceived (assuming a gestation length of 180 ± 7 days). We considered a female to be non-fertile (NF) during periods in which she was pregnant or nursing. Female *A. caraya* do not exhibit a conspicuous genital swelling during ovulation. However, it is possible to detect a slight vaginal tumescence and color change associated with mating receptivity (Zunino pers. comm.; see also *Alouatta palliata* [Jones, 1985]). The term *fertile period* is used to describe the period during which a female was judged to be PFO (we did not collect endocrine profiles of adult females, and acknowledge that in using behavioral measures of fertility, we are likely to have misclassified some periods during which sexually active non-pregnant, non-lactating females were not ovulating [NF] as potentially fertile periods [PFO]). Quantitative data on mating behavior, copulations, and social interactions were analyzed and compared between PFO and non-PFO periods. We considered sexual solicitation or female mate choice to have occurred when a female actively pursued a particular male by grooming, touching, and following him, and by displaying a characteristic proceptive posture in which the female faced away from the male exposing her thighs, and then turned her head toward the male (Kowalewski and Garber, 2010).

## Results

### *Within-Group Male Affiliation*

Although male black and gold howlers were highly aggressive to solitary adult males or males from neighboring groups, they were highly tolerant of other resident males across a range of social contexts. For example, adult males were each other's nearest neighbors (within 0–2 m) during 40% of fruit-feeding bouts, 53% of flower-feeding bouts, and 56% of leaf-feeding bouts. During resting, which accounted for 59% of the howler activity budget, males were each other's nearest neighbor (0–2 m), 70% of the time. Although grooming is not a common activity in

*A. caraya* (accounting for only 4.6% of total activity budget), 12% of adult-grooming bouts were between resident adult males. Resident male black and gold howlers also were observed to engage in a behavior termed social embracing. Social embracing appeared to serve an important function in reaffirming male–male alliances during intergroup encounters and after bouts of within group male–male howling. Male–male embracing occurred at a rate of 0.07 embraces per hour. In total, 79% of male–male embraces occurred in the context of an intergroup encounter. The central male of each group was involved in social embracing in 77% of all cases.

In marked contrast to these patterns of affiliation and association, the frequency of intrasexual agonistic interactions among the four resident adult males in each study group was extremely low. On average, we observed only one aggressive interaction per resident male every 2 months (0.0036 agonistic interactions per hour per male in Group X and 0.0068 in Group G). This pattern was consistent across both howler study groups.

We also examined the strength of partner preferences within dyadic associations among resident males. This was accomplished using measures of grooming frequency and spatial proximity (Fig. 8.1a, b). Although males and females were each other's most frequent grooming partners, in Group G, Hermoso and Jose, both of whom acted as central males during part of our study, groomed each other more than each groomed any other male (Fig. 8.1a). In Group X, grooming patterns were less clear. For example Jesus received more grooming from Primo (his preferred partner) and from Gatti (the central male) than he provided to each of these other males.

To explore these results more fully, we constructed sociograms based on patterns of social tolerance or the amount of time individual males were scored as each other's nearest neighbor. Based on these data, there is evidence of strong individual partner preferences between resident adult males (Fig. 8.1b). In Group G, Jose and Hermoso, and Ova and Rocky, respectively, were each other's preferred social partner across all behavioral contexts. Ova and Rocky were half-sibs (the sons of Jose) and had matured in their natal group (Oklander, 2007). (After the death of their father, Jose in 2005, both Ova and Rocky successfully emigrated into different neighboring groups; Peker pers. comm.) In Group X, adult males Jesus and Primo were each other's preferred social partner. Resident adult males Primo and Jesus were characterized by strong partner preferences during resting, traveling, and feeding, whereas the central male of this group, Gatti, tended to have two adult females (Ana and Josefa) as his most frequent partners (Fig. 8.1b). In both social groups, we found that whereas the central male had an adult male as his nearest neighbor 46% of the time, subordinate males had other adult males as their nearest neighbor only 34% of the time.

Overall, we found that the mean association indices between howler dyads differed significantly from random ($p < 0.05$ for all the six male dyads in Group G and Group X, respectively), suggesting that dyads of male howlers associated more frequently than expected based on the number of potential social partners (for all analyses, the standard deviation of the original data set was greater than

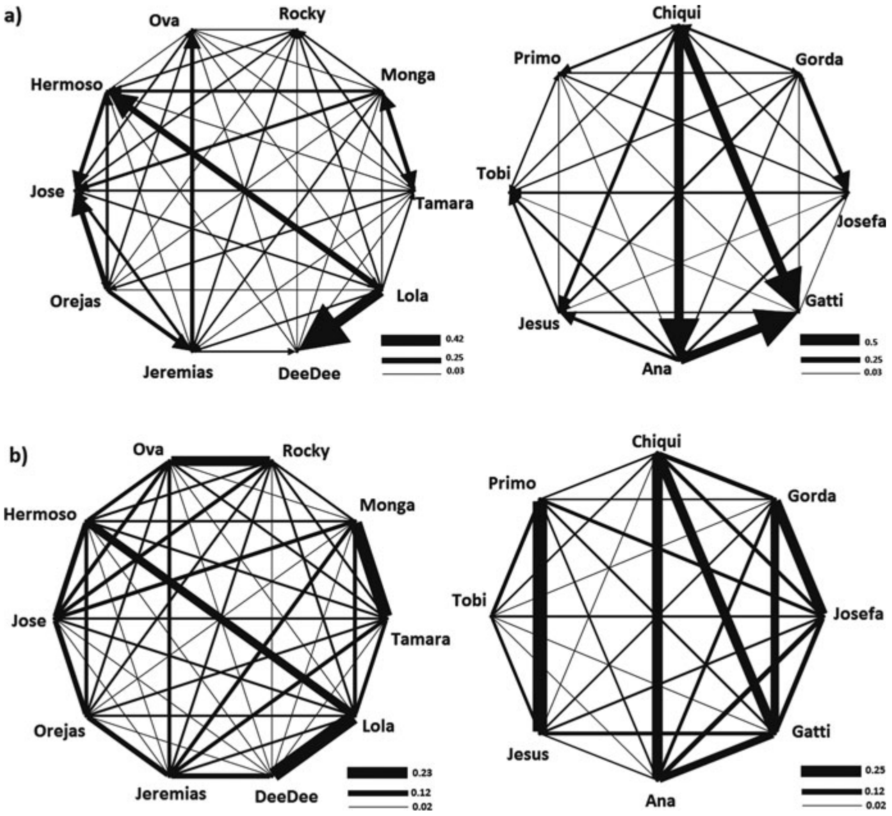


**Fig. 8.1** Sociograms based on (**a**) grooming relationships and (**b**) nearest neighbor distances (December 2003–November 2004). Composition of Group X. Adult males: Gatti, Primo, Jesus; Subadult male: Tobi, Adult females: Ana, Josefa, Chiqui, Gorda. Composition of Group G. Adult males: Jose, Hermoso, Ova, Rocky; Adult females: Tamara, Monga, Lola, Orejas; Juvenile males: Jeremias, ad Dee. The thickness of the *lines* represent the strength of the relationship

that of the random data set; male data set—Group X: 0.063 vs. 0.026; Group G: 0.060 vs. 0.017). In addition, we examined evidence for seasonal changes in patterns of male social interactions and changes in partner preferences across activities. This was accomplished by calculating association indices for each pair of adult male residents. We found no differences in frequency of association or in the strength of association across behavioral contexts (feed, travel, rest) for male dyads in Groups X or G (Group X: Association Index Kruskal–Wallis test: $H(2, N=18)=0.43$, $p>0.05$; strength of dyadic association : Kruskal–Wallis test: $H\ (2, N=18)=3.82$, $p>0.05$; Group G: Association Index Kruskal–Wallis test: $H(2, N=18)=0.36$, $p>0.05$; strength of dyadic association : Kruskal–Wallis test: $H\ (2, N=18)=2.01$, $p>0.05$) (Fig. 8.2). A comparison of seasonal variation in resident male–resident male association indices indicates that the amount of time males had

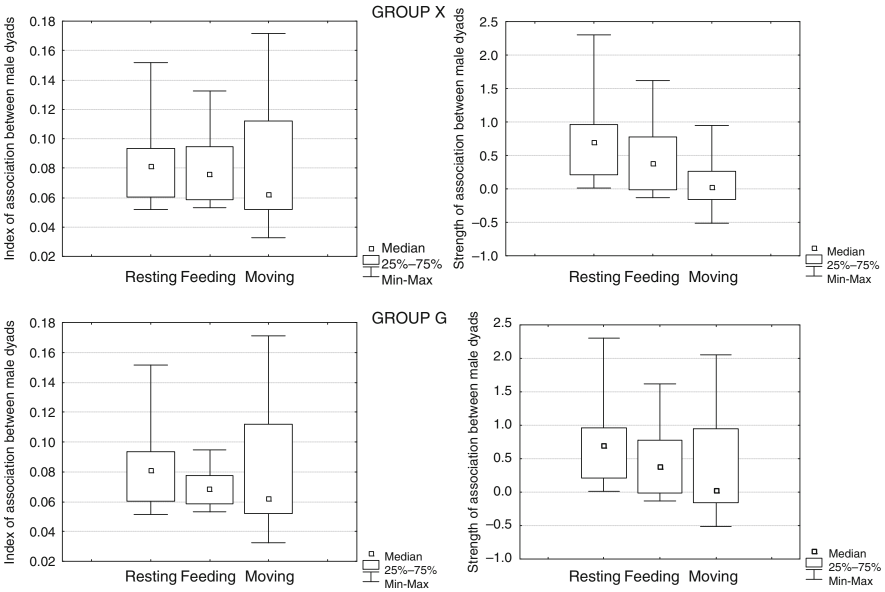


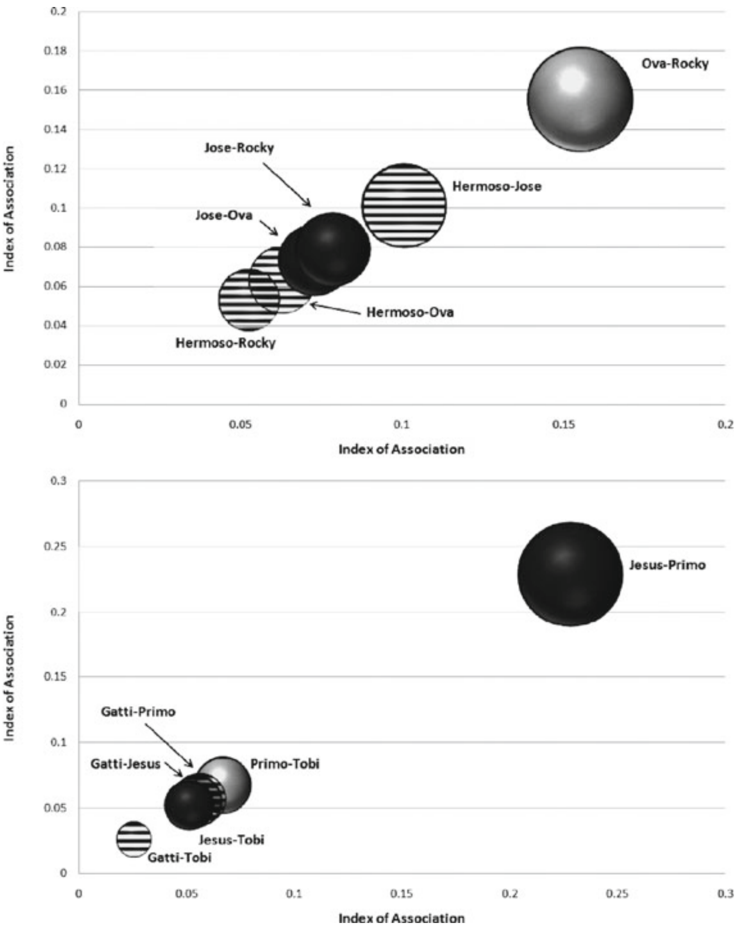
**Fig. 8.2** Variation in association index and the strength of associations of male dyads across behavioral contexts (resting, feeding, and moving)

other males as their nearest neighbor remained constant across the entire year (Two groups pooled data: Association Index Kruskal–Wallis test: $H(3, N=42)=0.57$, $p>0.05$; strength of dyadic association : Kruskal–Wallis test: $H\ (2, N=18)=0.41$, $p>0.05$).

Figure 8.3 displays the indices of association for male–male dyads during the study. In Group X, Primo and Jesus were the dyads with the highest index of association. In Group G, dyads composed of Ova and Rocky and dyads composed of Hermoso and Jose had the strongest associations. Moreover, during months of the year in which within-group copulations increased, there was no evidence of an increase in the frequency or severity of within-group adult male intrasexual aggression (aggression over females was so low throughout the year that we could not conduct statistical tests of changes in aggression during the period of female fertility). Thus, despite seasonal changes in food availability as well as monthly differences in female receptivity and fertility, male black and gold howlers maintained strong and persistent affiliative social relationships.

## *Within-Group Mating Patterns*

Our results indicate that adult male black and gold howlers were highly tolerant of mating activities between resident males and resident females but highly aggressive



Indices of Association for Group G (top) and Group X (bottom). The size of the bubble is proportional to the value of the index of association between males in each possibly dyad.

**Fig. 8.3** Indices of Association for Group G (*top*) and Group X (*bottom*) during the entire study period 2003–2004. The size of the bubbles are proportional to the value of the index of association between males in each possibly dyad

toward the mating activities of extragroup males. The eight resident females in the two study groups were observed to copulate with resident males on 149 occasions. Combining data for both study groups, resident females copulated with 3.5 ± 0.9 resident males during PFO periods that probably resulted in conception and 2.34 ± 1.5 resident males during non-fertile periods (pregnancy and gestation). Overall central males engaged in the majority of copulations (78%) with resident females, of which 69% were during potentially fertile periods. The central male in each group was observed to engage in mate guarding and followed potentially fertile females closely during a 2–3-day period. However, mate guarding by the central male did not result in mating exclusivity, and resident females also copulated with two or three other resident males during potentially fertile periods (59.5% of resident subordinate male–resident female copulations occurred during a female's potentially fertile period). In approximately 90% (51 of 56) of cases in which the dominant male directly observed resident males copulating with group females (42 of these cases were during the female's PFO period), he made no attempt to interfere with or breakup the copulation.

## *Male Participation During Intergroup Encounters*

Given their relatively small (6 ha) and overlapping home ranges (71% of the range of each study group overlapped with three neighboring groups), *A. caraya* are characterized by frequent intergroup encounters. Our two study groups engaged in intergroup encounters every 5.7 h of observation (Group X = 1 encounter per 4.7 h of observation; Group G = 1 encounter per 6.7 h of observation) or approximately twice per day. On average, resident male invested almost 2 h per day in intergroup encounters (Group X: 117.1 ± 94.4 min; Group G: 117.8 ± 94.2 min).

In *A. caraya*, intergroup encounters involved cooperative adult male boarder vigilance (56%), howling (41%), and fighting (3%). During these encounters, resident males acted collectively to expel intruder neighboring males from the group and to interfere with mating activities between non-resident males and resident females. On average 3 ± 0.8 resident males acted collectively during these encounters (Group G = 3 ± 0.27; Group X = 3 ± 1). In both study groups, the central male was actively involved in all cases of group defense. In Group G, 100% of intergroup encounters involved multiple resident males. In Group X, 89% of intergroup encounters involved coalitions of males. In the remaining 11% of cases (18 of 156), the central male of this group acted alone. In these 18 cases, we could identify no obvious or consistent factor(s) (e.g., intruder number, location in home range, response to particular neighboring group, female reproductive state) that explained the behavior of subordinate males.

We also examined the context of intergroup encounters. That is, whether these encounters primarily represent a form of resource defense and occur in the vicinity of a major feeding site. Our results indicate that Group X fed immediately before or immediately after in the quadrat in which the encounter took place in only 3.2% of cases. Group G fed in the same area before or after the encounter in 1.8% of cases. This suggests that areas of intergroup encounters did not generally coincide with the location of major feeding sites. In contrast, neighboring groups tended to exhibit greater overlap in their use of joint areas of their range during periods in which resident females were fertile. There was a significant positive correlation between the number of fertile females per group per month and each groups use of overlap quadrats (female fertility was determined based on counting back 180 days [average gestation length in *Alouatta*] from the birth of an infant) (Group X: Spearman correlation $N = 12$, $r = 0.58$, $p = 0.04$; Group X $N = 12$, $r = 0.59$, $p = 0.04$). These results indicate a pattern of increased use of overlap quadrats (greater intergroup spatial proximity) by howlers during which periods females in neighboring groups were fertile.

On six occasions, we observed a solitary male or a male from a neighboring group approach the study group and attempt to mate with a resident female (Kowalewski et al., 2006). In each case, resident males were highly aggressive to intruders and acted in a coordinated fashion to expel the foreign male. When engaged in coalitionary support, resident males chased and aggressively attacked intruder males. In five out of the six cases, at least three same-sex group members jointly attacked the intruder in what appeared to be a coordinated activity. This behavior may represent one tactic used by resident howler males to aggressively exclude same sex extragroup individuals attempting to mate with resident females.

## Discussion

Kin-biased affiliative behaviors and social bonds are well documented in primates (Thierry, 2007; Arnold and Aureli, 2007). However, recent studies on several species of nonhuman primates indicate that affiliative and cooperative behaviors also are common among unrelated or distantly related group members (Goldberg and Wrangham, 1997; Hashimoto et al., 1996; Mitani et al., 2002; Faulkes et al., 2003; Silk, 2005, Chapais, 2006; Sussman and Garber, 2007; Kitchen et al., 2004; Garber and Kowalewski, in press). For example, in common chimpanzees (*Pan troglodytes*), measures of social affiliation among males, such as proximity, coalition formation, meat sharing, and patrolling behavior occur more frequently among non-relatives of similar age and rank than among close relatives (Mitani et al., 2002; Lukas et al., 2005). Difficulties in separating the effects of familiarity, age, cohort, and rank in influencing social interactions have led some researchers to call into question the overall importance of kin selection in understanding social cooperation in primates (Chapais, 2006, Colmenares, 2004). In particular, Chapais (2006) has argued that social familiarity, partner competency, and partner reliability, irrespective of kin relatedness, are perhaps the most significant factors affecting the costs, benefits, and nature of primate social interactions.

Various forms of reciprocity and mutualisms have been proposed to explain social bonding and cooperative interactions among both kin and non-kin (Trivers, 1971, 2006; de Waal, 2000; de Waal and Brosnan, 2006). Reciprocity occurs when two or more individuals exchange beneficial services such as tolerance at a feeding site or grooming (de Waal and Brosnan, 2006). Generally, the exchange of benefits occurs over a relatively short period of time (i.e., days), and the cost to the initiator of aiding a conspecific is low. This is analogous to Trivers' (2006) description of a "Tit-for-Tat strategy" in which each of two partners repeats the last action of the other. Models of reciprocity do not require that individuals act as long-term partners, although this sometimes occurs (Kitchen et al., 2004; de Waal and Brosnan, 2006). Reciprocity does require that the direct benefits gained by each partner through cooperative and affiliative interactions are relatively equal over time and that individuals maintain predictable social relationships (Trivers, 2006). Reciprocity associated with grooming, coalitionary support, and food sharing between related and unrelated individuals has been reported in many primate species (Muroyama, 1991; Rowell et al., 1991; Barrett et al., 1999; Silk, 1992, Silk et al., 2004; Widdig et al., 2000; Horrocks and Hunte, 1986; Watts, 2000; Hauser et al., 2003; de Waal, 2000).

Mutualisms represent another class of affiliative or cooperative behaviors in which both the initiator and recipient receive a net benefit. These benefits need not be equal or symmetrical. Unlike reciprocity, however, all participants involved in mutual actions obtain an immediate and direct benefit. Perhaps the most common form of mutualism is by-product mutualism (Dugatkin, 1997). By-product mutualism is associated with affiliative, coordinated, and cooperative behaviors involving low or no additional cost to the participants because each would perform that behavior in the absence of a partner. Partners are expected to benefit from such coordinated behavior because the collective action of several individuals is more effective than the lone action of any single individual. These behaviors may include predator vigilance or alarm calls, thermoregulatory behavior, group-, resource-, or mate-defense, cooperative hunting, and foraging techniques such as prey flushing in which the collective action of several individuals enhances capture rates. Again, these represent behaviors that an individual must perform regardless of living alone or living in a group (Dugatkin, 1997). By-product mutualism may represent the most common and simplest type of cooperation because neither kinship nor “scorekeeping” mechanisms are needed for its development (Dugatkin, 1997; Sussman and Garber, 2007, 2011). We argue that concepts of reciprocity, mutualisms, and the benefits of collective action are central to an understanding of social tolerance and cooperative behavior among male black and gold howler monkeys (*A. caraya*).

Our data on *A. caraya* indicate that resident males are highly tolerant of each other across a range of contexts including feeding, foraging, resting, and mating. It is likely that tolerance is achieved over time and through individual experience during frequent and predictable social interactions. In the case of *Alouatta pigra*, for example, Kitchen et al. (2004) found that males who were co-residents in the same group for over 4 years were more likely to engage in collective action when exposed to playbacks of howling from one or three adult males compared to resident males who were characterized by a more short-term association.

Tolerance, spatial proximity, friendships, and trust (e.g., Gilby and Wrangham, 2008) among resident males appear to facilitate joint action. In *A. caraya*, males were often each other’s nearest neighbor or preferred associate and engaged in bouts of intrasexual grooming and embracing. In many cases, bonds among individual males have persisted over long periods of time. In Group X, Gatti held that position of central male for at least 6 years (Kowalewski, 2007). The other males were residents of this group from 4 to almost 6 years. In Group G, Jose became the central male in 2002 (Oklander, 2007). At that time he was at least 7 years old. As a result of this change in his status, the previous central male transferred to neighboring Group M (he became that group’s central male). In October of 2004, a natal adult male Hermoso, who was 6–7 years of age and unrelated to Jose (Hermoso was the son of a male in Group G who died in 2001 – Oklander 2007), began to act as a central male. During a 3–4-month period, Jose and Hermoso were codominant. Thereafter, Hermoso became the group's lone central male (Fernandez, pers. com). This change in dominance was not associated with any major social disruption in the group. Jose died while still a resident in Group G in June 2005. The remaining two adult males have been residents of Group G for 5 years.

Strong and persistent social bonds and mating opportunities within the group provide benefits to all resident males of collective action. Group defense by multiple resident adult males occurred on average twice per day and had a duration of 2 h. Given that groups were active for 12.2 h per day and resting accounted for 60–65% of each groups' daytime activity budget, male black and gold howlers devoted 41–47% of non-resting hours each day to group defense. Collective action principally involved relatively low-cost behaviors such as boarder vigilance (56%) and howling (41%). Only 3% of intergroup encounters ended in fighting. Although the dominant male of each group was found to engage in all intergroup encounters, 89–100% of these actions involved coalitions of two or three adult males.

Collective action resulting in enhanced benefits to individuals residing in an effective, cooperative, and coordinated social unit is an important component of theoretical models of primate sociality (Goodnight et al., 1992; Nunn, 2000; Altmann, 1990; Isbell, 1991; Sussman and Garber, 2007, 2011; Garber and Kowalewski, in press). In the case of many species of atelines (howlers, spider monkeys, muriquis, and woolly monkey), social interactions between resident males are affiliative and cooperative, and resident males act collectively via patrolling or intergroup encounters to exclude neighboring and extragroup males from entering the group (Nunn, 2000; Pereira et al., 2000; Kowalewski et al., 2006; Strier, 2000; Di Fiore and Campbell, 2007; Di Fiore, 2009). In these same species, females often transfer between groups and solicit copulations from both resident adult males and extragroup males during fertile and non-fertile periods. Given female promiscuity and opportunities for females to mate with extragroup males (in *A. caraya* 34% of all copulations were extragroup; Kowalewski and Garber, 2010), the collective action of resident males may benefit each by increasing the likelihood that offspring are sired by group males. Thus, between-group factors may act as primary drivers of within-group male social affiliation and cooperation.

Under conditions in which the costs to females of mating are low, dominant males face a set of behavioral options. These range from (1) aggressively excluding all males from the group, (2) tolerating some number of resident males but rigidly controlling their access to fertile females, to (3) forming mutually beneficial and reciprocal social bonds and alliances with several resident males (Nunn, 2000). In this latter case, even if the dominant male contributes disproportionately to the success of the alliance, by soliciting the aid of other group males, the dominant male can benefit by reduced risk of injury, increased probability of successful group/mate defense, reduced male takeovers, and increased tenure in the group.

In the case of subordinate males, by acting singly, each is likely to have very limited competitive success against extragroup males (Connor and Whitehead, 2005). Subordinate males benefit from acting together with the dominant male to take advantage of their joint competitive ability, displaying traits and abilities that are attractive to females and increasing the probability of alliance success. Being a member of a successful alliance increases individual opportunities to mate with resident females and sire offspring. Moreover, as additional group males participate in the alliance, the costs and risks of injury to each participant are reduced, especially if joint displays or vocalizations serve to intimidate single males or males from smaller alliances (strength in numbers). This type of cooperation has been described by Nunn (2000) as cooperation designed to promote the "collective good." Males that reside in groups with a greater number of males or a set of more strongly socially bonded and affiliative males have advantages over solitary males, socially intolerant males, or males living in groups with non-cooperative males, in increasing the likelihood that offspring born in the group are sired by resident males and survive to maturity. In addition, groups with affiliative and cooperative males may attract a larger number of adult females if these groups offer females advantages in increased group stability, access to multiple mates, opportunities for mate choice, reduced infanticide risk, increased predator detection, increased infant survivorship, and access to higher quality resources (Kowalewski and Garber, 2010). Based on an examination of the size and age/sex composition of 29 howler groups representing five different species, Treves (2001: 61) found that "groups with a greater proportion of adult and subadult males contained more juveniles than expected from the population average." Thus, female reproductive success, and ultimately male reproductive success, appears to be positively affected by the presence of several socially tolerant males residing together in a group.

In some platyrrhine taxa, male philopatry, parallel male migration, or paired male migration may contribute to the strength of male alliances by maintaining social relationships and partner preferences over the course of years and in some cases for decades (Strier, 1994, 2000; Jack and Fedigan, 2007; Garber et al., 1993; Di Fiore and Campbell, 2007). However, the degree to which kinship alone can explain many instances of male intrasexual cooperation remains unclear. In woolly monkeys, black and gold howler monkeys, and some groups of *Ateles*, *Saguinus*, and *Callithrix* (Di Fiore, 2009; Faulkes et al., 2003; Kowalewski, 2007), resident males are less closely related to each other than are resident females. Nevertheless, male–male social tolerance and alliance formation remain strong. In this regard, many forms of cooperative behavior among both kin and non-kin may be explained in terms of the mutual and reciprocal benefits that individuals receive by maintaining coordinated, strong, and predictable social bonds that enhance group cohesion. In many instances cooperative and affiliative actions represent relatively low-cost behaviors that offer immediate or near-term benefits to the actors (Dugatkin, 1997, 2002). Once these bonds are formed, they may offer group members ecological and social advantages in terms of access to food resources and grooming partners, opportunities for social learning, enhanced mating success (especially if females are attracted to groups with several males), increased offspring survivorship, and predator protection. We argue that although individuals may compete for access to reproductive partners, greater attention needs to be paid to the role of non-aggressive behavior such as sperm competition, socioendocrinological mechanisms of reproductive suppression, female mate choice, and the advantages to both males and females of living in a more effectively functioning social group in evaluating the costs and benefits to individual males and females of cooperative and collective behavior (Garber, 1997; Sussman and Garber, 2007, 2011; Manson, 2007).

**Acknowlegments** We want to thank our field assistants and collaborators: Silvana Peker, Romina Pave, Vanina Fernandez, Nelson Novo, Soledad Diaz, Laura Prosdocimi, Manuela Chomnalez, Nancy Lopez, Ezequiel Noriega, Lilian Ferre, Mariana Carro, Juan Emilio Sala, Diego Bombelli, and Raul Sobrero. We thank the support of Dr. Gabriel Zunino during the field work and for stimulating discussions on the topic. We also thank Escuela Comunitaria Guacara-Isla del Cerrito for logistical support. This study was funded by The Graduate College-UIUC, The Wenner Gren Foundation Grant #7034, The Leakey Foundation, IdeaWild and American Society of Primatologists. The study complied with the current laws and permission of the United States and Argentina (IACUC protocol #01071) and adhered to the ASP principles for the ethical treatment of nonhuman primates. Finally, PAG wishes to thank Sara, Jenni, and Chrissie for their love, support, patience, and cooperation in allowing him to explore ideas of primate social bonds.

## References

Agoramoorthy, G. and Hsu, M.J. 2000. Extragroup copulations among wild red howler monkeys in Venezuela. Folia Primatologica 71: 147–151.

Altmann, J. 1974. Observational study of behavior: Sampling methods. Behaviour 49: 227–267.

Altmann, J. 1990. Primate males go where the females are. Animal Behaviour 39: 193–195.

Arnold, K. and Aureli, F. 2007. Postconflict reconciliation. In: C.J. Campbell, A. Fuentes, K.C. MacKinnon, M. Panger and S.K. Bearder (eds.), *Primates in Perspective* (pp. 592–608). New York: Oxford University Press.

Barrett, L., Henzi, S.P., Weingrill, T., Lycett, J.E. and Hill, R.A. 1999. Market forces predict grooming reciprocity in female baboons. Proceedings of the Royal Society of London B266(1420): 665–670.

Boyko, R.H. and Marshall, A.J. 2009. The willing cuckold: optimal paternity allocation, infanticide and male reproductive strategies in mammals. Animal Behavior 77(6): 1397–1407.

Bravo, S.P. and Sallenave, A. 2003. Foraging behavior and activity patterns of *Alouatta caraya* in the northeastern Argentinean flooded forest. International Journal of Primatology 24(4): 825–846.

Brown, A.D. and Zunino. G.E. 1994. Habitat, density and conservation problems of Argentine primates. Vida Silvestre Neotropical 3(1): 30–40.

Cairns, S.J. and Schwager, S.J. 1987. A comparison of association indices. Animal Behaviour 35: 1454–1469.

Calegaro-Marques, C. and Bicca-Marques, J.C. 1993. Reprodução de *Alouatta caraya* Humboldt, 1812 (Primates,Cebidae). Primatologia no Brasil 4: 51–66.

Chapais, B. 2006. Kinship, competence and cooperation in primates. In: P.M. Kappeler and C.P. van Schaik (eds.), *Cooperation in Primates and Humans: Mechanisms and Evolution* (pp. 47–64). Berlin, Germany: Springer-Verlag.

Chapman, C.A. and Chapman, L.J. 2000. Determinants of group size in primates: the importance of travel costs. In. S. Boinski and P.A. Garber (eds.), *On the Move: How and Why Animals Travel in Groups* (pp. 24–42). Chicago: The University of Chicago Press.

Clarke, P.M.R., Henzi, S.P. and Barrett, L. 2009. Sexual conflict in chacma baboons, *Papio hamadryas ursinus*: absent males select for proactive females. Animal Behavior 77(5): 1217–1225.

Clutton-Brock, T. 2002. Breeding together: kin selection and mutualism in cooperative vertebrates. Science 296: 69–72.

Colillas, O. and Coppo, J. 1986. Breeding *Alouatta caraya* in Centro Argentino de Primates. In: D.L. Chivers and W. Lane-Petter (eds.), *Recent Advances in Primatology, Vol. 2: Conservation* (pp. 201–214). New York: Academic.

Colmenares, F. 2004. Kinship structure and its impact on behavior in multilevel societies. In: B. Chapais and C.M. Berman (eds.), *Kinship and Behavior in Primates* (pp. 242–270). Oxford: Oxford University Press.

Connor, R. and Whitehead, H. 2005. Alliances II. Rates of encounter during resource utilization: a general model of intrasexual alliance formation in fission-fusion societies. Animal Behaviour 69(1): 127–132.

Cooper, M.A., Chaitra, M.S. and Singh, M. 2004. Effect of dominance, reproductive state, and group size on body mass in *Macaca radiata*. International Journal of Primatology 25(1): 165–178.

Crockett, C.M. and Eisenberg, J.F. 1987. Howlers: variations in group size and demography. In: B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wangham and T.T. Struhsaker (eds.), *Primate Societies* (pp. 54–68). Chicago: University Chicago Press.

Crockett, C.M. and Janson, C. 2000. Infanticide in red howlers: female group size, male membership, and a possible link to folivory. In: C.P vanSchaik and C. Janson (eds.), *Infanticide by Males and its Implications* (pp. 75–98). Cambridge: Cambridge University Press.

Crockett, C.M. and Sekulic, R. 1982. Gestation length in red howler monkeys. American Journal of Primatology 3: 291–294.

de Waal, F.B.M. 2000. Primates: A natural heritage of conflict resolution. Science 289: 586–590.

de Waal, F.B.M. and Brosnan, S.F. 2006. Simple and complex reciprocity in primates. In: P.M. Kappeler and C.P. van Schaik (eds.), *Cooperation in Primates and Humans: Mechanisms and Evolution* (pp. 85–105). New York: Springer.

Dias, P.A.D. and Rodriguez Luna, E. 2006. Seasonal changes in male associative behavior and subgrouping of *Alouatta palliata* on an island. International Journal of Primatology 27(6): 1635–1651.

Di Fiore, A. 2009. Genetic approaches to the study of dispersal and kinship in New World primates. In: P.A. Garber, A. Estrada, J-C Bicca Marques, E. Heymann and K.B. Strier (eds.), *South American Primates: Comparative Perspectives in the Study of Behavior, Ecology, and Conservation* (pp. 211–250). New York: Springer.

Di Fiore, A. and Campbell, C.J. 2007. The Atelines: variation in ecology, behavior, and social organization. In: C.J. Campbell, A. Fuentes, K.C. MacKinnon, M. Panger and S.K. Bearder (eds.), *Primates in Perspective* (pp. 155–185). New York: Oxford University Press.

Dugatkin, L.A. 1997. *Cooperation among Animals: An Evolutionary Perspective*. New York: Oxford University Press.

Dugatkin, L.A. 2002. Animal cooperation among unrelated individuals. Naturwissenschaften 89:533–541.

Faulkes, C.G., Arruda, M.F. and Monteiro da Cruz, A.O. 2003. Matrilineal genetic structure within and among populations of the cooperatively breeding common marmoset, *Callithrix jacchus*. Molecular Ecology 12(4): 1101–1108.

Garber, P.A. 1988. Diet, foraging patterns, and resources defense in a mixed species troop of *Saguinus mystax* and *Saguinus fuscicollis* in Amazonian Peru. Behaviour 105(1–2): 18–34.

Garber, P.A. 1997. One for all and breeding for one: cooperation and competition as a tamarin reproductive strategy. Evolutionary Anthropology 5: 187–199.

Garber, P.A., Encarnacion, F., Moya, L. and Pruetz, J.D. 1993. Demographic and reproductive patterns in moustached tamarin monkeys (*Saguinus mystax*): Implications for reconstructing platyrrhine mating systems. American Journal of Primatology 29(4): 235–254.

Garber, P.A. and Estrada A. 2009. Advancing the study of South American primates. In: P.A. Garber, A. Estrada, J-C Bicca Marques, E. Heymann and K.B. Strier (eds.), *South American Primates: Comparative Perspectives in the Study of Behavior, Ecology, and Conservation* (pp. 3–19). New York: Springer Press.

Garber, P.A. and Kowalewski, M.M. in press. Male cooperation in pitheciines: the reproductive costs and benefits to individuals of forming large mulitmale and multifmale groups. In L. Veiga, A. Barnett and M.A. Norconk (eds.), *Evolutionary Biology and Conservation of Titis, Sakis and Uakaris* (pp.). Cambridge: Cambridge University Press.

Gilby, I.C. and Wrangham, R.W. 2008. Association patterns among wild chimpanzees (*Pan troglodytes schweinfurthii*) reflect sex differences in cooperation. Behavioral Ecology and Sociobiology 62(11): 1831–1842.

Glander, K.E. 1980. Reproduction and population growth in free-ranging mantled howling monkeys. American Journal of Physical Anthropology 53: 25–36.

Goldberg, T.L. and Wrangham, R.W. 1997. Genetic correlates of social behaviour in wild chimpanzees: evidence from mitochondrial DNA. Animal Behaviour 54: 559–570.

Goodnight, C., Schwartz, J. and Stevens, L. 1992. Contextual analysis of models of group selection, soft selection, hard selection, and the evolution of altruism. American Naturalist 140: 743–761.

Hashimoto, C., Furuichi, T. and Takenaka, O. 1996. Matrilineal kin relationship and social behavior of wild bonobos (*Pan paniscus*): Sequencing the D-loop region of mitochondrial DNA. Primates 37(3): 305–318.

Hauser, M.D., Chen, M.K., Chen, F. and Chuang, E. 2003. Give unto others: Genetically unrelated cotton-top tamarin monkeys preferentially give food to those who altruistically give food back. Proceedings of the Royal Society of London B270(1531): 2363–2370.

Henzi, P. and Barrett, L. 2003. Evolutionary ecology, sexual conflict, and behavioral differentiation among baboon populations. Evolutionary Anthropology 12(5):217–230.

Horrocks, J.A. and Hunte, W. 1986. Sentinel behaviour in vervet monkeys: Who sees whom first? Animal Behaviour 34(5): 1566–1567.

Isbell, L.A. 1991. Contest and scramble competition: patterns of female aggression and ranging behavior among primates. Behavioral Ecology 2(2): 143–155.

Jack, K. and Fedigan, L.M. 2007. Why be alpha male? dominance and reproductive success in wild white-faced capuchins (*Cebus capucinus*). In: A. Estrada, P.A. Garber, M.S.M. Pavelka and L. Luecke (eds.), *New Perspectives in the Study of Mesoamerican Primates: Distribution, Ecology, Behavior, and Conservation* (pp. 367–386). New York: Springer.

Janson, C. 1988. Food competition in brown capuchin monkeys (*Cebus apella*): quantitative effects of group size and tree productivity. Behaviour 105: 53–76.

Jones, C.B. 1985. Reproductive patterns in mantled howler monkeys: estrus, mate choice and copulation. Primates 26(2): 130–142.

Kappeler, P.M. and van Schaik, C.P. 2002. Evolution of primate social systems. International Journal of Primatology 23(4): 707–740.

Kitchen, D.M. and Beehner, J.C. 2007. Factors affecting individual participation in group-level aggression among non-human primates. Behaviour 144(12): 1551–1581.

Kitchen, D.M., Cheney, D.L., Seyfarth, R.M. and Beehner, J.C. 2009. A link between focal testosterone and an honest signal – the loud ′wahoo′ vocalizations of chacma baboons. American Journal of Physical Anthropology (Suppl 48): 166.

Kitchen, D.M., Horwich, R.H. and James, F.A. 2004. Subordinate male black howler monkey (*A. pigra*) responses to loud calls: experimental evidence for the effects of intra-group male relationships and age. Behaviour 141: 703–723.

Kowalewski, M.M. 2007. *Patterns of Affiliation and Co-operation in Howler Monkeys: An Alternative Model to Explain Social Organization in Non-human Primates*. Ph. D. thesis, Department of Anthropology, University of Illinois at Urbana-Champaign.

Kowalewski, M.M. and Garber, P.A. 2010. Mating promiscuity and reproductive tactics in female black and gold howler monkeys (*Alouatta caraya*) inhabiting an island on the Parana River, Argentina. American Journal of Primatology 72: 734–748.

Kowalewski, M.M., Garber, P.A. and Zunino, G.E. 2006. Alternative mating strategies in black and gold howler monkeys. American Journal of Primatology 68(Suppl 1): 95.

Kowalewski, M.M. and Zunino, G.E. 2004. Birth seasonality in *Alouatta caraya* in Northern Argentina. International Journal of Primatology 25(2): 383–400.

Lukas, D., Reynolds, V., Boesch, C. and Vigilant. L. 2005. To what extent does living in a group mean living with kin? Molecular Ecology 14(7): 2181–2196.

Manson, J.H. 2007. Mate choice. In: C.J. Campbell, A. Fuentes, K.C. MacKinnon, M. Panger and S.K. Bearder (eds.), *Primates in Perspective* (pp. 447–463). New York: Oxford University Press.

Mitani, J.C., Watts, D.P. and Muller, M.N. 2002. Recent developments in the study of wild chimpanzee behavior. Evolutionary Anthropology 11(1): 9–25.

Muroyama, Y. 1991. Mutual reciprocity of grooming in female Japanese macaques (*Macaca fuscata*). Behaviour 119(3–4): 161–170.

Newton-Fisher, N.E. 1999. Association by male chimpanzees: A social tactic? Behaviour 136(6): 705–730.

Noe, R., van Schaik, C.P. and van Hooff, J.A.R.A.M. 1991. The market effect: An explanation for pay-off asymmetries among collaborating animals. Ethology 87(1–2): 97–118.

Nunn, C.L. 2000. Collective benefits, free-riders, and male extra-group conflict. In: P.M. Kappeler (ed.), *Primate Males: Causes and Consequence of Variation in Group Composition* (pp. 192–204). Cambridge: Cambridge University Press.

Nunn, C.L. and Lewis, R.J. 2001. Cooperation and collective action in animal behavior. In: R. Noe, J.A.R.A.M. van Hoff and P. Hammerstein (eds.), *Economics in Nature: Social Dilemmas, Mate Choice and Biological Markets* (pp. 42–66). Cambridge: Cambridge University Press.

Oklander, L.I. 2007. *Estructura Social y Relaciones De Parentesco En Poblaciones Silvestres De Monos Aulladores (Alouatta caraya) Del Noreste Argentino*. Ph.D. Dissertation, Universidad de Buenos Aires, Argentina.

Pereira, M.E., Clutton-Brock, T.H. and Kappeler, P.M. 2000. Understanding primate males. In: P.M. Kappeler (eds.), *Primate Males: Causes and Consequence of Variation in Group Composition* (pp. 271–277). Cambridge: Cambridge University Press.

Pope, T.R. 2000. Reproductive success increases with degree of kinship in cooperative coalitions of female red howler monkeys (*Alouatta seniculus*). Behavioral Ecology and Sociobiology 48(4): 253–267.

Pradhan, G.R. and van Schaik, C. 2008. Infanticide-driven intersexual conflict over matings in primates and its effects on social organization. Behaviour 145(2): 251–275.

Rowell, T.E., Wilson, C. and Cords, M. 1991. Reciprocity and partner preference in grooming of female blue monkeys. International Journal of Primatology 12(4): 319–336.

Shoemaker, A.H. 1979. Reproduction and development of the Black howler monkey *Alouatta caraya* at Columbia Zoo. International Zoo Yearbook 19: 150–155.

Silk, J.B. 1992. Patterns of intervention in agonistic contests among male bonnet macaques. In: A.H. Harcourt and F.B.M. de Waal (eds.), *Coalitions and Alliances in Humans and Other Animals* (pp. 215–232). New York: Oxford University Press.

Silk, J.B. 2005. The evolution of cooperation in primate groups. In: H. Gintis, S. Bowles, R. Boyd and E. Fehr (eds.), *Moral Sentiments and Material Interests: The Foundations of Cooperation in Economic Life* (pp. 43–73). Cambridge, MA: MIT Press.

Silk, J.B., Alberts, S.C. and Altmann, J. 2004. Patterns of coalition formation by adult female baboons in Amboseli, Kenya. Animal Behaviour 67(3): 573–582.

Sousa Fialho de, M. and Setz, E.Z.F. 2007. Extragroup copulations among brown howler monkeys in southern Brazil. Neotropical Primates 14:28–30.

Sterck, E.H.M. and van Hooff, J.A.R.A.M. 2000. The number of males in langur groups: Monopolizability of females or demographic processes? In: P.M. Kappeler (ed.), *Primate Males: Causes and Consequence of Variation in Group Composition* (pp. 120–129). Cambridge: Cambridge University Press.

Sterck, E.H.M., Watts, D.P. and van Schaik, C.P. 1997. The evolution of female social relationships in nonhuman primates. Behavioral Ecology and Sociobiology 41(5): 291–309.

Strier, K.B. 1994. Brotherhoods among atelins: kinship, affiliation, and competition. Behaviour 130(3–4): 151–167.

Strier, K.B. 1997. Mate preferences in wild muriqui monkeys (*Brachyteles arachnoides*): reproductive and social correlates. Folia Primatologica 68: 120–133.

Strier, K.B. 2000. From binding brotherhoods to short-term sovereignty: the dilemma of male Cebidae. In: P.M. Kappeler (ed.), *Primate Males: Causes and Consequence of Variation in Group Composition* (pp. 72–83). Cambridge: Cambridge University Press.

Sussman, R.W. and Chapman, A. 2004. *The Origins and Nature of Sociality*. New York: Aldine De Gruyter.

Sussman, R.W. and Garber, P.A. 2007. Cooperation and competition in primate social interactions. In: C.J. Campbell, A. Fuentes, K.C. MacKinnon, M. Panger and S.K. Bearder (eds.), *Primates in Perspective* (pp. 636–651). New York: Oxford University Press.

Sussman, R.W. and Garber, P.A. 2011. Cooperation, collective action, and competition in primate social interactions. In: C.J. Campbell, A. Fuentes, K.C. Mackinnon, S.K. Bearder and R. S.M. Stumpf (eds.), *Primates in Perspective: 2nd Edition* (pp. 587–599). New York: Oxford University Press.

Sussman, R.W., Garber, P.A. and Cheverud, J.M. 2005. The importance of cooperation and affiliation in the evolution of primate sociality. American Journal or Physical Anthropology 128: 84–97.

Thierry, B. 2007. Unity in diversity: lessons from macaque societies. Evolutionary Anthropology 16(6): 224–238.

Thierry, B. 2008. Primate socioecology, the lost dream of ecological determinism. Evolutionary Anthropology 17(2): 93–96.

Treves, A. 2001. Reproductive consequences of variation in the composition of howler monkey (*Alouatta* spp.) groups. Behavioral Ecology and Sociobiology 50: 61–71.

Trivers, R.L. 1971. The evolution of reciprocal altruism. Quarterly Review of Biology 46: 25–57.

Trivers, R. 2006. Reciprocal altruism: 30 years later. In: P.M. Kappeler and C.P. van Schaik (eds.), *Cooperation in Primates and Humans: Mechanisms and Evolution* (pp. 67–84). New York: Springer.

van Belle, S., Estrada, A., Ziegler, T.E. and Strier, K.B. 2009. Sexual behavior across ovarian cycles in wild black howler monkeys (*Alouatta pigra*): male mate guarding and female mate choice. American Journal of Primatology 71: 153–164.

van Noordwijk, M. and van Schaik, C.P. 1999. The effects of dominance rank and group size on female lifetime reproductive success. Primates 40: 105–130.

van Schaik, C.P. 1989. The ecology of social relationships amongst female primates. In: V. Standen and R.A. Foley (eds.), *Comparative Socioecology: The Behavioural Ecology of Humans and Other Mammals* (pp. 195–218). Oxford: Blackwell Scientific Publications.

van Schaik, C.P. and Kappeler, P.M. 2006. Cooperation in primates and humans: closing the gap. In: P.M. Kappeler and C.P. van Schaik (eds.), *Cooperation in Primates and Humans* (pp. 3–21). Heidelberg: Springer.

van Schaik, C.P., Pradhan, G.R. and van Noordwijk, M.A. 2004. Mating conflict in primates: infanticide, sexual harassment and female sexuality. In: P. Kappeler and C.P. van Schaik (eds.), *Sexual Selection in Primates, New and comparative perspectives* (pp. 131–150). Cambridge: Cambridge University Press.

Wang, E. and Milton, K. 2003. Intragroup social relationships of male *Alouatta palliata* on Barro Colorado Island, Republic of Panana. International Journal of Primatology 24: 1227–1244.

Watts, D.P. 2000. Grooming between male chimpanzees at Ngogo, Kibale National Park. II. Influence of male rank and possible competition for partners. International Journal of Primatology 21(2): 211–238.

Widdig, A., Streich, W.J. and Tembrock, G. 2000. Coalition formation among male Barbary macaques (*Macaca sylvanus*). American Journal of Primatology 50(1): 37–51.

Zunino, G.E., Kowalewski, M.M., Oklander, L. and Gonzalez, V. 2007. Habitat fragmentation and population size of the black and gold howler monkey (*Alouatta caraya*) in a semideciduous forest in northern Argentina. American Journal of Primatology 69(9): 966–975.

# Chapter 9
# Mechanisms of Cohesion in Black Howler Monkeys

**Mary S.M. Pavelka**

All diurnal primates live in social groups but with a great range of variation in the types of groups they form. Primate societies vary in group size, composition, dispersal patterns, levels of cohesion, and the extent of overt social interaction or differentiation of relationships within the group. They also vary in the flexibility seen in these aspects of social organization. For example, cross-population studies as well as diachronic studies suggest that black howlers are constrained to live in highly cohesive groups of no more than 10 individuals, despite considerable variation in group composition (Pavelka and Chapman, 2006; Van Belle and Estrada, 2006). Other species, such as Muriquis, reveal considerable flexibility in group size and cohesion; an increase in population size over a 25-year period produced significantly larger social groups and a shift from cohesive to flexible fission–fusion grouping pattern in which members regularly fission and fuse into parties of ever-changing size and composition (Dias and Strier, 2003).

The focus of this chapter is on cohesion and the question of what holds social groups together. I also suggest two possible mechanisms of cohesion not previously considered for primates. It is traditionally assumed that primate groups are held together by the social relationships among group members. These relationships are built and maintained by affiliative interactions such as social grooming (Dunbar, 1999; Cooper and Bernstein, 2000; Seyfarth, 1983). In the 1980s Robert Hinde offered a framework for social groups in which interactions among and between individuals, over time, developed into relationships among those individuals, and the web of these relationships essentially formed the social group. This framework began with the assumption that individuals are different, and their differences shape their interactions and the relationships they form. In Hinde's words "a first requirement for understanding the causal basis of social behavior is an understanding of how individuals differ in their propensities to behave and in their behavior with particular others" (Hinde, 1983:4). He describes a continuous dialectic between the

---

M.S.M. Pavelka (✉)
Department of Anthropology, University of Calgary, Calgary, AB T2N 1N4, Canada
e-mail: pavelka@ucalgary.ca

R.W. Sussman, C.R. Cloninger (eds.), *Origins of Altruism and Cooperation*,
Developments in Primatology: Progress and Prospects 36, DOI 10.1007/978-1-4419-9520-9_9,

natures of individual animals and the interactions and relationships in which they participate, and the need for us, as researchers, to know how individuals are shaped by their social experiences. “A second requirement for understanding the causal basis of social behavior is a set of principles concerned with how interactions affect subsequent interactions within the same relationship, and, more generally, with the development of relationships” (Hinde, 1983:5). In Hinde’s model, “each relationship is set in a nexus of other relationships, which mutually affect each other” and the social group is “constituted by those relationships”. In other words, interactions among individuals with different natures and life experiences lead, over time, to relationships (specifically *differentiated* relationships) which themselves constitute the fabric of the social group. These social relationships hold the group together; they are the mechanism of cohesion.

For many well-studied species, Robert Hinde’s framework for the foundation of social groups seems particularly apt. Japanese monkeys are a classic example of a female-bonded or resident nepotistic society in which females remain throughout their lives in their natal groups, and their social relationships are highly differentiated by kinship, dominance, personality, and individual social and reproductive history (Pavelka, 1993). Social groups are comprised of, and appear to be held together by, an array of complex interactions and relationships. Large provisioned groups with artificially enhanced and locally provided food supplies are probably somewhat inflated in terms of matriline size and social complexity, but even smaller unprovisioned Japanese monkey groups on Yakushima Island have distinctly differentiated individuals and relationships (personal observation). This type of social group, described by many who studied female-bonded cercopithecines, and characterized by Hinde, was for some time regarded as typical of primates.

It is clear now that there is no “typical” primate (Strier, 1994) and that many primate species are not female bonded. Some form groups in which females are not related, and have undifferentiated, egalitarian relationships with weak social bonds (van Schaik, 1989). However, from the perspective of Hinde’s framework, it is unclear that how undifferentiated relationships, and weak social bonds, can hold a group together. If unrelated females in a group interact little, what is the basis of the relationships? And without strong relationships among group members, what is the basis of the social group? How are groups comprised of unrelated, undifferentiated individuals held together?

This question led me to switch, over 10 years ago, from the terrestrial, provisioned, female-bonded old-world Japanese monkeys to wild, arboreal, bisexually dispersing Central American black howler monkeys in Monkey River, Belize. Compared to Japanese macaques, black howlers engage in almost no overt social interactions (within the group). Other than juvenile play (with other juveniles and with subadult males), they interact very little. They rarely groom or fight or displace each other and exchange few if any visual or vocal social signals that are detectable to observers. While they do regularly have intergroup interactions in which they roar at the neighbors (see more below), it is rare for anything to happen within the group. There are no apparent dominance hierarchies, since there are few interactions of any kind. On very rare occasions, such as when a new monkey is trying to join the group, some fighting does occur among group members, but these are rare enough to prove the general rule that they do not usually do much that is social.

But there is the following paradox: while they engage in extremely low levels of social interaction, and thus have no visible relationships, they live in perhaps *the most cohesive* of primate societies. Social groups are consistently small (<10) with small group spread (rarely greater than 10 m). While resting (and they are "resting" or inactive for 60–80% of the time), it is not uncommon for the entire group to be in the same tree. They show very low levels of what are now called fission–fusion dynamics (Aureli et al., 2008) and do not form subgroups unless group size increases to beyond 10 individuals, which it rarely does. Considering them from the Hinde framework and Japanese monkey (and baboon) perspective, they beg the question – what is holding the group together in the absence of overt social interactions or social signals? What is the mechanism of group cohesion in the absence of active affiliation or coalitionary support? How do they manage extremely high within group cohesion with extremely low levels of social interaction?

I suggest the following two possible alternative mechanisms for social cohesion in species such as black howlers in which intragroup social interaction and opportunities for reciprocity and altruism are rare: behavioral synchrony and intergroup encounters. I also present data supporting a climate-related constraint on group size.

In addition to the small group size and spread, black howlers are highly synchronous in their behavior and highly coordinated in their activity. Our data show that in over 85% of scan samples, all group members are engaged in the same activity (inactive, forage, travel, social). The group almost gives the impression of being an organism in itself. Members sit tight in their sleeping tree until 9 am. Then the whole group defecates, one after another, and the whole group moves off to find food. They travel and forage together, within 10 m of one another, until they all settle, often in the same tree, for several hours of inactivity. Two individuals doing something social, such as playing, is the source of the non-synchronous scans.

Activity synchrony has not been considered as a possible mechanism of social cohesion in primates; however, studies of other mammals (e.g., Muskoxen; Cote et al., 1997; sheep, Michelena et al., 2006; Rook and Penning, 1991; and Ibex, Ruckstuhl and Neuhaus, 2001) suggest that activity synchrony, the tendency for all group members to engage in the same activity at the same time, may function to maintain cohesion. Reproductive synchrony, the widespread tendency for individuals to carry out some stage of their reproductive cycle simultaneously with other members of the population, has long been viewed as a possible antipredator strategy (Darling, 1938; Ims, 1990). Activity synchrony might function to increase cohesion and reduce predation (Ruckstuhl and Neuhaus, 2001). Synchronizing activities with other group members may be an adaptation to maintain contact with the group (Jarman, 1974) and decrease predation risk by dilution and detection effects (Dehn, 1990). Activity synchrony helps to keep members of the group in close proximity since it prevents individuals being left behind when the others become active (Dunbar and Dunbar, 1980). However, individuals of dissimilar body size to the other group members might not be able to follow their optimal activity budget if they are synchronized with other group members (Ruckstuhl, 1998, 1999). This may explain in part why males and females in sexually dimorphic social ungulates segregate into single sex groups outside the breeding season (Main et al., 1996). Within these groups, individual activity budgets are similar and synchrony of activities is generally high (Conradt, 1998; Ruckstuhl, 1998, 1999; Conradt and Roper, 2000).

In terms of cohesion, black howlers may be contrasted with the highly dispersed fission–fusion societies of chimpanzees and spider monkeys, in which community members form subgroups of changing size and composition in response to food availability and predation risk. Black howlers and spider monkeys represent the ends of a continuum, with the highly cohesive howlers at one end and the highly dispersed spiders at the other, with much variation in between. Recognition of flexibility in intragroup cohesion over time (e.g., Muriquis above) and of variation in grouping patterns in other primate species (e.g., Hamadryas baboons range by day in stable cohesive one-male units that fuse into "super-troops" at night) is leading to a rethinking of the dichotomous treatment of cohesive versus fluid groups and to increased interest in the range of fission–fusion dynamics (FFD) that may exist within and between species and the conditions that produce them. In a recent paper in *Current Anthropology*, Filipo Aureli et al. (2008) have suggested that social systems characterized by fluid (high FFD) versus cohesive (low FFD) grouping patterns may be qualitatively different in their socioecology, social interactions, and cognitive abilities. Different levels of cohesion, or fission–fusion dynamics, may play an important role in determining the kinds of inter-individual behaviors seen in different groups.

Do high or low cohesion levels favor the evolution of complex social signals and intragroup dynamics, including, for example, the evolution of altruism or reciprocity? On the one hand, high fission–fusion dynamics would presumably require complex social skills as group members are constantly negotiating and renegotiating (sub)group entrance and membership. Individuals have to be able to keep track of a large number of group members and relationships without the benefit of regular contact. On the other hand, where fission–fusion dynamics are high, individuals may not need to develop such high levels of social skill and complexity since they can use subgroup formation to get away from one another. Fission–fusion dynamics are seen first and foremost as a means to avoid direct competition for food and would likewise make it possible to avoid many kinds of social interactions. Animals in captivity often display patterns, such as reconciliation, that are absent in their wild conspecifics. In this vein, tightly cohesive groups such as black howlers might be expected to show fairly complex intragroup dynamics and social signaling. But they do not.

To address the question of what kinds of grouping require what kind of interactions and signals, Aureli et al. (2008) have envisioned a social landscape with two axes (degree of cohesiveness and degree of differentiation of social relationships) and four quadrants. From the examples given in each of the quadrants, it seems that the most socially and cognitively complex primates fall into the category of least cohesive (high FFD) with highly differentiated relationships (quadrant IV). Chimpanzees, spider monkeys, and humans fit this description and thus fall into this

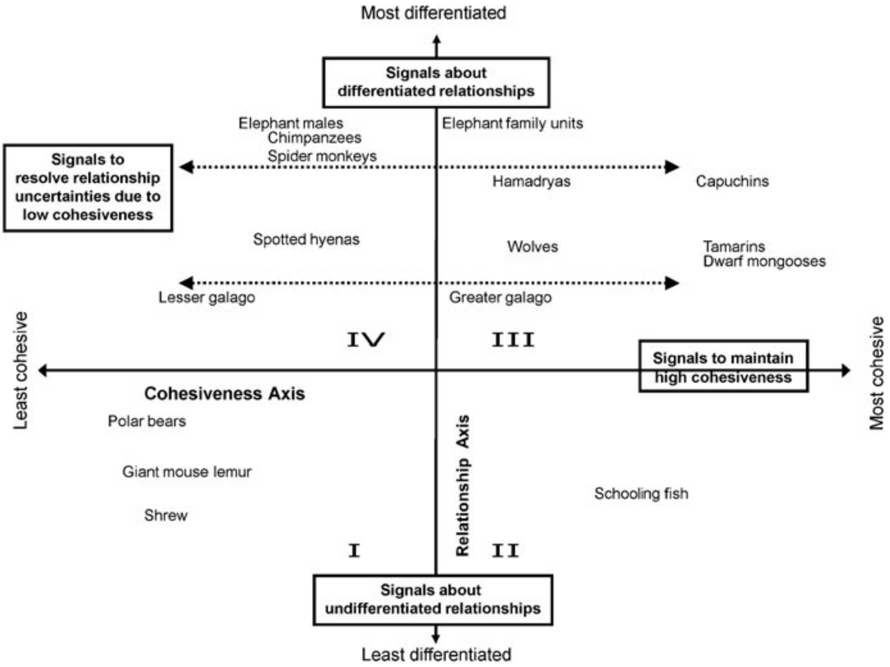


**Fig. 9.1** Model of social landscapes related to amount of cohesion (from Aureli et al. 2008)

quadrant. Humans, for example, have highly differentiated social relationships and social signals, yet are highly dispersed in terms of spatial cohesion. Whether in traditional foraging or modern societies, group members split up and spread out during the daytime, although they may regroup regularly at night when the risk of predation is highest. Primates characterized by high cohesion (lower FFD) and highly differentiated relationships also exist (quadrant III). Many of the classic female-bonded or resident nepotistic species, such as macaques, baboons, and cebus monkeys, fall into this category. But what of the situation described in this chapter for black howlers: high cohesion combined with undifferentiated relationships and few social signals? In the social landscape of Aureli et al., this category exists but no primate examples are given. The only example in the most cohesive and least differentiated quadrant is schooling fish. Are black howler monkeys the primate equivalent of schooling fish? High levels of synchrony maintain cohesion and act as a predator avoidance strategy in schooling fish. If there are many biological and behavioral mechanisms that humans and nonhumans primates use to reinforce social and cooperative behavior, then behavioral and activity synchrony could be such a mechanism, operating in the absence of strong bonds, differentiated relationships, and complex social signals within the group.

There is also no real evidence of predation on the black howler monkey groups at Monkey River. The monkeys exhibit very low levels of vigilance and despite the presence of jaguars in the area, seem completely undisturbed by and even uninterested in researchers moving around on the forest floor beneath them. Furthermore, disappearances of individuals in these very stable social groups are rare. The apparent absence of predation combined with the very low levels of social interactions and relationships begs the question as to why the monkeys do not wander off to forage on their own. What is holding them together? The absence of within-group feeding competition may reduce the costs of living in a group but in itself does not explain what holds them together. Here one may need to look to the deep at neurophysiological adaptations for sociality that are the subject of other chapters in this volume. It may be as "simple" as the monkeys feeling anxious when alone and thus preferring the company of known others (Louise Barrett, personal communication).

Another of the multiple mechanisms for sociality may be, as social and cultural anthropologists have long known, a common foe. The low levels of intragroup interaction of any kind in black howlers contrast with the quite high levels of intergroup interaction. On an almost daily basis, group members engage in howling bouts with adjacent groups. These can be quite dramatic and they are certainly loud. Primarily adult males, but often adult females as well, will lunge and roar at the neighbors, who are doing the same to them. Many researchers have attempted to identify the cause or function of intergroup encounters, all basically assuming that these interactions relate first and foremost to between group feeding and reproductive competition. Results are mixed and many hypotheses exist to explain what might be the motivation for individuals to engage in such energetically costly behavior, which also brings the risk of injury. Observations of intergroup encounters in the black howlers of Monkey River are particularly puzzling in that they do not appear to result in any clear winners or losers. These dramatic encounters are generally followed by both groups settling down to a period of peaceful inactivity, often in adjacent trees. This may last for several hours after which one or both groups moves off without incident. They occur in areas of home range overlap, which are quite large, and thus within the normal home range of both groups. Notably, the members of each group gather in a small area with small group spread. In other words, the encounter appears to function to increase bonding and cohesion *within* each group and to have few if any consequences in terms of territory holding, access to food supplies, or changes in group membership. In this regard, apparently agonistic intergroup encounters in the highly cohesive yet highly undifferentiated black howlers may have more in common with sporting events than with warfare in humans.

Why do black howlers have such undifferentiated social relationships? Possibly because they are folivores, with leaves comprising 60% of their annual diet. Socioecological models of primate social groups (Wrangham, 1980; van Schaik, 1989; Sterck et al., 1997) have predicted that folivores should be characterized by female dispersal and subsequent undifferentiated relationships between and among the unrelated adults in the group, such as we see in the bisexually dispersing and egalitarian black howlers. The evenly distributed food supply also permits the spatial cohesion that we see, there being no reason for the animals to spread out to find food. Even during periods of high frugivory in our study groups, small group size means that all members can feed together in a patch. So the consistently small groups make it much easier to be spatially cohesive. But the small group size is hard to explain, since we have found no evidence of feeding competition even in the largest of our study groups (Knopff and Pavelka, 2006). The small group size makes it possible for them to remain tightly cohesive, but what enforces the small group size if not feeding competition?

The consistently small yet unexplained group size in *Alouatta pigra*, compared with its geographic neighbor and close relative *Alouatta palliata* (that live in groups of up to 40 individuals), was one of the main factors leading to its designation as a separate species (Smith, 1970). *A. palliata* is found throughout Central America while *A. pigra* has a very limited distribution on the eastern side of the Yucatan peninsula in Belize, Mexico, and Guatemala. It is not clear why there are two such closely related species living side by side in such a small geographic area.

In October of 2001, 3 years after we began the black howler study in southeastern Belize, the study site was devastated by Hurricane Iris. The population was immediately reduced by 40% and continued to decline for 3 years before stabilizing (Pavelka et al., 2003; Pavelka et al., 2007; Pavelka and Behie, 2008). Prior to the storm, eight stable social groups (53 monkeys) lived in adjacent overlapping home ranges within a 52-ha study area. The storm devastated the forest and the monkey population. The period of 12 weeks after the storm is best described as a period of social chaos with solitary monkeys and small unstable groups wandering throughout and in and out of the area. All food sources and known arboreal pathways were gone and many individuals were gone. After 12 weeks, social groups began to coalesce. We do not know to what extent these groups were new or contained fragments of


Before Hurricane Iris

After Hurricane Iris

**Fig. 9.2** Study site before and after Hurricane Iris the pre-hurricane groups. Interestingly, while social groups had reestablished themselves after 12 weeks, these groups did not settle into stable home ranges for almost a year.

The effect of the storm on social behavior was harder to document, since for several months we were unable to enter the forest. All trails had been destroyed and deadfall, including many large fallen trees, and made access impossible. Procuring local assistance to open new trails proved difficult since the local human population was dealing with their own homelessness and lack of power or water. Our observations for the first 3–4 months were limited to what we could see from the river and the road that border the site, and did not permit scrutiny of intragroup dynamics, although we did observe a severe fight between two adult males that led to the death of one. For the remainder of that next year, we did have good focal animal data and these show no significant change in the amount of time spent in social contact. The primary change was a significant increase in the time spent inactive (Behie and Pavelka, 2005) which may have been due to the changes in the food supply (Pavelka and Behie, 2005), which led to complete folivory where the monkeys had previously consumed almost 40% fruit annually. Furthermore, the low population density and unstable home ranges lead to less contact between social groups, if frequency of howling bouts is taken as an indication of these. Certainly the forest became a comparatively quiet place compared to before the storm. It may be that without stable home ranges, intergroup encounters were more risky, with outcomes less predictable. The newly formed groups may have opted to avoid each other in the forest for that first year before home ranges stabilized.

In addition to the dramatic reduction in population and group density, another effect of Hurricane Iris was a significant reduction in the size of the already small groups (from a modal group size of eight before the storm to a maximum group size of five for several years after). In 1999, Pat Wright suggested that there might be a connection between cyclones in the north of Madagascar and the consistently small group sizes found in lemur species in this area (Wright, 1999). This led us to ask the following question: is group size and species distribution in *A. pigra* related to the weather patterns in their range? We conducted a preliminary investigation of hurricane tracks in and around Central America over the past 150 years (NOAA, 2007), which shows a concentration of hurricanes crossing onto land in precisely the range of *A. pigra* (see maps below). In fact, since 1858, 315 Atlantic hurricanes and tropical storms have crossed into coastal regions populated by *A. pigra* (825 km of coastline), where only 120 have crossed in the range of *A. palliata* (1360 km of coastline), producing a hurricane to coastline ratio of 0.382 for *A. pigra* and only 0.088 for *A. palliata*.

These data raise the intriguing possibility that natural disasters play a role in determining, or constraining, group size and perhaps even in explaining speciation. We do not know of a mechanism by which storm frequency in an area might constrain group size; however, if group size is constrained by such an external factor, high levels of cohesion might be permitted even in a folivore and in the absence of social interactions among group members. In the case of black howlers, the small groups permit high levels of cohesion, with all group members able to feed together

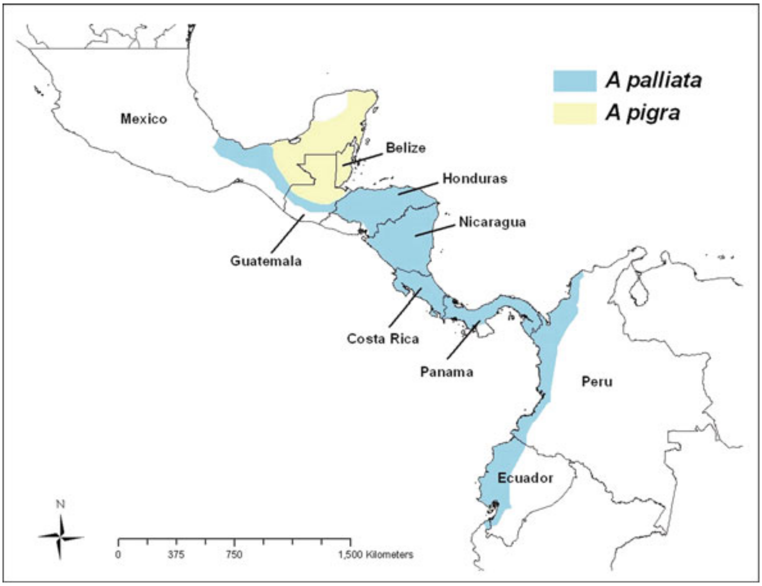


**Fig. 9.3** Distribution of *A. palliata* and *A. pigra*

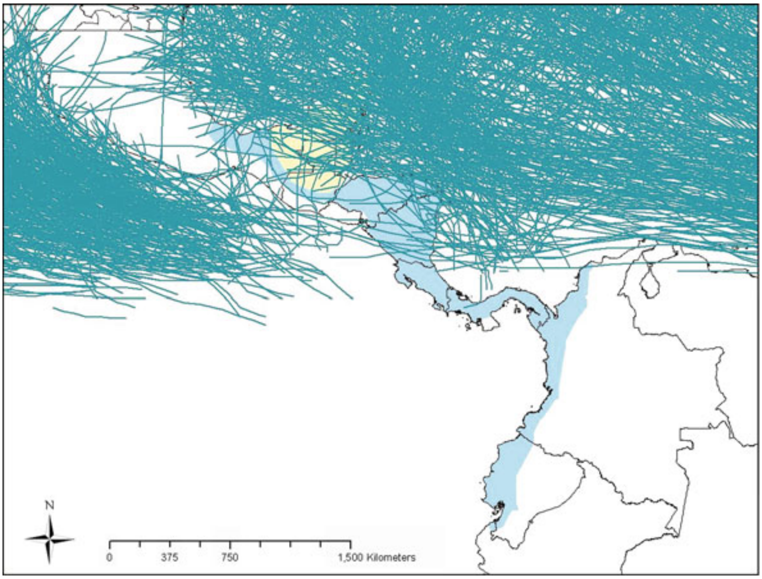


**Fig. 9.4** Hurricane tracks in and around Central America over the past 150 years

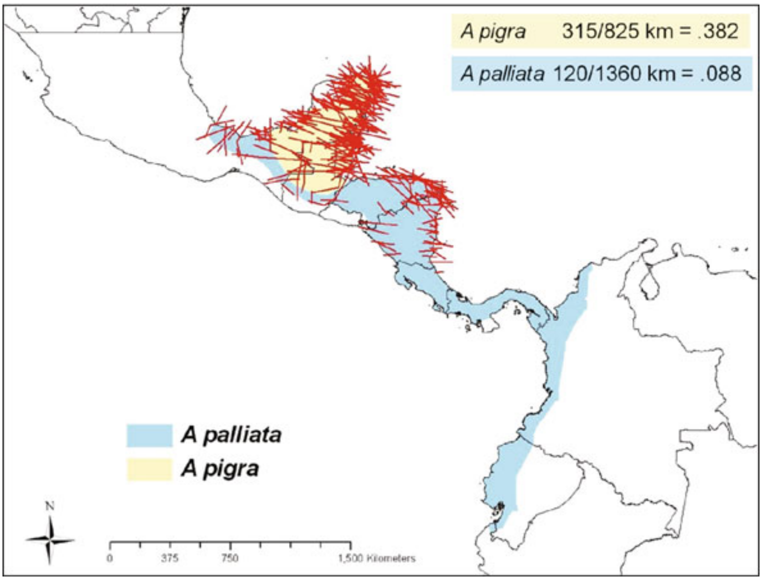


**Fig. 9.5** Hurricane tracks in relationship to the ranges of *A. palliata* and *A. pigra*

in a patch, and the absence of feeding competition within the group favors undifferentiated relationships. To the question of what holds such a group together under conditions of low levels of social interaction and indifferent "relationships", activity synchrony and intergroup encounters are suggested alternate mechanisms of cohesion, working in concert with the evolved neurophysiological adaptations for sociality which are the subject of much of this volume.

**Acknowledgments** I would like to thank Bob Sussman for inviting me to be part of this very interesting project. Also many thanks to the graduate and undergraduate students who have worked on the Monkey River project, as well the people of Monkey River for their many years of support. In particular I acknowledge Travis Steffens and Tracy Wyman who are working with me on the hurricane to coastline study mentioned briefly in this paper, and Dr. Alison Behie of Australia National University, who spent several years in the forest observing the black howler monkeys. The Monkey River project was supported by the Natural Sciences and Engineering Council of Canada (NSERC), The Province of Alberta, National Geographic, and the University of Calgary.

## References

Aureli, F., Schaffner, C.M., Boesch, C., Bearder, S.K., Call, J., Chapman, C.A., Connor, R., Di Fiore, A., Dunbar, R.I.M., Henzi, S.P., Holekamp, K., Korstjens, A.H., Layton, R., Lee, P., Lehmann, J., Manson, J.H., Ramos-Fernandez, G., Strier, K.B., and van Schaik, C.P. 2008. Fission-fusion dynamics: New research frameworks. *Curr. Anthropol.* 49(4):627–646.

Behie, A.M. and Pavelka, M.S.M. 2005. The short term effect of hurricane iris on the diet and activity budget of black howlers (*Alouatta pigra*) in monkey river, Belize. *Folia Primatologica*. 76(1):1–9.

Conradt, L. 1998. Could asynchrony in activity between the sexes cause intersexual social segregation in ruminants. *Proc. Roy. Soc. Lond*. 265:1359–1363.

Conradt, L. and Roper, T.J. 2000. Activity synchrony and social cohesion: a fisson-fusion model. *Proc. Roy. Soc. Lond*. 267: 2213–2218.

Cooper, M.A. and Bernstein, S.I. 2000. Social grooming in Assamese macaques (*Macaca assamensis*) *Am. J. Primatol.* 50:77–85.

Cote, S.D., Schaefer, J.A., and Messier, F. 1997. Time budgets and synchrony of activities in muskoxen: The influence of sex, age and season. *Can. J. Zool.* 75(10):1628–1635.

Darling, F.F. 1938. *Bird flocks and breeding cycle*. Cambridge University Press: Cambridge.

Dias, L.G. and Strier, K.B. 2003. Effects of group size on ranging patterns in *Brachyteles arachnoides hypoxanthus*. *Int. J. Primatol.* 24:209–221.

Dehn, M.M. 1990. Vigilance for predators: detection and dilution effects. *Behav. Ecol. Sociobiol.* 26:337–342.

Dunbar, R.I.M. 1999. Co-evolution of neocortx size, group size and language in humans. *Biomed. Life Sci.* 40(1):47–59.

Dunbar, R.I.M. and Dunbar E.P. 1980. The pairbond in klipspringer. *Anim. Behav.* 28:219–229.

Hinde, R.A. Ed. 1983. *Primate social relationships: An integrated approach*. Blackwell Scientific Publications: Boston, MA, pp. 182–190.

Ims, R.A. 1990. On the adaptive value of reproductive synchrony as a predator-swamping strategy. *Am. Naturalist* 136(4):485–498.

Jarman, P.J. 1974. The social organisation of antelope in relation to their ecology. *Behaviour* 48:215–267.

Knopff, K.H. and Pavelka, M.S.M. 2006. Feeding competition and group size in *Alouatta pigra. Int. J. Primatol.* 27(4):1059–1078.

Main, M.B., Weckerly, F.W., & Bleich, V.C. 1996. Sexual segregation in ungulates: new directions for research. *J. Mammal.* 77:449–461.

Michelena, P., Noel, S., Gautrais, J., Gerard, J.F., Deneubourg, J.L., and Bon, R. 2006. Sexual dimorphism, activity budget and synchrony in groups of sheep. *Oecologia* 148: 170–180.

National Oceanic and Atmosheric Administration. United States Department of Commerce. Accessed 2007. http://maps.csc.noaa.gov/hurricanes/download.jsp

Pavelka, M.S.M. 1993. *Monkeys of the Mesquite: The social life of the South Texas snow monkey*. Kendall/Hunt Publishing Co: Dubuque Iowa.

Pavelka, M.S.M. and Behie, A.M. 2005. The effect of hurricane iris on the food supply of black howlers (*Alouatta pigra*) in Southern Belize. *Biotropica*. 37(1):102–108.

Pavelka, M.S.M. and Behie A.M. 2008. Reduction and recovery of a black howler monkey population in response to a major hurricane. International Primatological Society, Edinburgh. *Primate Eye*. 96:88.

Pavelka, M.S.M., Brusselers, O., Nowak, D., and Behie, A.M. 2003. Population reduction and social disorganization in *Alouatta pigra* following a hurricane. *Int. J. Primatol.* 24(2): 1037–1055.

Pavelka, M.S.M. and Chapman, C., 2006. Population structure of black howlers (*Alouatta pigra*) in Southern Belize and responses to Hurricane Iris. In *New perspectives in the study of Mesoamerican primates: Distribution, ecology, behavior, and conservation*, A. Estrada, P. Garber, M.S.M. Pavelka, and L. Lueke (eds.), Developments in Primatology: Progress and Prospects, Springer, New York, pp. 143–163.

Pavelka, M.S.M., McGoogan, K., and Steffens, T. 2007. Population size and characteristics of *Alouatta pigra* before and after a major hurricane. *Int. J. Primatol.* 28(4):919–929.

Rook, A.J. and Penning, P.D. 1991. Synchronisation of eating, ruminating and idling activity by grazing sheep. *Appl. Anim. Behav. Sci.* 32:157–166.

Ruckstuhl, K.E. 1998. Foraging behaviour and sexual segregation in bighorn sheep. *Anim. Behav*. 56:99–106.

Ruckstuhl, K.E. 1999. To synchronise or not to synchronise: A dilemma in young bighorn males? *Behaviour* 136:805–818.

Ruckstuhl, K. and Neuhaus, P. 2001. Behavioral synchrony in IBEX groups: Effects of age, sex and habitat. *Behaviour* 138(8):1103–1046.

Seyfarth, R.M. 1983. Grooming and social competition in primates. In *Primate social relationships: An integrated approach*, R.A. Hinde (ed.), Blackwell Scientific Publications, Cambridge, MA, pp. 182–190.

Smith, J.D. 1970. The systematic status of the black howler monkey, *Alouatta pigra lawrence. J. Mammal*. 51:358–369.

Sterck, E.H.M., Watts, D.P., and van Schaik, C.P. 1997. The evolution of female social relationships in nonhuman primates. *Behav. Ecol. Sociobiol.* 41(5):291–309.

Strier, K. 1994. The myth of the typical primate. *Yearbook Phys. Anthropol.* 37:233–271.

Van Belle, S. and Estrada, A. 2006. Demographic features of *Alouatta pigra* populations in extensive and fragmented forests. In *New perspectives in the study of Mesoamerican primates*, A. Estrada, P.A. Garber, M. Pavelka, and L. Luecke (eds.), Springer, New York, pp. 121–142.

Van Schaik, C.P. 1989. The ecology of social relationships amongst female primates. In *Comparative sociobiology. The behavioural ecology of humans and other mammals*, V. Staden R.A. Foley (eds.), Blackwell Scientific Publications, Oxford, pp. 195–218.

Wrangham, R.W. 1980. An ecological model of female-bonded primate groups. *Behaviour* 75:262–300.

Wright, P.C. 1999. Lemur traits and Madagascar ecology: Coping with an island environment. *Yearbook Phys. Anthropol.* 42:31–72.

# Chapter 10
# Social Plasticity and Demographic Variation in Primates

**Karen B. Strier**

## Introduction

A basic assumption in contemporary models of primate behavioral ecology is that the social patterns we observe in wild subjects are adaptations, or the products of past evolutionary selection pressures. Yet, both ecological and demographic conditions can change during the course of an individual's life span, resulting in selection pressures that fluctuate on shorter time scales than the generations over which evolutionary processes occur. The varying fitness consequences of particular social patterns under different conditions can result in behavioral polymorphisms within populations and in high levels of intraspecific behavioral variation between populations (Strier, 2003, 2009). Social behavior is especially sensitive to local conditions, which reflect the demographic histories of groups and populations (Sussman, 1977; Strier, 1997a; Struhsaker, 2000, 2008; Henzi and Barrett, 2003; Sapolsky and Share, 2004) in addition to the phylogenetic histories of species. If evolution has favored "expedience," or "the ability to select whatever tactic is necessary to solve an immediate problem, regardless of the possible long-term consequences of such action," as Barrett and Henzi (2005, p. 1868) have suggested, then a great deal of primate social behavior may not be adaptive in a genetically determined, evolutionary sense.

Traditional approaches to investigating the relationships between social variables, such as levels of competition and cooperation, and ecological and demographic variables, have focused on interspecific comparisons (e.g., Sterck et al., 1997; Nunn and Barton, 2001). These approaches have been effective in identifying behavior patterns that segregate with phylogeny, such as the concentration of female kin networks and matrilocality among the cercopithecines (Di Fiore and Rendall, 1994; Strier, 1994). However, because the comparative method compresses intraspecific variation into species-specific norms, it fails to take into account the contributions of group and population histories in shaping variation in social patterns among populations of the same species or within populations over time

K.B. Strier (✉)
Department of Anthropology, University of Wisconsin, Madison, WI 53706-1393, USA
e-mail: kbstrier@wisc.edu

R.W. Sussman, C.R. Cloninger (eds.), *Origins of Altruism and Cooperation*,
Developments in Primatology: Progress and Prospects 36, DOI 10.1007/978-1-4419-9520-9_10,

(Strier, 1997a). Longitudinal studies can provide data for evaluating predictions about the ways in which primates adjust their behavior in response to changing ecological and demographic conditions and therefore contribute to more dynamic models that are sensitive to the fluctuating selection pressures under which primate sociality has evolved (Strier, 2009).

In this chapter, I have used data on the demographic changes that have occurred over a long-term field study of wild northern muriquis (*Brachyteles hypoxanthus*) to explore some predictions about the ways in which their social dynamics might be expected to change over time. Our long-term research on northern muriquis at the Reserva Particular Pâtrimonio Natural-Feliciano Miguel Abdala (previously the Estação Biológica de Caratinga) in Minas Gerais, Brazil, has revealed that they live in an unusually egalitarian society in which males are philopatric and the majority of females disperse from their natal groups prior to the onset of puberty (Strier, 1990; Strier et al., 2006). Rates of aggression among and between males and females are low compared to many, but not all, other primates (Sussman et al., 2005), and there is no evidence of agonistically based dominant relationships among or between males and females within groups (Strier, 1992). Females avoid direct competition with one another over access to food by avoiding close proximity while feeding (Strier, 1990), and there is no overt competition among males for sexual access to females (Strier, 1992). Females routinely mate with multiple partners (Strier, 1997b; Possamai et al., 2007), and male access to females can best be described as scramble competition (Strier et al., 2002). Indeed, the high proportion of time that males spend in close spatial proximity to one another suggests that social monitoring plays an important role in mating success of male.

The peaceful characteristics of the muriqui's society have persisted, despite more than a fivefold increase in the size of the study group and a corresponding increase in the size of the population over the past 28 years (updated from Strier et al., 2006). Nonetheless, demographic pressures have stimulated other behavioral changes in this group. For example, we have previously documented a shift from cohesive grouping patterns to fluid associations (Dias and Strier, 2003), similar to the fission–fusion associations that reduce direct feeding competition in other primate and non-primate societies (Aureli et al., 2008). More recently, we documented a 20-fold increase in the muriquis' use of terrestrial substrates, consistent with the expansion of their vertical niche in response to increased population density and habitat saturation (Tabacow et al., 2009a). Yet, despite these clear indications of their behavioral plasticity and sensitivity to changing demographic conditions, the social dynamics among group members have remained remarkably constant (Strier et al., 2000).

Ongoing evidence of group and population growth and a shift from female- to male-biased infant sex ratios over the past 10 years are predicted to pose new social challenges when members of these recent birth cohorts mature and enter the breeding population (Strier et al., 2006; Strier & Mendes, In press). The 294 individuals in the study population (as of February 2010) are distributed among four mixed-sex groups, all of which are confined to a forest fragment less than 1,000 ha in size. Although recent sightings of dispersing females from the study population are consistent with the increase in population density in the forest (Tabacow et al., 2009b), the study site's isolation precludes the recruitment of individuals from other populations. Consequently, the increasing number of individuals and the increasingly male-biased breeding sex ratio are occurring in the context of a closed population, similar to those of other primates whose habitats have undergone extensive fragmentation. These conditions provide a unique opportunity to evaluate how the northern muriqui's social dynamics, intergroup dispersal patterns, and life histories respond to demographic changes.

## Historical Background

Systematic observations were initiated in June 1982 on one of the two original muriqui groups at the study site (Matão group), yielding individual-based behavioral and life history data since July 1983. The Matão group has grown from 22 to 105 individuals, and the study population has increased from an estimated number of 40–45 individuals (Valle et al., 1984) to the 294 individuals that comprise the population as of February 2010. The other group present in 1982 (Jaó group) has fissioned on two occasions, resulting in the establishment of the M2 group in 1987 and of the Nadir group in 2002 (Strier et al., 1993, 2006). Systematic observations were initiated on these groups in 2002, yielding individual life history data on the entire population since 2003. Currently (February 2010), these groups range in size from 46 (M2 group) to 63 (Jaó group) and to 70 (Nadir group) individuals.

Muriquis are not territorial but, indicative of group integrity, they do engage in agonistic intergroup encounters in areas where their home ranges overlap. The Matão group shifted its home range to the south when the M2 group was established (Strier et al., 1993; Dias and Strier, 2003), and there is extensive home-range overlap among all of the groups except the Matão and Jáo groups, whose home ranges overlap with the other groups but not with one another's (Boubli et al., 2005).

The growth of the population reflects its recovery from past disturbances and the prohibitions against hunting that have been enforced since the mid 1940s, when the ranch in which the forest is situated was established (Strier and Boubli, 2006). Nonetheless, there are reasons to suspect that the population may be approaching the carrying capacity of the forest. In addition to the high degree of home-range overlap and the vertical niche expansion that we have documented in the Matão group (Tabacow et al., 2009a) there has been a measurable decline in the density of sympatric brown howler monkeys, which consume many of the same food species as muriquis (Almeida-Silva et al., 2005). Although the muriqui population is still growing, habitat saturation and the increasingly male-biased infant sex ratios (which may be a response to habitat saturation) suggest that the population may have reached or is approaching the forest's carrying capacity, and that its growth rate will be slower in the future than it has been in the past.

The Matão group has been the target of numerous behavioral, ecological, and reproductive studies since the onset of the project, with studies on the other groups beginning once their members were habituated (Strier and Boubli, 2006). Data on adult male and female spatial relationships and social interactions were collected during systematic observations of the Matão group over different years (males: 1996–1997; females: 1998–1999) and under different demographic conditions, and include a combination of the same individuals, all natal males and three natal females that matured in the group, and immigrant females. These behavioral data provide a basis for generating predictions about the effects of projected demographic changes on male and female social dynamics. In addition to their exceptionally low rates of agonistic interactions, northern muriquis do not groom one another (Strier, 1992), and rates of affiliative interactions are low compared to those of many other primates (Sussman et al., 2005). However, their spatial associations, particularly during resting bouts, are indicative of their high levels of social tolerance and social preferences (Strier, 1997c; Strier et al., 2002). Males are classified as adults from the date on which they achieve their first complete copulation, defined as a copulation that terminates with ejaculation (Possamai et al., 2005). Females are classified as adults when they begin to copulate, which is coincidental with the onset of ovarian cycling in this species (Strier and Ziegler, 2000).

## Sex Differences in Social Patterns

*Kinship*: Male and female northern muriquis exhibit sex-biased social patterns that can be attributed, at least in part, to the effects of male philopatry and female dispersal. Co-residence among philopatric males permits males to maintain lifelong associations with one another and with their mothers, whereas females leave both their parents and male kin behind when they disperse from their natal groups prior to the onset of puberty. Females may transfer into the same groups with members of their age cohorts, who may be paternally related sisters, or into groups that older, familiar, maternally related sisters previously joined, but access to the more extended kinship networks that are available to philopatric males is severed when females disperse (Strier, 2004, 2008).

Despite the availability of familiar maternal kin, nepotism does not appear to play a detectable role in the structuring of the muriqui's social dynamics. Maternally related brothers do not maintain closer spatial associations with one another or engage in more frequent affiliative embraces than expected by chance (Strier et al., 2002). There is also no evidence that mothers bias their associations in favor of their juvenile or adult sons over other males in the same age classes, or that the variation in the strength of associations between mothers and their juvenile daughters affects their daughters' subsequent dispersal decisions (Tolentino et al., 2008). Three of some 34 females that have survived to dispersal age to date (Strier & Mendes, In press) have remained and reproduced in their natal Matão group (Fig. 10.1), but only one of the three mother-adult daughter dyads associated more often than expected by chance (Tolentino et al., 2008). Intriguingly, this mother was also the only one to engage in grandmaternal care when her daughter's first son was born, but that may

**Fig. 10.1** A rare mother–adult daughter embrace. BS (*back*) embraces her adult daughter (BR), who is carrying her infant and BS's granddaughter. BR is one of only three females that have remained and reproduced in their natal group to date. Photo by C.P. Nogueira

have been because she was not caring for an infant of her own like the other female with maternal grandoffspring in the group (Assunção et al., 2007).

Despite the lack of strong kin bonds, the indirect evidence of close inbreeding avoidance suggests that northern muriquis may recognize familiar, maternally related kin. Copulations between mothers and sons, and between maternally related males and the females that have remained in their natal group, have been extremely rare compared to copulations involving non-maternally related individuals of similar age classes, who would be similarly familiar with one another as maternal relatives who avoid one another as mates (Strier, 1997b; Possamai et al., 2007). In addition, females have dispersed non-randomly into groups that are unlikely to include related males (Strier et al., 2006). For example, females born in the Jaó and Nadir groups have dispersed exclusively into the M2 and Matão groups, and with one recent (November 2008) exception, Matão females have dispersed exclusively into the Jaó and Nadir groups, thereby avoiding the M2 group, where a cohort of Jaó males that previously made incursions into the Matão group and copulated with Matão females now resides (Strier, 1997b; Strier et al., 2006). However, factors other than maternal kinship and the histories and relationships among the groups could affect female mate choices and dispersal decisions, respectively, and interpretations about inbreeding avoidance, especially without knowledge of paternal relatedness, should be treated cautiously.

*Social and Spatial Dynamics*: During the 1996–1997 study period, the 13 adult males in the Matão group spent more than 60% of their time within a 5-meter radius of at least one other adult male (Strier, et al., 2002). By contrast, during the 1998–1999 study period, the 19 adult females in the group spent only about 50% of their time in proximity to one another (Nogueira and Strier, Unpublished). Dyadic association indices (calculated as $N_{AB}/(N_A + N_B + N_{AB})$, where $N_{AB}$ = the frequency at which individuals A and B were seen together and $N_A$ and $N_B$ = the frequencies at which individuals A and B were observed in proximity to other individuals in their age/sex class without the other [Martin and Bateson, 1986]) were significantly higher for male dyads (0.15 $\pm$ 0.10, median = 0.13, range = 0.05–0.59, $N$=78;

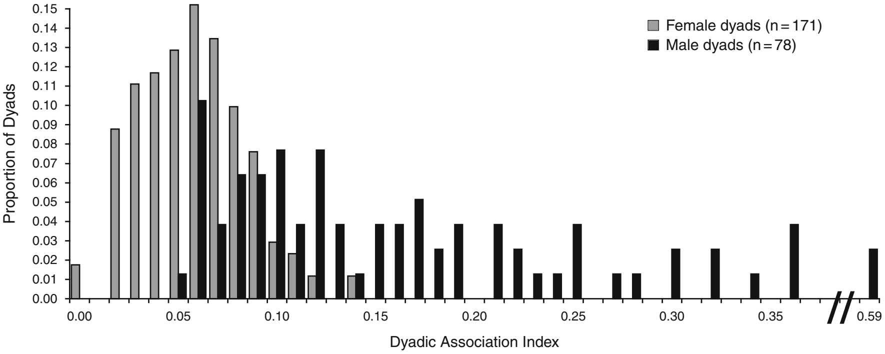


**Fig. 10.2** Sex differences in dyadic association indices. See text for sources of data and calculations

Strier, et al., 2002) than for female dyads (0.05 ± 0.03, median = 0.05, range = 0–0.13, $N = 171$; $z = 10.19$, $p < 0.0001$; Fig. 10.2).

Dyadic embrace indices, calculated similarly to the association indices, also differed significantly between the sexes, with higher embrace indices among female dyads (0.05 ± 0.01, median = 0.0, range = 0–0.50) than among male dyads (0.04 ± 0.02, median = 0.03, range = 0–0.11; $z = 4.98$, $p < 0.0001$). However, only 27% of the 171 possible female dyads engaged in embraces, 100% of which were dyadic ($n = 61$). By contrast, 86% of the 78 possible male dyads engaged in embraces, and 59% of male embraces were polyadic ($n = 39$).

Comparisons of association and dyadic embrace indices for individual female and male dyads illustrate distinct, sex-specific patterns in their social dynamics (Fig. 10.3). In general, female dyads associated relatively rarely, and females interacted with fewer partners more intensively than males, who not only associated with one another at higher rates but also distributed their interactions more evenly among a higher proportion of the same-sexed partners available to them. Thus, females can be described as interacting with only a few "best friends," whereas males can be described as interacting within extensive social networks.

The one exceptional female dyad involved a female (EL) who had immigrated into the Matão group in 1995 and gave birth to her first infant in June 1998, and another (MO) who was present as a nulliparous female in 1982 and gave birth to her sixth infant in July 1998. While it is tempting to infer that EL and MO interacted so often with one another because of their similar status as nursing mothers, neither of the other two females that also gave birth in June 1998 interacted disproportionately more often with one another or with EL or MO during this study period. The one exceptional male dyad involved the two most popular males in the Matão group, one (CL) being an older male whose popularity was a result of the high rates at which other males approached him, and the other being a younger male (RB) whose popularity was a result of the exceptional initiative he took in approaching other males (Strier et al., 2002). Interestingly, there are indications that at least some associations correspond with the ages of male and female dyads, and with the reproductive

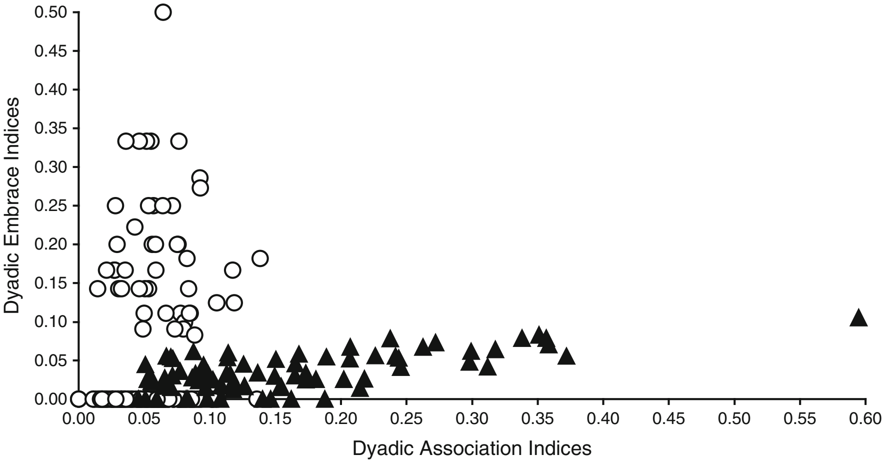


**Fig. 10.3** Sex differences in social dynamics of female (*open circles*) and male (*black triangles*). Sex text for sources of data and calculations

conditions of female dyads. However, younger males are generally more responsible for initiating proximity with older males, suggesting that proximity and the access it provides to interacting with other males in their extended social networks is an important element in the social maturation and integration of males (Strier et al., 2002).

## Effects of Demographic Changes on Social Patterns

*Increases in the Number of Social Partners*: Considering the sex differences in northern muriqui social patterns, demographic pressures can be predicted to affect males and females in different ways. For example, an increase in the number of possible social partners should impact female social dynamics less than those of males, whose associations and interactions are based on extended, integrated networks. Consequently, while the number of female social partners might be expected to increase proportionately with an increase in the number of females in their groups, the number of male social partners should increase exponentially (Fig. 10.4).

Ecological or cognitive constraints might preclude the maintenance of male social networks if the number of males in a group exceeds some maximum threshold. Forest structure and canopy size may limit the number of males that can maintain close spatial associations, while the time and energy required to monitor a greater number of male group members may become prohibitive if doing so interferes with the time and energy required to meet their basic subsistence needs. Time constraints may play a particularly important role in limiting group size in other primates in which social networks are important (Dunbar et al., 2009).

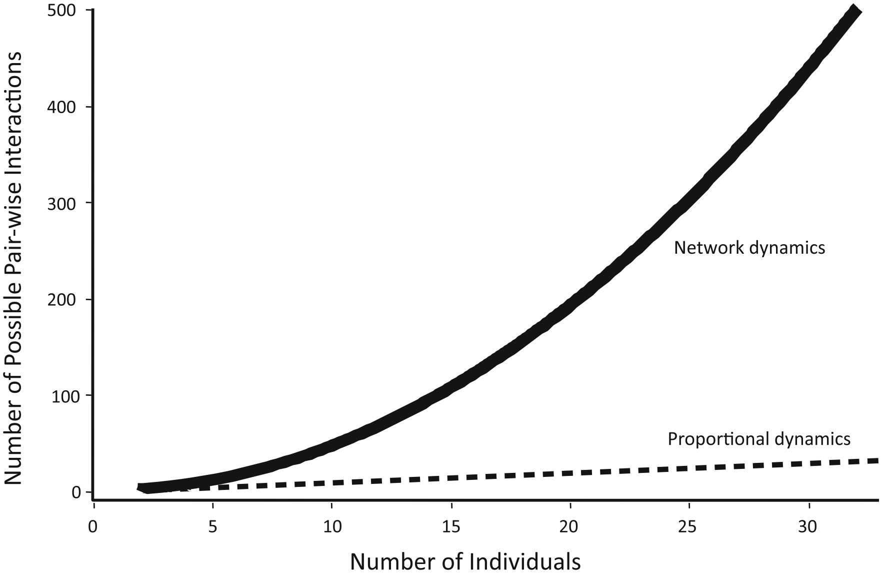


**Fig. 10.4** Predicted effects of increases in the number of social partners for male (*upper solid line*) and female (*lower dashed line*) northern muriquis. Redrawn from Goldsmith and Zimmerman (2001, Fig. 11.14)

*Changes in Breeding Sex Ratios*: Increases in the number of males would not necessarily lead to the disruption of male social networks per se. Instead, male networks might be predicted to cluster along the strength of their dyadic affiliations, becoming more clique-like within the larger context of the group and ultimately be susceptible to fissioning along these lines. Although we do not know whether males or females were responsible for the two prior fissioning events of the Jaó group, in both cases, cohorts of 6 and 14 males from the parent group maintained transient associations until ultimately joining the newly established M2 and Nadir groups, respectively (Strier et al., 2006). During the second group fissioning event, one cohort of Jaó males remained in the Jaó group with a subset of females, another cohort of Jaó males joined the subset of females that founded the Nadir group from the outset, and a third cohort of Jaó males associated in an all-male unit that alternated between associating with the Nadir group and ranging on its own. Although we lack data on the social dynamics of members of the Jaó group prior to its fissions, it is clear that both male and female relationships were sufficiently differentiated to diverge when the group fissioned. Indeed, when efforts to habituate and identify individuals in the Jaó group were initiated, experienced observers could recognize two distinct subgroups based on the consistency of their associations at the time. When the Jaó group clearly fissioned later that year, it did so along these predictable, previously identified lines (Boubli et al., 2005).

Increases in the number of male muriquis should not affect levels of male–male competition for access to mates unless they are accompanied by a decrease in the relative number of females. Although the adult sex ratio in the Matão group has remained fairly stable to date, the recent shift from female- to male-biased infant sex ratios in the population since 2000 implies that levels of competition will increase when the members of these male-biased birth cohorts have matured. The mortality costs of female dispersal, which are estimated to be up to 33% (Strier, In press), will further exaggerate the effects of male-biased birth sex ratios on adult sex ratios in the future.

Increasingly limited access to females can be expected to stimulate behavioral responses by males, but an increase in overt competition is only one of the possible options. For example, rates of agonistic interactions could increase among males, resulting in a shift from the tolerant, egalitarian relationships that have persisted to date, to more antagonistic, hierarchical relationships. Other philopatric male primates (e.g., spider monkeys and chimpanzees) compete for rank with one another despite their cooperation in inter-community encounters (Aureli et al., 2006; Langergraber et al., 2007). However, in contrast to these species, northern muriquis lack the sexually dimorphic canines (Lemos de Sá et al., 1993) associated with sexual selection pressures on canine size for male aggression or aggressive displays (Plavcan, 1999). Whether intraspecific, inter-population variation in demographic conditions could lead to corresponding population differences in levels of canine dimorphism is not so implausible considering that intraspecific variation in other morphological traits has been documented in other primates (e.g., body mass in howler monkeys [Glander, 2006]; testicular size in baboons [Jolly and Phillips-Conroy, 2006]).

An alternative response to increased levels of male–male competition associated with male-biased breeding sex ratios would be a shift from male philopatry to male dispersal. Secondary dispersal into groups with more favorable breeding sex ratios and reproductive opportunities is common among male primates (e.g., ring-tailed lemurs [Sussman, 1992]; Hanuman langurs [Moore, 1992]; howler monkeys [Glander, 1992]), and one case of dispersal has been reported in male bonobos, despite their typical pattern of male philopatry (Hohmann, 2001).

Whether the benefits of male muriqui dispersal would outweigh the costs would depend on the extent of the variation in breeding sex ratios in other groups in the population relative to the breeding sex ratio in their natal groups. It would also depend on the risks of being targeted for aggression by philopatric male networks in the groups they seek to join. Indeed, at least some of these risks might be avoided if, instead of dispersing from their natal groups, males opportunistically or deliberately can gain extra-group mating opportunities with other females in the population. The episodic incursions of a cohort of Jaó males into the Matão group from 1987 to 2001 were usually met with agonistic challenges by Matão males, but copulations between Matão females and extra-group males still accounted for 13% of the more than 500 copulations observed during a 60-month period from July 1990 to June 1995 (Strier, 1997b). Although Matão males have never been observed to associate or copulate with females in any of the other groups, the precedent for the behavior in this population has been set.

A third possible response to increased competition would be either an acceleration or a delay in the age of male sexual maturation. Males in the Matão group have reached sexual maturity and entered the breeding population between

5.21 and 8.36 years of age (mean ± sd = 6.75 ± 0.83, median = 6.62 years, $N = 21$; Strier, In press). One of the two males that reached sexual maturity in 2007 was among the youngest of these males (5.21 years), while the other male was older (7.35 years) than the median age of male maturity in this group to date. Accelerated maturation is associated with life history strategies in which adult survivorship is low, whereas delayed maturation is generally associated with high adult survivorship (Charnov and Berrigan, 1993). Declines in adult male survivorship could be caused by increased competition over food as well as mates, as the population continues to grow and the habitat becomes increasingly saturated, with similar advantages on earlier maturation.

However, it is more likely that the effects of competition over access to food or mates would result in delayed maturation before it could impact adult survivorship. Passive exclusion from adult male social networks, or the inability of young males to attract or gain cooperation from females, could also result in maturational delays. During conception months, male age was positively and significantly correlated with the proportion of copulations that terminated with ejaculation and negatively correlated with copulation-to-ejaculation durations (Possamai et al., 2005). In addition to age-related differences in male experience and in the rapidity of male physiological responses, female preferences for older males might also play a role in shaping male mating opportunities and hence the age at which male northern muriquis enter the breeding population.

Currying female favor might be a fourth response to males faced with increased levels of competition for access to mates due to unfavorable sex ratios in their groups. Behaviors associated with gaining female favors in other male primates include the care and protection of infants that may or not be their own (Smsuts, 1985; Paul, 1999). Past interactions between adult males and infants in our study group were characterized by the indifference that males displayed on rare occasions in which infants approached them (Guimarães and Strier, 2001). However, in recent months, a number of different adult males have not only been observed to initiate affiliative interactions with various infants, but in some cases, also have carried the infants while the infants' mothers were resting or feeding nearby (Kaizer et al., In press).

None of the males were maternally related to the infants with whom they interacted, raising the intriguing possibility that their recent interest in infants may be a form of mating effort that has not been observed in this species before. Whether males that attend to infants now will be preferred by the infants' mothers as future mates' remains to be seen when the mothers resume cycling and copulate again in upcoming years. Nonetheless, the high energetic cost of infant carrying, which appears to be as expensive as lactation in this species (Guedes et al., 2008), suggests that male contributions to infant care might be a sufficiently valued currency among females to bias their mate choices in favor of male caretakers. Although it is difficult to envision that current rates of male infant carrying are sufficient to increase infant survivorship or reduce maternal energetic costs enough to shorten their parturition-to-cycling delays (Strier, 1996), monitoring the variation in infant survivorship and parturition-to-cycling intervals among infants that are carried and those that are not will provide further insights into the possible ways in which new behavioral patterns among males can affect other components of the muriquis' life histories.

## Phenotypic Plasticity and its Significance for Social Evolution

Whether new behavioral patterns can be definitively attributed to demographic pressures, or might be introduced through equally influential initiatives unrelated to demography, remains to be evaluated. Nonetheless, by proposing some of the alternative behavioral responses that muriquis might be expected to make as demographic conditions in their groups and population change, I have attempted to move considerations of primate social behavior beyond commonly held assumptions about its inherent adaptiveness. There is no a priori reason to assume that the muriquis'—or any other primates'—responses to changing local conditions are necessarily adaptive. To the contrary, the opportunism of phenotypic plasticity is as likely to result in selectively neutral or even deleterious social patterns as it is in adaptive ones. The assumption that adaptive responses will become fixed through selection processes ignores the potential for them to become established as learned, nongenetic local traditions. Particularly in long-lived, slow-reproducing species such as primates, the social transmission of behavioral patterns may be a faster and more efficient process, as well as one that can respond more effectively to fluctuations in local demographic conditions.

Frequency dependent selection on learned behavior patterns may be a better paradigm for understanding the range of social responses that primates make to fluctuating demographic conditions. Local conditions can favor cooperation or competition at different times in an individual's life span. The ability to move between cooperative and competitive modes, and social plasticity in general, may be the underlying adaptation of primate social evolution.

**Acknowledgments** The initial concept for this chapter was presented in the symposium, Man the Hunted, The Origin and Nature of Human Sociality, organized by Robert W. Sussman at the Annual meeting of the AAAS in February 2006. A longer version was presented at the Conference on Man the Hunted: Sociality, Altruism, and Well-Being (March 12–14, 2009, Washington University) co-organized by Robert W. Sussman and C. Robert Cloninger. I thank Jonathan Marks and John Martin for early conversations and Robert Sussman for comments on the manuscript. The data on the sociality of female muriquis were collected by the late Claudio P. Nogueira, who also contributed to the long-term monitoring of the Matão group and to the habituation and early monitoring of the Jaó and Nadir groups. I am grateful to him and to the many other people and funding agencies that have made the long-term field study possible. I also thank the Brazilian CNPq for research permission, the Sociedade para a Preservação do Muriqui for permission to work in their forest, and Sérgio L. Mendes for his long-term collaboration on the project.

## References

Almeida-Silva, B., Cunha, A. A., Boubli, J. P., Mendes, S. L., & Strier, K. B. (2005). Population density and vertical stratification of four primate species at the Estacao Biologica de Caratinga/RPPN-FMA, Minas Gerais, Brazil. *Neotropical Primates, 13(Suppl)*, 25–29.

Assunção, M. L., Mendes, S. L., & Strier, K. B. (2007). Grandmaternal infant carrying in wild northern muriquis (*Brachyteles hypoxanthus*). *Neotropical Primates, 14*, 120–122.

Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., Connor, R., Di Fiore, A., Dunbar, R. I. M., Henzi, S. P., Holekamp, K., Korstjens, A. H., Layton, R., Lee, P. C. Lehmann, J., Manson, J.,H., Ramos-Fernandez, G., Strier, K. B., & van Schaik, C. P. (2008). Fission-fusion dynamics: New research frameworks. *Current Anthropology, 49*, 627–654.

Aureli, F., Schaffner, C. M., Verpooten, J., Slater, K., & Ramos-Fernandez, G. (2006). Raiding parties of male spider monkeys: Insights into human warfare? *American Journal of Physical Anthropology, 131*, 486–497.

Barrett, L., & Henzi, P. (2005). The social nature of primate cognition. *Proceedings of the Royal Society of London, B, 272*, 1865–1875.

Boubli, J. P., Tokuda, M., Possamai, C., Fidelis, J., Guedes, D., & Strier, K. B. (2005). *Dinâmica intergrupal de muriquis-do-norte, Brachyteles hypoxanthus, na Estação Biológica de Caratinga, MG: o comportamento de uma unidade de machos (all male band) no vale do Jaó.* Livro dos Resumos, XI Congresso Brasileiro de Primatologia, Porto Alegre, Brasil, p. 41.

Charnov, E. L., & Berrigan, D. (1993). Why do female primates have such long lifespans and so few babies? or life in the slow lane. *Evolutionary Anthropology, 1*, 191–194.

Dias, L. G., & Strier, K. B. (2003). Effects of group size on ranging patterns in *Brachyteles arachnoides hypoxanthus*. *International Journal of Primatology, 24*, 209–221.

Di Fiore, A., & Rendall, D. (1994). Evolution of social organization: A reappraisal for primates by using phylogenetic methods. *Proceedings of the National Academy of Sciences USA, 91*, 9941–9945.

Dunbar, R. I. M., Korstjens, A. H., & Lehmann, J. (2009). Time as an ecological constraint. *Biological Reviews of the Cambridge Philosophical Society, 84*, 413–429.

Glander, K. E. (1992). Dispersal patterns in Costa Rican mantled howling monkeys. *International Journal of Primatology, 13*, 415–436.

Glander, K. E. (2006). Average body weight for mantled howling monkeys (*Alouatta palliata*): An assessment of average values and variability. In A. Estrada, P. A. Garber, M. S. M. Pavelka, & L. Luecke (Eds.), *New perspectives in the study of Mesoamerican primates: Distribution, ecology, behavior, and conservation* (pp. 247–263). New York: Springer.

Goldsmith, T. H., & Zimmerman, W. F. (2001). *Biology, evolution, and human nature*. New York: Wiley.

Guedes, D., Young, R. J., & Strier, K. B. (2008). Energetic costs of reproduction in female northern muriquis (*Brachyteles hypoxanthus*, Primates, Platyrrinhi). *Revista Brasileira de Zoologia, 25*, 587–593.

Guimarães, V. O., & Strier, K. B. (2001). Adult male-infant interactions in wild muriquis (*Brachyteles arachnoides hypoxanthus*). *Primates, 32*, 395–399.

Henzi, P., & Barrett, L. (2003). Evolutionary ecology, sexual conflict, and behavioral differentiation among baboon populations. *Evolutionary Anthropology, 12*, 217–230.

Hohmann, G. (2001). Association and social interactions between strangers and residents in bonobos (*Pan paniscus*). *Primates, 42*, 91–99.

Jolly, C. J., & Phillips-Conroy, J. E. (2006). Testicular size, developmental trajectories, and male life history strategies in four baboon taxa. In L. Swedell & S. R. Leigh (Eds.), *Reproduction and fitness in baboons: Behavioral, ecological, and life history perspectives* (pp. 257–275). New York: Springer.

Kaizer, M. C., Coli, A. Z., Mendes, S. L., & Strier, K. B. (In press). Interações de machos adultos e infantes em *Brachyteles hypoxanthus* (Kuhl 1820). In J.M.D. Miranda and Z.M.B. Hirano (Eds.), *A Primatologia no Brasil - 12*. Paraná, Brasil: Sociedade Brasileira de Primatologia.

Langergraber, K. E., Mitani, J. C., & Vigilant, L. (2007). The limited impact of kinship on cooperation in wild chimpanzees. *Proceedings of the National Academy of Sciences USA, 104*, 7786–7790.

Lemos de Sá, R. M., Pope, T. R., Struhsaker, T. T., & Glander, K. E. (1993). Sexual dimorphism in canine length of woolly spider monkeys (*Brachyteles arachnoides*, E. Geoffry, 1806). *International Journal of Primatology, 14*, 755–763.

Martin, P., & Bateson, P. (1986). *Measuring behavior*. New York: Cambridge University Press.

Moore, J. (1992). Dispersal, nepotism, and primate social behavior. *International Journal of Primatology, 13*, 361–378.

Nunn, C. L., & Barton, R. A. (2001). Comparative methods for studying primate adaptation and allometry. *Evolutionary Anthropology, 10*, 81–98.

Paul, A. (1999). The socioecology of infant handling in primates: Is the current model convincing? *Primates, 40*, 33–46.

Plavcan, J. (1999). Mating systems, intrasexual competition and sexual dimorphism in primates. In P. Lee (Ed.), *Comparative primate socioecology* (pp. 241–269). Cambridge: Cambridge University Press.

Possamai, C. B., Young, R. J., Mendes, S. L., & Strier, K. B. (2007). Socio-sexual behavior of female northern muriquis (*Brachyteles hypoxanthus*). *American Journal of Primatology, 69*, 766–776.

Possamai, C. B., Young, R. J., Oliveira, R. C. F., Mendes, S. L., & Strier, K. B. (2005). Age-related variation in copulations of male northern muriquis (*Brachyteles hypoxanthus*). *Folia Primatologica, 76*, 33–36.

Sapolsky, R. M., & Share, L. J. (2004). A pacific culture among wild baboons: Its emergence and transmission. *PLoS Biology, 2*, E106.

Smuts, B. B. (1985). *Sex and friendship in baboons*. New York: Aldine.

Sterck, E. H. M., Watts, D. P., & van Schaik, C. P. (1997). The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology, 41*, 291–309.

Strier, K. B. (1990). New World primates, new frontiers: Insights from the wooly spider monkey, or muriqui (*Brachyteles arachnnoides*). *International Journal of Primatology, 11*, 7–19.

Strier, K. B. (1992). Causes and consequences of nonaggression in woolly spider monkeys. In J. Silverberg & J. P. Gray (Eds.), *Aggression and peacefulness in humans and other primates* (pp. 100–116). New York: Oxford University Press.

Strier, K. B. (1994). Myth of the typical primate. *Yearbook of Physical Anthropology, 37*, 233–271.

Strier, K. B. (1996). Male reproductive strategies in new world primates. *Human Nature, 7*, 105–123.

Strier, K. B. (1997a). Behavioral ecology and conservation biology of primates and other animals., *Advances in the Study of Behavior, 26*, 101–158.

Strier, K. B. (1997b). Mate preferences of wild muriqui monkeys (*Brachyteles arachnoides*): Reproductive and social correlates. *Folia Primatologica, 68*, 120–133.

Strier, K. B. (1997c). Subtle cues of social relations in male muriqui monkeys (*Brachyteles arachnoides*). In W. G. Kinzey (Ed.), *New world primates: Ecology, evolution, and behavior* (pp. 109–118). Hawthorne, NY: Aldine de Gruyter.

Strier, K. (2003). Demography and the temporal scale of sexual selection. In C. Jones (Ed.), *Sexual selection and reproductive competition in primates: New perspectives and directions* (pp. 45–63). Norman, OK: American Society of Primatologists.

Strier, K. B. (2004). Sociality among kin and nonkin in nonhuman primate groups. In R. W. Sussman & A. R. Chapman (Eds.), *The origins and nature of sociality* (pp. 191–214).

Strier, K. B. (2008). The effects of kin on primate life histories. *Annual Review of Anthropology, 37*, 21–36.

Strier, K. B. (2009). Seeing the forest through the seeds: Mechanisms of primate behavioral diversity from individuals to populations and beyond. *Current Anthropology, 50*, 213–228.

Strier, K. B. (In press). Northern muriqui monkeys: Behavior, demography, and conservation. In J. Yamagiwa & L. Karczmarski (Eds.), *Primates and cetaceans: Field research and conservation of complex mammalian societies*. New York: Springer.

Strier, K. B., & Boubli, J. P. (2006). A history of long-term research and conservation of northern muriquis (*Brachyteles hypoxanthus*) at the Estação Biológica de Caratinga/RPPN-FMA. *Primate Conservation, 20*, 53–63.

Strier, K. B., Boubli, J. P., Possamai, C. B., & Mendes, S. L. (2006). Population demography of northern muriquis (*Brachyteles hypoxanthus*) at the Estação Biológica de Caratinga/Reserva Particular do Patrimônio Natural-Feliciano Miguel Abdala, Minas Gerais, Brazil. *American Journal of Physical Anthropology, 130*(2), 227–237.

Strier, K. B., Carvalho, D. S., & Bejar, N. O. (2000). Prescription for peacefulness. In F. Aureli & F. B. M. de Waal (Eds.), *Natural conflict resolution* (pp. 315–317). Berkeley, CA: University of California Press.

Strier, K. B., Dib, L. T., & Figueira, J. E. C. (2002). Social dynamics of male muriquis (*Brachyteles arachnoides hypoxanthus*). *Behaviour, 139*, 315–342.

Strier, K. B., & Mendes, S. L. (In Press). The northern muriqui (*Brachyteles hypoxanthus*): Lessons on behavioral plasticity and population dynamics from a critically endangered primate. In P. Kappeler & D. Watts (Eds.), *Long-Term Studies of Primates*. Heidelberg: Springer-Verlag.

Strier, K. B., Mendes, F. D. C., Rímoli, J., & Odalia Rímoli, A. (1993). Demography and social structure in one group of muriquis (*Brachyteles arachnoides*). *International Journal of Primatology, 14*, 513–526.

Strier, K. B., & Ziegler, T. E. (2000). Lack of pubertal influences on female dispersal in muriqui monkeys, *Brachyteles arachnoides*. *Animal Behaivour, 59*, 849–860.

Struhsaker, T. (2000). Variation in adult sex ratios of red colobus monkey social groups: Implications for interspecific comparisons. In P. Kappeler (Ed.), *Primate males* (pp. 108–119). Cambridge: Cambridge University Press.

Struhsaker, T. T. (2008). Demographic variability in monkeys: Implications for theory and conservation. *International Journal of Primatology, 29*, 19–34.

Sussman, R. W. (1977). Feeding behaviour of *Lemur catta* and *Lemur fulvus*. In T. H. Clutton-Brock (Ed.), *Primate ecology* (pp. 1–36). New York: Academic.

Sussman, R. W. (1992). Male life history and intergroup mobility among ringtailed lemurs (*Lemur catta*). *International Journal of Primatology, 13*, 395–413.

Sussman, R. W., Garber, P. A., & Cheverud, J. M. (2005). Importance of cooperation and affiliation in the evolution of primate sociality. *American Journal of Physical Anthropology, 128*, 84–97.

Tabacow, F. P., Mendes, S. L., & Strier, K. B. (2009a). Spread of a terrestrial tradition in an arboreal primate. *American Anthropologist, 111*, 238–249.

Tabacow, F. P., Possamai, C. B., Melo, F. R., Mendes, S. L., & Strier, K. B. (2009b). New sightings of northern muriqui (*Brachyteles hypoxanthus*) females in forest fragments surrounding the Estação Biológica de Caratinga-RPPN Feliciano Miguel Abdala, Minas Gerais. *Neotropical Primates 16*(2), 67–69.

Tolentino, K., Roper, J. J., Passos, F. C., & Strier, K. B. (2008). Mother-offspring associations in northern muriquis, *Brachyteles hypoxanthus*. *American Journal of Primatology, 70*, 301–305.

Valle, C. M. C., Santos, I. B., Alves, M. C., Pinto, C. A., & Mittermeier, R. A. (1984). Preliminary observations on the behavior of the monkey (*Brachyteles arachnoides*) in a natural environment (Fazenda Montes Claros, Município de Caratinga, Minas Gerais, Brasil). ria Press. In M. Thiago de Mello (Ed.), *A primatologia no Brasil* (pp. 271–283). Belo Horizonte: Imprensa Universitária Press.

# Part III
# Altruism and Cooperation Among Humans: The Ethnographic Evidence

# Chapter 11
# Altruism and Cooperation Among Humans: The Ethnographic Evidence: Introduction Part III

**Peter Benson**

In everyday life, we clearly discern acts of altruism. There are goodness and kindness in the world. Individuals partner with each other and make sacrifices for others. They engage in charity and in the giving of gifts, resources, and knowledge. Parents care for their offspring. Friends or strangers lend helping hands. Families and communities take shape around cooperation and care-giving. There is probably as much love as there is animus in the human condition. But altruism is a tricky subject. Here is the 64,000-dollar question (or, given the scale of global philanthropy a la the Gates Foundation, the 64 billion). Is the giver, in giving, or the partner, in cooperating, not acting in a way that, while seeming to sacrifice, maximizes that individual's fitness, status, prestige, or security? Is what appears on the surface to benefit others or the common good indeed selfish?

Scholars attempt to understand the meaning of these acts, the influence of biology and the environment on human behavior, and the function and purpose of altruism in the organization and evolution of the species. At the heart of this quest to understand what seems so apparently communal and sacrificial is an *aporia*, literally an impasse. The undergraduate student who participates in community service projects is also padding his/her resume and maximizing life chances. The corporation that massively funds philanthropy in the areas of cancer awareness and research also realizes a significant tax deduction and acquires symbolic capital through its public relations. The parents who shower kindness on their children are ensuring that their genes are promoted. Altruism is an *aporia* because the question of *true* motive is indeterminate.

Lately it seems that the shoe has been dropping on the side of skepticism. Research in fields such as economics and evolutionary psychology attempts to explain all of human experience in terms of reproductive fitness and individual competition. Even for cases that seem to confound a desire to pass along genes, there are "just so" explanations. The gay man is a good uncle. The nun's oath of chastity is a strategy to ensure that scarce family resources go to her siblings or to communities

---

P. Benson (✉)
Department of Anthropology, Washington University, St. Louis, MO 63130, USA
e-mail: pbenson@artsci.wustl.edu

R.W. Sussman, C.R. Cloninger (eds.), *Origins of Altruism and Cooperation*,
Developments in Primatology: Progress and Prospects 36, DOI 10.1007/978-1-4419-9520-9_11,

in which her genetic materials reside. Adopting a child emboldens the emotional and psychological well-being of the childless couple who are now better equipped to be better relatives and members of a genetic pool. All individuals are out for number one. Cooperative and associative behavior are reduced to being the means of individual fitness rather than an essential part of what defines the human species, so that competition ultimately drives altruistic behavior. "Slap one hypothesis down," R. Brian Ferguson writes in Chapter 10, "another pops up. True believers see confirmation of our evolved violent nature everywhere they turn, and they have forcefully presented this bleak view to the public and policy makers."

Trying to account for the fact that altruistic and solidaristic behaviors occur in every human society "always leads to some variation of the same, rather silly, circular arguments," an economic anthropologist notes. He illustrates the point with the following fictional dialog:

> Q: If people only act to maximize their gains in some way or another, then how do you explain people who give things away for nothing?
> A: They are trying to maximize their social standing, or honor, or prestige that accrues to them by doing so.
> Q: Then what about people who give anonymous gifts?
> A: Well, they're trying to maximize the sense of self-worth, or the good feeling they get from doing it. (Graeber, 2001:8)

The search for hidden motives, something beneath the surface of human behavior, has a deep intellectual history in Western philosophy and science. There have been various well-known challenges to this kind of skepticism, such as the Cartesian certainty principle, Kant's critique of pure reason, British empiricism, phenomenology, and American pragmatism. But according to the French philosopher Paul Ricoeur (1970), a distinctively skeptical approach, what he calls the "hermeneutics of suspicion," defined the work of many of the major modern intellectuals. For Friedrich Nietzsche cruelty and the will to power lie beneath appearances. When the judge, magistrate, or landlord shows benevolence, like forgiving a debt, he is instilling thankfulness and obedience, a more efficient form of power than physical force (Foucault, 1977). For Karl Marx it was the profit motive. The factory owner provides the workforce with "free" coffee and cigarettes at break time, increasing productivity while also inducing loyalties and massaging potential conflict (Mintz, 1986).

The particular brand of scepticism that most defines contemporary thinking about evolution and how altruism fits into the picture is liberal political economy. Theories of the market that arose in the mercantile period have become the dominant paradigm for thinking about all of human behavior. Research on human evolution now looks quite similar to research done in microeconomics, and there is exceptional synergy in fields like evolutionary psychology, where the underlying assumptions about rational choice, decision making, and sociality come from classical and neoclassical economics. Adam Smith's notion of the invisible hand serves as a blueprint. In *The Wealth of Nations* (2000 [1776]), he famously observed that "it is not from the benevolence of the butcher, the brewer, or the baker that we expect our dinner but from their regard to their own self-interest. We address ourselves, not to their humanity but to their self-love." Through such narrative sketches, Smith shows how competition between actors free to pursue their own self-interests can create efficiencies that benefit everyone. In his take on utilitarianism, it is not cooperation but competition that benefits the whole. "Every individual generally neither intends to promote the public interest nor knows how much he is promoting it," Smith wrote, "he intends only his own gain, and he is in this led by an invisible hand to promote an end which was no part of his intention."

Marx might agree with the cynical reading of altruism. But he also wrote passionately and sensitively about the diversity of pre-capitalist societies. Contrary to the assumptions of liberalism, he did not understand self-interest to be the most foundational aspect of human nature. Nor did he equate self-interest with the greediness of maximizing economic behavior. Marx understood greed as a dangerous moral value promoted and excused within a particular set of historical and social conditions and then naturalized in the philosophies and doctrines of the academy. What liberalism saw as natural, Marx argued, was in fact one concrete way of behaving in the world, and with Max Weber and Emile Durkheim he was interested in enriching rather than narrowing the epistemology of human nature and nurture.

Perhaps the most famous statement in social theory on altruism and one of the most significant challenges to the liberal perspective comes from Marcel Mauss. His book *The Gift* (1990 [1954]) argued that there is no such thing as a gift. Any act of giving is part of a context of reciprocity in which some kind of return, whether material or symbolic, is expected and delivered. A primary function of social institutions is to continuously promote and maintain social solidarity through gift exchange. Acts that are essential to the survival of individuals and social groups, such as the provisioning of resources and the maintenance of ecological balance, are accomplished through the dynamics of reciprocity. The argument is not that people are not self-interested. Mauss relished in the fact that social relationships are interested and motivated, and that the ecological and economical functions of exchange masquerade behind such notions as uninterested gifts and unmotivated generosity. Yet, he wrote against the reduction of gift exchange to any one impulse or to individual motivation. Reducing altruism to a biological function, for instance, misses the holistic social context in which altruistic behavior takes place and has consequences. Solidarity is not the result of accumulated individual maximizing decisions. Rather, the very ability of individuals to flourish depends on social and environmental influences and nourishment from communities. This is a very different portrait of human nature than what the methodological individualism of classical liberal thought provides.

Whether or not something called altruism exists as part of human nature may not be the best jumping-off point for debates about the function of cooperative, sacrificial, or generous behaviors. It is not a question of whether an act is wholly selfish or selfless, profane or sacred. "I do not think," Walter Goldschmidt writes in his chapter, "the word altruism fits into the scientific paradigm, and I believe it should be replaced with the recognition of the dynamic role of love in social life." In other words, the question of altruism is really a question that involves apprehending and understanding a whole range of prosocial behaviors and their impact on the immediate lives of those involved as well as the longer range trajectory of the species. An evolutionary perspective that takes prosocial behavior as natural is better equipped to explain why people engage in particular kinds of altruistic acts than one that relies on assumptions about individual fitness.

The first chapter in this part, by Bruce Knauft, begins with an argument regarding the immense diversity of the use of lethal violence among humans, while also noting that a distinctive pattern has developed over the past several centuries. In general, current rates of human killing are higher in the most economically undeveloped countries and lower in the most developed countries. "The ostensible peace dividend of economic late modernity," he writes, "has been complemented if not intensified by the redirection, export, facilitation, and failure to forestall slaughter and human wastage in poor countries, including by structural means and the exploits of the international political economy, from which rich countries benefit." The staggering statistics and historical geography of combat and violence that he provides contest the promise of perpetual peace that Kant envisioned in the Enlightenment.

Knauft then looks at the specific case of the Gebusi, a small-scale society in Papua New Guinea. A group that once had some of the highest levels of homicide in the ethnographic record, with killing closely linked to a culture of sorcery accusation and compounded by high levels of predation from neighboring groups, now has a very low homicide rate. Knauft explains the shift by examining the group's peaceful cultural revival in which long-standing customs and practices have been reinvigorated and sorcery has become increasingly defunct. The shift occurred without effective pressure exerted on Gebusi from government officials, development workers, or missionaries. "As Gebusi linger on the margins of the global political economy, their 'undeveloped' state does not please them," he writes. "But they have taken initiative on their own terms to craft what has been for several decades now a positive way of turning marginality into their own meaningful and peaceful cultural development."

Douglas P. Fry's chapter also emphasizes a need to contextualize patterns of violence in terms of historical, social, and ecological processes. He draws on his extensive work with present-day nomadic foragers to show how these groups, which are often taken as stand-ins for human ancestors and used to supplement archaeological and primatological research on human evolution, exhibit a set of social patterns that defy the "Man the Warrior" stereotype that has been built up in much science and in the popular culture. These social patterns include an emphasis on sharing and cooperation, high levels of egalitarianism, including gender egalitarianism, minimal material property accumulation, minimal private ownership of resources, loosely defined territorial ranges, lots of reciprocal exchange among individuals as well as within and between groups, a devaluation of physical aggression, lack of warrior values, and the exertion of social control via cultural forms more often than through violence. Fry argues that the flexibility and sheer diversity of these human groups belie any single characterization, and that aggression, when it does manifest, is usually more personal, as in the case of spousal jealousy, than societal or organized. "The actual ethnographic evidence does not support the portrayal of nomadic foragers as warlike," he writes. "Such a view is a myth. It is out of touch with the facts."

Ferguson's chapter likewise confronts myths found in the science of human nature. He looks at violent behavior among chimpanzees and asks whether there is in our common evolutionary heritage a predisposition to organized violence. Challenging the dominant work in this area, the view of chimps as "natural born killers," Ferguson argues that primates have evolved a most flexible nature. The presence of violence and warfare in primate populations does not for Ferguson indicate the evolution of a violent brain, but rather a mix of impulses that includes cooperation and prosociality and which, given particular ecological circumstances such as food shortage, leads to cooperative efforts to engage in severe fighting. The violence that is taken to be natural by many primatologists is thus linked by Ferguson to the human impact on the contemporary environments of chimpanzees and the processes through which chimpanzees and other animals are socialized in those environments. The same analytical misstep he diagnoses has occurred in cultural anthropology where colonial and other external impacts were ignored in portraits of timeless cultures (Clifford and Marcus, 1986). The idea that violence arises in response to increased resource competition and other disruptions is very different than the idea that it is the normal expression of evolved propensities. "Primatology should avoid that mistake," Ferguson writes. "The way to understand behavior is to examine responses to changing circumstances." Working carefully through evidence from primatology, archaeology, and field ethnography, Ferguson offers a powerful challenge to the notion that humans and our closest primate relatives are inclined to war and that the economy of reproductive success underpins a common aggressive nature.

The chapters in this part attempt to reframe our understanding of human nature at the same time as they raise questions about the ethics of the fields in which human evolution is studied. The authors insist that other motivations besides economic self-interest must be considered part of human nature, and human nature itself must be understood as dynamic and entwined with the developmental contexts of the social world. We should not forget that Adam Smith argued that just as important as self-interest is the human passion of sympathy, what he called "fellow-feeling." In speaking of the dynamism of human behavior as a phenomenon which confounds the binaries of nature and nurture, sacred and profane, the chapters also point to the political and ethical dangers of scientific research which fails to reflect on its use of narration and its capacities for reification.

In the final chapter of the section, Goldschmidt writes of the need to arrive at an account of human nature for the "third millennium." This involves a more rounded appreciation of the role of cooperative social behavior. He provides considerable evidence for the evolution of affection and creativity from the hominid fossil record and the analysis of human language and cognition. The capacity for positive affect to be transmuted through culture, and for natural survival impulses to be oriented around generous, socially directed behavior, is an essential part of an adaptive society. His effort to expand and temper the scientific view of human nature converges with, among other intellectual currents, the rise of behavioral approaches in economics. Behavioral economics is redefining the meaning of rationality by showing that human psychology is not always adept at or geared toward maximizing individual economy. Some of the more interesting findings from the subfield include the diverse meanings of utility across societies, the ways that individual attachments to communities and identities promote social behaviors that would not be predicted by neoclassical economics, and the fact that various kinds of cooperative behavior exist alongside competitive impulses in business and markets. We also learn that social and organizational environments significantly impact levels of cooperation (Akerlof and Kranton, 2000; Akerlof and Shiller, 2010; Ensminger, 2002).

Goldschmidt's approach also involves a critical, reflexive attitude about the messages and values that science communicates. His argument reflects the increased awareness in fields such as cultural anthropology, the history and sociology of science, and social theory about what Ian Hacking (1995) calls the "looping effect." The language used in science affects the empirical world and therefore the outcomes of future research in human populations. "It is about how a causal understanding can change character," writes Hacking, arguing that audiences are influenced by scientific reporting on human nature, such that science "can change the kind of people that they are" (351). Meanwhile, the dominant ideologies of the wider culture influence the theories that scientists develop, which are nonetheless purported to be unbiased, timeless, and natural. Much of evolutionary psychology reflects the model of human behavior that is espoused in neoliberal economics, which emphasizes the contraction and marketization of state functions in order to unleash individual entrepreneurship and competition in the private sector. In large measure, one scholar comments (McKinnon, 2006), evolutionary psychology is the intellectual arm of the global trade regime, espousing theories of "neoliberal genes" that underwrite harsh policy measures.

Goldschmidt expands on this critique to show that theories about human evolution, in neglecting to take full account of prosociality, can become self-fulfilling prophecies and have a negative impact on the quality of life and capacities for creativity, adaption, and nurturance in contemporary societies. He counters with the argument that because the nervous system of mammals is not completely developed at birth, acts of caring are in fact vital to human life, encouraging adaptive biological, psychological, and social development. Goldschmidt's phrasing is exacting: "a *social act* is essential for the members of the species to have *the physical capability* for psychosocial competence."

All of the chapters in this section reiterate the key argument of this volume that cooperative behavior is a powerful disposition in human evolution and behavior, while also showing how the science of human nature has warped our understanding to the point of naturalizing harsh social policies and economic systems. The chapters collectively reiterate the point that while human behavior involves interesting, motivating, and maximizing strategies, this is not simple or mechanical, but rather a result of particular ecologies of circumstance in which nature and nurture are inseparable. There are powerful social and cultural influences that shape and channel human biology so that we can perhaps speak of biology itself as being local, contingent, and flexible. And local worlds can oftentimes be dangerous so that violence arises not in spite of cooperation and cohesion but as a result of these forms of sociality (Kleinman, 1998).

Knauft shows that a diminishing reality and perception of external political threat can be linked to reduced levels of aggression and violence in one society. Likewise, Ferguson and Fry encourage an understanding of human and primate violence that takes account of the relevant social and ecological contexts, the impact of external forces, and the changing dynamics of subsistence, security, and vulnerability in populations. Knauft connects this anthropological perspective to a critique of the neoliberal order.

> In the broader current context of macro-political economy and the direct and indirect export or structural facilitation of high rates of violence in underdeveloped countries and world areas, a similar point may be made. To the extent that world area powers and the interests of the international community fuel the sense and the reality of external political threat within and between underdeveloped countries, the rate of lethal violence tends to increase. Polarizations, exploitations, and vested interests to maintain rather than reduce conflict intensify.

Returning to the earlier discussion of classical liberalism, it seems necessary to reintegrate something like Smith's "fellow-feeling" into political economy and evolutionary history rather than banishing sympathy from our understanding of who we are and where we are going. The imperative to nurture, Goldschmidt writes, "is inextricable to mammalian nature, but it must be developed, through social contact, in each individual." These chapters resonate with the work done on violence and suffering in cultural and medical anthropology in recent decades. Anthropologists have shown how violent behavior gets transmuted from generation to generation, not through the simple mechanism of a rigidly violent "culture" (as in Oscar Lewis's old idea of the culture of poverty or in Napoleon Chagnon's [apologies to Lewis] sociobiological theory of culture) but rather through complex social and cultural dynamics, such as the spread of bitterness and trauma throughout social groups, the normalization of violence in a local moral order, and the trickle-down and trickle-out impacts of macro forces of political economy, extractive industry, and environmental change (Kleinman et al., 1999). In many cases it is not that an imperative to nurture is lacking but that the exact form that nurture takes can involve neglect or the incitement of brutal and violent behavior (Scheper-Hughes, 1993). To view urban gang violence or ethnic conflict as evidence of inborn aggression—as some primatologists do, the chapters here critically note—tells us nothing about the complexly woven circumstances that induce people to kill or do harm to other people and leaves us with no traction in terms of changing those conditions. On the contrary, it shovels tacitly racial stereotypes; forsakes the chance to scientifically understand how environmental conditions shape biological conditions, human psychology, and social behavior; and encourages bourgeois readers of popular science magazines to take social distance from depraved and difficult life circumstances through the faux experience of epistemological proximity.

If Goldschmidt is right that "mutuality is as important as antagonism for species survival," then these chapters should lead us to think with urgency about the globalization of values like greed and competition and all of the discursive work, scientific and otherwise, that goes into making these values seem fixed. There is a great deal of consent around the idea that we are individuals always and only looking out for number one. The Nobel-winning economist Gary Becker (1976) argued that spousal contracts arise out of individual calculations of value made with an eye toward utility and fitness maximization. We know from our intimate relationships that they are not the simple outcomes of market exchange, and yet this jaded theory has directly influenced our largest and most powerful economic systems. In helping us to better understand the depth and scale of altruism in our genealogy, these chapters should also encourage us to behave in more humane ways. They invite us to think about how social systems might be differently organized precisely because we are not irredeemably combative and competitive. They push us to consider how we might treat each other with respect and dignity, how we might behave altruistically while eschewing ulterior motives, because, as the late French moral philosopher Emmanuel Levinas (1998) might say, we live not only with others but also for them.

## References

Akerlof, George A., and Rachel E. Kranton. 2000. Economics and Identity. Cambridge, MA: MIT Press.

Akerlof, George A., and Robert J. Shiller. 2010. Animal Spirits: How Human Psychology Drives the Economy, and Why it Matters for Global Capitalism. Princeton, NJ: Princeton University Press.

Becker, Gary S. 1976. The Economic Approach to Human Behavior. Chicago, IL: University of Chicago Press.

Clifford, James, and George E. Marcus, eds. 1986. Writing Culture: The Poetics and Politics of Ethnography. Berkeley, CA: University of California Press.

Ensminger, Jean. 2002. Theory in Economic Anthropology. Boulder, CO: Altamira Press.

Foucault, Michel. 1977. Discipline and Punish: The Birth of the Prison. Alan Sheridan, trans. New York: Random House.

Graeber, David. 2001. Toward an Anthropological Theory of Value: The False Coin of Our Own Dreams. New York: Palgrave.

Hacking, Ian. 1995. The Looping Effect of Human Kinds. In: Causal Cognition: An Interdisciplinary Approach, pp. 351–383. D. Sperber, ed. Oxford: Oxford University Press.

Kleinman, Arthur. 1998. Experience and Its Moral Modes: Culture, Human Conditions, and Disorder. The Tanner Lectures on Human Experience, Stanford University, April 13–16. Electronic document, http://www.tannerlectures.utah.edu/lectures/documents/Kleinman99.pdf.

Kleinman, Arthur, Veena Das, and Margaret Lock, eds. 1999. Social Suffering. Berkeley, CA: University of California Press.

Levinas, Emmanuel. 1998. Entre Nous: Thinking-of-The-Other. Michael B. Smith and Barbara Harshav, trans. New York: Columbia University Press.

Mauss, Marcel. 1990 [1954]. The Gift: The Form and Reason for Exchange in Primitive Societies. London: Routledge.

McKinnon, Susan. 2006. Neo-Liberal Genetics: The Myths and Moral Tales of Evolutionary Psychology. Chicago, IL: Prickly Paradigm Press.

Mintz, Sidney. 1986. Sweetness and Power: The Place of Sugar in Modern History. New York: Penguin.

Ricoeur, Paul. 1970. Freud and Philosophy: An Essay on Interpretation. Denis Savage, trans. New Haven, CT: Yale University Press.

Scheper-Hughes, Nancy. 1993. Death Without Weeping: The Violence of Everyday Life in Brazil. Berkeley, CA: University of California Press.

Smith, Adam. 2000 [1776]. The Wealth of Nations. New York: Modern Library.

# Chapter 12
# Violence Reduction Among the Gebusi of Papua New Guinea – And Across Humanity

**Bruce M. Knauft**

One of the striking variations across humanity is the degree to which people kill, or do not kill, one another. The homicide rate in Japan, at 0.44 per 100,000 populations, is less than one-twelfth the U.S. homicide rate (approximately 5.4 killings per 100,000 people). The U.S. rate is itself almost ten times less than the current homicide rate in Honduras, at 58 per 100,000 per annum. Overall, homicide rates across the world currently vary by a factor of approximately 133.

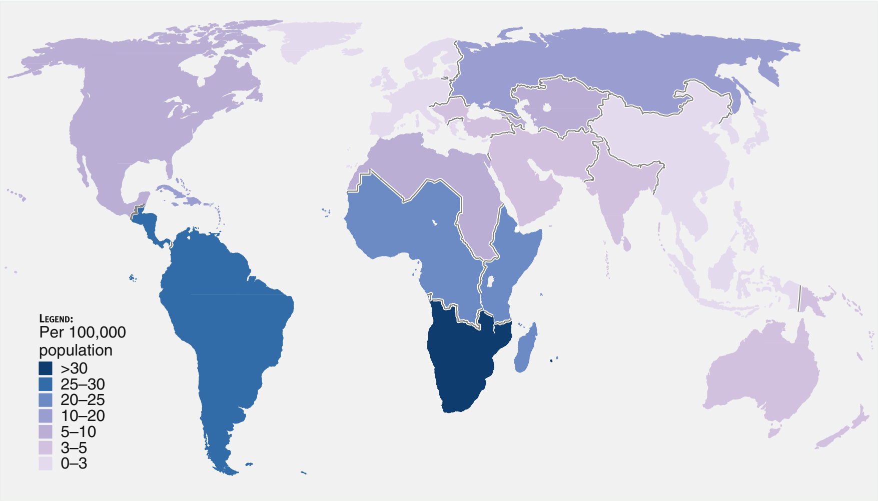
Human diversity in lethal violence is also amply evident over time. The rate of killing from all sources in Europe during World War II—the bloodiest conflict known to date—claimed between 50 and 60 million lives, resulting in a homicide rate that can be estimated to be between approximately 455 and 600 persons per 100,000 per annum. Against this, the homicide rate has in recent decades been between 0 and 3 persons per 100,000 persons annually in Western Europe. (Liechtenstein has registered a killing rate of zero out of a population of more than 35,000 in most recent years.) The rate is somewhat higher in Eastern Europe, between 5 and 10 per 100,000. Averaging out these figures and comparing them against the mid-point of killings during World War II, it can be said that the rate of lethal violence from all sources in Europe is currently less than 1/100th of what it was during the 6 years between 1939 and 1945.

On a global basis, the rate of homicide, as reflected in international homicide statistics of the United Nations Office on Drugs and Crime (UNODC), shows a rather expectable pattern. The most economically developed parts of the world, such as Europe, East and Southeast Asia, North America, Australia, have a dramatically lower rate of homicidal killing than does sub-Saharan Africa. At the same time, however, rates of killing are also high in many countries of Latin America and are moderately high also in Russia. In addition, homicide rates in the mid-East are reported to be relatively low apart from violence associated with warfare and related conflicts (Fig. 12.1).

---

B.M. Knauft (✉)
Department of Anthropology, Emory University, Atlanta, GA 30322, USA
e-mail: antbk@emory.edu

R.W. Sussman, C.R. Cloninger (eds.), *Origins of Altruism and Cooperation*,
Developments in Primatology: Progress and Prospects 36, DOI 10.1007/978-1-4419-9520-9_12,



**Note:** The boundaries and designations used on this map do not imply endorsement or acceptance.
**Source:** UN Office on Drugs and Crime (UNODC) estimates

**Fig. 12.1** Intentional homicide, rate per 100,000 population, by subregion, 2004 (from UNODC, 2010)

Questions can immediately be raised about the quality and coverage of such data. Indeed a range of methodological challenges confront the comparative study of human killing in modern times much less prehistoric or evolutionary ones (cf., Knauft. 1987c, 1991). Not only do modern governments generally keep violence associated with warfare or other forms of state-sponsored violence separate from interpersonal killings as “homicides” or “murders,” the relationship between violent deaths, reporting, registering of information, and national tabulation of killings and their categorization is highly variable between as well as within countries.

Given what we know about these factors in general and qualitative terms, it seems plausible to assert in general terms that current rates of human killing from all causes are high and in some cases very high in the most economically undeveloped countries while being low to very low in the most highly developed countries. The economic rise of East Asia, including China, previously Japan, and now Southeast Asia and India, is consistent with this trend, as is the continuing high rate of killing in Sub-Saharan Africa as well as in Latin America, which harbors the greatest economic disparity between rich and poor people of any world area.

In terms of large political units, it seems evident when comparing the first half of the 20th century to the current period from the end of World War II to the present, that bloody conflicts between major world powers—as also occurred between kingdoms or empires in the past —have now been sharply reduced, resulting in low rates of killing in most developed countries. For instance, the United States has not been afflicted by massive loss of life through violence since the Civil War, which claimed between 600,000 and 700,000 lives. This toll amounts to many times more violent deaths than the United States has sustained cumulatively from violent deaths from all causes since that time.

However, this reduction—the ostensible peace dividend of economic late modernity —has been complemented if not intensified by the redirection, export, facilitation, and failure to forestall slaughter and human wastage in poor countries, including by structural means and the exploits of the international political economy, from which rich countries benefit. As Melko (1990), among others, has documented, relative peacefulness among developed countries and world areas corresponds with the increase and concentration of violence within poorer and less developed countries which are for the most part former colonies of Western political powers. These processes variously involve proxy combat, covert support, and the indirect impacts of violence—in addition to occasional direct invasion by foreign powers themselves. This pattern of external exploitation is related to and complemented by internal dissension, weak government, and bloody feuding between local or internationally supported militias within many of the world's most violent and unstable countries and between factions across them. Even when violent conflict is not caused by external threat and coercion, it is certainly exacerbated, sometimes exponentially, by these.

In Iraq, for instance, detailed statistical calculations document that at least 601,000 Iraqis died in war-related violence between March 2003 and July 2006 (Burnham et al., 2006). Given that the population of Iraq during this period of three and one-third years was approximately 26.5 million, the resulting homicide rate is approximately 680 per 100,000 per annum. This is significantly higher than the upper estimate of the rate of killing in Europe during World War II. Though it may be debated how much of this violence was directly as opposed to indirectly caused by the U.S. invasion of Iraq, the impact of American military invasion and its related effects have resulted in a rate of killing that was more than 100 times greater than the current U.S. homicide rate of 5.4.

It is not surprising that tallies and rates of killing are kept vigilantly separate by state governments for actions sanctioned or supported by the state itself and those considered voluntaristic or personal in nature. The latter are typically characterized and publicized as "crimes," whereas the former, when they are publically calculated and publicized at all, are considered legitimate acts of national security. It should be noted in this respect that the United States intervened militarily against 24 countries since the end of World War II, an average of one country every two-and-a-half years. Armed interventions in a range of countries, including Viet Nam, Laos, Cambodia, Chile, El Salvador, and Nicaragua—as well as Afghanistan and Iraq—have resulted in significant increased rates of killing in those countries during resulting periods of political instability. These more formal military intrusions are in addition to proxy interventions and "black-bag" wars by the United States and other world areas across parts of Latin America and other world areas (e.g., Grandin, 2006). In a post-colonial era, such incursions are typically designed to topple political regimes or, alternatively, repress political resistance rather than annex new territory outright (see Knauft, 2007c). These interventions may not directly cause or explicitly sanction ensuing national or regional violence, but they pave the way for and abet its escalation.

Patterns by which internal armed conflict is triggered, fueled, or facilitated by the interests of regional and world powers beyond or in addition to the United States are characteristic of a number of the world's other major trouble spots. These prominently include eastern sections of the Democratic Republic for of the Congo (DRC), which provide a large treasure trove of mineral wealth that is easily exploited, smuggled, and exported, and which creates huge profits for interests from Rwanda, Uganda, the numerous forces of the United Nations forces (which have now been asked to leave by the President of the DRC) as well as international interests, which increasingly include the Chinese as well as Europeans, a few Americans, and those from other African countries in addition to the Congolese army and a plethora of local militia factions (see Reyntjens, 2009). These vested interests maintain political instability and ensure a large area of effectively tax-free exploitation by continuing to fuel devastating conflict in an area that has seen the most catastrophic loss of human life in the world —now five-and-a-half million persons in East Congo—since World War II and the Holocaust (IRC, 2008).

Immiserating conflicts that have decimated population in places such as southern Sudan, Somalia, and Western Columbia, and Rwanda dovetail with this pattern particularly insofar as regional and international interests support and polarize (if not historically create) opposing sides and preclude effective resolution to conflict (see Mamdani, 2001, 2009; Grandin, 2006). In a larger view, it is unsurprising that the violent upheavals generated by the world's "great powers" during the 19th and early 20th century—what Niall Ferguson (2006) calls the calamitous "War of the World"—has directly and indirectly exported violent consequences to the underdeveloped world —at the same time that the developed world has itself, since World War II, become increasingly "peaceful."

## The Gebusi: Past or Forward?

Against this macro-background, this chapter attempts to draw comparative implications from marked reduction in lethal violence in a small-scale decentralized society—the Gebusi of interior Papua New Guinea (see Figs. 12.2 and 12.3).

In particular, this chapter charts, analyzes, and draws general implications from striking and enduring changes in homicidal violence among the Gebusi people of Papua New Guinea from (a) the late pre-colonial period through the early 1960s, (b) the colonial and early post-colonial era of the late 1960s, 1970s, and early 1980s, (c) a dramatic period of introduced cultural change during the late 1980s and 1990s, and (d) challenges faced by Gebusi during a period of major economic decline and closure of the region's airstrip and government station in 2007–2008. In conclusion, I consider the implications of the marked reduction of violence among Gebusi for our understanding of human plasticity against assertions that human violence is genetically determined or hard-wired, particularly among men. I also link a more flexible understanding of human violence back both to our understanding of global macro-patterns of contemporary violence and, on the other hand, to features of what we know about the long-standing evolution of violence among humans as a species.

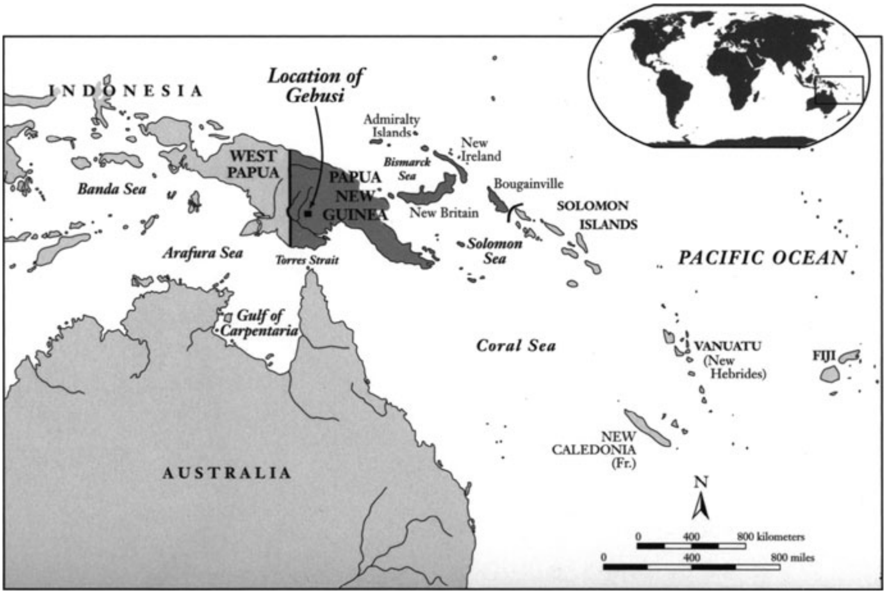


**Fig. 12.2** Location of Gebusi

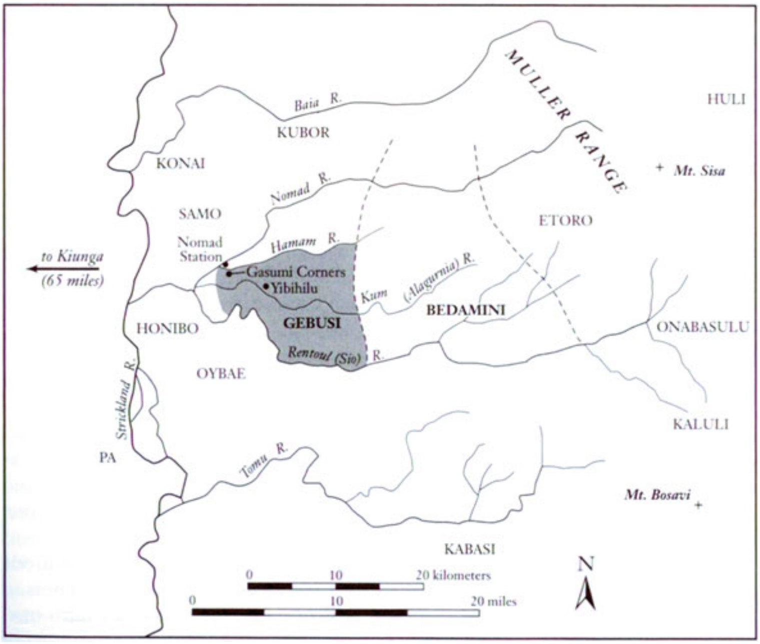


**Fig. 12.3** Gebusi in regional context, Strickland-Bosavi area, Papua New Guinea

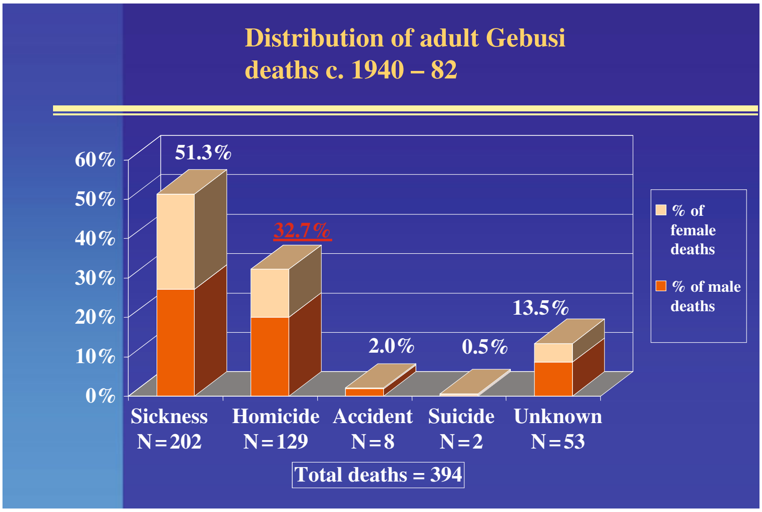


**Fig. 12.4** Distribution of adult Gebusi deaths, *c.* 1940–1982

Expressed in colloquial terms, the Gebusi are remarkable in having gone from virtually worst to virtually first concerning the extent of lethal violence documented ethnographically in a small-scale human society.

During the pre-colonial era, Gebusi had one of the highest homicide rates documented in a decentralized society: at least 39.0% (97/249) of all adult men and women (Knauft, 1985:116; cf. Knauft, 1987c). This homicide rate reduced to 23% of adult deaths (224/103) during the period of Australian administration (1963–1975) and then to 19% (8/42) of all adult deaths during the early post-colonial period (1975–1982). Composite figures are graphed in Fig. 12.4.

In aggregate, the 163 homicides documented across these periods—verified and cross-checked from genealogies of 15 clans that comprised 72% of the entire Gebusi population —were a combination of raids against suspected Gebusi sorcerers by the neighboring Bedamini people (21%) and the killing of suspected sorcerers by and largely within Gebusi communities themselves (65%). Further back in the pre-colonial period, a higher percentage of Gebusi homicides would likely have been caused by massive Bedamini raids. In the sample, by contrast, only 5.5% of the homicides resulted from battles or combat staged by Gebusi themselves, while 3% were insanity related, and the cause was unknown in 5% of the cases.

For purposes of comparative method, as documented elsewhere (Knauft, 1985, 1987c), care was taken to document a maximal Gebusi population size against which homicide rates could be reliably and conservatively ascertained on a per capital basis per annum. The Gebusi rate of killing was found to be equivalent to 683 per 100,000 population per year during the pre-colonial era and still 419 during the early post-colonial era. This rate is exceeded by estimates that can extrapolated from information pertaining to a few other areas of interior New Guinea (see

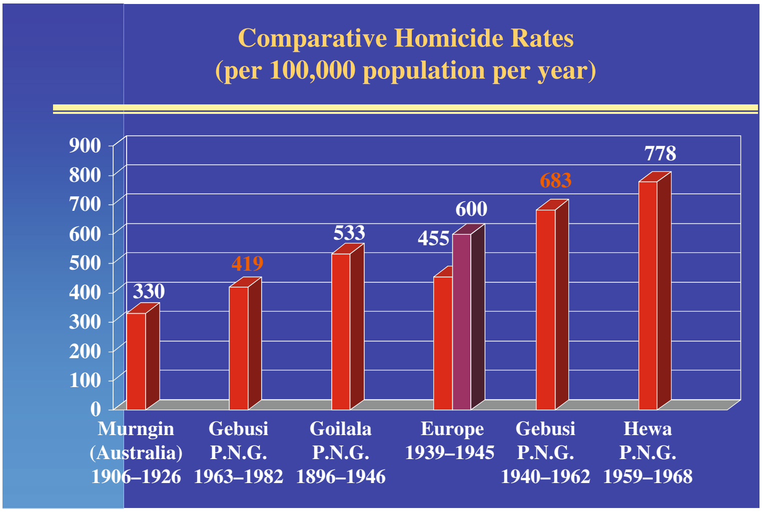


**Fig. 12.5** Selected comparative homicide rates per 100,000 population/annum

Knauft, 1985:379, 1991; Steadman, 1971 concerning the Hewa and Kelly, 1993 concerning the Etoro). But Gebusi homicide rates remain among the highest effectively documented—and higher than the upper estimate of all killings in Europe (including Western Russia) during World War II (see Fig. 12.5). The rate of pre-colonial killing was almost exactly the same as that mentioned above in Iraq from 2003 to 2006.

Several caveats may be underscored. First, patterns of Gebusi violence are contexted by historical and cultural specifics that are not necessarily typical even within the general context of the country of Papua New Guinea. As documented elsewhere (Knauft, 1985, 1987c, 1991), Gebusi's own patterns of pre-colonial violence evoke the sporadic but sometimes intense internal violence of simpler human societies and even bands of foragers more than they do the blood feuding and warfare classically associated with the so-called "big-man" societies of highland New Guinea (cf., Meggitt, 1977; see more generally Knauft, 1990).

Second, Gebusi pre-colonial rates of internal killing were strongly influenced by the impact of the larger and more densely populated Bedamini population, who predated Gebusi in their less-fecund downstream rainforest environment. Indeed, if it had not been for Australian pacification of the Bedamini between the mid-1960s and mid-1970s, Gebusi would very likely have been reduced to a remnant population or completely have been killed out and/or absorbed, losing their cultural identity.

As against this, Australian colonial intervention beginning in 1962–1963 eventually forestalled Bedmini incursion while having little immediate colonial impact on Gebusi themselves, who were seldom directly contacted by the Australians and hence left by and large to their own devices in their remote and marginal parts of the rainforest. As a result, Gebusi were free to continue their own practices, including their own internal violent sorcery inquests, while being spared many colonial and post-colonial intrusions that have been common in other world areas such as significant land alienation, taxation, cash cropping, expatriate missionization, physical coercion, or expropriation of natural resources by either international or national post-colonial forces, organizations, or agents. It is notable, for instance, that Gebusi stands of timber in virgin rainforest are not quite plentiful or extensive enough, relative to other areas of interior New Guinea, to have yet been subject to logging or deforestation.

Amid the large-scale portrayals made at the outset of this chapter, the specific history of the Gebusi is cautionary in underscoring, first, that not all external impacts are necessarily negative in terms of facilitating or abetting violence, and, second, that violence can often be the product of regionally endogenous causes, including those of long-standing cultural proclivity. These facts do not contravene larger trends—any more than singular counterexamples invalidate statistical generalities. However, they throw into relief the significance of what the Gebusi case may reveal by considering their changed patterns of violence over time.

## *Cultural and Social Context: 1980–1982*

During my initial fieldwork, Gebusi were "traditional" in the sense of being unchristianized and not exposed to significant Westernization. I was hence able to observe and document substantial aspects of indigenous Gebusi social organization and exchange, spirit mediumship; sorcery divinations and inquests; beliefs and practices concerning sickness, health, healing, and death; myths and folktales concerning supernatural beings and forces; and rituals of spiritual commemoration, initiation, curing, community celebration, and for a host of other reasons and causes (see Knauft, 1985, 1986, 1987a–c, 1989a+b, 1991, 1998a).

Intra-community killing of Gebusi sorcery suspects seldom corresponded with outstanding social grievances adduced between the killer and the victim of homicide; in only 9 of 69 intra-community, sorcerer-killings (13%) were a preceding social cause attributed. Instead, the cause of the sorcerer's purported anger was simply that "he (or she) is just a bad person; he sent sickness and death just because" (Knauft, 1987c:456; 1985:142–49). The sorcerer was believed to keep animosities hidden and to be motivated by an irrationally malicious and generally misanthropic spirit.

Gebusi cosmology in 1980–1982 encoded a mirror world and generally inverse relationship between unseen spirits, including those of the natural environment and the world of living humans. Communication with this world was variously possible through spiritual mediums (or shamans) and through ritual practices and divinations to commune, communicate with, benefit from the superordinate awareness of, and enjoy the world of unseen spirits.

The flipside of the Gebusi's generally positive and beneficent cosmological tie between the human and unseen realms was a strong belief in sorcery, including the belief that virtually all deaths by sickness or accident are in fact caused by people. Gebusi exhibited a correspondingly strong commitment to take revenge against accused sorcerers. More than one-fourth (56/211, 26.5%) of all adult deaths individually precipitated the killing of an alleged sorcerer or sorcery-related homicide. At least 65% of adult Gebusi men had committed homicide, with an overall average of 1.2 killings per man. Killing was preeminently determined by social context, especially in the aftermath of a sickness death in the community. Outside of that context, killing was rare, while within it, even the mildest man easily became a killer.

Both victims and perpetrators of sorcery could be of either sex, and victims could be of any age. Alleged perpetrators of sorcery could also be young or older adults, but children were rarely accused (contrast Kelly, 1976), and young women in teens and early 20s—the key segment of the population in terms of demographic reproduction—were almost never accused or attacked. However, I obtained no evidence that any Gebusi actually collected leavings, retained sorcery paraphernalia, or conducted the alleged magical rites that sent sickness; the sending of sorcery was an attributed and supposed cultural fact rather than a demonstrated behavioral reality.

In practice, the likelihood of sorcery accusation increased with the age of the alleged sorcerer, though some men and women were considered especially congenial and slow to anger and were never suspected of sorcery as they got older. As part of this pattern, Gebusi homicide did not appear to negate the demographic viability of their society, though it did further deplete the number of able-bodied men and women who would, in pre-colonial days, have been able to resist Bedamini attacks.

In significant respects, sorcery attributions and killings among Gebusi functioned as what Christopher Boehm (1999) has described in evolutionary terms as a “reverse” or “counter” dominance hierarchy, whereby potential prerogatives of seniority or leadership are undercut. This is consistent with Gebusi’s political organization, which is highly decentralized and had no position of “big-man,” headman, or village leader. In practice, the spirit medium—who was in daily life a person with no special rights, title, or prerogative —was key in congealing community consensus concerning the identity of the sorcery suspect. This occurred especially in the course of all-night spirit séances, which took place on the average of once every 11 days and considered a range of social and spiritual issues. Among these was the identity of sorcery suspects and the proper inquests to validate their guilt and the action to be taken against them.

Gebusi sorcery inquests and divinations were influenced and in some cases directed by the spirits of the Gebusi medium, and they included corpse divination, sago divination, searching for ostensible (but magically transformed) sorcery paraphernalia, and other means. Inquest proceedings were scrupulously observed by the kin of the suspect as well as by the community at large to ensure they were ostensibly unbiased. By various means, indictment by the medium’s spirits was “objectively” validated by divinations, in many of which the spirit medium himself played no part (see Fig. 12.6).

Following an unfavorable divinatory outcome—sometimes very difficult to avoid—the suspect could be killed on the spot or, more likely, told to “forget the

**Fig. 12.6** Armed Gebusi men witness the results of a sago divination undertaken by a sorcery suspect, 1981. (Photo credit: Eileen Knauft)

matter," after which he or she could be killed days or weeks later when accompanied by only a few supporters or relatives deep in the forest. Sometimes suspects were publicly tortured before being dispatched. After the killing, the body of the executed sorcerer was traditionally cooked and eaten by the community at large—excepting by close relatives, who were typically upset by the killing. As such, the person killed was treated "just like a wild pig or cassowary" —since the deceased was considered to have become inhuman and having acted like an animal in resorting to lethal sorcery.

In terms of larger cultural patterns, the killing of Gebusi sorcerers was a negative reciprocity dimension of their pronounced emphasis on exact exchange. This included the ideal of direct exchange of women in sister-exchange marriage, sharing and reciprocity between hosts and visitors at feasts, the exchange of the medium's spirit for those of the spirit world during séances, and direct reciprocity that demanded the life of the accused sorcerer in exchange for the life of victim he or she had allegedly killed by sickness.

Given this larger context, Gebusi perceptions of their own violence were culturally unsurprising but striking from a Western perspective. Gebusi considered themselves peace-loving and friendly people. And outside of the context of sickness death and sorcery attribution, they generally were. Given the small size of their dispersed settlements (26.5 persons, on average), the speed of generational turnover (about 15 years), and the fact that each settlement sustained a killing on average not more than once every 7 years, Gebusi did not consider homicidal violence to be a significant problem. And it was directed, in their view, to *eliminate* rather than perpetrate lethal violence, that is, to excise persons who had betrayed Gebusi trust and become heinous sorcerers within their communities.

Given these patterns and the strength of their beliefs, I considered it most unlikely when I left the field in 1982 that Gebusi would substantially change their orientations or practices in the future.

At the time, I sensed that Gebusi had internalized a pronounced sense of insecurity and ultimate suspicion of each other that had been intensified by their decimation and occasional wholesale slaughter by raiding parties of the intruding Bedamini. On one occasion in which Bedamini marched into my settlement of residence, the man who was the target of their attentions quickly and fully agreed to give up his one large domesticated pig for the Bedamini to kill and eat—in lieu of the man himself. For several days after the Bedamini departed, the village was rife with fears of sorcery attack, with mothers holding their children close and warnings repeated about going into the forest activities without adequate armed escort. Gebusi fears of sorcery were not caused by the Bedamini but they were intensified, further substantialized, and to an extent redirected among Gebusi themselves in the wake of this powerful influence and impact. With the progressive cessation of Bedamini raiding, these fears eased but were still strongly evident and appeared to have become internalized among Gebusi themselves.

## *Major Changes: 1998*

When I returned to the Gebusi in 1998, after a hiatus of 16 years, a principal research question concerned developments in Gebusi patterns of violence and their beliefs and practices of sorcery. On the one hand, between roughly 1940 and 1982, the rate of homicide had declined from 39% to 23% to 19% of all deaths. But on the other hand, Gebusi beliefs in sorcery had seemed very strong, and the comparative evidence from other parts of Papua New Guinea suggested that tribal fighting—as well as beliefs in sorcery—often intensified along with the increasing absence of Australian colonial officials and their police, including in outstation areas (e.g., Zelenietz and Lindenbaum, 1981).

During my absence, Gebusi had undergone many changes (see Knauft, 2002a+b, 2003, 2007a+b, 2010). My community of residence had moved their whole settlement several miles to reconstruct their village next to the Catholic Church, itself built near the airstrip, government station, school, market, and other facilities of the Nomad Sub-District Office (see Knauft, 1998b).

Changes included the following:

- daily weekday attendance at the Nomad school by Gebusi school-age children
- weekly attendance at church and also at other church meetings and teachings
- attendance by most women Gebusi of Gasumi Corners at the twice-weekly Nomad market, including bringing heavy bags of forest and garden produce to sell
- regular attendance and participation by men and boys at rugby, soccer, basketball, and other games arranged in regular league competition at the Nomad sports field (see Fig. 12.7)

**Fig. 12.7** Sports teams on the Nomad ball field, 1998. (Photo credit: Bruce Knauft)

- attendance at and active participation in government projects and meetings at the Nomad Station, including various economic and development projects
- walking to Nomad to celebrate and materially participate in festivities for various public holidays and related public festivities—especially at Independence Day, Christmas, New Year, and Easter
- walking to Nomad for free clinic health care or hospital services
- visiting the Nomad police station to lodge complaints or check on the progress of open investigations
- leisure pursuits at Nomad such as attending the Nomad video night, buying petty items at the small Nomad stores, or simply taking a "spin" to the station to see what was going on.

As titled in my 2002 book on the subject, Gebusi in 1998 said they were "exchanging their past" for ways associated with Christianity and the modern practices of the Nomad station and its educated outsiders, including government, school, market, development projects, and market. In this sense, their notion of direct reciprocity in traditional exchange was itself recast to exchange in a modern, asymmetrical way—the past practices themselves for locally modern practices that were hoped to lead to new and successful ways of life. When I asked Nomad school children to draw pictures of themselves as they envisaged their life in the future, their pages burgeoned with bright color drawings of themselves as soldiers, police officers, heavy equipment operators, pilots, rock musicians, teachers, doctors, nurses, and modern-dressed housewives (Knauft, 2002a:199–200). Only a tiny percentage of the students drew their anticipated future selves as traditional farmers, dancers, or villagers.

Amid this strong and powerful drive to access the future at the self-avowed expense of the past, Gebusi also had strongly internalized a sense of political and spiritual as well as economic dependency upon the authority, knowledge, and beneficence of outsiders. Their ability to lead or meaningfully influence developments at school, market, government, or even the local church was trumped by educated Papua New Guineans from other parts of the country.

Changes did not prevent continuation of traditional sensibilities in some areas of Gebusi life, including in subsistence, forays to the forest, and interest in performing traditional dances (if mostly in government competitions at the Nomad parade ground). But in comparison to my observations and understanding of Gebusi beliefs and practices in 1980–1982, it did seem that major and transformational shifts in so-called traditional cultural practices had taken place, as Gebusi themselves emphasized.

The agents as well as the subjects of this conversion were primarily Gebusi themselves. I use “conversion” here at one and the same time for both Christian conversion and conversion of social life and orientations more generally to locally modern forms. Indeed, it is difficult among Gebusi and perhaps among many Oceanian peoples to divorce the notion of conversion in a religious sense from that of adopting other forward-looking and locally “modern” practices (see Knauft, 2002c).

In collective social terms, changes to Gebusi culture included Christian baptism of 84% of the population, and the associated demise and general discontinuation of traditional spirit mediumship, divination (including for sorcery), ritual fights, male–male sexual practices, traditional dancing, and initiation. Relatedly, there was a pronounced decline in Gebusi killings or executions of sorcery suspects. With demise of spirit mediumship, Gebusi averred generally that they had little way to communicate with spirits or maintain effective contact with the unseen spirit world.

It is important to note that these changes were the primary choice and decision of Gebusi themselves. Never subject to teaching by Western (white) missionaries, Gebusi have been evangelized by a combination of Papua New Guinean preachers from other parts of the country and by their own lay prayer leaders and teachers. Revealingly, none of the outside church leaders realized or argued against the persistence of Gebusi spirit mediumship or spirit séances, including in relation to sorcery divinations and accusations. Rather, it was Gebusi themselves who considered “singing to God” in church to be inimical to and a replacement for “singing to the spirits” in traditional Gebusi spirit séances. By 1998, Gebusi spirit mediums in all but in the most remote villages had given up the practice and “cut their ties” to the spirits in favor of becoming Christians and going to church.

As seen in Fig. 12.8, the period 1982–1998 saw a significant decline in the incidence of Gebusi inquest séances by the spirit medium following a sickness death in the community, as well as a decline in divinations and the public naming of a sorcery suspect. The co-decline of death séances, divination, and sorcery accusation, depicted graphically in Fig. 12.9, isolates the important role of the spirit séance itself in influencing whether divination and sorcery accusation occur (see Knauft, 2002a:ch. 5 for details).

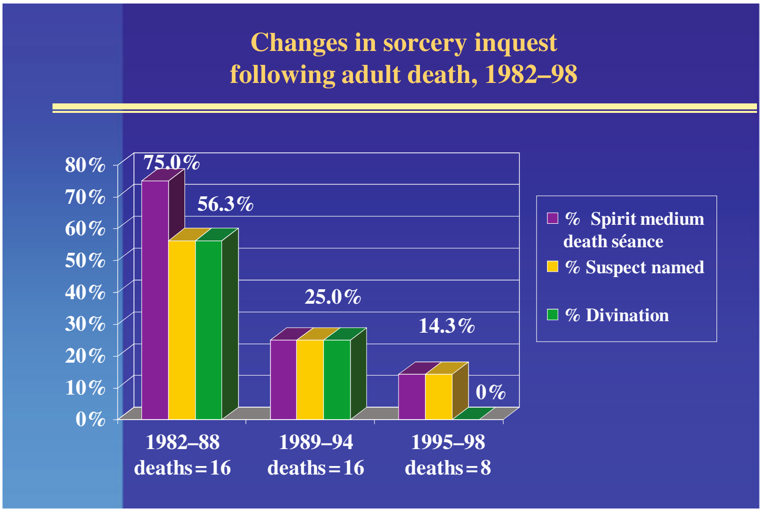


**Fig. 12.8** Changes in sorcery inquest following adult death, 1982–1998

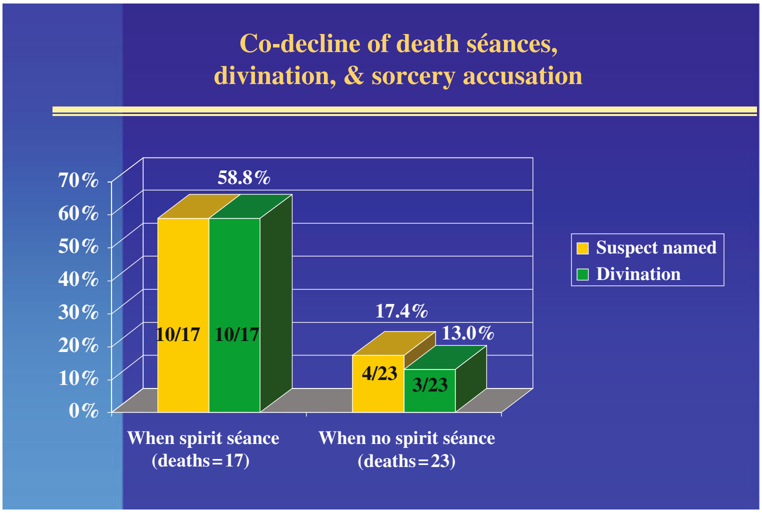


**Fig. 12.9** Co-decline of death séances divination, and sorcery accusation, 1982–1998

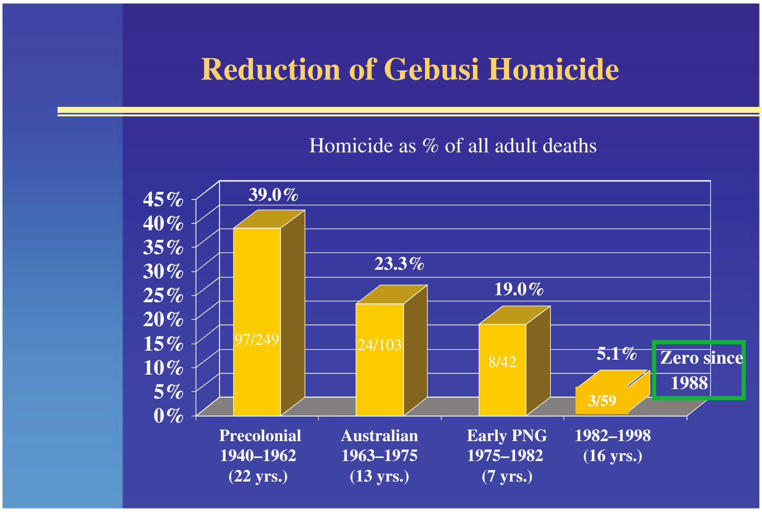


**Fig. 12.10** Reduction of Gebusi homicide

It is consistent with these trends that the rate of Gebusi homicide also declined markedly. As shown in Fig. 12.10 below, the rate of Gebusi killing dropped to 5.1% between 1982 and 1998, with just three killings. Furthermore, all of these deaths occurred during 1982 and 1988; since that time, the homicide rate in this community of some 122 persons had been zero. This community was about 1/6 (16.2%) of the enlarged Gebusi population of approximately 750 persons at the time. Analysis of police records at Nomad as well as discussions with Gebusi in other communities suggested that the rate of homicide among Gebusi generally and indeed in the Nomad sub-district as a whole had fallen off very dramatically, and among some groups, as among western Gebusi, has declined to zero (Knauft, 2002a:64, 108).

This great reduction of homicide—and of violence more generally—is striking given the depth of preceding Gebusi cultural beliefs in sorcery and the extent and diversity of their violent retribution against alleged sorcerers. Though Gebusi often privately admitted still believing or suspecting sorcery, especially when one of their own close relatives died of sickness, they consistently agreed that there was little means to verify, validate, or muster consensus around these suspicions or to take concrete action against a presumed sorcerer in the absence of collective spirit séances, divinations, and publically announced discussions and accusations.

## Gebusi 2008

Against the backdrop of their social and cultural changes, a further twist in Gebusi trajectories was evident during recent fieldwork in the winter of 2008 (Knauft, 2010: ch. 12).

At the time, the Nomad airstrip—the region's life-line of supply to the outside world—had been closed for most of a year. (I was fortunate to be able to hire a chartered aircraft and an experienced bush pilot, and to make a test landing on the Nomad airstrip, which was thereafter re-opened on a provisional basis with some restrictions.) With no roads to anywhere, the Nomad sub-district—and the Gebusi within it—had sustained a major downturn if not collapse of government services, programs, development projects, trade, and income. The Nomad airstrip closure echoed patterns that are increasingly common in outstation areas of Papua New Guinea and other developing countries: lack of government infrastructure support or funding, corruption of officials, inefficiency, unwillingness of local workers to labor without pay, and departure of qualified officials and staff from remote areas back to major towns or cities. In the case of Nomad, almost all salaried government officials, health workers, and teachers left on the last departing plane flights and continued to receive their pay for work at Nomad while residing in the town of Kiunga or other locations in the province.

Upon arrival, I found that the elementary Nomad school was closed, the health clinic was moribund, and the government officers and development workers had left, including all police. With no salaries or significant monies coming in, the local cash economy had collapsed, and there was very little wage labor. The market that had been bustling twice a week at Nomad was desultory, with very few buyers and very high prices for any outside goods. The sports leagues were defunct and the large ball field at Nomad was covered with two-foot-high grass, with parts of the goalposts taken for firewood. Government houses were boarded up (see Fig. 12.11).

A prime research concern was the legacy of Gebusi conversion, both Christian and modern more generally. It was evident in short order that significant aspects of Gebusi indigenous life had reemerged. A large traditional longhouse had been built

**Fig. 12.11** Closed Nomad sub-district office building, 2008. (Photo credit: Bruce Knauft)

**Fig. 12.12** Gebusi man with his children, smoking a traditional tobacco pipe in men's section of the community longhouse where initiation was held, 2008. (Photo credit: Bruce Knauft)

in my same community of residence, and a major traditional initiation had been held to indoctrinate a large new cadre of young men. (A significant number in the previous cohort, too old to participate, had never been initiated at all.) Practices of customary male etiquette that had been highly developed and enthusiastically practiced in 1980–1982 but which had been moribund in 1998—including smoking and sharing tobacco in large bamboo pipes, drinking kava (*piper methysticum*), and boisterous displays of male sexual joking—had all been resuscitated and were strongly in evidence (see Fig. 12.12).

Within 2 days of my arrival, a traditional curing dance, with a visiting dancer in full indigenous costume, was held within a few minutes' walk of where I was staying—something that had not happened anywhere in the community during the 6 months of my stay with the Gebusi in 1998 (see Fig. 12.13).

However, some features of customary religious and spiritual life were not reasserted or re-established. Importantly, this included spirit mediumship and spirit séance singing. No new spirit mediums had been initiated, and none had replaced those who had died, retired, or "cut their ties" with the traditional spirits. As a result, the incidence of sorcery divinations, accusations, and violent action against potential sorcery suspects continued to be nil. There had been no homicides since my previous visit.

One major case of sorcery related dispute that had arisen was revealing. This concerned a young man who had gone to work at a logging operation in a distant other part of the province and who had not returned after the expected completion of his contract. His family accused another young man in the community of causing his death by sorcery while he had been gone. However, the matter was brought directly to the attention of the Catholic priest. He, in turn, was able through his contacts to get tenuous radio contact with the young man himself through the logging operations' base headquarters. When the disbelieving parents of the young man refused to believe that he was still alive, the Priest dispatched the man who had been

**Fig. 12.13** Dancer at a traditional curing rite, 2008. (Photo credit: Bruce Knauft)

considered to be his enemy to go to the distant logging camp himself and personally retrieve the overdue worker. When the two returned safely together—and having become friends in the interim—the matter was considered successfully resolved. In the mix, the attribution of sorcery was demonstrated to have been a definitive falsehood.

This case reveals not only that suspicions of sorcery linger but also that countervailing awareness, actions, and interpretations forestall their coalescence at the same time that effective means to orchestrate community consensus or action against potential sorcery suspects is undercut.

## *Gebusi Revisited*

During a period of approximately 50 years, Gebusi violence has changed from a consistent pattern of intense intercommunity and intra-community lethal violence—one of the highest rates of killing documented in the ethnographic record—to exhibiting a homicide rate that has dropped to zero. The former pattern of highly elevated homicide endured for a documented period of at least four decades—attenuating somewhat but still surprisingly high through the early 1980s—followed by a sharp diminution in killing that has reached and persisted at a rate of zero for 20 years from 1988 to 2008.

Underscoring the significance of these changes is the fact that Gebusi have not been particularly pressured much less coerced to initiate or maintain such alteration. It is true that Gebusi were both impressed by and beneficiaries of the Australian suppression of Bedamini raiding during the late 1960s and early 1970s. At the same time, Gebusi were considered, as one patrol officer put it, "quiet tractable people who have seldom given the Administration and difficulty" (Barclay, 1970–71: unpaginated). They carried out their own inquisitions against sorcery suspects internally but these often did not reach government attention.

Likewise, the choice of Gebusi in my community of residence to move near the Nomad Station, to become Christian, and to engage whole-heartedly in the activities and life-style associated with the Nomad sub-district station during the late 1990s was of their own volition. Deep in the rainforest, there was little effective pressure that was exerted or poised to bear on Gebusi from external sources. Unlike many forest peoples, Gebusi have been free to return to their ways of life in the rainforest—and they have indeed done so increasingly following the closing of the Nomad airstrip and the collapse of the local cash and trade good economy in 2007.

Amid this tradition, Gebusi have resuscitated, rediscovered, and/or reinvented many of their long-standing customs and practices, including traditional dances and initiations, residence, and patterns of male etiquette and song-fests. But these developments have consistently not included the practice of spirit mediumship, the singing of séances, divinatory inquests for sorcery, the public accusation of sorcery suspects, or the taking of violent action against them. All these practices continue to be moribund and have become increasingly defunct over a period that now extends to almost three decades. Increasingly during this same period, there is little state-sponsored or other authoritarian or coercive force to prevent Gebusi from taking up their historical patterns of accusing and killing sorcery suspects. If anything, the Nomad police and its legal system have become more vestigial and non-functional in terms of palpable village outreach than they have been at any time since Australian patrol officers first arrived and founded the Nomad station in 1962–1963. Neither have the Christian pastors nor priests been instrumental in combating or even identifying the key role that spirit mediumship and séances have had in both the previous maintenance of Gebusi sorcery beliefs and retributions and their later demise.

Both government officials and Christian leaders from other parts of the country have been significant influences and role models. But these influences have not—and especially in comparative terms —been targeted against the specific ways and means by which Gebusi violence has operated. There has been little to prevent or penalize Gebusi from taking up these practices again.

It is hard to escape the conclusion that directions of Gebusi cultural change—their own distinctive version of becoming at one and the same time locally modern and "traditional" —have been keys to their peaceful cultural revival. These developments have been initiated as well as mediated by the intentions and decisions of Gebusi themselves: not through intrusions of coercion and constraint but rather by Gebusi's own willful volition. It may indeed be the relative absence of outside pressure—the ability of Gebusi to determine their fate and their local future in their own terms—that has allowed them to avoid patterns of increasing violence that are common if not overdetermined in many undeveloped and so-called impoverished countries where such intrusion is more evident.

A major factor that has promoted these possibilities—and which highlights Gebusi as exceptional amid patterns of polarizing violence in significant parts of the underdeveloped world—is that their distinctive history of interaction with outside powers that has reduced rather than increased their susceptibility to external threat, including in their local regional context. Rather than being subject to massive or violent intrusion—economic, political, religious, or military—Gebusi were fortunate to have the predations of their tribal neighbors suppressed without having these replaced by other effective political agents or organizations, including those of state government, material resource extraction, or business interest.

As Gebusi linger on the margins of the global political economy, their "undeveloped" state does not please them. But they have taken initiative on their own terms to craft what has been for several decades now a positive way of turning marginality into their own meaningful and peaceful cultural development.

## The Future of the Past

I conclude with two observations that link together Gebusi patterns, current trends in violent world history, and our evolutionary past. The first is that human patterns of lethal violence are extremely variable and malleable in character and in degree, and in their intensity or absence. Given the adaptability and diversity of humans in many other regards, this should not be surprising. These trends contravene the notion that humans have an innate, genetic, or otherwise deeply predisposed nature to be violently aggressive, including among males (*pace* Wrangham, 1987; Wrangham and Peterson, 1996; Chagnon, 1988).

Second, one of the greatest ways that human violence can be effectively diminished is to reduce the reality and the perception of external political threat. To a significant extent, the high pre-colonial rate of Gebusi internal violence was contexted and predisposed by the systematic predation visited against Gebusi by Bedamini and neighboring groups. By contrast, agents of colonial intrusion were generally viewed as positive rather than as negative or threatening to Gebusi; they were seen as powerful benefactors if not saviors. The Gebusi's giving up of sorcery inquests, divinations, mediumship, and the intensity of their sorcery beliefs have not been so much the product of coercive administration (or of Christianization) as much as a response by Gebusi themselves to new opportunities and ways of life that they have associated with an ability to reformulate their lives beyond their more violent past.

In this sense, the particularities of colonial intrusion, pacification, and then departure in this case created a distinctive space for Gebusi to engage and cultivate their own path of violence reduction. This contrasts to many parts of the ex-colonial world, including large parts of the Papua New Guinea highlands, in which resurgence of so-called tribal fighting has been common if not endemic. It is beyond the scope of this chapter to address these differences in detail, but it may be mentioned that the effective reduction of external political threat experienced by Gebusi contrasts greatly with the continuing perception of risk from political rivalry and aggression experienced by large ethnic groups in highland Papua New Guinea.

In the broader current context of macro-political economy and the direct and indirect export or structural facilitation of high rates of violence in underdeveloped countries and world areas, a similar point may be made. To the extent that world area powers and the interests of the international community fuel the sense and the reality of external political threat within and between underdeveloped countries, the rate of lethal violence tends to increase. Polarizations, exploitations, and vested interests to maintain rather than reduce conflict intensify.

These patterns are not inevitable or irreversible. To the extent that external influences work not just in principle but in fact to reduce these external stresses, including by depolarizing competing economic interests among militias or other armed factions, the rate of internal violence is more easily and spontaneously reduced.

In a sense, as Boehm (1999) has persuasively argued, the defusing of aggressive domination and its polarizing politics is, in evolutionary terms, part and parcel of the marked evolutionary tendency among humans as a species toward what he terms counter-dominance hierarchies. These leveling mechanisms draw down rather than build up the constituencies of rival alpha males and, on a larger scale, of rival political powers. These tendencies are facilitated by widespread patterns of generalized reciprocity in simple societies and, in complementary fashion, by aversive reactions to the differential amassing of prerogatives—including disproportionate sexual access or material resources—by some individuals as opposed to others. This does not mean that violence is absent in simple human societies (Knauft, 1991, cf., Kelly, 2000). But it does mean that the potential for violent leveling mechanisms—as developed by Gebusi under conditions of external threat and duress—are themselves managed, mediated, and subject to amelioration by prosocial exchange and reciprocity.

Closing the loop among the understanding of violence in our species' past, our complicated present, and our willful future is not an easy task. But flexibility and enormous variation not just in patterns of human violence but in its relative or total absence in important cases are also very hopeful. Reduction of lethal violence is not just a pipedream but a reality across the spectrum of many developed countries as well as for peoples such as the Gebusi for whom such an outcome could scarcely have been imagined or expected by Western scholars. How to extend and expand this pattern, to reduce external political threat and economic exploitation rather than increasing and polarizing these, especially where people are most at risk and least able to combat and repel such pressures, remains not just a key issue but a plausible human goal.

## References

Barclay, R. E. 1970–71. Official Correspondence for Patrol Report No. 10. Nomad Sub-District Office. Western Province, Papua New Guinea.

Boehm, Christopher. 1999. *Hierarchy in the Forest: The Evolution of Egalitarian Behavior*. Cambridge, MA: Harvard University Press.

Burnham, Gilbert, Riyadh Lafta, Shannon Doocy, and Les Roberts. 2006. Mortality after the 2003 invasion of Iraq: A cross-sectional cluster sample survey. *The Lancet* October 11.

Chagnon, Napoleon A. 1988. Life histories, blood revenge, and warfare in a tribal population. *Science* 239:985–992.

Ferguson, Niall. 2006. *The War of the World: Twentieth-Century Conflict and the Descent of the West*. New York: Penguin.

Grandin, Greg. 2006. *Empire's Workshop: Latin America, The United States, and the Rise of the New Imperialism*. New York: Metropolitan Books.

IRC. 2008. The International Rescue Committee. "Mortality in the Democratic Republic of Congo: An Ongoing Crisis." On-line publication @ http://www.theirc.org/sites/default/files/migrated/resources/2007/2006-7_congomortalitysurvey.pdf.

Kelly, Raymond C. 1976. Witchcraft and sexual relations: An exploration in the social and semantic implications of the structure of belief. In *Man and Woman in the New Guinea Highlands*. Edited by Paula Brown and Georgeda Buchbinder. Washington, DC: American Anthropological Association.

Kelly, Raymond C. 1993. *Constructing Inequality: The Fabrication of a Hiearchy of Virtue among the Etoro*. Ann Arbor, MI: University of Michigan Press.

Kelly, Raymond C. 2000. *Warless Societies and the Origin of War*. Ann Arbor, MI: University of Michigan Press.

Knauft, Bruce M. 1985. *Good Company and Violence: Sorcery and Social Action in a Lowland New Guinea Society*. Berkeley, CA: University of California Press.

Knauft, Bruce M. 1986. Text and social practice: Narrative "longing" and bisexuality among the Gebusi of New Guinea. *Ethos* 14:252–281.

Knauft, Bruce M. 1987a. Homosexuality in Melanesia. *The Journal of Psychoanalytic Anthropology* 10:155–191.

Knauft, Bruce M. 1987b. Managing sex and anger: Tobacco and Kava use among the Gebusi of Papua New Guinea. In *Drugs in Western Pacific Societies: Relations of Substance*. Edited by Lamont Lindstrom, pp. 73–98. Association for Social Anthropology of Oceania, Monograph #11. Lanham, MD: University Press of America.

Knauft, Bruce M. 1987c. Reconsidering violence in simple human societies: Homicide among the Gebusi of Papua New Guinea. *Current Anthropology* 28:457–500.

Knauft, Bruce M. 1989a. Bodily images in Melanesia: Cultural substances and natural metaphors. In *Fragments for a History of the Human Body, Part Three*. Edited by Michel Feher, Ramona Naddaff, and Nadia Tazi, pp. 198–279. New York: Urzone.

Knauft, Bruce M. 1989b. Imagery, pronouncement, and the aesthetics of reception in Gebusi spirit mediumship. In *The Religious Imagination in New Guinea*. Edited by Michele Stephen and Gilbert H. Herdt, pp. 67–98. New Brunswick, NJ: Rutgers University Press.

Knauft, Bruce M. 1990. Melanesian warfare: A theoretical history. *Oceania* 60:250–311.

Knauft, Bruce M. 1991. Violence and sociality in human evolution. *Current Anthropology* 32: 381–428.

Knauft, Bruce M. 1998a. Creative possessions: Spirit mediumship and millennial economy among Gebusi of Papua New Guinea. *Bodies and Persons in Africa and Melanesia*. Edited by Michael Lambek and Andrew Strathern, pp. 197–209. Cambridge: Cambridge University Press.

Knauft, Bruce M. 1998b. How the world turns upside down: Changing geographies of power and spiritual influence among the Gebusi. In *Fluid Ontologies: Myth, Ritual, and Philosophy in the Highlands of Papua New Guinea*. Edited by Laurence R. Goldman and Chris Ballard, pp. 143–161. Westport, CT: Bergin and Garvey.

Knauft, Bruce M. 2002a. *Exchanging the Past: A Rainforest World of Before and After*. Chicage, IL: The University of Chicago Press.

Knauft, Bruce M. 2002b. Trials of the Oxymodern: Public practice at Nomad station. In *Critically Modern: Alterities, Alternatives, Anthropologies*. Edited by B. Knauft, pp. 105–143. Bloomington, IL: Indiana University Press.

Knauft, Bruce M. 2002c. Critically modern: An introduction. In *Critically Modern: Alterities, Alternatives, Anthropologies*. Edited by B. Knauft, pp. 1–54. Bloomington, IL: Indiana University Press.

Knauft, Bruce M. 2003. What ever happened to ritualized homosexuality? *Annual Review of Sex Research* 14:137–159.

Knauft, Bruce M. 2007a. From self-decoration to self-fashioning: Orientalism as backward progress among the Gebusi of Papua New Guinea. In *Body Arts and Modernity*. Edited by Elizabeth Ewart and Michael O'Hanlon, pp. 88–107. Wantage, Oxon: Sean Kingston Publishing.

Knauft, Bruce M. 2007b. Moral exchange and exchanging morals: Alternative paths of cultural change in Papua New Guinea. In *The Anthropology of Morality in Melanesia and Beyond*. Edited by John Barker, pp. 59–73. Burlington, Vermont: Ashgate.

Knauft, Bruce M. 2007c. Provincializing America: Imperialism, capitalism, and counterhegemony in the twenty-first century. *Current Anthropology* 48:781–805.

Knauft, Bruce M. 2010. *The Gebusi: Lives Transformed in a Rainforest World, 2nd edition*. New York: McGraw-Hill.

Mamdani, Mahmood. 2001. *When Victims Become Killers: Colonialism, Nativism, and Genocide in Rwanda*. Princeton, NJ: Princeton University Press.

Mamdani, Mahmood. 2009. *Saviors and Survivors: Darfur, Politics, and the War on Terror*. New York: Pantheon.

Meggitt, Mervyn J. 1977. *Blood is their Argument: Warfare Among the Mae Enga Tribesmen of the New Guinea Highlands*. Palo Alto, CA: Mayfield.

Melko, Matthew. 1990. *Peace in Our Time*. New York: Paragon House.

Reyntjens, Filip. 2009. *The Great African War: Congo and Regional Geopolitics, 1996–2006.* Cambridge: Cambridge University Press.

Steadman, Lyle B. 1971. Neighbors and Killers: Residence and Dominance among the Hewa of New Guinea. Ph.D. Dissertation. Department of Anthropology, Australian National University, Canberra.

UNODC. 2010. International Homicide Statistics (HIS). On-line publication @ http://www.unodc.org/unodc/en/data-and-analysis/ihs.html.

Wrangham, Richard W. 1987. The significance of African apes for reconstructing human social evolution. In *Primate Models of Hominid Evolution*, Edited by Warren G. Kinzey, pp. 51–71. Albany, NY: SUNY Press.

Wrangham, Richard W. and Dale Peterson. 1996. *Demonic Males: Apes and the Origins of Human Violence*. Boston, MA: Houghton Mifflin.

Zelenietz, Marty and Shirley Lindenbaum (eds.). 1981. *Sorcery and Social Change in Melanesia*. *Social Analysis*, no. 8, special issue. Adelaide.

# Chapter 13
# Human Nature: The Nomadic Forager Model

**Douglas P. Fry**

*For more than 99 percent of the approximately two million years since the emergence of a recognizable human animal, man has been a hunter and gatherer. . . .Questions concerning territorialism, the handling of aggression, social control, property, leadership, the use of space, and many other dimensions are particularly significant in these contexts. To evaluate any of these focal aspects of human behavior without taking into consideration the socioeconomic adaptation that has characterized most of the span of human life on this planet will eventually bias conclusions and generalizations. M. G. Bicchieri (1972:iii, iv–v)*

Smith (2007:81) asserts that "We've inherited our warlike nature from prehistoric bands that were able to kill their neighbors and acquire their resources. These groups flourished while the pacifists withered on the evolutionary vine." In a similar vein, Alexander (1979:222, 223) speculates that "At some early point in our history the actual function of human groups—their significance for their individual members—was protection from the predatory effects of other human groups. . . .Multi-male bands. . .stayed together largely or entirely because of the threat of other, similar, nearby groups of humans." Shaw and Wong (1989:17) assume that "warfare propensities are deeply entrenched in human nature." They portray human ancestors over the last one-to-two million years as living in "small, tight-knit groups" of kin that they dub *nucleus ethnic groups* (Shaw and Wong, 1989:14). In their view, "relationships between nucleus ethnic groups were shaped *largely by conflict* in an environment of scarce resources," and "intergroup competition and warfare over scarce resources would have had to be *widely prevalent* throughout evolution" (pp. 50, 54, italics added).

---

D.P. Fry (✉)
BARA, University of Arizona and Åbo Akademi University, P.O. Box 311, FIN-65101,
Vasa, Finland
e-mail: dfry@abo.fi

R.W. Sussman, C.R. Cloninger (eds.), *Origins of Altruism and Cooperation*,
Developments in Primatology: Progress and Prospects 36, DOI 10.1007/978-1-4419-9520-9_13,

Writings such as these portray a “Man the Warrior” view of humanity (Fry, 2006, 2007). We will see in this chapter that a “Man the Warrior” view is not supported by the actual data on nomadic foragers. We will examine the data for patterns—for recurring themes—among nomadic band societies and on this basis reconstruct the likely social features of ancestral humans. The rationale for drawing nomadic hunter–gatherer analogies is that the social and physical environments of current day nomadic foragers are similar in many ways to those under which early humans evolved. The task is to focus on *recurring patterns*, or *themes*, apparent across nomadic hunter–gatherer societies, rather than to grab idiosyncratic ethnographic tidbits from only a few cultures.

The first part of this chapter will consider several ways that the “Man the Warrior” view does not match the available data on nomadic band societies. Next, the central role of reciprocity within social relations will be discussed, which will lead into a discussion of the types of conflict that are typical of nomadic forager societies. It will become clear that most conflicts are interpersonal, not between groups, at the nomadic band level of social organization. And in terms of predominate interactional patterns, social life in band societies is built on principles of reciprocal sharing, assistance-giving, and egalitarianism. Conflicts do occur, of course, but the ethnographic data on nomadic forager societies show that most disputes and grievances are dealt with without violence. Avoidance of adversaries and restraint in the use of physical aggression are noteworthy responses to serious conflict. The final part of this chapter will consider patterns of conflict management within nomadic forager societies.

Two types of data on nomadic hunter–gatherers will be used in this chapter. The Standard Cross-Cultural Sample (SCCS) consists of 186 societies worldwide and includes 21 nomadic forager societies (see White, 1989). I have coded each of these 21 nomadic forager societies for variables dealing with conflict management and aggressive behavior. Some basic frequency data will be reported for this sample of 21 forager societies. Additionally, ethnographic examples will be presented both from societies in the sample and from some additional nomadic forager societies in order to bring to life the forager patterns.

We will begin with some myth busting. One assumption of the “Man the Warrior” view is that our nomadic foraging ancestors had a closed-off patrilocal, patrilineal form of social organization which facilitated raiding by a group of related males against other such groups. Wrangham and Peterson (1996:25) even propose that “The system of communities defended by related men is a human universal that crosses space and time.” As the imaginary bumper sticker says: “Males that raid together stay together.”

Turning to the actual evidence regarding nomadic hunter–gatherer group composition and descent, we discover that this proposed system of closed-off patrilocal–patrilineal communities is a myth. Examination of the 21 nomadic forager societies in the SCCS shows that bilateral descent, not patrilineal descent, is most common among nomadic foragers (Fig. 13.1). This finding replicates the results of a previous study by Knauft (1991). Both studies also found that a solid majority of nomadic

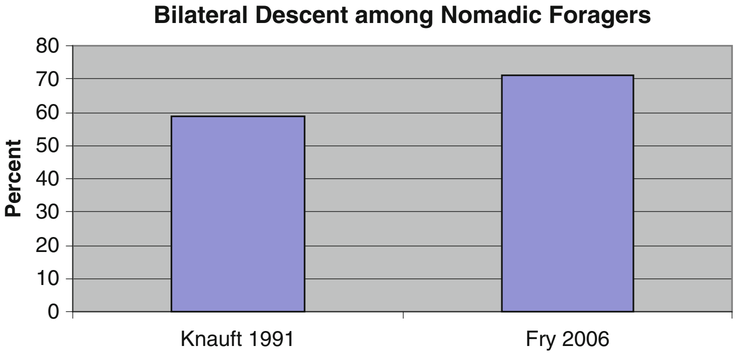


**Fig. 13.1** Nomadic forager societies coded by Murdock (1981) as having bilateral or ambilineal descent. Sample sizes are 39 societies for Knauft (1991) and 21 for Fry (2006), the latter being the nomadic band societies in the SCCS. Clearly the majority of both samples figure descent bilaterally, which contradicts a "Man the Warrior" assumption that nomadic foragers emphasize patrilineal descent. Additionally, 72% percent of the Knauft sample and 86% of the SCCS sample lack patrilineal kin groups of any type. For further discussions, see Fry (2006:166–168) and also Marlowe (2005)

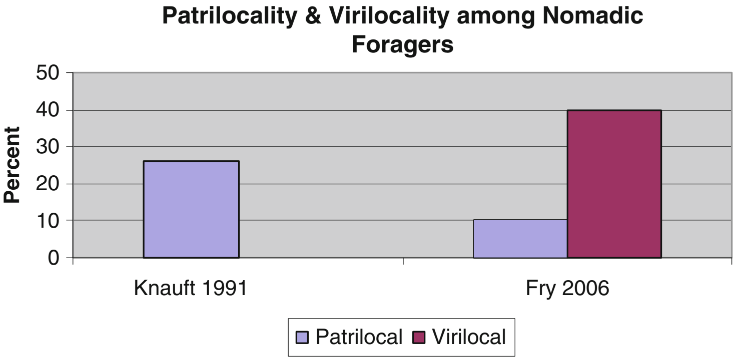


**Fig. 13.2** Nomadic forager societies coded by Murdock (1981) as having either patrilocal or virilocal residence. Sample sizes are 39 societies for Knauft (1991) and 21 for Fry (2006), the latter sample being the nomadic band societies in the SCCS. Clearly, in contradiction of a "Man the Warrior" assumption, patrilocality is not the most common form of residence among nomadic foragers. For further discussions, see Fry (2006:166–168)

foragers, 72% of the Knauft sample and 86% of the SCCS sample, lack patrilineal kin groups of any type. The "Man the Warrior" assertion of prevalent patrilocality is not supported either (Fig. 13.2).

Marlowe (2005:60) points out that: "Bilateral descent, tracing kin through both mother and father, is more prevalent among foragers (75%) than agriculturalists (25%). . . .Most foragers are multilocal; the couple resides in camps with the wife's kin at times, the husband's kin at other times, occasionally with both, and sometimes with neither." Such a pattern can be seen as discouraging intergroup hostilities and at the same time facilitating peaceful relationships among groups because relatives can be found spread out across different bands. As Marlowe (2005:60) explains, "an advantage of bilateral descent is that it maximizes the number of kin ties across camps, which facilitates visiting, finding mates, and moving to access seasonal resources."

The foregoing data on patterns of decent and residence in nomadic foraging societies illustrate a broader phenomenon about "Man the Warrior" propositions: They tend to be speculation-based and if they are checked against actual data on nomadic hunter–gatherers, "Man the Warrior" propositions tend not to hold water (Fry, 2006). We will now bust another "Man the Warrior" myth about nomadic foragers that is of central importance: the assertion that nomadic foragers, past and present, are warlike. Based on a much cited study by Ember (1978), Goldstein (2001:24) sees support for a conclusion that we shall soon see is unfounded: "Of 31 gathering-hunting societies surveyed in one study, 20 typically had warfare more than once every two years, and only three had 'no or rare warfare.' . . .If typical gathering-hunting societies found today represent the typical societies found before the rise of the state. . .then those original societies were warlike."

There are two major flaws with the Ember (1978) hunter–gatherer study that invalidate the conclusion about the warlike nature of nomadic forager societies (Fry, 2006, 2007). First, readers of the 1978 article are not told that "war" is being defined so broadly so as to include feuding and homicides if conducted by two or more persons. By this definition, the following event among Alacaluf foragers, for example, would count as an act of war. "A man once stole another man's wife. The husband tried to get her back by force, but was beaten off by his competitor. He returned in the night with his brother [and left a warning that he would attempt to murder the man]. The two brothers subsequently ambushed the rival and killed him with a spear" (Bird, 1946:71). Is this how we usually conceptualize war?

The second flaw with the Ember (1978) study is that almost half of the societies in the sample are *not* nomadic band societies. Twenty-three percent of this sample are equestrian hunters (Ute, Kutenai, Coeur D'Alene, Gros Ventre, Comanche, Crow, and Tehuelche). The use of horses to hunt game, such as bison on the North American plains, is a very recent cultural development, occurring only after the Spanish introduced the horse into the Americas a few hundred years ago. Another 26% of the sample are sedentary or semi-sedentary societies (Sedentary: Aleut, Yurok, and Bellacoola; Semi-sedentary: Squamish, Maidu, Nootka, Eastern Pomo, and Pekangekum). Seven out of these eight societies also have some degree of class stratification—a social feature reflecting complexity and *lacking in egalitarian nomadic foraging bands*. The overall point is that almost half of the sample (48%) are *not* nomadic hunter–gatherers at all. From a heterogeneous sample like this one, it is *fallacious* to conclude that the nomadic hunter–gatherers of the evolutionary past were warlike. When we also bear in mind the first flaw —that "war" is defined so unconventionally as to include certain homicides and feuding—then clearly we have a real mess to sort out.

## Are Nomadic Foragers “Warlike”?

To address this topic of “warlikeness,” the first step must be to untangle the different types of hunter–gatherers. Kelly (1995:293, italics added) notes that the image of simple nomadic foragers entails “small, *peaceful*, nomadic bands, men and women with few possession[s] and who are equal in wealth, opportunity, and status.” Kelly (1995:293, italics added, see also Binford, 2001:432) goes on to summarize that “complex hunter–gatherers are non-egalitarian societies, whose elites possess slaves, *fight wars*, and overtly seek prestige.” As mentioned, equestrian hunting societies arose only a few hundred years ago, and hence they are not the best model of ancestral bands. Lumping together nomadic foragers, complex foragers, and mounted hunters, and then offering interpretations about the likelihood of war in the nomadic past are sloppy endeavors doomed to create confusion from the onset.

Let us try a different approach. Hunter–gatherer societies overall can be operationally defined as those having *at most* 5% subsistence dependence on agriculture and animal husbandry. By this criterion, the SCCS contains 35 hunter–gatherer societies based on ratings in Murdock (1967, 1981). Murdock (1967, 1981) has published codes for settlement type, whether or not a society has a class system and, if so, what type, and, finally, whether horses are used in the society. An examination of these Murdock codes reveals that the 35 hunter–gatherer societies can be divided into three subgroups. The first group consists of nomadic or semi-nomadic societies that lack domestic animals including horses and that lack class distinctions. This is the type of social form that most closely resembles nomadic hunter–gatherers of the evolutionary past. Complex hunter–gatherers are those rated as *not* nomadic or as having social class distinctions. A third type of society of very recent origin are equestrian hunter–gatherers, those societies relying on horses for hunting. These classifications yield the 21 nomadic hunter–gatherer societies that we are focusing on in this chapter as well as nine complex hunter–gatherer societies and five equestrian hunter–gatherer societies (Fry, 2006:Table 8.2). *The essential finding is that all the complex hunter-gatherers and all the equestrian hunters make war, whereas a majority of the nomadic foragers do not* (Fry, 2006:Table 8.3). Both social complexity and adoption of the horse go along with warfare (see Table 13.1).

A consideration of war *intensity and severity* in nomadic versus complex and equestrian hunter–gatherers reveals an additional intriguing pattern: Warfare among complex hunter–gatherers tends to be more serious than it is among nomadic hunter–gatherers. Leacock (1978:249) writes of nomadic Montagnais-Naskapi bands, for example, that “warfare was minimal or nonexistent.” Regarding Gilyak bands, Shternberg (1933:247) singles out two motivations for “war” among these nomadic hunter–gatherers: competition over a woman and avenging the death of a clan member. “Indeed, what the Gilyak called wars in ancient times were in fact nothing more than sporadic clan skirmishes motivated by vengeance or, even more frequently, were over women. The Gilyak have never known war as a profession. . . .”

**Table 13.1** Presence or absence of warfare and type of society

| Hunter–Gatherers | Nonwarring | | Warring | |
|---|---|---|---|---|
| Nomadic | !Kung | Aranda | Montagnais | Gilyak |
| | Hadza | Copper Inuit | Ingalik | Micmac |
| | Mbuti | Andamanese | Botocudo | Kaska |
| | Semang | Saulteaux | Aweikoma | Yukaghir |
| | Vedda | Paiute | | |
| | Tiwi | Yahgan | | |
| | Slave | | | |
| Others | | | Bella Coola | Haida |
| | | | Gros Ventre | Yurok |
| | | | Comanche | Yokuts |
| | | | Chiricahua | Kutenai |
| | | | Tehuelche | Twana |
| | | | Klamath | Eyak |
| | | | Eastern Pomo | Aleut |
| | $n = 13$ | | $n = 22$ | |

Fisher's Exact test (one tailed) probability, $p = 0.0001$.
Nomadic hunter–gatherers are in the top row. Other types of hunter–gatherers (complex and equestrian) are in the bottom row. War is defined as involving armed combat between political communities and *not* merely as feuding and revenge homicide

Turning to complex hunter–gatherer societies, we see, as a *pattern*, an increase in the severity of fighting (Fry, 2006:106–107, Kelly, 1995). For instance, Murdock (1934:241) calls the complex hunting-and-gathering Haida "the Vikings of the coast" and reports that "they fight amongst themselves over real or fancied injuries, and they wage relentless war, partly for revenge but mainly for plunder, against the Tlingits, Tsimshian, and Bellabella." Overall, we have a dual conclusion: Not only is war more likely to exist in complex and equestrian hunter–gatherer societies than in nomadic foraging band societies but also when warfare is reported for nomadic foragers, the hostilities tend to be less severe than in other kinds of hunter–gatherer societies. The overall conclusion is that nomadic bands are not particularly warlike after all.

## The Reciprocity Principle

Westermarck (1924) developed a model of moral emotions that gave reciprocity a central position, and the nomadic forager data correspond with his theorizing about the importance of reciprocity. Westermarck (1924) used the term *retributive emotions* to refer to feelings associated with "paying back in kind," either *retributive kindly emotions* related to reciprocating good deeds or *resentment* for bad deeds.

To hazard a generalization, the preponderance of nomadic hunter–gatherer social interaction involves the doing and reciprocating good deeds. Boehm (1999, 2000) points out that nomadic foragers have egalitarian moral communities. An extensive survey of the ethnographic literature led Boehm (1999:72) to the conclusion that members of egalitarian moral communities are expected to be generous, cooperative, unbossy, and un-arrogant. The dominant cultural values among Australian Aborigines of the Western Desert region, for instance, include unselfishness, kinship solidarity, sharing, amicability, and peace (Tonkinson, 1974:57, 65, 79). Members of nomadic bands, with remarkable consistency, are cooperative and moralistically sanction deviants. “In effect, the band keeps a dossier on every individual, noting positive and negative points” (Boehm, 1999:73). A prominent feature of the nomadic hunter–gatherer group is “an ethic of sharing that selectively extends to the entire group the cooperation and altruism found within the family” (Boehm, 1999:67).

The key example is that nomadic foragers reciprocally share meat. Meat given today will be paid back tomorrow. Social life in band society involves a network of reciprocal obligations to cooperate, share, and participate in exchanges (Lee, 1993). The ubiquity of reciprocal meat sharing in nomadic hunter–gatherer society is unambiguous (Boehm, 1999:183; Knauft, 1991:393–394; Lee and Daly, 1999:4; Lee and DeVore, 1968a:12; Marlowe, 2005:62–63; for examples see Clastres, 1972; Endicott and Endicott, 2008:48–49; Honigmann, 1954:89; Leacock, 1954:7, 33; Lee, 1993; Marshall, 1961; Service, 1971:75; Woodburn, 1982). The Guayaki of South America have a rule for sharing manifested as a food taboo: a hunter should never eat the meat of the animals he has killed. This taboo reinforces the fact that people are interdependent and must share with each other; each hunter gives his game to others and in return receives meat from other hunters (Clastres, 1972:169).

The participants benefit from positive, reciprocal social exchanges, such as meat sharing, and sometimes their survival depends on them. Another aspect of nomadic forager reciprocity is to allow access to resources in times of need. Lee and DeVore (1968a:12) generalize:

> Local groups as groups do not ordinarily maintain exclusive rights to resources. Variations in food supply from region to region and from year to year create a fluid situation that can best be met by flexible organizations that allow people to move from one area to another. The visiting patterns create intergroup obligations, so that the hosts in one season become the guests in another. We think that reciprocal access to food resources would rank as equal in importance with exchange of spouses as a means of communication between groups.

Tonkinson (2004:101) provides an ethnographic illustration of how reciprocal access to resources benefits the participants. The Mardu of Australia’s Western Desert strive to maintain positive relationships that facilitate the reciprocal sharing of critical resources among bands. In Australia’s Western Desert, the rainfall is predictably unpredictable. In a given year, some areas may get no rain whatsoever.

> [This] necessitates a strong cultural stress on the permeability of boundaries and the maintenance of open and peaceful movement and inter-group communication within a huge area of desert. In these circumstances, to permit inter-group conflict or feuding to harden social and territorial boundaries would be literally suicidal since no group can expect the existing water and food resources of its territory to tide it over until the next rains; peaceful

> inter-group relations are imperative for long-term survival. . .It is not surprising, then, that the Mardu have no word for either "feud" or "warfare" and there is no evidence for the kinds of longstanding inter-group animosity one associates with feuding. The situation is one of small and scattered highly mobile groups moving freely within large territories rather than highly localized, solitary corporate groups contesting resources and maintaining boundaries. . .Everyone is mindful also of how much their survival rests on mutual hospitality and unfettered access to their neighbors' natural resources in both lean and bountiful times.

Intergroup sharing also occurs in times of local abundance (Wheeler, 1910:67; Birdsell, 1971:346). When a coastal group of Australian Aborigines discovered a beached whale with meat enough for many, they lit signal fires and neighboring groups flocked to the site to share in the bounty. The reciprocal sharing of periodic windfalls such as these among neighbors, in parallel to the ubiquitous sharing of meat within bands, means that over the long haul everyone benefits more than had each group simply hoarded abundant food.

Kelly (1995) (see also Birdsell, 1971; Cashdan, 1983) offers a thorough review of land use and resource sharing and concludes that nomadic foragers regulate access to resources though kinship, trade-relationships, spiritual beliefs, and various other cultural mechanisms that have nothing to do with defending boundaries through physical force, even when resources are limited. If we are looking for a suitable catch-phrase to describe a prevalent characteristic of our nomadic forager ancestors, "Reciprocal Sharer" is an appellation that matches the data on how nomadic foragers actually behave whereas "Man the Warrior" does not.

## Conflict and Its Management

We have seen that nomadic foragers, as a social type, actually are not "warlike." However, disputes do arise. What types of disputes do nomadic foragers have, and how do they deal with them? To answer these questions, we will turn to the 21 nomadic forager societies in the SCCS and consider various ethnographic illustrations. To foreshadow the findings, we will see that disputes tend to be very personal in nomadic forager society. A frequent dispute scenario entails two men fighting over a particular woman. Sometimes two women also fight over a man. Married couples may also become embroiled in a conflict due to jealousy or infidelity. Some fights involve the defense of honor as one party responds to an insult or an injury. Most disputes do not lead to homicide but occasionally someone is killed. The ethnographic data suggest that the most common reasons for homicide are the avenging of a previous killing and sexual matters such as adultery or elopement. In short, the data that we will examine are in tune with Service's (1966:60) assessment that disputes in band societies usually stem from "some kind of personal conflict, often caused by an elopement, or an illegal love affair of some kind, or simply an insult. There seems to be no evidence whatsoever in any of the band societies under review that warfare is actually undertaken for economic reasons, such as for booty or territorial acquisition." We will begin by looking into homicide.

## Homicide

We should bear in mind the generalization that most disputes are nonlethal, and many conflicts involve no physical aggression at all. For *7 out of the 21* band societies, or one-third of the sample, ethnographers assessed homicides to be uncommon, being described as follows: rare, very rare, never mentioned to occur, none known, and unknown.

Some nomadic forager societies are nonviolent. The Paliyan, for instance, live in accordance with a nonviolent ethos (Gardner, 1972:425; 1995, 2000a, b:93). Aggression is incompatible with their emphasis on the values of respect, equality, and individual autonomy. Gardner (2004:58) found no evidence of homicide and reports "a complete absence of feuding within Paliyan society and a corresponding total lack of war." Of the Jahai foragers of Malaysia, Sluys (1999:307) writes that the, "Jahai are known for their shyness toward outsiders, their nonviolent, non-competitive attitude, and their strong focus on sharing."

Granted that the homicide rates are variable across nomadic forager societies, a clear pattern is apparent in the descriptions of homicides: Men are usually the killers and also the victims. Occasionally a woman may be a victim, but extremely rarely does a woman commit homicide (Fry, 2006:221–222; Lee, 1979). The Pintupi of Australia, as described by Myers (1986:253), illustrates this nomadic forager pattern of sex-differences when it comes to homicide: "Pintupi men say, women are 'harmless.' Though fights including women are common, I have no record of deaths inflicted by women's weapons. Men, on the other hand, are responsible for the deaths of women as well as men."

The most common non-mutually exclusive reasons for homicide reported for the SCCS forager sample are as follows:

| | |
|---|---|
| Revenge homicide | 15 societies |
| Over a woman/adultery/sex | 12 societies |
| Crimes (theft, rape, trespass, etc.) | 7 societies |
| Execution (e.g., of a recidivist offender) | 6 societies |

Other less frequently mentioned reasons for homicide in the SCCS data include self-defense (three societies), punishment for a taboo violation (two societies) insults or "quarrels" (three societies), and due to starvation leading to cannibalism (one society). Accidental killings are mentioned as occurring among 7 of the 21 societies.

Revenge is the single most common motive for homicide among these 21 band societies. The revenge homicide pattern again illustrates the personal nature of disputes at this level of social organization. It also illustrates, in the extreme, Westermarck's (1924) observation about the reciprocity of paying back a bad deed with a bad deed. Someone is killed. The family of the victim may attempt to kill the killer. If they succeed, this typically ends the matter. The two deaths cancel each other (Fry, 2006:230). For example, the Montagnais-Naskapi thought that the appropriate pay back for committing homicide was death to the perpetrator of the crime. The death sentence should be carried out by a close male relative of the deceased (Lips, 1947:470). Among the Yukaghir of Siberia, traditionally the brother or another close relative of a homicide victim could seek blood revenge. "He does not kill directly, but requires from the murderer an explanation of his act, not infrequently letting him off with a ransom." (Jochelson.1926:132).

Among the Ingalik, when a person is killed, revenge may be exacted by the victim's father, son, brother, grandfather, grandson, or uncle, but not by more distant relatives. Once, in the heat of passion, a friend of a murdered man stabbed his friend's killer. His friend had no living relatives to avenge his death. Osgood (1958:54) recounts how a couple of days after the second killing, the new victim's uncle, brother, and father arrived at the killer's home and said:

"You had no business to kill that boy."

"I know that," he answered, "but he talked to me without politeness and having already killed my friend, it made me mad and I killed him. You would do the same in the circumstances."

Osgood (1958:54) continues the narrative: "The relatives were impressed by the statement and after considering the character of the one who had just been killed, they concluded that perhaps it was better he was dead." In this case, there was no further killing.

In the SCCS sample, disputes over women, adultery, or elopement run a close second to revenge as a reason for homicide in band society. Again, most such disputes over a woman do not lead to homicide. At the same time, sexual jealousy, adultery, and elopement would seem to be a very common, perhaps the most common, cause of conflict in nomad band societies, even in relatively nonviolent ones. Some examples of sexual themes as recurrent reasons for conflict follow (see Fry, 2006).

Woodburn (personal communication, October 29, 2009) explains that Hadza men fight for various reasons, but that "fights over women are a significant factor" and that "murders occur." At least some disputes among the Montagnais-Naskapi of North America involve competition over a woman. For example, one hunter killed another man and usurped his rival's wife (Lips, 1947:470). A common cause of disputes among the Ju/'hoansi is adultery which leads to fights between men over a woman, between women over a man, and between wives and husbands (Lee, 1979:377). Lee's ethnographic data demonstrate how adultery and sexual rivalry are a theme reflected in some Ju/'hoansi homicides: "a man attacked and killed a non-San [non-Ju/'hoansi] who had been sleeping with his wife... a man killed another and ran away with his wife...a man who had slept with another's wife was attacked by the husband but killed the husband...and a man killed his wife in an argument over her adultery" (Lee, 1979:392). Competition among Netsilik Inuit men over a particular woman also was a recurring reason for disputes that sometimes resulted in aggression (Balikci, 1970). In conclusion, these nomadic forager examples illustrate a broader pattern wherein many disputes within band society stem from sexual jealousy or competition between two men over a particular woman. The example we considered earlier of the Alacaluf husband, with the aid of his brother, spearing his rival also illustrates this recurring theme (Bird, 1946:71). Competition between women over a man also occurs, although the later tends to be less injurious and rarely results in homicide (Fry, 2006:222, 2007).

## Community Sanctioned Execution

Thieves, rapists, and poachers are killed on occasion in band society. In fact, one sure fire way to get yourself executed is to become a repeat offender, either by establishing a long rap sheet of crimes or, to expedite your own demise, by committing several murders (Boehm, 1999; Fry, 2006). In band society, no one likes a bully. The execution of overly violent men and bullies is a theme in ethnographic accounts of band societies. Damas (1991:78), writing about the Copper Inuit, explains that "Certain men were feared for their aggressiveness or violent tendencies, but they almost invariably met with violent ends themselves." Hoebel (1967:88) explains the typical fate of a recidivist killer:

> As a general menace, he becomes a public enemy. As a public enemy, he becomes the object of public action. The action is legal execution: a privilege-right of the executioner. The single murder is a private wrong redressed by the kinsmen of the victim. Repeated murder becomes a public crime punishable by death at the hands of an agent of the community.

Hoebel's observation that a recidivist killer is no longer killed simply due to the revenge-seeking of a victim's family but due to his status as a public outlaw is interesting. It corresponds with Lee's (1979:394) description of how a Ju/'hoansi recidivist killer was put to death by group action. "He had killed two people already, and on the day he died he stabbed a woman and killed a man. . . .No one came to his aid because all those people had decided he had to die. . . .They all fired on him with poison arrows till he looked like a porcupine."

In another case (Lee, 1979:393), a Ju/'hoansi man named Gau was considered a "lion" who "ate people." After he had killed three people, Gau was stabbed in the heart as he slept. He jumped up to attack his assailant but dropped dead in his tracks. Based on an extensive review of the forager literature, Boehm (1999:82, italics added) explains that "reports of execution of individuals who behave too aggressively are available for Eskimos, North American Indians, Australian Aborigines, and African foragers. . . .My suspicion is that the *pattern* may be generalized to nomadic foragers in general."

After reading many ethnographic accounts, I agree with Boehm's assessment. This observable pattern across widely separated forager societies reflects Westermarck's second type of reciprocity, which stems not from gratitude felt for the good deeds of others but instead is based on feelings of resentment for bad deeds. In band society, bullies, overly aggressive persons, serious troublemakers, and especially recidivist killers, because they endanger everyone, sooner or later receive their just desserts in accordance with this Westermarckian reciprocity principle. The community overall considers the killings of recidivist offenders to be morally justified.

## Contest, Ritualization, and Self-Restraint

How else do foragers deal with disputes? Animal aggression has been analyzed in terms of evolutionary costs and benefits, and a similar orientation may shed light on patterns of nomadic forager conflict as well (Fry, 2006:218–219). In the extreme case, as we have seen, recidivist killers run a high chance of being executed with the overall approval of the group. Overly aggressive individuals also may suffer increased chances of injury and death due to their frequent involvement in dangerous altercations and additionally may risk social penalties such as loss of support and even ostracism from the group (e.g., Endicott and Endicott, 2008:43, 50; Lips, 1947:469). In other words, acting aggressively toward others may lead to various negative paybacks as victims feel resentment and seek revenge against an attacker in accordance with Westermarck's (1924) reciprocity principle. For these various reasons, it is not surprising that restraint in the use of aggression, which is apparent in much animal aggression, also is apparent in various nomadic hunter–gatherer contexts. Exercising restraint regarding aggressive encounters may well be the outcome of strong selective forces operating over evolutionary time (Fry, 2006, 2007).

Gusinde (1937:887) provides one example of restraint for the Yahgan of South America: "A person will literally foam with rage. . . .Nevertheless, he can muster astonishing self-control when he realizes that he is too weak to stand against his opponent." Tonkinson's (1978:124) observation pertaining to the Mardu of Australia also illustrates a system of restraint: "When men fight each other, the unstated aim. . .is to allow maximum opportunity for the dispute to be aired *verbally*. This takes place in an atmosphere of great public drama and menace, so that honor is seen to be satisfied, but with a minimum of physical violence."

Researchers of animal aggression have pointed out how the ritualization of aggression in many species prevents injuries among contestants (Archer and Huntingford, 1994; Maynard Smith and Price, 1973). Among humans, contests with rules that limit aggression can allow for the resolution of differences with less risk of injury than might occur during less ritualized forms of fighting (Fry, 2005).

Contests have rules that promote restraint, and spectators take a role in enforcing the rules if necessary. The metacommunicative context of contests is that they are simultaneously *serious yet not serious* or at least not as serious as unbridled aggression. Winning by the rules enhances esteem, but winning through cheating—fighting unfairly—may have an opposite effect when the spectators and the social group are one and the same (Fry, 2005). Contests or duels are reported for settling disputes in 9 of the 21 SCCS nomadic forager societies.

Among the Siriono, Holmberg (1969:156) explains that disputes between men may be settled through wrestling matches. The wrestling matches have rules that limit aggression, and rivals for the most part adhere to the rules. If not, bystanders intervene to enforce them. Holmberg (1969:156) recounts how "Eantándu when drunk, struck an opponent with his fists. Everyone began to clamor that he was fighting unfairly, 'like a white man.' He stopped immediately."

Hoebel (1967:92) concludes that contests serve as a means for handling conflict without the loss of life in many Inuit societies. Contests are a form of socially institutionalized restraint. "Homicidal dispute, though prevalent, is made less frequent in many Eskimo groups by recourse to regulated combat—wrestling, buffeting, and butting. . .The object of the boxing and butting contests is not annihilation, but subjection." For example, the Netsilik Inuit utilize both physical and verbal contests to settle disagreements with minimal danger to the participants. According to the rules, two rivals stand opposite each other and take turns striking each other using blows directed at the forehead or shoulders. Eventually, one man gives up. A Netsilik informant explains that "After the fight, it is all over; it was as if they had never fought before" (Balikci, 1970:186). Verbal song duels also are used by the Netsilik to resolve disputes. Under the rules of song dueling, opponents have free range to blast their antagonists with derogatory words (Balikci, 1970).

Moving to the opposite end of the planet, the nomadic Ona of Tierra del Fuego also engage in wrestling contests. As among the Netsilik, wrestling provides a relatively safe, nonlethal context in which to settle disputes or to assert dominance. Gusinde (1931:645–646) describes Ona wrestling:

> The occasions are insult, defamation of honor, or slighting another man, who will not put up with such things. . . .[The wrestling] happens only if each believes he is a match for his opponent; otherwise the weaker one avoids challenging the other to fight.
>
> . . .The two move toward each other and seize each other tightly. The previous irritation and the heightened jealousy cause each to attack boldly; they summon their utmost strength and plant themselves against each other in desperate rage, until finally one must succumb, either by being pressed against a tree or thrown on the ground. With this the existing disagreement has been settled to some extent, at least for today, namely, to the disadvantage of the one defeated. . . .One who had to leave as the one defeated took this dishonor very seriously; his people also often reminded him of it.

To assess the degree of restraint during aggressive encounters, I coded the 21 nomadic forager societies in the SCCS pertaining to "rules for fighting." The results are as follows:

| | |
|---|---|
| Persons fight in a "no holds barred" fashion | 1 society |
| Rules for fighting are sometimes ignored | 2 societies |
| For the most part, participants adhere to the rules for fighting | 7 societies |
| Insufficient information to code | 11 societies |

Unfortunately, for 11 or 21 societies, there was no relevant data for this variable. Acknowledging this limitation, the findings do show that for the majority of these nomadic band societies for which there is information on this topic, individuals tend to show restraint and adhere to the rules for fighting. This restrained approach—which parallels the widespread pattern of restrained intraspecific competition across animal species—can be interpreted as evolutionary advantageous because it minimizes risks, bodily and social, for individuals engaging in aggressive behavior.

## Avoidance

Avoidance is mentioned for 16 out of the 21 nomadic band societies in the SCCS. Nomadic hunter–gatherers are renowned for "voting with their feet." This approach is relatively easy in nomadic societies. Of the !Kung (or Ju/'hoansi): "Conflict was resolved by moving apart." (Ritchie1986:314). If a dispute arises in a Paliyan band, one party or the other will just leave for a week or so (Gardner, 2004). Balikci (1970:192) refers to avoidance among the Netsilik as "a very important strategy for conflict resolution."

In short, members of nomadic bands often decide to separate in response to conflict. I should also point out that the regular use of avoidance by nomadic foragers is another reflection of restraint. Woodburn (personal communication, October 29, 2009) emphasizes avoidance among the Hadza as the typical response to serious conflict, such as between two men over a woman: "If a man stays in the social situation with a rival it is impossible to protect himself. When he is asleep or if off in the bush, he can be ambushed. Self-segregation is the best, safest approach."

## Third Parties: Friendly Peacemaking and Mediation

Black (1993) coins the term friendly peacemaker to refer to a third party that intervenes in a dispute to distract or separate the disputants but who does not otherwise address the issues of the dispute. If a third party delves into the problem in an attempt to help the disputants find a mutually agreeable solution, then the third party is playing a mediator role. Sometimes multiple third parties act as friendly peacemakers or mediators.

Friendly peacemaking was mentioned for 12 out of the 21 nomadic band societies in the SCCS. For these 12 societies, friendly peacemaking was coded as occurring "nearly always" for five, and occurring "sometimes" for six, with one society lacking sufficient information to allow a frequency assessment. In the nomadic foraging societies of the SCCS, mediation was mentioned as occurring in 10 out of the 21. Mediation was usually conducted by elders, other respected persons, or in some cases the entire band.

Gardner (2000a:224) explains that among the Paliyan of India, "a self-appointed conciliator distracts with wit or sooths with diplomacy, this is done in a respectful way, never at the expense of the principals." Various Australian Aborigine bands hold meetings or hearings as ways of mediating disputes (Berndt, 1965:176; Berndt and Berndt, 1996: Chapter 10; Tonkinson, 2004:102–104).

An example from Australia entails both mediation and friendly peacemaking. A married Aranda woman ran off with another man. About a year later, the new couple met up with the former husband's group. The matter was discussed at some length by others in the group while the husband and his rival remained silent and listened to the discussion. Spencer and Gillen (1927:468–469) explain that after some while, the wife-seducer got up, walked to an open space, and shouted to the husband:

"'I took your woman, come and growl.' Thereupon the man got up, and standing some distance off, threw spears and boomerangs at the first man, who skillfully guarded himself with his shield, but made no attempt to retaliate." The former husband moved in and attempted to punish the man by cutting him with a stone knife. The guilty party defended himself as best he could but did not retaliate against his punisher. Others then stepped in as friendly peacemakers, and calling loudly "*kulla impara*," which means "enough, leave him," they pulled the two men apart. Having had the opportunity to attack his rival, the husband renounced his claim to his former wife by waving his stone knife in the air and shouting "You keep together, I throw away, I throw away."

The foregoing case illustrates how others, besides the disputants, convened a hearing to air the grievance. To the extent that they were facilitating a resolution of the dispute, they were engaged in mediation. After listening to the discussion, the husband's rival accepted that he was in the wrong and allowed the husband to punish him bodily without attempting to retaliate. We see the onlookers acting as friendly peacemakers when they pull the two men apart and declare that the husband has now cut his rival enough. By allowing this type of resolution, the perpetrator acknowledges that he should allow the man he has wronged to punish him. In Westermarck's scheme, the wronged husband gets to express his resentment over the original bad deed he has suffered, while simultaneously getting even by inflicting a just punishment. The next section focuses further on punishment of offenders.

## Punishments and Social Control

Humans express moral disapproval and apply sanctions against those who violate the social rules (Black, 1993; Brown, 1991:138). In band society, disapproval ranges from nasty looks and malicious gossip through ridicule, sarcasm, and harangues to the infliction of injury, ostracism, and, as we have already considered, execution (Boehm, 1999, 2000; Fry, 2006). Group members individually and in concert effectively express moral disapproval and apply social control measures.

Among the Montagnais-Naskapi, social control was maintained by rewarding and encouraging positive behavior—that is, by showing moral approval—and also by applying ridicule and scorn that reflected negative public opinion—moral disapproval (see Reid, 1991:245; Speck, 1935:44). Such behavior is typical in nomadic hunter–gatherer societies (see Boehm, 1999, 2000). In response to the most serious transgressions, such as committing incest, constant troublemaking, or murder (if the killer was not killed by the victim's kin), the guilty party faced ostracism from the band. Le Jeune observed in the 1630s not only the generous and cooperative side of Montagnais-Naskapi life, but also, in accordance with Westermarck's reciprocity principle, the importance they placed on "getting even" with serious wrongdoers. He wrote, "So enraged are they against every one who does them an injury, that they eat the lice and other vermin that they find upon themselves—not because they like them, but only, they say, to avenge themselves and to eat those that eat them"

(Le June quoted in Leacock, 1981:194). In this example, we see that Westermarck's reciprocity principle is being applied even to lice!

Turnbull (1961) provides another illustration of how social control measures are used to uphold rules and obligations, this time in African Mbuti society, as he describes the antisocial behavior of one hunter. Cephu had flaunted the rules of cooperative hunting and meat sharing as he attempted to cheat the others out of some game. The band members responded with moral disapproval. They ridiculed, insulted, criticized, lectured, and laughed at Cephu before finally suggesting that he and his family could go elsewhere, a punishment that would have been disastrous for Cephu and his kin because such a small group could not have hunted effectively. When faced with criticism, ridicule, and the threat of ostracism, Cephu apologized profusely and turned over all of the ill-acquired game to the others.

Among nomadic hunter–gatherers, good behaviors typically include generosity, sharing, fulfilling obligations, and getting along with others without excessive violence or repeated troublemaking. Social rules tend to promote desired acts of generosity and respect for others. Among the Ju/'hoansi, for example, the ideal son-in-law "should be a good hunter, he should *not* have a reputation as a fighter, and he should come from a congenial family of people who like to do *hxaro*, the Ju/'hoan form of traditional exchange" (Lee, 1993:81, italics in original). Tonkinson (2004:94) writes that the ideal Mardu adult is "agreeable, unassuming, self-effacing, unselfish, and ever ready to share with kin and fulfill ritual and kinship obligations without complaint rather than being egotistical or boastful to excess." Social rules exist that prohibit exploitative behavior such as Cephu's greedy attempt to cheat the others. Violators are punished in various ways. Disapproved behaviors typically include theft, stinginess, rape, assault, and murder (see Boehm, 1999, 2000).

## Conclusions

Modern humans possess a legacy of adaptations acquired over many millennia. Until about 10,000 years ago, humans and their ancestors lived as nomadic hunter–gatherers. As a supplemental approach to archaeology, an examination of recurring patterns across extant nomadic hunter–gatherer societies can provide a basis for drawing inferences about the human nature and the past (Boehm, 1999; Fry, 2006). The existence of numerous recurring patterns in the social life of present-day nomadic foragers strongly suggests that ancestral groups also exhibited such features. Fry (2006:239) summarizes recurring patterns apparent in nomadic bands from around the world based on the nomadic forager literature (e.g., Bicchieri, 1972; Binford, 2001; Boehm, 1999, 2000; Endicott, 1999; Gardner, 1966, 1991; Guenther, 2002; Ingold, 1999; Ingold et al., 1988a, b; Kelly, 1995; Kent, 2002; Knauft, 1991; Leacock, 1978, 1982; Leacock and Lee, 1982; Lee and Daly, 1999; Lee and DeVore, 1968a, b; Marlowe, 2005; Murdock, 1968; Myers, 1986; Service, 1966; Steward, 1968; Woodburn, 1982):

> Nearly universal features of nomadic foragers include relatively low population densities, small band size (typically between 25 to 50 members), mobility, flexibility and fluctuations in group composition, concentration-dispersion patterns, interconnections among bands (especially among those that speak the same or similar languages), social emphasis on sharing and cooperation, high values placed on individual autonomy, bilateral systems of descent that emphasize connections both to maternal and paternal relatives, minimal leadership within groups, no overarching authority among groups, high levels of egalitarianism in both the ethos and as manifested in social relations, high levels of gender egalitarianism, decision making by consensus, sexual division of labor, hunting as primarily (but not exclusively) a male activity (with hunting large game being a male activity) and gathering as primarily (but not exclusively) a female activity, minimal material property, minimal private ownership of resources, loosely defined territorial ranges, patterns of reciprocal exchange among individuals within and between groups, a tendency to find spouses in other groups, the personal nature of disputes (e.g., involving sexual jealousy), group fission and/or interpersonal avoidance as a response to conflict (especially serious conflict), a devaluation of physical aggression, lack of warrior values, exertion of social control via gossip, ridicule, withdrawal of support, and in extreme cases, ostracism and execution.

Based on observations of extant nomadic foragers, the rates of aggression in the past probably were considerably variable from one group to the next. Much of the aggression that did occur likely entailed no use of weapons, but less frequently, attacks probably involved rocks, clubs, or spears. Third-party peacemakers and conflict resolution mechanisms are regular features of extant hunter–gatherer social life and no doubt also existed in the past (Boehm, 1999; Lee, 1993; Fry, 2000; Gardner, 2004; Tonkinson, 1978, 2004).

To highlight nomadic forager patterns of aggression and conflict management, it is important to recall that nomadic hunter–gatherers live in bands whose composition varies as people regularly transfer among groups. One implication of this type of social organization is that—in marked contrast to “Man the Warrior” assumptions—related males are spread out across the social landscape in neighboring bands whose membership is flexible and changing over time. Nomadic foragers also have few material possessions to plunder or fight over, are politically egalitarian, and tend to be widely dispersed. The obvious pattern is that disputes are personal, not collective, at the nomadic band type of social organization (Reyna, 1994; Service, 1966). The data show case-after-case of men competing over a particular woman, not bands of related men raiding other groups to capture women. The overall point is that nomadic hunter–gatherer bands tend not to engage in war or have militaristic value orientations (Fry, 2006; Steward, 1968; Kelly, 1995:Table 8.1). The actual ethnographic evidence does not support the portrayal of nomadic foragers as warlike. Such a view is a myth. It is out of touch with the facts.

Moreover, the amount of brawling and homicide varies within forager band societies. Some groups, such as the Paliyan (Gardner, 2004) and the Batek Semang of Malaysia (Endicott, 1979; Endicott and Endicott, 2008:50, 124–126), have nonviolent ideals, and physical aggression is extremely rare, whereas other band societies experience regular fighting and periodic killings (e.g., Balikci, 1970; Lee, 1993; Tonkinson, 1978, 2004). Boehm (1999) notes an overarching pattern wherein the members of band societies do not tolerate overly aggressive persons. We have seen that recidivist killers and otherwise dangerous persons are likely to be executed for the public good (Balikci, 1970; Boehm, 1999; Lee, 1993). Lacking authoritative leadership, courts, police, and mental hospitals, nomadic band societies nonetheless manage to deal with much conflict through avoidance, discussion, group meetings, contests, ostracism, and other nonviolent or aggression-limiting ways (Boehm, 1999; Fry, 2006). Nomadic foragers are especially famous for voting with their feet.

In short, the aggression in nomadic band society is not as rampant as sometimes assumed. When it does occur, it rarely resembles warfare. Furthermore, many nonviolent conflict management options exist as safer alternatives to aggression.

**Acknowledgment** Some of the data reported in this chapter were collected during the research funded by the National Science Foundation (Grant number 03-13670), whose financial support is gratefully acknowledged.

## References

Alexander, Richard (1979) *Darwinism and Human Affairs*. Seattle: University of Washington Press.

Archer, John and Huntingford, Felicity (1994) “Game theory models and escalation of animal fighting,” in M. Potegal and J.F. Knutson (eds.) *The Dynamics of Aggression: Biological and Social Processes in Dyads and Groups*, pp. 3–31. Hillsdale, NJ: Lawrence Erlbaum.

Balikci, Asen (1970) *The Netsilik Eskimo*. Garden City, NY: The Natural History Press.

Berndt, Ronald M. (1965) “Law and order in Aboriginal Australia,” in R. M. Berndt and C. H. Berndt (eds.) *Aboriginal Man in Australia: Essays in Honour of Emeritus Professor A. P. Elkin*, pp. 167–206. London: Angus and Robertson.

Berndt, Ronald and Berndt, Catherine (1996) *The World of the First Australians*, fifth edition. Canberra: Aboriginal Studies Press.

Bicchieri, M. G. (ed.) (1972) *Hunters and Gatherers Today*. Prospect Heights, IL: Waveland.

Binford, Lewis R. (2001) *Constructing Frames of Reference: An Analytical Method for Archaeological Theory Building Using Hunter-Gatherer and Environmental Data Sets*. Berkeley, CA: University of California Press.

Bird, Junius (1946) “The Alacaluf,” in J.H. Steward (ed.) *Handbook of South American Indians, Volume 1, The Marginal Tribes*, pp. 55–80 plus plates. Washington, DC: United States Printing Office.

Birdsell, Joseph B. (1971) “Australia: Ecology, spacing mechanisms and adaptive behaviour in aboriginal land tenure,” in R. Crocombe (ed.) *Land Tenure in the Pacific*, pp. 334–361. New York: Oxford University Press.

Black, Donald (1993) *The Social Structure of Right and Wrong*. San Diego: Academic Press.

Boehm, Christopher (1999) *Hierarchy in the Forest: The Evolution of Egalitarian Behavior*. Cambridge, MA: Harvard University Press.

Boehm, Christopher (2000) “Conflict and the evolution of social control” in L.D. Katz (ed.) *Evolutionary Origins of Morality: Cross-Disciplinary Perspectives*, pp. 79–101. Bowling Green, OH: Imprint Academic.

Brown, Donald E. (1991) *Human Universals*. New York: McGraw-Hill.

Cashdan, Elizabeth A. (1983) “Territoriality among human foragers: Ecological models and an application to four Bushman groups.” *Current Anthropology*, 24:47–66.

Clastres, Pierre (1972) “The Guayaki,” in M.G. Bicchieri (ed.) *Hunters and Gatherers Today*, pp. 138–174. Prospect Heights, IL: Waveland.

Damas, David (1991) “Copper Eskimo,” in D. Levinson (Editor in Chief) *Encyclopedia of World Cultures*, T. O’Leary and D. Levinson (volume eds.), *Volume I, North America*, pp. 76–79. Boston, MA: G.K. Hall.

Ember, Carol (1978) “Myths about hunter-gatherers.” *Ethnology*, 17:439–448.

Endicott, Karen L. (1999) “Gender relations in hunter-gatherer societies,” in R.B. Lee and R. Daly (eds.) *The Cambridge Encyclopedia of Hunters and Gatherers*, pp. 411–418. Cambridge: Cambridge University Press.

Endicott, Kirk (1979) *Batek Negrito Religion: The World-View and Rituals of a Hunting and Gathering People of Peninsular Malaysia*. Oxford: Clarendon Press.

Endicott, Kirk and Endicott, Karen (2008) *The Headman Was a Woman: The Gender Egalitarian Batek of Malaysia*. Long Grove, IL: Waveland Press.

Fry, Douglas P. (2000) “Conflict management in cross-cultural perspective,” in F. Aureli and F.B.M. de Waal (eds.) *Natural Conflict Resolution*, pp. 334–351. Berkeley: University of California Press.

Fry, Douglas P. (2005) “Rough-and-tumble social play in children,” in A.D. Pellegrini and P.K. Smith (eds.) *The Nature of Play: Great Apes and Humans*, pp. 54–85. New York: Guilford.

Fry, Douglas P. (2006) *The Human Potential for Peace: An Anthropological Challenge to Assumptions about War and Violence*. New York: Oxford University Press.

Fry, Douglas P. (2007) *Beyond War: The Human Potential for Peace*. New York: Oxford University Press.

Gardner, Peter (1966) “Symmetric respect and memorate knowledge: The structure and ecology of individualistic culture.” *Southwestern Journal of Anthropology*, 22:389–415.

Gardner, Peter (1972) “The Paliyans,” in M. G. Bicchieri (ed.) *Hunters and Gatherers Today*, pp. 404–407. Prospect Heights, IL: Waveland.

Gardner, Peter (1991) “Foragers’ pursuit of individual autonomy” *Current Anthropology*, 32: 543–572.

Gardner, Peter (1995) “Escalation avoidance and persistent Paliyan nonviolence.” Paper presented at the Meeting of the American Anthropological Association, November 15–19, Washington, DC.

Gardner, Peter (2000a) “Respect and nonviolence among recently sedentary Paliyan foragers.” *Journal of the Royal Anthropological Institute* (N. S.), 6:215–236.

Gardner, Peter (2000b) *Bicultural Versatility as a Frontier Adaptation among Paliyan Foragers of South India*. Lewiston, NY: Edwin Mellen Press.

Gardner, Peter (2004) “Respect for all: The Paliyans of South India,” in G. Kemp and D.P. Fry (eds.) *Keeping the Peace: Conflict Resolution and Peaceful Societies around the World*, pp. 53–71. New York: Routledge.

Goldstein, Joshua (2001) *War and Gender: How Gender Shapes the War System and Vice Versa*. Cambridge: Cambridge University Press.

Guenther, Mathias (2002) “Independence, resistance, accommodation, persistence: Hunter-gatherers and agropastoralists in the Ghanzi Veld, early 1800s to mid-1900s,” in S. Kent (ed.) *Ethnicity, Hunter-Gatherers, and the “Other,”* pp. 127–149. Washington, DC: Smithsonian Institution Press.

Gusinde, Martin (1931) *The Fireland Indians, Volume 1: The Selk’nam, on the life and thought of a hunting people of the Great Island of Tierra del Fuego*. In the electronic Human Relations Area Files, Ona, Doc. 1. New Haven, CT: HRAF, 1996, computer file.

Gusinde, Martin (1937) *The Yahgan: The Life and Thought of the Water Nomads of Cape Horn*, translated by Frieda Schütze. In the electronic Human Relations Area Files, Yahgan, Doc. 1. New Haven, CT: HRAF, 2003, computer file.

Hoebel, E. Adamson (1967) *The Law of Primitive Man: A Study in Comparative Legal Dynamics*. Cambridge, MA: Harvard University Press.

Holmberg, Allan (1969) *Nomads of the Long Bow: The Siriono of Eastern Bolivia*. New York: American Museum of Natural History. Originally published in 1950.

Honigmann, John J. (1954) *The Kaska Indians: An Ethnographic Reconstruction*. New Haven: Yale University Publications in Anthropology, number 51.

Ingold, Tim, Riches, David and Woodburn, James (eds.) (1988a) *Hunters and Gatherers, 1, History, Evolution, and Social Change*. Oxford: Berg.

Ingold, Tim, Riches, David and Woodburn, James (eds.) (1988b) *Hunters and Gatherers, 2, Property, Power, and Ideology*. Oxford: Berg.

Jochelson, Waldemar (1926) *The Yukaghir and the Yukaghirized Tungus*. The Jesup North Pacific Expedition Memoir of the American Museum of Natural History, Volume IX. New York: G. E. Stechert.

Kelly, Robert L. (1995) *The Foraging Spectrum: Diversity in Hunter-Gatherer Lifeways*. Washington, DC: Smithsonian Institution Press.

Kent, Susan (2002) "Interethnic encounters of the first kind: An introduction," in S. Kent (ed.) *Ethnicity, Hunter-Gatherers, and the "Other,"* pp. 1–27. Washington, DC: Smithsonian Institution Press.

Knauft, Bruce (1991) "Violence and sociality in human evolution." *Current Anthropology*, 32: 391–428.

Leacock, Eleanor (1954) *The Montagnais "Hunting Territory" and the Fur Trade*. Memoirs of the American Anthropological Association, *American Anthropologist*, 56(2), part 2, memoir number 78.

Leacock, Eleanor (1978) "Women's status in egalitarian society: Implications for social evolution." *Current Anthropology*, 19:247–275.

Leacock, Eleanor (1981) "Seventeenth-century Montagnais social relations and values," in W. C. Sturtevant (general ed.) *Handbook of North American Indians*, J. Helm (volume ed.), *Volume 6, Subarctic*, pp. 190–195. Washington, DC: Smithsonian Institution.

Leacock, Eleanor (1982) "Relations of production in band society," in E. Leacock and R. Lee (eds.) *Politics and History in Band Society*, pp. 159–170. Cambridge: Cambridge University Press.

Leacock, Eleanor and Lee, Richard (eds.) (1982) *Politics and History in Band Society*. Cambridge: Cambridge University Press.

Lee, Richard B. (1979) *The !Kung San: Men, Women, and Work in a Foraging Community*. Cambridge: Cambridge University Press.

Lee, Richard B. (1993) *The Dobe Ju/'hoansi*, second edition. Fort Worth, TX: Harcourt Brace College Publishers.

Lee, Richard B. and Daly, Richard (1999) "Introduction: Foragers and Others," in R.B. Lee and R. Daly (eds.) *The Cambridge Encyclopedia of Hunters and Gatherers*, pp. 1–19. Cambridge: Cambridge University Press.

Lee, Richard B. and DeVore, Irven (1968a) "Problems in the study of hunters and gatherers," in R.B. Lee and I. DeVore (eds.) *Man the Hunter*, pp. 3–12. Chicago: Aldine.

Lee, Richard B. and DeVore, Irven (eds.) (1968b) *Man the Hunter*. Chicago: Aldine.

Lips, Julian (1947) *Naskapi Law*. Philadelphia, PA: American Philosophical Society.

Marlowe, Frank (2005) "Hunter-Gatherers and Human Evolution." *Evolutionary Anthropology* 14:54–67.

Marshall, Lorna (1961) "Sharing, talking, and giving: Relief of social tensions among !Kung Bushmen." *Africa* 31:231–249.

Maynard Smith, J. and Price, G.R. (1973) "The logic of animal conflict." *Nature*, 246:15–18.

Murdock, George P. (1934) *Our Primitive Contemporaries*. New York: Macmillan.

Murdock, George P. (1967) "Ethnographic Atlas: A Summary." *Ethnology*, 6:109–236.

Murdock, George P. (1968) "The current status of the world's hunting and gathering peoples," in R.B. Lee and I. DeVore (eds.) *Man the Hunter*, pp. 13–20. Chicago: Aldine.

Murdock, George P. (1981) *Atlas of World Cultures*. Pittsburgh, PA: University of Pittsburgh Press.

Myers, Fred R. (1986) *Pintupi Country, Pintupi Self*. Berkeley, CA: University of California Press.

Osgood, Cornelius (1958) *Ingalik Social Culture*. New Haven, CT: Yale University Publications in Anthropology, number 53.

Reid, Gerald (1991) "Montagnais-Naskapi," in D. Levinson (Editor in Chief) *Encyclopedia of World Cultures,* T. O'Leary and D. Levinson (volume eds.), *Volume I, North America*, pp. 243–246. Boston, MA: G.K. Hall.

Reyna, S.P. (1994) "A mode of domination approach to organized violence," in S.P. Reyna and R.E. Downs (eds.) *Studying War: Anthropological Perspectives*, pp. 29–65. The Netherlands: Gordon and Breach.

Ritchie, Claire (1986) "From foraging to farmers: The Ju/Wasi of Nyae Nyae thirty years on," in M. Biesele with R. Gordon and R. Lee (eds.) *The Past and Future of !Kung*

*Ethnography: Critical Reflections and Symbolic Perspectives—Essays in Honour of Lorna Marshall*, pp. 311–325. Hamburg: Helmut Buske Verlag.

Service, Elman R. (1966) *The Hunters*. Englewood Cliffs, NJ: Prentice-Hall.

Service, Elman R. (1971) *Primitive Social Organization: An Evolutionary Perspective*, second edition. New York: Random House.

Shaw, R. Paul and Wong, Yuwa (1989) *Genetic Seeds of Warfare: Evolution, Nationalism, and Patriotism*. Boston, MA: Unwin Hyman.

Shternberg, Lev I. (1933) *Semya I Rod U Narodov Severo-Vostochnoi Azii*. English translation in the Human Relations Area Files, Id Number RX2. New Haven, CT: Human Relations Area Files.

Sluys, Cornelia M.I. van der (1999) “Jahai,” in R. B. Lee and R. Daly (eds.) *The Cambridge Encyclopedia of Hunters and Gatherers*, pp. 307–311. Cambridge: Cambridge University Press.

Smith, David L. (2007) *The Most Dangerous Animal: Human Nature and the Origins of War*. New York: St. Martin’s Griffin.

Speck, Frank G. (1935) *Naskapi: The Savage Hunters of the Labrador Peninsula*. Norman: University of Oklahoma Press.

Spencer, Baldwin and Gillen, Francis J. (1927) *The Arunta: A Study of a Stone Age People*. London: Macmillan.

Steward, Julian (1968) “Causal factors and processes in the evolution of pre-farming societies,” in R. B. Lee and I. DeVore (eds.) *Man the Hunter*, pp. 321–334. Chicago: Aldine.

Tonkinson, Robert (1974) *The Jigalong Mob: Aboriginal Victors of the Desert Crusade*. Menlo Park, CA: Cummings Publishing.

Tonkinson, Robert (1978) *The Mardudjara Aborigines: Living the Dream in Australia’s Desert*. New York: Holt, Rinehart, and Winston.

Tonkinson, Robert (2004) “Resolving conflict within the law: The Mardu Aborigines of Australia,” in G. Kemp and D.P. Fry (eds.) *Keeping the Peace: Conflict Resolution and Peaceful Societies around the World*, pp. 89–104. New York: Routledge.

Turnbull, Colin M. (1961) *The Forest People: A Study of the Pygmies of the Congo*. New York: Simon and Schuster.

Westermarck, Edward (1924) *The Origin and Development of the Moral Ideas*, in two volumes, second edition. London: Macmillan.

Wheeler, Gerald C. (1910) *The Tribe, and Intertribal Relations in Australia*. London: John Murray.

White, Douglas R. (1989) “Focused ethnographic bibliography: Standard cross-cultural sample.” *Behavior Science Research*, 23:1–145.

Woodburn, James (1982) “Egalitarian societies.” *Man*, 17:431–451.

Wrangham, Richard and Peterson, Dale (1996) *Demonic Males: Apes and the Origin of Human Violence*. Boston, MA: Houghton Mifflin.

# Chapter 14
# Born to Live: Challenging Killer Myths

**R. Brian Ferguson**

This chapter is an anomaly in this volume. It is about cooperation among primates, but cooperation for deadly violence against others of the same species. It is about warfare by chimpanzees and by humans. Whether chimpanzees make war depends on your definition. Mine has always been elementary: organized, potentially lethal violence against members of another group. Using this definition, there is no question that chimpanzees have the capability to make war and have done so on occasion. The patrols that often precede attacks, and the attacks themselves, display a high degree of intelligent cooperation. Male coalitional aggression is the label that has been aptly applied to chimpanzees and humans too.

What is very much in question is whether chimpanzees, and humans, are *predisposed* to war, whether our common evolutionary heritage has selected into our genes a tendency, a predilection, to attack and kill members of other groups. Just that claim has been made by many authors, most notably by Jane Goodall (1986), Richard Wrangham (Wrangham and Peterson, 1996), and Michael Ghiglieri (1999), in many forums both scientific and popular. I argue that it is wrong, fundamentally wrong. Chimpanzees—about which I am currently writing a book—have evolved a most flexible nature. With human beings, living in immensely complex social and symbolic worlds, that flexibility is squared. This is not to claim that we are born noble and peaceful. We are not species-ifically inclined against war either. Our orientation toward war, for it or against it, and our practice, depends on situations, inclusively defined as running from basic environmental circumstances, through social structures, to values and beliefs.

Challenging the myth of innate depravity, as Ashley Montagu (1968a) once called it, is the academic equivalent of whack-a-mole. Slap one hypothesis down, another pops up. True believers see confirmation of our evolved violent nature everywhere they turn, and they have forcefully presented this bleak view to the public and policy makers. Again and again, in this way and in that way, they claim

---

R.B. Ferguson (✉)
Department of Sociology and Anthropology, Rutgers University, Newark, NJ 07102, USA
e-mail: bfergusn@andromeda.rutgers.edu

R.W. Sussman, C.R. Cloninger (eds.), *Origins of Altruism and Cooperation*,
Developments in Primatology: Progress and Prospects 36, DOI 10.1007/978-1-4419-9520-9_14,

that humans may be able to learn peace, but they are naturally inclined toward war. Furthermore, they warn, if we do not accept this unpleasant truth, we doom ourselves to unending violence.

I have been researching war for over three decades, and I think that anthropology has some important things to say about mass violence in our world today (see Ferguson, 1999, 2003, 2006a, 2009). But those points are covered over by the smoke and mirrors of evolved predispositions to kill. This chapter takes a very broad approach to assertions of an evolved war-proneness, touring through a number of overlapping sorts of arguments. The basic point is that although psychological Darwinist claims are extensive, they are not supported by evidence. What *is* supported is the basic premise of this volume, that it is human beings' evolved nature to keep themselves alive and well, by means of cooperation and altruism. Sometimes, that means going to war.

## Chimpanzees as Natural Born Killers

A demonic perspective on chimpanzees provides foundation for the current psychological Darwinist perspective on war. As Wrangham (1999a:6) puts it, "selection has favored, in chimpanzees and humans, a brain that in appropriate circumstances, seeks out opportunities to impose violence on neighbors. In this sense, the hypothesis is that we have evolved a violent brain." "Chimpanzees and hunter gatherers. . . seek, or take advantage of, opportunities to use imbalances of power for males to kill members of neighboring groups" (Wilson and Wrangham, 2003:384). "a *necessary and sufficient* condition for intercommunity aggression is a perception that an opponent is sufficiently vulnerable to warrant the aggressor(s) attacking at low risk to themselves" (Wrangham, 1999b:15, my emphasis). And one more, to make clear I am not making up a straw-man:

> [S]election has favored a human tendency to identify enemies, draw moral divides, and exploit weaknesses pitilessly across boundaries. Among hunter-gatherer societies, inner-city gangs, and volunteer militias at the fringes of contested national territories, there are similar patterns of violence. The spontaneous aggressiveness of humans is a harsh product of natural selection, part of an evolutionary morality that revels in short-term victory for one's own community without regard for the greater good (Wrangham, 2005:19).

This scholarly version of this dramatic picture has been called the Rival Coalition Reduction Hypothesis (Wilson et al., 2004). Any opportunity to kill males of another group with impunity will be seized because loss of fighters reduces their ability to compete over the longer term. No immediate conflicts of interest are necessary. Against that, the RCRH, is the RCH or Resource Competition Hypothesis—where severe fighting across chimpanzee groups is a direct effort to protect food resources. I side with the latter to a point. My position is that heightened food competition, and other disturbances, all *linked to human impact*—or the Human Impact Hypothesis—are what lead to deadly conflicts between groups and other violence as well. This can be called RCH+HIH. (In this and later discussions of chimpanzees, summary statements are based on a book manuscript in progress, *Chimpanzees, Men and War*, and documentation will be provided there.)

Where did the idea of killer chimpanzees come from? It developed out of three field situations. At Gombe in Tanzania, there was the Four-Year War from 1974 to 1977. The story is almost as familiar as Cain and Able. Beginning in 1972, one intermingling community of chimpanzees split into northern and southern groups. In 1974, members of the northern Kasakela community began entering the rangelands of the southern Kahama group and brutally attacked individuals from it, especially males, whenever they caught one alone. By 1978, Kahama was entirely gone—presumed exterminated—and Kasakela began using their rangelands (Goodall, 1986:503–514).

The second situation also occurred at Gombe, right after the Four-Year War. From 1978 to 1982, the large Kalande community, formerly south of the now-gone Kahama, gradually began expanding their ranging northward, encroaching on Kasakela, which fearfully avoided the intruders. This "invasion from the south" is portrayed as a violent repeat of the Four-Year War (Goodall, 1986:514–517).

The third situation occurred 60 km south of Gombe, at Mahale. Adult male chimpanzees of K-group had disappeared over the years, one by one, starting in 1970. By 1982, all but one K-group male was gone. The larger, ever encroaching M-group assimilated K-group's range and a number of K-group females who remained in place. Little was made of the disappearances when they happened, but after the Four-Year War became known, Mahale researchers reinterpreted these disappearances as possible killings by M-group (Nishida et al., 1985). In many secondary sources, the killing off of K- by M-group is reported as a documented fact. The invasion from the South and the end of K-group were taken as confirmation of the dark vision that it is in their nature for chimpanzees groups to war on their neighbors.

Margaret Power (1991) is the main critic of this view. Her work has been largely discounted by chimpanzee researchers. I believe she was on the right track. Power stressed that both Gombe and Mahale were subject to major artificial provisioning, and that early observations there, and at Budongo and elsewhere, of non-provisioned chimpanzees, showed them to be less exclusive and hostile then the later Gombe portrait. But this difference between early and later observations has been blamed, by others, on fission–fusion confusion—researchers were misunderstanding normal separation and joining of individuals within one group, with two different groups coming together (Ghiglieri, 1984:8, 173–174). Yet the specificity of early observations goes against that interpretation, such as known Gombe males observed in the center of another group's rangeland (Goodall, 1968:214) or geographically distinct groups in the Ugandan Budongo Forest occasionally sharing a rich food source with each other and then going back their on separate ways (Sugiyama, 1968).

Power sees this difference in reports as a record of social change driven by artificial food provisioning. At Gombe, violence centered on banana distribution got so intense that it was cut back drastically via a series of experiments in controlled distribution (Wrangham, 1974). Power hypothesizes that this reduction, and the way the new banana systems operated, led to intense frustration. That generated aggressiveness among chimpanzees which were already socialized to violence, and they took it out on Kahama, the Four-Year War. Frustration led to aggression.

I follow all that, but go farther. My position is that the new ways of provisioning led to a serious food scarcity, evidenced by sharply declining body weights, and that a policy of banana-favoritism toward Kahama gave Kasakela a good reason to be extremely hostile toward them. While the local Kasakela chimpanzees had to wait in frustration for a bunch of bananas per week, the prodigal Kahama chimpanzees got bananas whenever they showed up (Goodall, 1986:503) Plus, there was a lot of sex and politics involved. (Now there is a good comparison to humans). Subsequently at Gombe, the "invaders from the south" appeared to be drawn to the feeding station (Goodall, 1986:516). Regarding Mahale, it seems that everyone agrees that what pulled M-group into K lands was the researchers' provisioning. I will return to this topic of human impact.

Gombe and Mahale 1974–1982 were the basis of the idea that chimpanzees, and so humans, are inherently warlike. It took time for this to reach maximum public spread in major publications (especially in Goodall, 1986; Wrangham and Peterson, 1996; Ghiglieri, 1999). Paradoxically, during that time of writing and presentation, violence dropped off, with only one clear outside adult male killing from 1983 to 1998. Doubts about the normality of those type-case situations began to grow. But events since then, at several sites, especially at Gombe and Kibale in Uganda, seem to support the demonic view. It is common to read statements such as, "A growing body of evidence suggests that lethal intercommunity aggression is typical for chimpanzees across Africa" (Gros-Louis et al., 2003:341). However, if one sticks with the cases, (and if one leaves aside highly artificial captive-introduction experiments), there are only 13 instances where evidence indicates certain or very likely intergroup killings of adult males, in over 200 years of reported observations.

Nine of the thirteen killings come from three short periods, Gombe 1974–77 and 2000–2004 and Kibale 1999–2004. My count (to be documented in *Chimpanzees, Men, and War*) is as follows: at Gombe, 2 in 1974–1977 (Sniff and Charlie), 1 in 2002 (Rusambo); at Kibale, 5 from Ngogo in 2002–2004, at Kanyawara, 2, 1 in 1991–1992 (Ruwenzori) and 1 in 1999; plus 3 other singletons, 1 at Kalinzu in 2003, 1 at Tai in 2005, and 1 at Loango in 2005. Highly noteworthy, but typically unnoted, some of those situations are characterized by other forms of intense violence, not associated with the Gombe war vision: internal and external infanticides, internal killings of adult males, severe violence against outside or inside adult females, killing and eating of human infants, and markedly increased hunting. This broad spectrum of bloodletting suggests chimpanzee populations under stress–stress from humans.

Power's emphasis on the impact of banana provisioning was countered by evidence of territorial clashes and killings at unprovisioned sites, most notably Kibale. Proponents of evolved warlike tendencies routinely equate human impact with provisioning only. If no provisioning, then human impact is ruled out. There is much more to human impact than that. Habitat loss in unprotected areas and around or even within protected areas has eliminated chimpanzee rangeland. Snare poaching and retaliation for crop raiding has added to rangeland impaction, even within Parks. This has led, I argue, to intensifying territorial competition. Epidemics, some introduced through humans, caused major demographic disruption, and with social consequences we are only beginning to discern. Other huge unknowns are the effects of research and tourism, which are often extremely intrusive. We cannot specify their effects but are unwise to discount them.

The exclusion of human impact is part of a broader problem in field research, the nearly complete separation of writings on scientific research questions from discussions of human threats and conservation. Anthropology too was reluctant to acknowledge that their study populations were far from "pristine"—"they were hardly affected by the outside world when *I* got there." Primatology should avoid that mistake. The way to understand behavior is to examine responses to changing circumstances. This is very relevant to violence. Human impact on chimpanzee populations has increased greatly in recent years. Note that 10 of the 13 intergroup adult male killings occurred after 1998. As human impact intensifies in the future, I predict substantially more male/male intergroup attacks, and more of other sorts of violence, in sharp contrast to field observations from 1983 to 1998, just as colonial intrusions intensified indigenous warfare in tribal zones all over the world (Ferguson and Whitehead, 2000). As with human warfare, to be understood, chimpanzee violence must be seen in its historical context. If these acts of violence are seen as expressions of a dark chimpanzee nature, international support for their protection may decrease. If, on the other hand, they are seen as a consequence of human disturbance, support for protection may grow.

## Unanswered Darwinian Questions

In an important sense, there is no necessary contradiction between my situational explanation of collective violence and views that posit evolved tendencies. Now, we are all nature–nurture interactionists. But in substance, the perspective that intense chimpanzee violence is associated with increased resource competition and other disruptions due to a human presence is very different from the idea that intense violence in the normal expression of evolved propensities. After all, if the point of the demonic and related arguments is not that chimpanzees and humans are *born* inclined toward war, that this inclination is coded in their genes, then what is the point? Yet, for all the emphasis on evolved tendencies, the evolutionary process leading to fixation of these tendencies remains surprisingly fuzzy, on several counts.

The ABC of Darwinism is variation and selective retention. Some individuals have a trait, some do not, and those that have it breed more. Add in consideration of inclusive fitness, and it is not just individuals that get selected but gene-sharing kin. Regarding chimpanzee wars, kin selection supposedly operates because males are philopatric. They (usually) do not leave their natal group, and so it is surmised that they share more genes with males of their own group than those of others, potential adversaries. This has not been demonstrated. Genetic comparisons showed no or only slightly higher relatedness of males within a group than among females, who typically migrate in from outside (Vigilant et al., 2001). No one has specified the demographic *model* that is supposed to select for demonic traits. It is by no means obvious how such selection could occur. If females regularly move to neighboring groups, generation after generation, then intergroup conflict means fighting with uncles, cousins, and nephews. In most theoretical applications of kin-selection, relatives that close would be working for *common* genetic interests.

Furthermore, the assumption that human hunter–gatherers are, like chimpanzees, patrilocal—and so the unspecified selection model works for us too (Wrangham and Peterson, 1996:65–66)—runs up against extensive evidence of residential variation and flexibility among foragers (Fry, 2006:167; Chapter 13, this volume). According to Wrangham and Peterson, one of the key parallels between chimpanzees and tribal peoples—specifically the Yanomami—is that females leave their own group to marry elsewhere. Unfortunately for that conclusion, the typical Yanomami marriage is village endogamous and both males and females stay where they are (Chagnon, 1968:69–73). So any selection model based on chimpanzee patterns would have only a variable *potential* application to simpler human societies.

Even if some statistical genetic benefit could be modeled for the very overlapping "us vs. them" of chimpanzees, the competitive advantage supposedly gained by eliminating individual males from neighboring groups could be swamped by the large fluctuations in group size. Killing off one enemy warrior would not make much difference in subsequent intergroup showdowns. The Gombe "invasion from the south" was supposedly halted by the maturation of a few Kasakela males.

The idea that this unspecified selection process fine-tuned a particular predisposition exemplifies an outmoded bean-bag image of genes, particular to particular traits. We now know it is hardly that simple. Genes are expressed in complex layers of interactions—systems of systems—all with external inputs. Their effects typically are not discrete. For instance, much attention has been given in humans to SLC6A4, the so-called anxiety gene. But this gene has also been associated (in the NCBI Entrez Gene database) with—alphabetically—aggressive behavior in children, alcoholism, anorexia nervosa, attention deficit hyperactivity disorder, autism, chronic fatigue syndrome, depression, heroin dependence, longevity, lymphoma, migraine, myocardial infarction, neuroticism, obsessive compulsive disorder, pulmonary veno-occlusive disease, schizophrenia, sleep apnea, sudden infant death syndrome, suicidal tendencies, and violent behavior. Select for one connection, select for all the others too. A "gene for" any aspect of violent intergroup competition would affect many other areas as well. Any inclusive fitness benefit of selection for intergroup violence would be weighed against countless other effects on lifetime reproductive success.

Moreover, in the demonic perspective, what is asserted to have evolved is not some single, simple tendency—such as a low-flash point for violence—but a complex suite of behaviors, including stealthy patrolling of borders, entering neighbors rangelands, careful monitoring of signs of adversaries, calculating numerical advantage, and collectively attacking. This would involve many, many genes.

Positing an inborn predisposition to this complex set of social actions stands quite apart from most understandings of chimpanzee behavior, which for decades has looked to flexible ecological adaptation rather than inherited tendencies. While most social behaviors display ranges of variation, this war suite is said to be fixed. As Wrangham puts it: “Does this mean chimpanzees are naturally violent? . . .Alas, the evidence is mounting and it all points the same way. . . In this cultural species, it may turn out that one of the least variable of all chimpanzee behaviors is the intense competition between males, the violent aggression they use against strangers, and their willingness to maim and kill those that frustrate their goals.” (Wrangham, 1995:7).

But why fix *this* set of behaviors, when evolution left the rest flexible in responding to circumstances? What is the reproductive advantage of having the temperamental dial set to attack, rather than in neutral? How does that expectably lead to more genes in future generations than an open, unbiased disposition, to go with whatever works best, be it violence, avoidance, or tolerance? The demonic view holds that even when there may be advantages to getting along, chimps and humans will opt for violence, start a war. What is the reproductive advantage of an orientation that leads to sub-optimal actions? How does that enhance fitness, individual or inclusive?

The alternative for chimpanzees is that a violent disposition to others is acquired. We are all aware of chimpanzees’ prodigious ability to learn. Different groups have different learned traditions. (Some would say cultures but I would not). Some of these traditions seem related to environmental conditions but many do not. Still, that catalog of learned behaviors remains mostly limited to techno-environmental interactions, much like the trait lists of anthropology a century ago. It is more than possible that complex, patterned social behaviors can be learned and passed along, for example, the differing degrees of bisexual bonding comparing Tai, Gombe, and elsewhere, or even many of differences between chimpanzees and bonobos. What would happen if a bonobo were raised among chimpanzees or vice versa? I expect their behaviors would reflect the local custom.

## Evolution of Violent Humans

Let us say for the sake of argument that chimpanzees are genetically predisposed to war. What does that mean about humans? The basic idea of the chimpanzee/human war analogy is that we share this violent predisposition—albeit much more elaborated among humans—because we inherited it from our last common ancestor. That ancestor was said to be pretty much a chimpanzee. As Wrangham and Peterson (1996:63) put it, “modern chimpanzees are not merely fellow time-travelers and evolutionary relatives, but surprisingly excellent models of our direct ancestors. . . [C]himpanzee-like violence preceded and paved the way for human war, making modern humans the dazed survivors of a continuous, 5-million-year habit of lethal aggression.”

Others see our apical ancestors quite differently. A behavioral synthesis in a 2008 issue of the *Journal of Anatomy*, explicitly focused on the last common ancestor, hypothesized “that the LCA displayed regional variation in certain behavioral traditions, ‘self-awareness’, and an enhanced ability to follow the gaze of other social agents. . . these behavioral characteristics are related to increased capacity of executive control to inhibit conventional responses in favor of social tolerance and seeking novel and flexible solutions to problems.” (Sherwood et al., 2008:431). The chimpanzee model has been further undermined by recently released findings on 4.4-million-year-old fossil *Ardipithecus ramidus*, which showed less sexual dimorphism and smaller canine teeth than anticipated. As Owen Lovejoy (2009:74) puts it: “Comparisons of the *Ar. ramidus* dentition with those of all other higher primates indicate that the species retained virtually no anatomical correlates of male-to-male conflict. Consistent with a diminished role of such agonism the body size of *Ar. ramidus* was only slightly larger than that of females.”

This is not the first time that living primates have been imagined as our ultimate progenitors. Baboon models were in vogue for some time (Jolly, 1970). A spirited case was made for the more peaceable, sexy, and female-bonded bonobo as the human template (Zihlman et al., 1978). The obvious point to be made is that no species living today represents our common ancestor 5–6 million years ago. But for argument, let us assume that our extremely great-grandpa did have an inborn predisposition to attack and kill his neighbors. Would modern men have gotten it from him, passed along over millions of bloody years?

If one considers all about those 5–6 million years, the huge unknowns that alone should be enough to dismiss any assertion of continuity in specific behavioral patterns. Wrangham and Pilbeam acknowledge this problem. Referring to human/chimpanzee parallels in lethal raiding, Wrangham and Pilbeam (2001:13) concluded whether this pattern of patrols and attacks was found in the LCA does not matter: “phylogentic continuity is impossible to confirm when it must traverse the great unknowns of 5 million years of hominid evolution. And more importantly, it has no explanatory value. The reasons why a behavior is shared must still be articulated for each species.” There you have it from the author of *Demonic Males*—chimpanzee’s collective violence provides no explanation for human collective violence, except, perhaps, by analogy.

Perhaps this proclivity was not passed down continuously from 5 million BP, they acknowledge. Without reference to the not-yet-described *Ardipithecus*, they note the reduction in both canine and body dimorphism in the later human line, a trend which usually is taken as an indicator of reduced male–male competition. Since later hominins thus appear to be comparatively nonviolent, they suggest that the bloody proclivities of the chimpanzee-like common ancestor were selected out, only to be selected back in at a more recent date. With bonobos, they were selected away, never to return.

If recent ancestors were inclined to war, then one would expect to find warfare present throughout the human archaeological record. That is what psychological

Darwinists routinely claim to be so, repeatedly citing two books (Keeley, 1996; LeBlanc with Register, 2003) which support that view. Those claims do not withstand scrutiny (Haas, 1999; Otterbein, 2004; Thorpe, 2003). They suffer from a compound misinterpretation: they note ancient cases where signs of war are present and extrapolate from them to the many more ancient cases where none are; they conflate later archaeological records with earlier records; and they assume that ethnographically recorded warfare of peoples in recent centuries is representatives of people millennia ago (Ferguson, 2006b; Chapter 13, this volume). That is assuming the ancient universality of war not documenting it.

War leaves archaeologically recoverable remains, in skeletal and settlement materials, and sometimes in tools and art. Globally, the pattern is that war signs are absent in the earlier archaeological records even where recovery of materials is sufficient to show war. After time—chronologies vary enormously in different regions—war signs unmistakably appear, and usually never go away. The appearance or intensification of war usually follows some combination of preconditions, including larger populations, greater sedentism (though not necessarily agriculture), increased trade, hierarchy, social bounding, and often, environmental reversals. The first established war findings date to around 10,000 years ago and gradually become more widespread and more intense around the world, ultimately leading to the frequently violent ethnographic universe recorded in recent centuries. The sum of early archaeological records from around the world contradicts the idea that recent, in evolutionary terms, human societies were characterized by violent competition and war (Ferguson, 2006b).

These are all scholarly objections. For the larger public, "chimps R us" carries the day. In the genes, they are 98% plus identical to humans. If we are so close in our DNA, how different could we be? This is a key icon of modern biomythology. As Marks (2003) details, and as post-genomic science continually updates, this figure is meaningless for the kind of behavioral questions we are discussing, especially as it seems gene regulation is the name of the game in our species' differentiation.

In the churning sea of questions about human evolution, a few things are clear. What separates humans from chimpanzees includes a vastly expanded neocortex and cognitive abilities, and commensurate capacities for language and symbol. These watershed differences provided the basis for culture, which—emergent—actualized humanity's "adaptive dimension" (Montagu, 1968b). The same human infant has the potential for being a pre-industrial hunter–gatherer or an astronaut, for being a genocidal slaughterer or a pacifist monk. That is pretty darn flexible, and humans can do it because culture *is* our nature. It is culture that made possible human beings' spectacular reproductive success. It is culture that enables us to live cooperatively and interdependently, pooling our efforts to collectively cope with any environment on earth. It is culture that provides the means for our material and reproductive well-being. Yet in psychological Darwinism, even after this quantum leap in collective flexibility, we remain inherently violent because violence increases inclusive fitness.

## Violence for the Genes

But claims for evolved tendencies for war are reinforced by assertions that both chimpanzees and humans actually *do* use deadly violence in ways that maximize their inclusive fitness. That is the ultimate commonality claimed to span the two species. The claim rests on little evidence.

For chimpanzees, if that were true, then certain kinds of killings should be expected according to the logic of inclusive fitness and certain kinds not. Expected would be killing not only of outside adult males but also of outside male infants. Not expected would be killing of adult or infant males within the group, which costs a present or future coalition member, or the killing of outside females of any age, who might immigrate and thus help propagate male genes. What is the record (in *Chimpanzees, Men, and War*)? Considering certain and very likely killings (and once again leaving out the captive introductions), there are 23 consistent with maximizing inclusive fitness and 25 that go against inclusive fitness—pretty much of a wash.

For humans, the violence-for-reproduction claim rests upon Chagnon's (1988) study of the Venezuelan Yanomami, which supposedly demonstrates that *unokai*—which Chagnon equates with men who have killed enemies—have more children than *non-unokai*. It would be hard to find a more thoroughly debunked claim in contemporary anthropology. Field ethnographers challenged Chagnon's data (Albert, 1989; Lizot, 1989). Fry (2006:184–199) and myself (1989; 2001:106–108) have taken on his statistical analysis. These rebuttals show that killers' alleged reproductive success is distorted by the following facts: (1) headmen, who have more wives, are all in the *unokai* category, thus raising *unokais'* apparent reproductive advantage, (2) the likelihood of becoming *unokai and* of having more children both increase with age, so age is a confounding variable that also inflates *unokais'* advantage, and (3) the sample is limited to living men. Known killers are often targeted for revenge killings, and dying younger obviously lowers lifetime reproductive success. If you only looked at the winners, then gambling would seem to be a good deal too.

Meanwhile, Moore's (1990) study of Cheyenne war and peace chiefs shows the latter had higher reproductive success. Dedicated warriors lived shorter lives with fewer children. If war-proneness were under genetic control, and conditions remained stable, the trait would be selected out quickly. Similarly, though on a group level, Younger's (2005) extensive computer modeling of social groups on islands shows that those led by more aggressive leaders tend rapidly toward extinction. The notion that being inclined to war leads to greater reproductive success is without empirical foundation.

Tooby and Cosmides (1988) posted an often-cited evolutionary psychological explanation of war on their website. They ask, since warriors often die, and being dead is bad for reproductive success, why would men risk combat? They posit three necessary conditions that would make our supposedly modular mind compute war as worthwhile in reproductive terms: "cheaters or non-participants must be identified and excluded (or punished) . . . the participants are rewarded or punished in proportion to the risks they have run, and in proportion to how important their contribution was to success." They do not provide a single example where these three conditions apply, so I (2001:110) considered them in relation to Chagnon's descriptions of Yanomami. None of the conditions hold true.

Mesquida and Wiener (1999) adopt Daly and Wilson's (1988:168–171) concept of a young male syndrome and apply it to war. They claim that wars are launched by young men because it suits their reproductive interests, to obtain mates directly or the resources needed for the attraction and retention of mates. For evidence, they cite national statistics which associate larger numbers of young men with more frequent or intense warfare. This association is real, as for example in Rwanda, and a good explanation already exists: those bulges of rootless young men are easily and cheaply recruited in political fights launched and controlled by older political leaders (Collier and Hoeffler, 2004).

As for tribal societies—such as the Yanomami (Ferguson, 1995), the Meru (Fadiman, 1982), the Cheyenne (Hoebel, 1978), or the Enga (Meggitt, 1977)—military decisions are typically made by middle-aged or older men, not young hotheads dreaming of glory and mates. In tribal combat, younger men generally are supervised and protected by their elders until they mature in the ways of war. Mesquida and Wiener's claimed behavioral generalization crashes against ethnography. In fact, one source they cite to show an association of intense warfare with the presence of more young men is the article previously mentioned (Moore, 1990), showing Cheyenne war leaders had lower reproductive success.

The biggest argument for war as reproductive contest is also the simplest: winners often prosper at the expense of losers. True, large population benefits and losses can accompany war. Evaluating that point requires consideration of a theoretical point of crucial significance. My longstanding materialist position is that wars occur when those who make decisions for war believe it is in their practical self-interest to do so. Practical self-interest means protecting or enhancing all the resources at one's disposal, the costs of obtaining them, physical safety, and—where such exists—political power (Ferguson, 1990). This is an all-important difference from psychological Darwinism, which holds that in addition to material well-being, humans also compete *directly* over reproductive success (Chagnon, 1990).

While that may seem to be a theoretical fine point, it leads to critically different expectations and understandings. It means that even if there is no competition over material resources, reproductive interests will still pit men against other men. In a broad sense, this goes directly against the key point of this volume: that cooperation is the more common, "natural" tendency in human evolution and behavior. More specifically, it means there is *always* a reason to make war. This is a testable theoretical difference: are conflicts over practical material issues more predictive of actual war than "reproductive" conflicts, even broadly defined. The basic goal of my book *Yanomami Warfare* (1995) was to evaluate these contrasting hypotheses against every reported case of warfare. Conflicts over access to the introduced necessities of steel tools and other Western manufactures are predictive. Disputes over women, in any form, are not predictive.

## Monumental Myths

All of the particular theories previously discussed carry weight in popular discussions because they rest comfortably within larger cultural assumptions that humans are, by evolution, by nature, born to kill others. This part considers several of these larger, mythic frameworks. It could start with "Man the Hunter," but in this volume that is better left to others. Instead, it begins with the idea that men are "naturally aggressive," an opinion I frequently get from my students.

Research and speculation on the biology of aggression deal with individuals. War is a property of social groups, with dynamics that can only be understood at the group level. The disjuncture between the two is well-illustrated by Konner's (2006) state of the art review of the biology of aggression and war. He summarizes the neurology of aggression, effects of brain trauma, heritability studies, etc. All of that is dropped when he moves on to explaining war, where he invokes pseudospeciation (below) and long-standing psychological research on mass psychology and authoritarianism, which "does not contradict current views in evolutionary psychology" (p. 23). Then psychology is somehow put in harness with Malthus, who, Konner claims, explains the colonization of the Americas, both World Wars, creation of the USSR, Vietnam, etc. Konner opens this article with the standard biological pitch: "there is in human nature a natural tendency to violence and, additionally, to war, and. . . the failure to fully recognize this tendency – a common failure in academic circles – increases the risk" (p. 1). So it is instructive to read in closing, just how this bio-realization is important: only if we concede that war is natural, like disease, will the international community be sufficiently motivated to do something to prevent it (28). How does that follow?

Konner and many others use biology to explain why war is a male activity. This too is said to apply to both chimpanzees and humans. Wrangham titled his book *Demonic Males* because female great apes were, in comparison, nonviolent. This clear distinction has eroded because of accumulating evidence of severe attacks by females. Still, it remains true that males do more of it.

For humans, collective violence usually is a male thing. Regarding whether or what role biology plays in this, I am agnostic. Measures of male and female aggression vary. Domestic violence, in the current English-speaking world, is slightly more likely to be initiated by females, though males are much more likely to do serious harm (Archer, 2000). Adult males have far more testosterone than females, but testosterone levels rise and fall with social events and may be as much an effect as a cause of aggression (Sapolsky, 1997). Young boys routinely test out as more aggressive than girls, but this is already after significant gender socialization (Condry and Condry, 1976; Sidorowicz and Lunney, 1980). We know, from many, many cases, that women can both order and fight wars (Davis-Kimball, 2002; Edgerton, 2000; Jones, 2005), so this cannot be a simple question of biological capabilities.

A solid, empirically grounded biosocial theory (Eagly and Wood, 2003) can explain gender segregation in war, without invoking inborn predispositions. Two prominent cases of warrior women lend it support. The famous women warriors of early 19th century Dahomey had to bow to social mores, as they said they had become men (Edgerton, 2000). Contemporary women soldiers of Eritrea fought with distinction and ruthlessness alongside men, enabled and encouraged by that country's revolutionary ideology. When the war ended and they went home, they found great difficulty reentering the traditional female role (Bernal, 2001). In both cases, women excelled as warriors, but they could not be warriors and culturally defined "women" at the same time.

Perhaps men are more aggressive than women. What does that tell us about war? Maleness is one part of biology. Biology is one part of aggression. Aggression is one part of combat. Combat is one part of war. An explanation of a part of a part of a part of a part of a social pattern says very little. It can be argued with at least as much support, that it is militarism in society that conditions male proclivities for violence (Goldstein, 2001). Could there be socialization for gender roles among chimpanzees and bonobos?

If innate male aggression were an important cause of war, we might expect men to relish the chance to kill enemies, to seek it out, as chimpanzees are alleged to. The record of the US military is totally the opposite. Men seek to avoid killing enemies and are traumatized when they do. A great deal of training is needed to make even them shoot (Grossman, 1996). An article by an Army major (Pierson, 1999) in *Military Review* advised commanders to identify the less than 4% of troops who are psycho or sociopathic because they are the ones who can be counted on to willingly kill. ("[A] controlled psychopath is an asset on the killing fields" [p. 61]) A recent evolutionary psychology book (Smith, 2007), premised on the evolutionary benefit of deadly violence, tries to deal with this conundrum by compounding inborn mental modules. A people-making module makes us unwilling to kill, but that can be overridden by other evolved modules compelling us to kill prey, predators, or sources of infection. If so, why then is there so much psychological stress, what turns the different modules on and off, and what is the "I" that puts all these modules together?

It is a short step to the next biological shibboleth, "pseudospeciation," the idea that humans have an inborn tendency to categorize enemies as less than human, and so to find it easier to kill (Eibl-Eibesfeldt, 1979:109–111). Dehumanization of enemies frequently occurs in war, and Goodall even applied the concept at Gombe, where Kasakela was said to "de-chimpize" Kahama (Goodall, 1986:532). But if this were an inborn human propensity, then there would be no inhibitions against killing. Obviously, in any war, a line must be drawn, which categorizes those on the other side—often people one knows very well—as meriting death. That can happen in many different ways and does not necessitate seeing enemies as less than human. Idioms of witchcraft and revenge often provide both moral and emotional reason to kill, but the concepts apply very clearly to human beings and only to humans. Pseudospeciation, like so much biological reductionism, slaps a label on the more complicated, and more interesting, practice of morally categorizing enemies.

Dehumanization takes us to the next mythic area, a big one—ethnocentrism. This tendency seems firmly grounded in chimpanzee behavior. Adult male chimpanzees routinely make agonistic displays at signs of outsiders—although there are also instances of tolerance. Goodall (1986:531–532) posits "an inherent fear of, or aversion to strangers, expressed by aggressive attack." There is more here than mere xenophobia, she emphasizes. Gombe chimpanzees drew a line cutting off *known* individuals, former friends, and "de-chimpized" them to make them suitable to kill. But this is actually a theoretical challenge—not support—for the ethnocentrism explanation of war. The mother of all chimpanzee conflicts developed *within* one group, which only became separate as the conflict intensified.

The idea of in-group amity and out-group enmity comes from Spencer, and the term ethnocentrism from Sumner, both lead thinkers of Social Darwinism (Van der Dennen, 1995:448–452). Their ideas were consistent with the Hobbesian images of savages held by their contemporaries Tylor (1888:221) and Boas (1912). Skipping ahead over decades, ethnocentrism was given a sociobiological stamp by Shaw and Wong (1989) (also see Reynolds et al.,1987), who portray it as an expression of genetic competition—"our kind" share more of "our genes" —and take it up through ethnic and national conflicts. Ghiglieri makes the point with characteristic bluntness:

> Unfortunately, every race, ethnic group, and tribe has its prejudices. Nearly all have led to atrocities, many lethal, often including full-scale war. The message here is that the human psyche has been equipped by kin selection to urge men to eliminate genetic competitors... War itself, declared or otherwise, is often motivated by these instinctive genocidal goals. I believe this happens because men are born ethnocentric and xenophobic by nature (Ghiglieri, 1999:215).

This is not a fringe position. It is a cornerstone, for instance, of Niall Ferguson's (2006:xliv–xlv) recent book explaining "twentieth-century conflict and the descent of the west."

It is an erroneous position. Contra the social Darwinist imaginings, most tribal war is not between culturally distinctive groups, but similar ones, as illustrated by the segmentary forms of opposition so common around the world (Otterbein, 1973; Sahlins, 1961). The theoretical value of kin selection drops to practically nil a few steps away from ego (Chapais, 2001). Self-sacrifice for "our kind" does not make genetic sense in those terms, though it can be argued to do so in terms of mutualism, cooperation, and altruism—principal themes of this volume. Cultural assertions of common ancestry at the tribal level may be complete fictions, as one recent genetic study of Central Asian tribes has demonstrated—they are no more related within the tribe than the mean kinship of the regional population as a whole (Chaix et al., 2004). The notion that recent "ethnic" or "sectarian" conflicts involve longstanding cultural groups struggling against ancient rivals, has been debunked thoroughly and repeatedly. I call these "identerest conflicts," emphasizing their highly variable fusions of identities and interests. Identerest groups are constructed in conflict, and they are constructed opportunistically, using multiple criteria, by political entrepreneurs seeking to forge a following (Ferguson, 2003).

Ethnocentrism, to some degree, exists in the very nature of culture. Humans learn that the way their group does things is the way things should be done. "Our ways" get the highest evaluations. But an empirical test of ethnocentrism in East Africa demonstrates that in-group/out-group contrasts beyond that baseline are extremely variable, concluding that Sumner's image of natural and stark oppositions—the image adopted today by psychological Darwinism—represents the negative pole in variable patterns of intergroup relations (Brewer and Campbell, 1976:144). “Social identity theory does find that [in our competitive society at least], intergroup categorization in itself regularly produces favoritism toward the in-group and discrimination against the out-group.” However, regarding actual intergroup conflicts, this “subjective” tendency is seen as playing a secondary role to the “objective” issues of history, society, economics and politics (Tafjel and Turner, 1986:14, 23). Intense ethnocentrism does not explain war, it accompanies war.

Which brings this tour of biological war myths to its last stop, territoriality. The concept itself developed in the study of birds and fish and then spread to other animals. As it spread, it became fuzzier. Does territoriality require active defense, or just regular usage? Is there a line between defense and advertisement (Van der Dennen, 1995:286–289)? Tinbergen (1968) projected the territoriality he saw in herring gulls on to human beings. Ardrey (1966) spread the idea as in *The Territorial Imperative*. It was a hit, a meme if you will, entering every day understandings and language. One reason for its popularity is that—loosely defined—it seems to apply to so many situations, as in Van den Berghe’s (1974) sweeping effort to “bring beasts back in” to the study of human conflict.

Territoriality is a major interest of primatology. For chimpanzees, some question if the concept applies since chimpanzee groups commonly share extensive overlapping ranges (Mitani and Rodman, 1979). But agonistic displays in the presence of others, and the specific behaviors at Gombe, convinced Goodall that the label fit. She thinks that for chimpanzees, what truly departs from standard conceptions of territoriality is the deadly violence involved. That, of course, is the link to humans (1986:525–528). As put by Ghiglieri (1988:259), “Primitive hunting and gathering societies the world over exhibit. . . territorial defense and warfare basically identical in form *and* function to that of chimpanzees.”

With the expansion of field observations over the years, it is clear that different chimpanzee groups relate very differently to the space they occupy. Some patrol borders, others do not; some male ranges are much larger than females, others only a little, etc. It is not too much to say that each study area has its own particular patterns. In some cases, lethal violence has been observed, in other cases, not. If lethal violence is seen as one variable aspect of territoriality, and if territoriality itself is situationally variable, how can there possibly be an innate predisposition to collective intergroup attacks?

Variation in human beings’ social orientations to space dwarfs that of chimpanzees. With people, the concept always involves the added dimension of symbolic construction (Ingold, 1987). In some cases, territorial defense seems a predictable response to concentrations of resources (Dyson-Hudson and Smith, 1978). In some cases it does not (Cashdan, 1983). Territorial identification is often more about social incorporation than perimeter defense (Kelly, 1995:185–189). Among Australian aborigines, foraging bands themselves are made up of members of multiple clans. Recognized clan titles to territory are not about restricting foraging by others—which is allowed—but about limiting access to sacred sites (Layton, 1986:22). As one ethnographer put it, “one could say that to own is to have the obligation to share” (Williams quoted in Ingold, 1987:134).

What about territoriality and war? For Ardrey, it was relevant for defense, to protect against intrusion, without which war would not occur. Tinbergen (1981), who was an inspiration for Goodall at Gombe, took it further to planned conquest and destruction of neighbors. The demonic perspective on apes and humans emphasizes territorial *acquisition.* Chimpanzees are said to go to war for "lebensraum," (Ghiglieri, 1999), to expand (Goodall, 1986:528; Wrangham, 1999b). In that they are said to be just like humans.

Obviously, many human groups do gain territory through war. Some of the earliest ecological models stressed this (Vayda, 1961). New Guinea warfare was at first proposed to be a "struggle for land" (Brookfield and Brown, 1963). More work, however, revealed that much New Guinea warfare lacked that dimension (Knauft, 1990:268–272). The case for Amazonian warfare as territorial expansion is even more tenuous (Ferguson, 1989b). In the ethnology of war, direct territorial acquisition—conquest—comes to the fore with developed social hierarchy—chiefdoms and above—where what is at stake is not the land itself, but the social wealth produced by subjugated peoples. In contemporary ethnonationalist struggles, land often becomes a potent symbol, worth killing for, not because there is too little of it to farm, but because land can be a potent symbol for self-aggrandizing ethnic entrepreneurs, a useful tool for mobilizing us against them. Territoriality is not a first principle that somehow explains human warfare. Rather it is a variable, and its expression and connection to intergroup violence is something that needs *to be* explained.

All these big, vague ideas—man the hunter, naturally aggressive males, pseudospeciation, ethnocentrism, and territoriality—are all too familiar aspects of our existence. We can see examples with our own eyes, at least through the media, and they repeatedly loom large in war. In that familiarity, they help create a public receptive to a simple explanation, that war is the product of a human nature evolved to struggle for reproductive superiority. These big notions provide a conceptual bridge from humans to chimpanzees that lend credence to all the smaller hypotheses discussed. But these half-formed concepts are just vague metaphors, with the patchiest empirical support. There is no evidence that they are orientations somehow encoded in our genes.

Proponents of biological explanations of war do not say it is some kind of fixed instinct. They always emphasize that our biological tendencies are mediated, channeled, and even redirected by culture. They do say humans have a decided tilt toward violence against outside groups, and that this leaning is a necessary factor for understanding war, from tribal peoples to world conflicts today. My position is that there *is no tilt*, no predisposition toward or against war.

Human beings—oriented to cooperation with others, living in symbolically constructed and learned social universes, and possessing language and the ability to communicate over time and space—are capable of almost anything. This, in my view, explains our unique evolutionary success. In this way, we *are born to live*, not to kill. But as Morton Fried (1973:355) once wrote on the idea of innate aggressiveness and war, "you can't kill a bad idea." He was probably right.

Still, anthropology does offer alternatives, very different answers to the question of "why war?" What follows is my alternative, developed over a few decades of studying war in many different contexts (see Ferguson, 1984, 1990, 1995, 2001, 2003, 2006a, 2009).

## An Anthropological Alternative

With some oversimplification, my position holds that wars occur when those who make the decisions to start fighting believe that it is in their practical self interest to do so. Self interest is defined in terms of maintaining or enhancing: access to important resources, their costs, safety, and where applicable power. This is the position I have long argued against both biological reductionism, and those many anthropologists who claim that war is the acting out of a particular culture's symbols and scripts, and is *not* about practicalities.

However, the symbolic dimension is very real and important. Particular cultures have their own expectations about war. Purely cognitive factors affect who is considered friend or enemy, within more fundamental structuring forces. They establish what kind of actions are thought appropriate in war, and how war is emotionally experienced, understood, and remembered. The practical and the symbolic are integrated in war. For example, if one considers the warfare that follows Western intrusions into indigenous areas over the past 500 years, patterns are very comparable across world areas. Yet, any detailed investigation finds those war patterns are informed and acted out according to understandings, symbols, and values that are particular to one local culture. The general and practical—and the particular and symbolic—as incomparable as they are, are joined in actual practice. How can we understand this in theory?

My approach to that question goes under the label of *moral conversion*—practical interests are converted into moral claims to persuade others and to justify oneself. As a conflict situation builds, and different courses of actions are weighed, people who participate in the decisions will convert their own perceived self-interest into the highest applicable moral standards, whether that is preserving democracy or avenging witchcraft. No one would tell others, "risk your life because it is good for me." They say, "if you are a man, this is what you should do." This is manipulation, but not just manipulation. People try to minimize cognitive dissonance, and I think it is common, probably the norm, that those advocating wars that serve their interests, come to believe those wars are righteous. As I say, this *is* an oversimplification, but that is the gist of my approach.

To understand war, then, one must focus on the decision makers. That directs attention to the sociopolitical structure of a society. What different kinds of people, groups, and institutions contribute in what ways to decisions, and what are their interests in a given situation? Those interests are as much, sometimes *more*, about the decision makers' position than concerned with the relationships between the groups in conflict. How will one course of action or another, whether toward war or toward peace, affect leaders' standing among their own?

In relatively egalitarian societies, every man decides for himself on war. Yet, even there, there are often recognizable leaders, headmen, inconspicuous except in war, able to persuade and cajole but not able to give anyone orders. Even at that level, by virtue of their position, these elementary leaders have somewhat distinctive interests in any conflict situation and greater influence than others. One of the most common consequences of war is an intensification of control by those in leadership positions, that is, unless things go wrong and they end up with their head on a pike. War leaders' positions get elevated in wartime. Often, leaders favor war, because war favors leaders.

Among the relatively egalitarian Yanomami, fine-grained study reveals their Machiavellian maneuvering (Ferguson, 1995). Among the more conspicuous Big Men of New Guinea that maneuvering is easily seen (Sillitoe, 1978). With chiefdoms around the world, probably the most common explanation for their incessant warfare is "chiefly ambitions." With kings, it is almost too obvious to mention. In the archaeological record, one of the preconditions contributing to war is the development of hierarchy. The self-interest of leaders in contemporary world conflicts is plainly evident for anyone who cares to look.

This is hardly a new idea. What rarely is recognized, however obvious, is that this may be the central explanatory principle of war. Ask people why we have wars, and many will reply, just like that, that it is in human nature. Very few will say that it is because of the self-interest of leaders, although they will say "of course" if asked about that directly. When reporters contact me, they want to hear about human nature, not the machinations of decisions makers. But that is where we should be looking. That is where we should direct the public's attention. For me, this is the biggest problem with biological "explanations" of war. They lay down a smoke screen, closing out an alternative explanation which is much better grounded in theory and evidence, that encourages citizens to foreground the question they really need to ask. When leaders call for war, what is in it for them?

## References

Albert, B. (1989). Yanomami "violence": Inclusive fitness or ethnographer's representation? *Current Anthropology, 31*, 637–640.

Archer, J. (2000). Sex differences in aggression between heterosexual partners: A meta-analytic review. *Psychological Bulletin, 126*, 651–680.

Ardrey, R. (1966). *The territorial imperative*. New York: Atheneum.

Bernal, V. (2001). From warriors to wives: Contradictions of liberation and development in Eritrea. *Northeast African Studies, 8*, 129–154.

Boas, F. (1912). An anthropologist's view of war. Carnegie Endowment for International Peace, International Conciliation Pamphlet no. 52.

Brewer, M.B., & Campbell, D.T. (1976). *Ethnocentrism and intergroup attitudes*: *The east African evidence*. New York: Wiley.

Brookfield, H.C., & Brown, P. (1963). *Struggle for land: Agriculture and group territories among the Chimbu of the New Guinea Highlands*. New York: Oxford University Press.

Cashdan, E. 1983. Territoriality among human foragers: Ecological models and an application to four bushman groups. *Current Anthropology, 21*(1), 47.

Chagnon, N. (1968). *Yanomamo: The fierce people.* New York: Holt, Rinehart Winston.

Chagnon, N. (1988). Life histories, blood revenge, and warfare in a tribal population. *Science, 239*, 985–992.

Chagnon, N. (1990). Reproductive and somatic conflicts of interest in the genesis of violence and warfare among tribesmen. In J. Haas (Ed.), *The anthropology of war* (pp. 77–104). Cambridge: Cambridge University Press.

Chaix, R., Austerlitz, F., Khegay, T., Jacquesson, S., Hammer, M.F., Heyer, E., & Quintana-Murci, L. (2004). The genetic or mythical ancestry of descent groups: Lessons from the Y chromosome. *American Journal of Human Genetics, 75*, 113–116.

Chapais, B. (2001). Primate nepotism: What is the explanatory value of kin selection? *International Journal of Primatology, 22*, 203–229.

Collier, P., & Hoeffler, A., (2004). Greed and grievance in civil war. *Oxford Economic Papers.*

Condry, J., & Condry, S., (1976). Sex differences: A study in the eye of the beholder. *Child Development, 47*, 812–819.

Daly, M., & Wilson, M. (1988). *Homicide*. New York: Aldine de Gruyter.

Davis-Kimball, J. (2002). *Warrior women: An archaeologist's search for history's hidden heroines.* New York: Warner Books.

Dyson-Hudson, R., & Smith, E. (1978). Human territoriality: An ecological reassessment. *American Anthropologist, 80*, 21–41.

Eagly, A.H., & Wood, W. (2003). The origins of sex differences in human behavior: Evolved dispositions versus social roles. In C.B. Tavris (Ed.), *Evolution, gender, and rape* (pp. 265–304). Cambridge: MIT Press.

Edgerton, R.B. (2000). *Warrior women: The amazons of Dahomey and the nature of war*. Boulder, CO: Westview Press.

Eibl-Eibesfeldt, I. (1979). *The biology of peace and war: Men, animals, and aggression*. New York: Viking.

Fadiman, J. (1982). *An oral history of tribal warfare; The Meru of Mt. Kenya*. Athens: Ohio University.

Ferguson, N. (2006). *The war of the world: Twentieth-century conflict and the descent of the west*. New York: The Penguin Press.

Ferguson, R.B. (1984). Introduction: Studying war. In R.B. Ferguson (Ed.), *Warfare, culture, and environment* (pp. 1–81). Orlando, FL: Academic.

Ferguson, R.B. (1989a). Do Yanomamo killers have more kids? *American Ethnologist, 16*, 564–565.

Ferguson, R.B. (1989b). Ecological consequences of Amazonian warfare. *Ethnology, 28*, 249–264.

Ferguson, R.B. (1990). Explaining war. In J. Haas (Ed.), *The anthropology of war* (pp. 26–55). Cambridge: Cambridge University Press.

Ferguson, R.B. (1995). *Yanomami warfare: A political history*. Santa Fe: School of American Research Press.

Ferguson, R.B. (1999). A paradigm for the study of war and society. In K. Raaflaub & N. Rosenstein (Eds.), *War and society in the ancient and medieval worlds: Asia, the Mediterranean, Europe, and Meso-america* (pp. 409–458). Cambridge, MA: Center for Hellenic Studies and Harvard University Press.

Ferguson, R.B. (2001). Materialist, cultural and biological theories on why Yanomami make war. *Anthropological Theory, 1*, 99–116.

Ferguson, R.B. (2003). Violent conflict and the control of the state. In R.B. Ferguson (Ed.), *The state, identity, and violence: Political disintegration in the post-Cold War era* (pp. 1–58). New York: Routledge.

Ferguson, R.B. (2006a). Tribal, "ethnic," and global Wars. In M. Fitzduff & C. Stout (Eds.), *The psychology of global conflicts: From war to peace, Vol. 1: Nature vs. nurture* (pp. 41–69). Westport, CT: Praeger Security International.

Ferguson, R.B. (2006b). Archaeology, cultural anthropology, and origins and intensifications of war. In E. Arkush & M. Allen (Eds.), *The archaeology of warfare: Prehistories of raiding and conquest* (pp. 469–523). Gainesville, FL: University of Florida Press.

Ferguson, R.B. (2009). Ten points on war. In A. Waterston (Ed.), *An anthropology of war: Views from the frontline* (pp. 32–49). New York: Beghahn Books.

Ferguson, R.B., & Whitehead, N.L. (2000). *War in the tribal zone: Expanding states and indigenous warfare.* Santa Fe: School of American Research Press.

Fried, M. (1973). On human aggression. In C. Otten (Ed.), *Aggression and evolution* (pp. 355–362). Lexington, MA: Xerox College Publishing.

Fry, D.P. (2006). *The human potential for peace.* New York: Oxford University Press.

Ghiglieri, M.P. (1984). *The Chimpanzees of the Kibale Forest: A field study of ecology and social structure.* New York: Columbia University Press.

Ghiglieri, M.P. (1988). *East of the Mountains of the Moon: Chimpanzee society in the African rain forest.* New York: The Free Press.

Ghiglieri, M.P. (1999). *The dark side of man: Tracing the origins of male violence*. Reading, MA: Perseus Books.

Goldstein, J.S. (2001). *War and gender: How gender shapes the war system and vice versa.* New York: Cambridge University Press.

Goodall, J. (1968). The behaviour of free-living chimpanzees in the Gombe Stream Reserve. *Animal Behaviour Monographs, 1*, 165–311.

Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behavior*. Cambridge, MA: Belknap Press of Harvard University Press.

Gros-Louis, J., Perry, S., & Manson, J.H. (2003). Violent coalitionary attacks and intraspecific killing in wild white-faced capuchin monkeys (*Cebus capucinus*). *Primates, 44*, 341–346.

Grossman, D. (1996). *On killing: The psychological cost of learning to kill in war and society.* New York: Little, Brown and Company.

Haas, J. (1999). The origins of war and ethnic violence. In J. Carman & A. Harding (Eds.), *Ancient warfare: Archaeological Perspectives* (pp. 11–24). Phoenix Mill: Sutton Publishing Ltd.

Hoebel, E.A. (1978). *The Cheyennes: Indians of the great plains*, 2nd ed. New York: Holt, Rinehart, and Winston.

Ingold, T. (1987). *The appropriation of nature: Essays on human ecology*. Iowa City, IA: University of Iowa Press.

Jolly, C.J. (1970). The seed eaters: A new model of Hominid differentiation based on a baboon analogy. *Man, 5*, 5–26.

Jones, D.E. (2005). *Women warriors: A history.* Washington, DC: Brassey's.

Keeley, L.H. (1996). *War before civilization: The myth of the peaceful savage*. New York: Oxford University Press.

Kelly, R.B. (1995). *The foraging spectrum: Diversity in hunter-gatherer life ways.* Washington, DC: Smithsonian Institution Press.

Konner, M. (2006). Human nature, ethnic violence, and war. In M. Fitzduff & C. Stout (Eds.), *The psychology of global conflicts: From war to peace, Vol. 1: Nature vs. nurture* (pp. 1–40). Westport, CT: Praeger Security International.

Knauft, B. (1990). Melanesian warfare: A theoretical history. *Oceania, 60*, 250–311.

Layton, R. (1986). Political and territorial structures among hunter-gatherers. *Man, 21*, 18–33.

LeBlanc, S.A., with Register, K. (2003). *Constant battles: The myth of the peaceful, noble savage.* New York: St. Martin's Press.

Lizot, J. (1989). Sobre la guerra: Una respuesta a N.A. Chagnon (*Science* 1988). *La Iglesia en Amazonas, 44(April)*, 23–34.

Lovejoy, C.O. (2009). Reexamining human origins in light of *Ardipithecus ramidus*. *Science, 326,* 74, 74e1–74e8.

Marks, J. (2003). *What it means to be 98% chimpanzee.* Berkeley, CA: University of California Press.

Meggitt, M. (1977). *Blood is their argument: Warfare among Mae Enga tribesmen of the New Guinea Highlands*. Palo Alto, CA: Mayfield.

Mesquida, C.G., & Wiener, N.I. (1999). Male age composition and severity of conflicts. *Politics and Life sciences, 18*, 181–189.

Mitani, J.C., & Rodman, P.S. (1979). Territoriality: The relationship of ranging pattern and home range size to defendability, with an analysis of territoriality in primates. *Behavioral Ecology and Sociobiology, 5*, 242–251.

Montagu, A.M.F. (1968a). The new litany of "innate depravity," or original sin revisited. In A.M.F. Montagu (Ed.), *Man and aggression* (pp. 3–17). New York: Oxford University Press.

Montagu, A.M.F. (1968b). (Ed.) *Culture: Man's adaptive dimension*. New York: Oxford University Press.

Moore, J.H. (1990). The reproductive success of Cheyenne war chiefs: A contrary case to Chagnon's Yanomamo. *Current Anthropology, 31*, 322–330.

Nishida, T., Haraiwa-Hasegawa, M., & Takahata, Y. (1985). Group extinction and female transfer in wild chimpanzees in the Mahale National Park, Tanzania. *Zeitschrift fur Tierpsychologie, 67*, 284–301.

Otterbein, K. (1973). The anthropology of war. In J. Honigmann (Ed.) *Handbook of social and cultural anthropology* (pp. 923–958). Chicago: Rand McNally College Publishing.

Otterbein, K. (2004). *How war began*. College Station, TX: Texas A&M Press.

Pierson, D. (1999). Natural killers–turning the tide of battle. *Military Review (May–June)*, 60–65.

Power, M. (1991). *The egalitarians–human and chimpanzee: An anthropological view of social organization.* New York: Cambridge University Press.

Reynolds, V., Falger, V.E.E., & Vine, I. (Eds.). (1987). *The sociobiology of ethnocentrism: Evolutionary dimensions of xenophobia, discrimination, racism and nationalism*. London: Croom Helm.

Sahlins, M. (1961). The segmentary lineage: An organization of predatory expansion. *American Anthropologist, 63*, 322–345.

Sapolsky, R.M. (1997). *The trouble with testosterone*. New York: Scribner.

Shaw, R.P., & Wong, Y. (1989). *Genetic seeds of warfare: Evolution, nationalism, and patriotism.* Boston, MA: Unwin Hyman.

Sherwood, C.C., Subiaul, F., & Zawidzki, T.W. (2008). A natural history of the human mind: Tracing evolutionary changes in brain and cognition. *Journal of Anatomy, 212*, 426–454.

Sidorowicz, L.S., & Lunney, G.S. (1980). Baby X revisited. *Sex Roles, 6*, 67–73.

Sillitoe, P. (1978). Big men and war in New Guinea. *Ethnology, 16*, 252–271.

Smith, D.L. (2007). *The most dangerous animal: Human nature and the origins of war*. New York: St. Martin's Press.

Sugiyama, Y. (1968). Social organization of chimpanzees in the Budongo Forest. *Primates, 9*, 225–258.

Tafjel, H., & Turner, J.C. (1986). The social identity theory of intergroup behavior. In S. Worchel & W.G. Austin (Eds.), *Psychology of intergroup relations*, 2nd ed. (pp. 7–24). Chicago: Nelson-Hall.

Thorpe, I.J.N. (2003). Anthropology, archaeology, and the origin of warfare. *World Archaeology, 35*, 145–165.

Tinbergen, N. (1968). On war and peace in animals and man: An ethologist's approach to the biology of aggression. *Science, 160*, 1411–1418.

Tinbergen, N. (1981). On the history of war. In L. Valzelli & L. Morgese (Eds.), *Aggression and violence: A psychobiological and clinical approach* (pp. 31–38). Saint Vincent: Edizioni Centro Culturale.

Tooby, J., & Cosmides, L. (1988). The evolution of war and its cognitive foundations. *Institute for Evolutionary Studies Technical Report 88–1.* Accessed June 7, 2011. http://www.psych.ucsb.edu/research/cep/papers/Evolofwar.pdf

Tylor, E. (1888). *Anthropology: An introduction to the study of man and civilization*. New York: D. Appleton and Co.

Van den Berghe, P.L. (1974). Bringing beasts back in: Toward a biosocial theory of aggression. *American Sociological Review, 39*, 777–778.

Van der Dennen, J.M.G. (1995). *The origin of war: The evolution of male-coalitional reproductive strategy*. Groningen, Netherlands: Origin Press.

Vayda, A.P. (1961). Expansion and warfare among swidden agriculturalists. *American Anthropologist, 63*, 346–358.

Vigilant, L., Hofreiter, M., Siedel, H., & Boesch, C. (2001). Paternity and relatedness in wild chimpanzee communities. *Proceedings of the National Academy of Sciences, 98*, 12890–12895.

Wilson, M.L., Wallauer, W.R., & Pusey, A.E. (2004). New cases of intergroup violence among chimpanzees in Gombe National Park, Tanzania. *International Journal of Primatology, 25*, 523–549.

Wilson, M.L., & Wrangham, R.W. (2003). Intergroup relations in chimpanzees. *Annual Review of Anthropology, 32*, 363–392.

Wrangham, R.W. (1974). Artificial feeding of chimpanzees and baboons in their natural habitat. *Animal Behaviour, 22*, 83–93.

Wrangham, R.W. (1995). Ape cultures and missing links. *Symbols*, Spring, 2–9, 20.

Wrangham, R.W. (1999a). Is military incompetence adaptive? *Evolution and Human Behavior, 20*, 3–17.

Wrangham, R.W. (1999b). Evolution of coalitionary killing. *Yearbook of Physical Anthropology, 42*, 1–30.

Wrangham, R.W. (2005). Planet of the apes. *Harper's, 310 (January)*, 15–18.

Wrangham, R., & Peterson, D. (1996). *Demonic males: Apes and the origins of human violence*. New York: Houghton Mifflin Company.

Wrangham, R., & Pilbeam, D. (2001). African apes as time machines. In B. Galdikas, N.E. Briggs, L.K. Sheeran, G.L. Shapiro, & J. Goodall (Eds.), *All apes great and small: Vol. 1: African apes* (pp. 5–17). New York: Kluwer/Plenum Publishers.

Younger, S.M. (2005). *Leadership, violence, and warfare in small societies: A simulation approach*. Los Alamos: Los Alamos National Laboratory.

Zihlman, A.L, Cronin, J.E., Cramer, D.L., & Sarich, V.M. (1978). Pygmy chimpanzee as a possible prototype for the common ancestor of humans, chimpanzees, and gorillas.

# Chapter 15
# Notes Toward a Human Nature for the Third Millennium

**Walter Goldschmidt**

## The Quest for Man's Nature

Every society needs to come to an understanding of what makes humans tick. For millennia, religion was the primary frame societies had for finding the answers. Theology assigned an outside influence on all behaviors; evil was the work of the devil or the consequences of sin, good was the result of purity and piety. During The Enlightenment, this quest left the hands of religious institutions and gradually turned to scientific enquiry, leaving to the field of anthropology this particular quest.

Early seekers turned first to biology, ideas of inheritance, and soon to the new genetics. These led to such ideas as "criminal types," Kretschmer's body types and, above all, race. These ideas faded within the field because they did not stand close scrutiny, and anthropologists turned to culture, the customs, and mores handed down by oral tradition. But how to explain culture? The cultural anthropologists tried to account for humanity's quirks through Freud, Durkheim, and evolutionary ecology with interesting findings but had little success at seeing the whole. Anthropologists were sure that biology was not the answer and some thought it not even relevant. The generation that came out of the dissidence of the Viet Nam war simply walked away from the issue as if it was of no importance, declaring that no scientific paradigm would work. They settled for saying that it was the nature of man to have culture—an empty phrase.

That explanatory vacuum was quickly filled by students of animal behavior and geneticists and by adherents to the emerging schools of Sociobiology and Evolutionary Psychology. They did not recognize the reality of culture, calling cultural phenomena "epigenetic" or reducing them to "memes," a continuation of biological evolution, but now transmitted by learning. While the concept of "human nature" has largely disappeared from discourse, it is implicit in the assumptions

---

Walter Goldschmidt: Deceased

W. Goldschmidt (✉)
Department of Anthropology, University of California, Los Angeles, CA 90095-1553, USA
e-mail: rwsussma@artsci.wustl.edu

R.W. Sussman, C.R. Cloninger (eds.), *Origins of Altruism and Cooperation*,
Developments in Primatology: Progress and Prospects 36, DOI 10.1007/978-1-4419-9520-9_15,

of geneticists and evolutionists, who treat humans as being motivated solely to preserve their genetic heritage (except for some motives sponsored by an "altruistic gene"), and economists, who assume humans are rational actors seeking only material rewards. Both these notions are not merely wrong, they are harmful to the preservation of the social order, for they sponsor social antagonism and are thus divisive. It is time for anthropologists to take back the understanding of human nature as our responsibility to social theory. This essay is my contribution to what I hope will be an extended and fruitful discussion.

## The Two Faces of Love

Love must surely be the most talked about, fought over, complex, and misunderstood word in the English language. It takes a lot of nerve to address it openly and with the express intent not only to clarify it but also to say that it is even more important than we have realized. The word is colloquially used very loosely, from the love of God to the love of a rare and juicy steak. But these are merely analogical uses, extending sentiments that are part of our biological heritage to more trivial matters. There really are just two kinds of love that come to us from two separate evolutionary sources with very different functions calling for quite different sentiments. The first is sexual (or romantic) love and the other is nurturant (or affectionate) love. They both make us feel good, they both involve stimulation of some of the same erogenous areas, and involve the secretion of the same hormones. Still, nurturant love must be decoupled from sex.

## Affect Hunger

The evidence for the role of affection in human social systems and of other social mammals was sufficiently compelling to me over a half century ago that, in *Man's Way* (Goldschmidt, 1959) I postulated a "need for positive affect" as a universal human characteristic. Growing evidence has emboldened me to be more straightforward and refer to it as "affect hunger." Affect (with the stress on the first syllable) is commonly used in psychology to refer to a feelings or sentiment, either positive or negative, about a person, thing, or event. I am using the phrase to refer to an aspect of human nature that is a biological imperative to seek gratification from affectionate responses. We all need to receive expressions of affect and this need is one of the most powerful forces in the service of the social order. It is not only limited to humans but also found among all social mammals from rodents to whales.

Unlike sexual love, which is as old as dual sexuality itself (and so far as animals are concerned, that means virtually forever), affectionate love only entered into the stream of evolution with the first mammals, when mothers had to take care of the infants they had produced by means of that older kind of love. This second kind of love lacks the drama and intensity of the sexual imperative, but is constantly at work, quietly, insidiously finding its way into every situation involving human interaction and many where even that is wanting. It came into our heritage as part of the shift from laying eggs to producing highly dependent living offspring. Caring for these infants can reasonably be thought of as the evolutionary reason for the origin of affectionate love using endogenous hormones, most notably oxytocin, which is an opiate that induces pleasant sensations and euphoria.

The word hunger refers primarily to a self-engendered, strongly felt desire for food, but the word is used more generically for any self-generated desire for life's necessities, such as water, oxygen, or sleep and, of course, food itself. *Thus, to say humans have "affect hunger" is a claim that humans have an inherent compelling need for receiving demonstrations of positive feeling from other humans in order to preserve their own humanity.* This is a very strong assertion of a very basic issue in the understanding of humanity and it deserves to have compelling supportive evidence. And we find a substantial amount of support—certainly, a lot more than has been put forward for the current *deus ex machina*: a wayward gene for altruism.

There was a time when received wisdom held that the brain was the one organ that was complete at the time of birth, undergoing no modification later. This egregious error has had remarkable staying power despite much information that leads to contrary conclusions. It has long been known that the caring acts of at least some social mammals are responsible for important modification of the nervous system. Dog, cat, and rodent mothers lick their newborn infants to promote the full growth of the dendrites and the synapses on the nerve endings; grooming among primates and caressing among humans achieve the same results. This physical care is demonstrably necessary less for sanitation than for a much more powerful need—to achieve the mental potential of the newborn infant. We must recognize in this the fact that among social mammals, a *social act* is essential for the members of the species to have *the physical capability* for psychosocial competence. As if this were not remarkable enough, we must also recognize that, contrary to our subliminal assumption that structure comes first and behavior follows, in this instance *behavior creates structure*. Please note that I am not making a guess or hypothesis here but merely calling attention to the results of research by psychologists and biologists.

Subsequent research has built an increasingly persistent case for the imperative need for social interaction to bring about the full potential of the individual. By mid-century there was sufficient evidence for assuming the biological basis for these universal social needs. For instance when the psychiatrist René Spitz had studied the living conditions and medical records of a sample of orphanages and found that children who were given fully adequate physical care but no affection had higher rates of mortality, morbidity, and mental disorders. (Notice the use of the term "affection;" this is a euphemism for the word "love" as there is a kind of taboo among psychologists against having any contact with the emotion of "love." Spitz's work was dismissed as Freudian psychoanalysis, while the Freudians frowned on empirical research that might contradict their master's teachings.)

The psychologist James Olds, who from the outset was concerned with the nature of motivation, joined the laboratory of Donald O. Hebbs in the mid-1950s. In his very first empirical observations, Olds discovered the existence of an endogenous reward system among mammals. This discovery was the first step in the direction of understanding that mammals can *choose to act* in response to rewards and are not merely preprogrammed machines.

A few years later, Harry Harlow, a psychologist at the University of Wisconsin, initiated studies of affect deprivation among macaques. His most dramatic work was on the reactions of infant monkeys to two constructed "wire mothers," one with open framework and a milk bottle at her breast, the other with the frame covered with terrycloth but without the milk. It had long been known that baby monkeys hung on to blankets and other rags, like Linus of "Peanuts." These monkeys regularly preferred contact with the cloth-covered surrogate mother over the one with food. When frightened, they always ran to the cloth mother. The hunger for affection appears to be stronger than for food.

Among the many experiments, Harlow and his team did were some on total isolation in infancy that rendered the monkeys psychopathic. Females who were completely deprived of affect would not copulate and when artificially inseminated would not take care of the infant. The infants generally showed characteristic signs of psychosis and suffered in health and in physical, sexual, social, and mental development. One anomalous infant, however, was so persistent in demanding affection that it finally stimulated its mother's latent capacity for affection and she ended up being an ideal mother. I find this incident particularly revealing. This event in Harlow's labs dramatizes the strength of these biological imperatives, mothering and affect need. This mother, motivated by her insistent infant, was able to counteract the destructive effects of her life experience. The nurturant imperative is inextricable to mammalian nature, but it must be developed, through social contact, in each individual. Harlow was fully aware that he was tapping into the deep well of love, and the public was intrigued. He was by nature a contrarian, and by publicly claiming to be studying love, he put himself at odds with the contemporary treatment of this emotion among the psychologists who were then pussyfooting around the topic.

Harlow's research made headlines, but it was also very cruel to the monkeys. The pictures of young monkeys crouched in psychotic positions are haunting, and brought an intense reaction from animal rights activists while Harlow's disregard for academic prejudices kept his fellow psychologists from coming to his defense. The continuing harassment of the students who were continuing Harlow's seminal work after he died brought this seminal line of research to a premature end, and serious examination of love among the monkeys was lost to science.

The British psychiatrist John Bowlby was the first to build on the deeper implications of Spitz's and Harlow's researches in his development of his theory of "attachment." Attachment is a social tie, much like bonding, but far more flexible, that infants and small children normally make with one or more adults. The psychologist Mary Ainesworth devised a way to measure the "quality" of such attachments and it became a measure for judging how well a child was adjusted. The anthropologist Thomas Weisner pointed out that different cultures called for different styles of attachment. Attachment measurement is now a regular feature of child development studies for it is a vital part of the mechanism for socialization. The infant wants—needs, really—a dependable source of affectionate care and works hard to get it. On the cover of my book dealing with these issues (*The Bridge to Humanity,* Goldschmidt, 2005) is a reproduction of an early Picasso depicting a nursing mother making eye contact with her baby, transmitting both nurturance and affection at the same time—a perfect symbol for the theme of that book.

Research on early infant behavior has uncovered a number of inherent traits that are designed to promote affiliation with their caretakers, traits that appear just days (and sometimes just hours) after birth. These include the tracking on the human face (or a representation of one) when it will track on no other object, imitating facial gestures, adapting to the rhythms and give-and-take as in adult "conversations" in which mother and child exchange affect rather than information. Sarah Hrdy showed that such manifestations of sociability and their appeal for affection had survival value. Infant death through neglect or infanticide is not infrequent among tribal peoples and throughout human history, as well as among the monkeys that had caught Hrdy's attention. Mothers are often responsible for such deaths. The infant that endears himself or herself is less likely to meet such an end. Adults must also be programmed to respond to these infantile blandishments, best exemplified by the baby's smile that, when it first appears, is a red-letter day for the family. All adults are softened by this expression of the child's pleasure. Look at ads for watches; they are almost always set with the hands pointing to the ten and two; the smiley face sells watches as well as babies.

These findings have not appealed to evolutionists, who have been so focused on the competitive side of natural selection that they rarely see the collaboration in the animal kingdom; the many living creatures that are huddled together in swarms, flocks, herds, schools, or the like. Even microorganisms collaborate to form mushrooms, while two alien species collaborate to create lichen. This suggests that mutuality is as important as antagonism for species survival. It certainly is for most primates and for humanity.

We have even more compelling evidence that it is no longer necessary to rely on an imaginary Good Samaritan gene; instead, we have real chemicals that give inducements or rewards for sociability. These are the oxytocin and vasopressin (and perhaps other hormones) that give the "altruist" good feelings and even euphoria when he or she engages in caring behavior. Oxytocin has long been known to be involved in inducing mothering behavior, which we may think of as the original purpose of and model for mammalian caring. Parental sacrificial acts have always been seen as essential for genetic continuity. However, these hormones that serve Olds's endogenous motive are not merely concerned with mothering behavior but with the whole gamut of social behavior, varying in detail from one mammalian species to another. These peptides do the work that evolutionists have been seeking to explain with a hypothetical "altruistic gene." We must understand, however, that the genes that are regulating these hormones are not creating altruists but are giving rewards for affectionate acts. And in these rewards, we see that the research that began with Old's discovery of endogenous motivation has begun to reveal that the biological mechanism for human sociality is love.

It is almost inconceivable to me that it took so long for psychologists to explore this phenomenon. A few years ago, when I was writing *The Bridge to Humanity*, I got only one reference that hinted that oxytocin was an opiate that gave a seductive reward for sacrificial behavior, but now it is being intensely investigated by science, perhaps inspired by the marketability of a "Hormone of Love." A 2005 review of the studies on the neurology of social affiliation includes comments by 35 scholars and scientists, who collectively cite over 700 references to field investigations and laboratory studies of primate and rat behavior. Oxytocin appears in the title of 87 of them. The authors say:

> A broad range of evidence suggests a role for endogenous opiates in sociosexual behavior. Endogenous opiate release or receptor binding is increased in rats, monkeys and humans by parturition, lactation and nursing, sexual activity, vaginocervical stimulation, maternal social interaction, brief social isolation, and grooming and other nonsexual tactile stimulation such as play. (Depue and Morrone-Strupinksy, 2005, p. 323)

I do not think the word altruism fits into the scientific paradigm, and I believe it should be replaced with the recognition of the dynamic role of love in social life. This enables us to escape the fool's errand of looking for a special gene, and turn to what we know exists, namely a system of endogenous rewards that are found throughout the mammalian world and have played a central role in establishing the phenomenon of culture. This gives us the other side of the almost universally recognized duality between the impulses that lead to self-aggrandizement and the impulses that lead to the need for expressions of affection and approval from others. We are genetically programmed to do mean and selfish things and to do kind and generous things. The duality between selfish need and affection is found elsewhere in the mammalian world. The new alpha male in the pack of wild dogs will immediately kill newborn pups so the bitch will get in heat and deliver his, but he aids all the dogs in the pack in their highly collaborative hunting, and shares the food with them. Dolphins will gladly share the care of each other's infants, but groups of males have repeatedly been seen raping solo females. *Homo sapiens* has brought this conflict into the realm of consciousness and, in the process, has given itself the power of culture.

Human nature can be understood only if we recognize that this duality *is human nature* and that the struggle to be human always involves finding the balance between the selfish and the compassionate. It is no accident that most religions have focused on this duality, because ambivalence lies deep in the minds and hearts of people everywhere. One of the difficulties with the word altruism is that it tends to obscure this duality, reducing our sense of love to a kind of "time out" from self-interest.

## Grammatical Language

We must now examine two elements characteristic of humanity that are distinct from the issue of love and affection; these are the capacity to make original and copied artifacts, and to articulate sounds according to grammatical rules that enable them to communicate things, real or imagined. The hominid fossil record shows the continuous growth of the brain case; that is, of the brain. It is only reasonable to assume that this growth enabled these two functions that are so distinctively human. The logic that goes into step-by-step manufacture of things, and the articulation of words into a complex message involve similar mental processes.

Hans Kummer (1971), in his classic *Primate Societies,* about baboon social behavior describes an "argument" between the Alpha and Beta male over which direction their trek for the day should go. This is all done with gestures, Beta running up the path he wants and Alpha merely sitting on his haunches and gazing up the other path. It seems clear to me that these two animals had pictures in mind of what they would find on the route they chose. I can imagine Alpha thinking, "he just wants to see if there are some females ready for him in that band down there." And I can imagine Beta thinking, "the old guy doesn't want to climb that steep hill on that route." But they cannot share these thoughts.

This momentary event that took place in Ethiopia many years ago shows us the limitations of animal communication. These baboons can express their preferences through sign language but cannot explain them. They may remember the hazards or delights they experienced in the past and they may project images into the future, but they have no way of sharing these images and expectations. Such limitations make it impossible to create narratives—and culture is built on shared narratives. The failure of the many scholars who have so assiduously attempted to teach various other primates to use grammar and syntax supports the contention that this talent is limited to the human biological heritage. Most, if not all, animals communicate in one way or another whether by sound, smell, gesture, facial expression, or some combination of these, and we also often use such devices in communication. But human language is unique; it has grammar. Grammar is the device by which a communication can place events discussed in time, location, context, and circumstances and how the entities in the discourse relate to one another. None of these has ever been done or taught to other animals, nor observed in the wild, yet all normal children learn them in the first few years of life. All animal discourse is about events taking place in the here and now. If there is no past tense you cannot discuss history and therefore cannot shape a society; if you have no future tense, you cannot talk about loans or interest and therefore cannot have an economic system and if you cannot talk about what goes on elsewhere, you cannot gossip about what you saw happening in the bushes and therefore cannot formulate a moral order. Humans can do this. Moreover, the special genius of these abilities lies in the fact that what we inherit is not the language or the culture, but the capacity to learn whatever language and cultural rules are in operation in the place we happen to have been born.

## Metamorphosis

We are in a desert; on the horizon are mountains with shale scree and giant bare boulders overlooking the dry, almost barren plains, and we wonder that if anything can live on this land, not even the kangaroo and other marsupials, primitive mammals appropriate to this primitive world. But the Aranda have, from time immemorial, enjoyed a cultural life that is rich in ritual, story, and philosophy, knowing that when they die their spirits will return to the "Dream Time" to join their ancestors until they again return to the earth.

Think of yourself now as a baby born in this world, riding astride your mother's left hip as she goes in search of food on this desert, her naked body keeping you warm in the early morning air. From the very beginning these outings make you feel good, you find the smell and the rhythm of your mother's body a kind of intoxicant and you are storing all this in your "intrinsic memory," as the psychologists call things you remember from before you could speak, and in your future life these memories may come to you unbidden and affect your mood. As your mother walks, she tells you stories about each place you pass, sometimes pointing to plants and naming them; sometimes pointing out where you can dig down to water or showing you great craggy rocks and telling you which ancestor had thrown them there in some heroic deed during the "Dream Time." She has told you these before, but the more she tells them the more vivid they become and certain you are that they are true. This goes on almost daily, year after year, the lessons becoming more and more explicit as your knowledge of the language grows. Like lacquer dripping on a figurine, her words are slowly shaping your contours with layer after layer of cultural sentiments, knowledge, beliefs, and manners. Without conscious volition, you have learned the bases and presumptions that underlie the way of life of the Aranda along with the language you speak.

One day, when you have lost your babyhood and are a young boy, a group of men snatch you and carry you out of sight of the women. Over and over, the men toss you as high as they can and hit you with switches as you come down, telling you what you have done wrong and how you must now conduct yourself. With this brief initiation you have become an Aranda man-child. You have crossed two lines you had not known existed before, though you may have been dimly aware of them: one between infancy and childhood and the other between the world of women and the world of the men. You now learn what the men know about the desert, the hunting rules and skills, and your ever-expanding role in the social order of your community.

This is the way every Aranda boy and girl imbibe the Aranda culture, though the sexes each learn their own version. This is the way every normal *Homo sapiens* has acquired his or her culture since the species originated.

## Culture

W*e do not inherit our language nor do we inherit our culture*. What we inherit is the ability to learn the language and culture we are born into. Thus we can fit into the ongoing society from the get-go. We who live in modern complex societies undergo the same generic experience as our Aranda boy, but the specifics vary widely and the baby in the crib next to ours will take a different journey.

Just as no two people see the same rainbow, so no two people have identical culture. Even in the most homogeneous of tribes, each child learns his culture from a different person under unique circumstances and only later, through storytelling and ritual, does the culture coalesce. Culture is the evolutionary solution to making a species so adaptable that it can live in virtually every terrestrial environment. *Homo sapiens* had to learn to find, prepare, and eat different kinds of food, it had to find ways to make the world habitable throughout the seasons and it had to be flexible enough to maintain social cohesion under diverse conditions.

Culture provides a system of motivations, highly flexible, that overlie or reshape the fixed biological ones. The basic motive for living matter is survival, the production of offspring and giving them their start in life. The struggle for survival is riveting, and its inherent drama appeals to the macho outlook of the biologically oriented scholars, so that they dwell on the competitive aspect of human culture without regarding the quiet nurturance that fills our daily life. It is the desire for nurturant love, which we have named "affect hunger," that preserves our social systems. The ancient heritage of antagonistic relationships among members of our species, that originally served the assurance of the continued welfare of our progeny, has been co-opted. The rivalry that is universally demonstrated among humans has been turned away from its original biological purpose, and now reinforces the more peaceable rivalries that make for social cohesion. This rivalry, centering on the social rewards that in sum express one's status in the community, fosters creativity that is also a part of human nature; this creativity has also led to the technology that has enabled the cultural evolution that has taken us so far away from our animal origins. We can point to many self-serving traits that have been transferred to the service of the social self by means of culture. This perception is fundamental to my whole take on human nature. It is clear that the animal instincts are alive and well but that every human being has the power to suppress them, to freely choose not to do harmful things. The things culture empowers humans to suppress, territorialism, hostility, sexual competitiveness, and violence, are the very traits that are emphasized by the evolutionists and anthropologists who ascribe to the notion of the "selfish gene." These mammalian characteristics have been made subject to human control so that humans can have humanity. This is the way Mark Solms and Oliver Turnbull (2002) say it:

> From the neuroscientific point of view, ironically perhaps, the essence of "free will" appears to be the capacity for inhibition – the capacity to choose not to do something. What distinguishes human beings more than anything else from their nearest primate relatives is the development of a higher-level "self" system, which is organized fundamentally on *inhibitory* mechanisms. These mechanisms, which have their physical locus in the prefrontal lobes (the crowning glory of the human brain), bestow on us the capacity to suppress the primitive, stereotyped compulsions that are encoded in our inherited emotional memory systems. On this basis, the inhibitory prefrontal lobes may be regarded, with some justification, as the very tissue of our humanity. (p. 281)

Thus we that find the dualism between good and evil, which forms part of the philosophy of most religions and the subject of much debate in Western philosophy, lies deep in our brains, the consequence of being human. We cannot cast aside our biological heritage as if we had all arrived by immaculate conception, and we cannot wish away the uniqueness of humanity by reducing ourselves to a variety of chimp.

The spectacular growth in the size of the brain has distanced our species from all others. These two resulting human features, grammatical language and making things, are both open-ended and have infinite possibilities. This unending adaptability is what makes culture possible; the beaver dam and the weaverbirds nest are remarkable constructions but they were developed over time by the evolutionary process and now require only the ability to follow instructions. Some birds can pick up new songs to imitate, but this ability is far removed from the self-generating creativity of humans. The Japanese poet is challenged to write the perfect haiku, the English poet to write the perfect sonnet, but each can face the other's challenge at will. This formulation lets us do away with Freud's mystical sounding "pleasure principle" and Dawkins' mythic "gene for altruism" and imaginary "memes," as well as overriding economists' assumptions about the bottom line. When the prefrontal lobe of the brain that Solms and Turnbull called its crowning glory is filled with the neurons that control our speech and that inhibit our animal excesses, can we really see culture as just bundles of memes? Should we continue to be caught in the folk meaning of love as an ineffable force after we have deconstructed it, and found that it has two separate origins, serves different social purposes, and evokes different kinds of behavior?

Freud's description of the dynamics of family life seems just right, but the bestial violence of rape and murder he evokes to explain it does not. If the infantile desire for the comforts of early nurturance is the kind of love each child desires, then Oedipus is not the appropriate model. But the sibling rivalry and father–son conflict are still an insightful perception of the social dynamics of family life.

## The Fundamentals of Human Nature

We are now in a position to articulate the underlying features that characterize *Homo sapiens.* All human beings are guided in their social interaction, perhaps in all action, by two sets of mutually inconsistent directives, one from the biological imperative for genetic survival and the other learned from the people taking care of him during his extended dependency. This appears to be the opposition of good and evil but that is an over-simplification. The former directives prompt the actor to serve his own interests with strength and passion and the latter induces a more generous, socially directed behavior. Passionate self-interest can be put to good purpose and should not automatically be labeled evil. The actual behavioral syndromes found in diverse societies vary; for example, the British suppresses the free expression of affect while the Italians encourage it. Again, the readiness to confront and fight an antagonist as against a readiness to negotiate is shaped by this alternative choice of action; the Plains Indians welcome violent conflict while the Pueblo dwellers of our Southwest are reluctant warriors. In our culture we have both; we call them "hawks" and "doves," and they are products of different socialization in our complex society. This duality, enigmatic and pervasive, is the core feature of human nature, reverberating through all philosophies and all religions. Trust no one who says "it is human nature to do [any single thing]."

The second core feature is the human need for the company and approval of other humans; what I have called "affect hunger." It is a need that must be met in childhood if the individual is to survive and flourish. It will continue to be needed throughout life in the process of becoming competent in the local culture and to preserve one's sense of self as one grows older. Affect hunger never dies.

The third feature of the species is the capacity to believe. Humans innately create a constructed world that is inseparable in our perception from the physical one. I doubt that a cultural world could exist without this human attribute. When you stop to think about it, language itself depends on belief; we have to accept as given from the very start that the words actually mean what we have been told they do. These are merely the first products of the "self-fulfilling prophesy," as Robert Merton labeled the quality of believing that establishes itself as true by the very act of believing it to be true.

But believing is not really that simple. Believing, like other traits of humanity, must remain flexible to serve the adaptability so essential to the cultural way of life. As with the concept of love it deserves close examination. At the same time that there is belief there is doubt – there are changes of mind or of heart, there is even the capacity to "sincerely" believe mutually contradictive things, things which cannot both be true at the same time. The scientific world has given inadequate attention to this vital, enigmatic, aspect of human nature.

I think these three covert elements are universal to the species and make our peculiar and unique mode of life possible. I have passed over some of the more overt traits such as the capacity to learn both language and culture and to internalize rules and expectations and undoubtedly many others, but I see my task as being no more than to open the discourse on this overlooked topic with the hope it will entice many of you to join in.

## References

Depue, R. A. and J. V. Morrone-Strupinksy. 2005. A neurobehavioral model of affiliative bonding: Implications for conceptualising a human trait of affiliation. *Behavioral and Brain Sciences* 28:313–395.

Goldschmidt, W. 1959. *Man's Way: A Preface to Understanding Human Society.* New York, Holt, Rinehart and Winston.

Goldschmidt, W. 2005. *The Bridge to Humanity: How Affect Hunger Trumps the Selfish Gene.* New York, Oxford University Press.

Kummer, Hans. 1971. *Primate Societies; Group Techniques of Ecological Adaptation*. New York, Aldine.

Solms, M. and O. Turnbull. 2002. *The Brain and the Inner World; An Introduction to the Neuroscience of Subjective Experience.* New York, Other Press.

# Part IV
# Neurological and Hormonal Mechanisms for Cooperation and Altruism

# Chapter 16
# Behavior Meets Neuroscience: Achievements, Prospects, and Complexity: Introduction Part IV

**Jane Phillips-Conroy**

This volume has as its goal to address the evolution and nature of cooperation and "altruism". This perspective challenges the pervasive public perception of Darwinian evolution as a process necessarily "red in tooth and claw", a view often promoted by media looking for an attention-getting headline to lead with in the evening news or on the front pages of a popular magazine. Aggression and violence are emotions with high valence and thus easily attract attention. Any of us who has experienced a powerfully aversive event recalls it readily and with little effort can easily retrieve the emotions, even though the event may have occurred in the far distant past. Positive experiences and emotions rarely have the same salience—nor do they receive the same attention in the popular media. The dark appeal of aggression has found a receptive audience and is translated into a conviction that this is how the world works, that aggression, is fundamental and, most important, that it forms the dominant explanatory base for theories that deal with the origins of human behavior and sociality.

Evolutionary biologists, of course, are aware that the popular view of how natural selection works is at best only half of the story. Though natural selection necessarily involves competition—there are winners and losers in the game of differential fitness—competition by no means always implies hostility, let alone physical violence or aggression. It may even involve cooperative and apparently altruistic behaviors—that appear on average to cost the actor more in fitness than he or she gains by the act. Nevertheless, it could be argued that even evolutionary biologists have been overly focused on aggressive and violent behaviors and the hormonal and genetic substrates that underlie them. This volume offers a multidimensional approach, with a broad reach, to correct this bias. It incorporates studies of contemporary human and nonhuman primate populations, and extant reconstructions of ancient life ways from the archeological and paleoanthropological records. The offerings in other parts of this volume confirm the pervasiveness of

---

J. Phillips-Conroy (✉)
Department of Anatomy and Neurobiology, and Anthropology, Washington University School of Medicine, St. Louis, MO 63110, USA
e-mail: baboon@pcg.wustl.edu

R.W. Sussman, C.R. Cloninger (eds.), *Origins of Altruism and Cooperation*,
Developments in Primatology: Progress and Prospects 36, DOI 10.1007/978-1-4419-9520-9_16,

cooperation among social mammals including humans and other primates and make the case that cooperation, not aggression, is the default option in most social behavioral interactions, not a socially strategized position. But if these observations are correct, and our social nature is at its base cooperative, can we identify the neurological pathways and underlying genetic substrates that promote cooperative behaviors? Such mechanisms should be ancient, detectable in our primate (and non-primate) relatives. Genes "for" aggression and violence have attracted much attention. For instance, individuals with low activity of the monoamine oxidase A gene (MAOA) may present with a more aggressive behavioral phenotype and are described as having "warrior genes" (McDermott et al., 2009). The perpetrator's genotype has been offered (and accepted) in some legal domains as a mitigating factor in cases of lethal aggression. Of course, the very fact that we recognize such genotypes as abnormal presupposes the existence of a "normal" genotype, promoting prosocial behavior, that is shared by most of the population.

Current thinking also emphasizes the developmental complexity that is concealed by an expression like "a gene for violence". Like much of our current knowledge of the relationship between the now-sequenced human genome and disease, our understanding of the pathway between gene and behavior is incomplete and prospective. Little is known about influences that are active between gene and phenotype, the complexity of individual (and life-history) variation, and perhaps most important of all, the pervasive influence of epigenetic interactions (Jiang et al., 2008).

The presentations in this part of the volume all focus on this aspect of causation, often called "proximate", and distinguished from the "ultimate" causation that is expressed in terms of Darwinian selection and adaptation. As such, they represent the comparatively recent resurgence of the study of proximate causes and mechanisms, undoubtedly stimulated by the many new, tools in the biologist's physiological and genetic armamentarium. Studies of neuropeptides and steroid hormones in the context of behavior speak to the biological underpinnings of social fundamentals (Snowdon); neuroimaging studies allow us to situate behavior in a functional anatomical context and to localize areas within the brain that are key in certain classes of behavior (Rilling), and the interplay of early experience and later brain function and neural connections are addressed by Pollack. These new techniques have spawned fields with new names (e.g., "social neuroscience" and "neuroeconomics" inter alia) that address proximate causes or the mechanisms directly underlying the behaviors.

In their contribution to the superb volume from a 1996 New York Academy of Sciences meeting "The Integrative Neurobiology of Affiliation" (Carter et al., 1999), Levine et al. (1999) comment that, as a stand-alone topic, affiliation had seen relatively little attention for many years. However, in the two decades preceding the conference, there was a 10-fold increase in the affiliation literature published in Medline. It is not coincidental that in these years, there was also a tremendous increase in the understanding of the mechanisms of social bond formation and notably the roles of neurotransmitters and hormones in behavior. The combination of studies of New World primates and the now-famous story of prairie and mountain voles, with their differing social systems and correlated levels of oxytocin (in females) and vasopressin (in males), has offered an enriched perspective. Information on the neurochemical underpinnings of behavior, combined with studies of the localization of the relevant receptors in the brain, and responses of particular brain regions to cooperative, conflict, or altruistic behaviors, have made it possible to examine complex behaviors along with their hormonal-neuropeptide-and neuroanatomical correlates.

In this volume, Snowdon addresses a series of behavioral and neuroendocrine mechanisms that support and enhance sociality. Grooming, so widely found among most primate taxa, is shown to reward both groomer and groomee, with evidence that it not only stimulates the production of oxytocin but also it has other salubrious effects. Studies have shown that intranasal administration of oxytocin can increase levels of trusting behavior in humans, and that oxytocin, trust, and affiliative behavior are causally linked. Sexual behavior, in itself intrinsically rewarding, results in elevated oxytocin levels which function in forming and cementing social relationships. Similarly, the effects of oxytocin in the central nervous system can be seen in fMRI studies: oxytocin reduces activation of the amygdala and therefore the fear (or lack of trust) response; by contrast, fMRI studies show that activation of the caudate reinforces cooperation. Cooperation is immediately rewarding because these centers receive input from the mesolimbic dopamine system. Clearly, the formation and maintenance of oxytocin-mediated pathways by which collaborative behavior is rewarded have often been favored by natural selection in the evolutionary history of primates and other vertebrates.

Recent work also shows that the role of other steroid and peptide hormones is less straightforward than is often assumed. Testosterone, so often reflexively allotted to the category of hormones implicated predominantly in aggression, has a role as an estrogen precursor. In species where males care for infants, prolactin, typically implicated in maternal care, is elevated in males to levels comparable to those found in females.

These papers collectively demonstrate the unique value of laboratory-based studies, which, by allowing for manipulation of variables in a controlled social setting, offer prospects for arriving at the proximate causes of behavior. As a primatologist, I inevitably reflect how the promise and accomplishments of the perspectives presented in these three papers can translate into our efforts to understand affiliation, cooperation, and aggression in wild primates. The challenges posed by individual and life-history variation are obvious, as is the complexity of getting at the bases of these behaviors in large groups of animals, living in highly uncontrolled social environments. But given these caveats, to what extent is it possible to apply hormonal and neuroscience approaches to the study of wild primate behavior? The conditions imposed by fieldwork are significantly more challenging than that by laboratory studies, and obviously limit the types of studies that can be done. We cannot import an fMRI machine into the field, and behavioral experimentation, while not confined to laboratory environments, is far more difficult to be achieved in the field. Nonetheless, the divide between lab and field is narrowing, and adaptations of these approaches have become increasingly common as field researchers recognize how these lab-based methods may aid in addressing their research questions as well.

Studies of baboons that my colleagues and I have carried out in the field illustrate some of the ways this integration can be achieved. Baboons come in many forms (we recognize six species). Decades of study, by many researchers, have established that there are basic features of social behavior shared by baboons, and many other monkeys also—female philopatry, polygynandrous mating, large multimale groups, and so on. But there are also crucial inter-populational differences in behavior. An example is the Kinda baboon, a small form found in Zambia, Angola, southwest Tanzania, and the Democratic Republic of Congo. Before we began our research, little or nothing was known about their ecology or social behavior. In our work in Zambia over the last 6 years, we have observed hitherto unsuspected behaviors in Kindas (Phillips-Conroy et al., 2009a, b; Weyher, 2010). In particular, Kindas seem distinctly different from other baboons in their patterns of affiliation: male Kindas groom lactating females at frequencies not seen in any other baboons (Kinda males are the active partners in 70% of all grooming interactions compared with values ranging from 1 to 20% in all other baboon taxa). This male behavior is seen in the larger context of Kinda small body size (adult males are the size of adult female chacma baboons), correlated low-size dimorphism, and the increased engagement of females in vigilance behavior. The overall picture is of a baboon with reduced levels of somatic and behavioral dimorphism. We suspect that these seemingly distinctive patterns of affiliative behavior are part of a suite of morpho-physio-behavioral features characteristic of Kindas. In our planned field program, areas of investigation will include comparisons between males and females in their levels of testosterone, assayed from feces, and prolactin, assayed from serum, both of which have been implicated in competitiveness vs. affiliativeness and parenting (Ziegler et al., 2009; Shur, 2009; Beehner et al., 2009).

The classic example of species-specific behavioral variation in baboons is, however, the hamadryas, and its social organization, which is based upon close-knit, harem-like One Male Units. Our study has focused on the differences between hamadryas and the neighboring population of anubis baboons, which show more conventional baboon behavior. We were able to use techniques in the field that enabled us to examine levels of neurotransmitter metabolites in cerebrospinal fluid. Such studies—requiring animals to be captured and sampled by cisternal puncture—are comparatively unusual. Until our studies on the baboons of Ethiopia, only one other study of a naturally functioning population (involving provisioned, semi-free ranging macaques) had been undertaken (Mehlman et al., 1997).

There are clear contrasts in the ontogeny of behavior of male anubis and hamadryas baboons: Anubis males disperse from their natal group at puberty; hamadryas males, by contrast, normally remain for life in the group where they were born. Adult anubis males form temporary consort relationships with periovulatory females, while hamadryas males are typically bachelors without harems as young adults; only as they age are they successful in accumulating females. Bachelor males attempt to find mating opportunities by sneaking copulations or by trying to form harems by kidnapping juvenile hamadryas females. These inherently risky strategies, however, are not typical of mature adult hamadryas males.

We sampled CSF from 49 anubis and 54 hamadryas males. Dental eruption sequences and dental wear patterns allowed us to estimate the ages of individuals, and therefore to explore the relationship between levels of these neurotransmitters and age. Our working hypothesis was that 5-HIAA, reflecting serotonin activity, would be low in anubis males, as had been found in rhesus monkeys that left their natal group earlier than average (Mehlman et al., 1997). Contrary to our prediction, we found that, overall, adult anubis males had a lower HVA/5HIAA ratio (and therefore relatively higher serotonin) than adult hamadryas males (Jolly et al., 2008). In male anubis, the dopamine metabolite (HVA) drops markedly relative to that of 5-HIAA, the serotonin metabolite, in adulthood. By contrast, young adult male hamadryas' have a high HVA/5-HIAA ratio, which apparently falls in later adulthood to levels comparable to those seen in anubis.

Comparative studies on humans and rhesus monkeys enabled us to provide a *post hoc* explanation for the unpredicted finding. High central serotonergic activity has been linked to positive social interactions in human subjects (Knutson et al., 1998) and in male macaques (Botchin et al., 1993; Higley et al., 1992). Some researchers report the ratio of the dopaminergic to serotonergic metabolites to be particularly predictive. Departures from normal HVA/5–HIAA balance, in either direction, are associated with behavioral problems (Oades, 2002; Roy et al., 1986). In particular, Soderstrom et al. (2003) associate a low HVA/5–HIAA ratio in human subjects with impulsivity, irresponsibility, and outward-directed aggression. Such traits are regarded as reprehensible in human males, but might represent a viable reproductive strategy for a young adult male hamadryas, living in the permissive environment of his natal group, and mating opportunistically as he attempts to accumulate a harem of his own.

When he becomes a harem holder, the hamadryas male demonstrates less impulsive, more measured, and socially responsible behavior. This transformation from "bachelor" to harem-holding male generally has occurred by the time the male reaches the age at which his HVA/5–HIAA levels have seemingly dropped considerably.

The male anubis' social trajectory is quite different. He typically does not breed until he has joined a new group, and he never accumulates a "harem". Success throughout his reproductive life is therefore dependent upon effective social negotiation with animals to whom he is unrelated: with females for admission to the group and for collaboration in mating, and with other adult males, for tactical alliances and status. Impulsivity is unlikely to bring consistent reproductive rewards at any age. Thus, our interpretation of these differing trajectories is based on the dispersing and philopatric ontogenies of anubis and hamadryas males, respectively. Interestingly, as hamadryas males develop the social skills similar to those required of adult anubis males, their metabolite levels reflect that change and the initially divergent paths of metabolite ratios of young anubis and hamadryas adult baboons begin to converge.

The Zambian and Ethiopia projects exemplify the application of endocrine and neuroscience approaches to field studies, testing hypotheses suggested by work, such as that reported by Snowdon, in the complicated context of wild animal behavior. In particular, they illustrate the fact that both "aggressive" and "affiliative" behaviors are likely to shape natural social systems and that the contexts in which each is manifested are likely to be very taxon-specific and to differ even among very closely related species. Without information about behavior and population structure in a natural setting, interpretation of this variation would be very difficult—and is likely to be written off as “noise”.

The flow of inspiration and information between lab and field should, however, go in both directions. Much as the laboratory-generated findings of correlations between neurotransmitters and behavior suggested this field study, so too can field studies suggest relevant laboratory investigations. The differences between anubis and hamadryas male behavior with regard to their interactions with females (hamadryas mate-guarding, while anubis typically form estrus-dependent temporary consort interactions) might well be reflected in differing patterns of oxytocin and vasopressin receptor localization and densities in the brain, as has been found in voles (Insel and Shapiro, 1992). Similarly, differences we observed in wild Ethiopian baboons may well be reflected in contrasting features in the serotonin- and dopamine-relevant regions of the brain. While earlier experimental approaches using autoradiography involved sacrificing animals, PET imaging studies using radioactive ligands for specific transmitters (Rilling, 2008), in theory, now can allow pursuit of these questions via neuroimaging methods.

While Rilling’s and Snowdon’s studies suggest links between neuroendocrine factors, neural regions and behavior, more complex pathways are presented in Pollack’s study. Pollack examines the ontogenesis of appropriate social adaptation and the factors that cause it to derail. While the presumption is that some basic neural circuitry is “preconfigured” in the human brain, Pollack highlights the importance of social experience in configuring human brain function. Behaviors that allow the developing individual to survive in a negative environment often set the stage for adverse outcomes and deviant behaviors in later life. While the patterns of these behaviors suggest a possible genetic basis for aberrant behavior, these early events prime future behaviors by altering set points for sensory thresholds. For example, abused children show greater attention to angry faces than to those with less emotional valence, and when presented with faces with ambiguous expression, they interpret the expression as one of anger. The “acquired salience of certain emotional signals” is associated with the failure of regulatory capabilities in individuals who have received strong social stressors early in life, together with neural correlates such as reduction in the size of cortical areas responsible for cognitive function. But—and this is the important and exciting finding—potential negative behavioral outcomes that this might predict can be offset by supportive social intervention.

The stress regulatory system, centered in the hypothalamic–pituitary–adrenal axis of the limbic system, is fundamental in this pathway, with glucocorticoids being the major players. Pollack’s relating of how social environment, regulation, and neural circuitry interact calls to mind the elegant experiments of Meaney et al. at McGill. Over many years they have been exploring the link between the behavior of mother rats and their offspring—as infants and in later life—and more recently have extended their findings to human behavioral pathology as well (Fish et al., 2004; McGowan et al., 2009). Their findings clearly show that even variation in normal maternal behavior affects their infants' response to stress and their regulation of the stress response. "High-care" mothers show high levels of licking and grooming and they nurse their pups in an arched-back posture that facilitates access to the nipple. Their offspring show lower levels of the stress hormones ACTH and corticosterone and a muted response of the HPA axis to stress. While a number of behavioral pathologies have had a genetic component attributed to them, in these studies cross-fostering of pups' shows that it is a maternal behavior, not genes, which is responsible.

How is it that these lower levels of stress hormones were produced? The whole story is a complex one, featuring the intricate interplay of molecules, physiology, and behavior. Meaney et al. discovered that the state of methylation of the glucocorticoid receptor promotor in the hippocampus is key. Reduced methylation is correlated with increased glucocorticoid receptor production; more receptors bind more GC and thus yield a reduced stress response. While pups of both low-care and high-care mothers are born showing equivalent amounts of methylation, this condition changes in the first week of life. In infants of high-care mothers, the GR promoter is significantly demethylated which, in turn, leads to increased production of glucocorticoid receptors and consequently a less-reactive behavioral phenotype in the infant. These changes are stable over life; thus infant females of high-care mothers themselves become nurturant mothers. Thus the mother's behavior influences gene expression of the offspring, and the changes that ensue are heritable via non-genetic pathways. (This has been described as "non-genomic transmission of individual differences in stress reactivity across generations" (Weaver et al., 2004). Should there be any lingering believers in the reality of the nature-nurture dichotomy, this wonderful demonstration of epigenetic interactions should certainly persuade otherwise. Their more recent work on stress, depression, and suicide in humans, shows similar processes at work: the hippocampus of abused individuals who committed suicide had higher levels of DNA methylation and lower levels of GC receptor expression than that seen in non-abused individuals who committed suicide, or in individuals who had died suddenly but not of suicide (McGowan et al., 2009). These studies thus suggest a common regulatory mechanism in rats and humans

## Conclusion

The advances in the fields of neuroendocrine and neuroimaging studies, together with their integration with behavioral studies in humans and nonhuman primates, make this potentially an exciting and exceptionally productive time both for anthropology and for functional neuroscience. Neurochemistry is being woven into stories with larger and complex contexts: a recent study proposes connections among intermittent food scarcity in human evolution, with consequent varying levels of dietary cholesterol, serotonin levels (cholesterol being a precursor to serotonin), and aggression (Wallner and Machatschke, 2009). Whether or not this particular scenario is eventually confirmed, such formulations attest to a growing awareness of the complex interactions among human ecology, neurophysiology, and culture.

One of the exciting implications of recent advances in neurobiological technique and understanding is that new light may be thrown onto historically important debates in the study of human and primate evolution. One such is Dart's notion of early hominins as "killer apes," whose intraspecific aggressiveness was rooted in a new-found, habitual carnivory. The scenario has been highly influential, but its archeological foundation has been severely shaken by reinterpretation of the supposed osteodontokeratic material culture (Shipman and Phillips-Conroy, 1977; Brain, 1981; Chapter 3, this volume). Ethologists, meanwhile (Hart and Sussman, 2009; Chapter 3, this volume), have pointed out that, in habitual mammalian carnivores, the fixed action patterns involved in hunting are quite distinct from those seen in intra-specific aggression. Lorenz famously suggested that social carnivores are more likely than "peaceable" omnivores to have evolved effective behavioral mechanisms to defuse aggressive impulses (Lorenz, 1952). Developments in primate neuroscience should make it possible to test this hypothesis at the physiological and neuroanatomical levels, and in species whose carnivory is opportunistic, and whose biological heritage and general physiology is much closer to our own.

Similarly, Snowdon's argument that sexual behavior stimulates sociality (through the common medium of oxytocin), though very different in its details, harkens back to Zuckerman's argument, advanced some 70 years ago or more (Zuckerman, 1932), that sociality and sexuality were intimately intertwined. However, today, we understand that neurochemical mediators are released in sexual behavior that promote trust and affiliation and hence allow for social bonding.

Finally, and on a somewhat lighter note, it is instructive to see how the popular culture manages to adapt new scientific findings to accord with its own obsessions—inevitably, money, power, and sex. Oxytocin is touted as a magical antidote to social failure—a "hormone of love" or "cuddle hormone." A visit to the Verolabs site (http://www.verolabs.com/) offers the following voice-over for its prime product "Liquid Trust:" "Imagine for a moment that everyone trusted... .you! You would sell more, love more, and accomplish far more than you imagined." Its narration in somnolent, honeyed tones adds to the image and message: your genes may have made you in one way; but a mere inhalation of our product can make you into a trusting, cooperative individual. One of the (many) things left unsaid is that a number of studies of the oxytocin system suggest that altruism and some forms of aggression (i.e., "defensive" aggression) may be quite closely related. This has been observed in studies of prairie voles, where neonatal exposure not only induces pair bonding but also affects mate-guarding behavior (Bales and Carter, 2003). Similar findings derive from a recent experimental study in which administration of oxytocin during a prisoner's dilemma game was observed to promote not only in-group trust and cohesion as expected but also defensive (not offensive) aggression toward the out-group (De Dreu et al., 2010) The authors conclude that the "parochial altruism" induced by oxytocin administration both influences social bonding AND makes individuals ready to defend the group. Such studies, and studies as are exemplified by the following three contributions, highlight the promise—and the challenges—to be faced by scientists in this research area.

**Acknowledgements** This manuscript was significantly improved; thanks to the astute comments of Cliff Jolly.

## References

Bales KL, Carter CS. 2003. Sex differences and developmental effects of oxytocin on aggression and social behavior in prairie voles (*Microtus ochrogaster*). Hormones and Behavior 44(3):178–184.

Beehner J, Gesquiere L, Seyfarth R, Cheney D, Alberts S, Altmann J. 2009. Testosterone related to age and life-history stages in male baboons and geladas. Hormones and Behavior 56(4): 472–480.

Botchin M, Kaplan J, Manuck S, Mann J. 1993. Low versus high prolactin responders to fenfluramine challenge: Marker of behavioral differences in adult male cynomolgus macaques. Neuropsychopharmacology 9(2):93–99.

Brain C. 1981. The hunters or the hunted?: An introduction to African cave taphonomy. University of Chicago Press, Chicago.

Carter C, Lederhendler I, Kirkpatrick B. 1999. The integrative neurobiology of affiliation. The MIT Press, Cambridge, MA.

De Dreu C, Greer L, Handgraaf M, Shalvi S, Van Kleef G, Baas M, Ten Velden F, Van Dijk E, Feith S. 2010. The neuropeptide oxytocin regulates parochial altruism in intergroup conflict among humans. Science 328(5984):1408.

Fish E, Shahrokh D, Bagot R, Caldji C, Bredy T, Szyf M, Meaney M. 2004. Epigenetic programming of stress responses through variations in maternal care. Annals of the New York Academy of Sciences 1036(The Uterus and Human Reproduction):167–180.

Hart D, Sussman RW. 2009. Man the hunted: Primates, predators, and human evolution: Expanded edition. Westview Press, Boulder, CO.

Higley J, Mehlman P, Taub D, Higley S, Suomi S, Linnoila M, Vickers J. 1992. Cerebrospinal fluid monoamine and adrenal correlates of aggression in free-ranging rhesus monkeys. Archives of General Psychiatry 49(6):436.

Insel T, Shapiro L. 1992. Oxytocin receptor distribution reflects social organization in monogamous and polygamous voles. Proceedings of the National Academy of Sciences of the United States of America 89(13):5981.

Jiang Y, Langley B, Lubin F, Renthal W, Wood M, Yasui D, Kumar A, Nestler E, Akbarian S, Beckel-Mitchener A. 2008. Epigenetics in the nervous system. Journal of Neuroscience 28(46):11753.

Jolly C, Phillips-Conroy J, Kaplan J, Mann J. 2008. Cerebrospinal fluid monoaminergic metabolites in *Wild Papio anubis* and *P. hamadryas* are concordant with taxon-specific behavioral ontogeny. International Journal of primatology 29(6):1549–1566.

Knutson B, Wolkowitz O, Cole S, Chan T, Moore E, Johnson R, Terpstra J, Turner R, Reus V. 1998. Selective alteration of personality and social behavior by serotonergic intervention. American Journal of Psychiatry 155(3):373.

Levine S, Lyons D, Schatzberg A. 1999. Psychobiological consequences of social relationships. The Integrative Neurobiology of Affiliation 83–92.

Lorenz K. 1952. King Solomon's ring: New light on animal ways. Routledge and Kegan Paul, London.

McDermott R, Tingley D, Cowden J, Frazzetto G, Johnson D. 2009. Monoamine oxidase A gene (MAOA) predicts behavioral aggression following provocation. Proceedings of the National Academy of Sciences 106(7):2118.

McGowan P, Sasaki A, D'Alessio A, Dymov S, Labonté B, Szyf M, Turecki G, Meaney M. 2009. Epigenetic regulation of the glucocorticoid receptor in human brain associates with childhood abuse. Nature Neuroscience 12(3):342–348.

Mehlman P, Higley J, Fernald B, Sallee F, Suomi S, Linnoila M. 1997. CSF 5-HIAA, testosterone, and sociosexual behaviors in free-ranging male rhesus macaques in the mating season. Psychiatry Research 72(2):89–102.

Oades R. 2002. Dopamine may be ‘hyper’ with respect to noradrenaline metabolism, but ‘hypo’ with respect to serotonin metabolism in children with attention-deficit hyperactivity disorder. Behavioural Brain Research 130(1–2):97–102.

Phillips-Conroy J, Jolly, CJ, Weyher, AH. 2009a. Observations of “Kinda” baboons (*Papio cynocephalus kindae*) in Zambia: Adult males as the active partner male-female grooming dyads. American Journal of Primatology 71(Suppl 1):65.

Phillips-Conroy J, Jolly CJ, Burrell AS, Rogers JA, Weyher AH. 2009b. Genetic and behavioral observations of “kinda” baboons (*Papio cynocephalus kindae*) in Zambia. American Journal of Physical Anthropology Suppl. 48:211.

Rilling J. 2008. Neuroscientific approaches and applications within anthropology. American Journal of Physical Anthropology 137(S47):2–32.

Roy A, Agren H, Pickar D, Linnoila M, Doran A, Cutler N, Paul S. 1986. Reduced CSF concentrations of homovanillic acid and homovanillic acid to 5-hydroxyindoleacetic acid ratios in depressed patients: Relationship to suicidal behavior and dexamethasone nonsuppression. American Journal of Psychiatry 143(12):1539.

Shipman P, Phillips-Conroy J. 1977. Hominid tool-making versus carnivore scavenging. American Journal of Physical Anthropology 46(1):77–86.

Shur M. 2009. Hormones associated with friendship between adult male and lactating female olive baboons, *Papio hamadryas anubis*. Rutgers, The State University of New Jersey, Brunswick, 155p.

Soderstrom H, Blennow K, Sjodin A, Forsman A. 2003. New evidence for an association between the CSF HVA: 5-HIAA ratio and psychopathic traits. British Medical Journal 74(7):918.

Wallner B, Machatschke I. 2009. The evolution of violence in men: The function of central cholesterol and serotonin. Progress in Neuro-Psychopharmacology and Biological Psychiatry 33(3):391–397.

Weaver I, Cervoni N, Champagne F, D’Alessio A, Sharma S, Seckl J, Dymov S, Szyf M, Meaney M. 2004. Epigenetic programming by maternal behavior. Nature Neuroscience 7(8):847–854.

Weyher AH. 2010. Behavioral observations of Kinda baboons (*Papio cynocephalus kindae*) in Zambia. American Journal of Physical Anthropology (Suppl 50):241–242.

Ziegler T, Prudom S, Zahed S, Parlow A, Wegner F. 2009. Prolactin’s mediative role in male parenting in parentally experienced marmosets (*Callithrix jacchus*). Hormones and Behavior 56(4):436–443.

Zuckerman S. 1932. The social life of monkeys and apes. Harcourt, Brace and World, New York.

# Chapter 17
# The Neurobiology of Cooperation and Altruism

**James K. Rilling**

> *"There is no duty more indispensable than that of returning a kindness. All men distrust one forgetful of a benefit."—Cicero*

Much of the cooperation and altruism observed in nonhuman animals is directed toward genetic relatives. However, cooperation among non-relatives also occurs, particularly in social mammals such as lions and meerkats, as well as in several species of primates. Most examples of cooperation among non-relatives in nonhuman animals are best explained by mutualism, in which both partners gain immediate benefits from their behavior (Clutton-Brock, 2009b). For example, in wild dogs, cooperation between hunting partners can increase their per capita success in catching or defending prey (Creel and Creel, 2001). An alternative form of cooperation among non-relatives is reciprocal altruism, in which providing assistance has net costs at the time it is provided which are offset by subsequent benefits (Trivers, 1971). One significant difference between mutualism and reciprocal altruism is that selection can favor cheating and exploitation in the latter but not in the former. It may be this barrier to the evolution of reciprocal altruism that accounts for the limited number of documented cases of reciprocal altruism among nonhuman animals. In contrast to the situation in nonhuman animals, however, reciprocal altruism is pervasive in human society (Clutton-Brock, 2009a), as evidenced by massive holiday gift exchanges and by the social debt we feel after having accepted a favor, as reflected in the commonly heard phrase, "I owe you one." Our penchant for reciprocity is also the very foundation of the division of labor upon which our economy is based.

At the most basic level, altruism toward non-relatives is an evolutionary puzzle since individuals who sacrifice personal fitness to increase the fitness of others will be selected against. However, a number of potential explanations have been offered for the evolution of altruistic behavior in humans. One is that the short-term costs

---

J.K. Rilling (✉)
Departments of Anthropology and Psychiatry and Behavioral Sciences, Emory University, Atlanta, GA 30322, USA
e-mail: jrillin@emory.edu

R.W. Sussman, C.R. Cloninger (eds.), *Origins of Altruism and Cooperation*,
Developments in Primatology: Progress and Prospects 36, DOI 10.1007/978-1-4419-9520-9_17,

of altruism can be outweighed by the benefits of future reciprocity, either from the original recipient (i.e., direct reciprocity) or another group member (i.e., indirect reciprocity). Another is that altruism will evolve if there are people or systems in place that will punish non-altruistic behavior. A third explanation is that altruism is a costly signal that attracts mates and therefore allows altruists to out-reproduce non-altruists (Fehr and Fischbacher, 2003; Henrich and Henrich, 2006; Ridley, 1996).

But why is it that reciprocal altruism among non-relatives seems to be so much more common in humans than in other primates? The explanation may be related to the fact that reciprocal food sharing is a critical adaptation for survival in traditional hunter–gatherer populations such as the !Kung Bushmen, whose lifestyle is similar to that of our ancestors throughout much of human evolution. Meat from wild game constitutes a significant proportion of the Bushman diet. But meat is a very clumped, unpredictable resource, so a hunter cannot be guaranteed success on every outing. Hence, it is critical that he be able to rely on his friends to share their bounty in his time of need so that he can feed himself and his family. If the Bushmen reveal something of the environment in which humans evolved and the selective pressures they faced, then we can imagine that our penchant for reciprocal exchange evolved in the context of the need to share meat in order to survive on the African savannah.

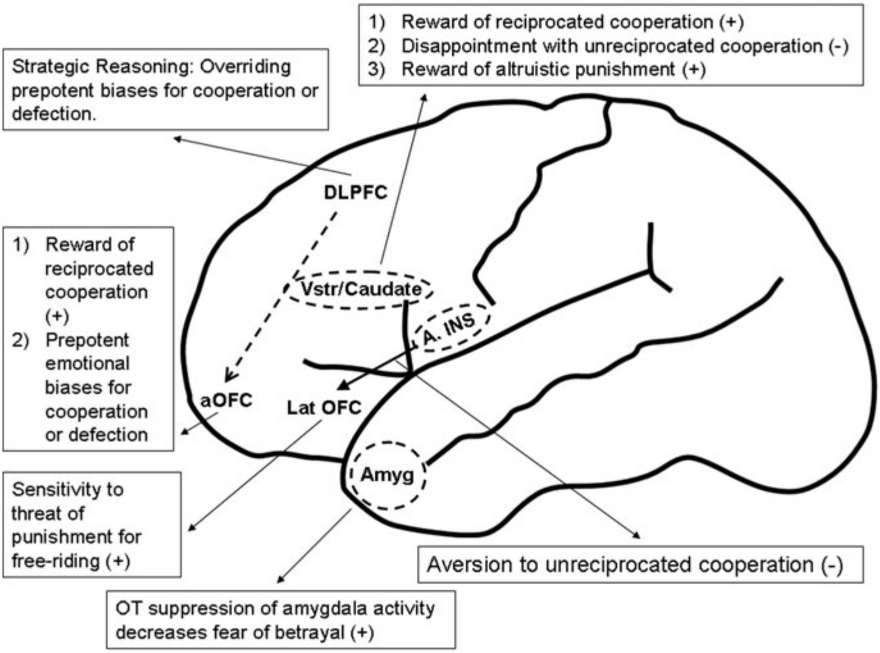


**Fig. 17.1** The neural basis of human altruism. Overall model of the neurobiology of human altruism. DLPFC, dorsolateral prefrontal cortex; VMPFC, ventromedial prefrontal cortex; Lat OFC, lateral orbitofrontal cortex; Amyg, amygdala; A. INS, anterior insula; Vstr, ventral striatum; OT, oxytocin; aOFC, anterior orbitofrontal cortex

As originally suggested by Trivers (1971), the evolution of human altruism would require the evolution of a suite of psychological adaptations to support it. Reciprocal altruism, for example, is inherently unstable, first because both parties are tempted to act in their short-term self-interest by accepting but not reciprocating a favor, and second because both parties fear the selfish impulses of their partner. Thus, the evolution of reciprocal altruism required the evolution of psychological adaptations (1) to overcome the temptation to accept but not reciprocate a favor and (2) to trust social partners and overcome the fear of betrayal. Additional psychological adaptations to support human altruism include (3) a tendency to discriminate against non-reciprocators, (4) a motivation to punish "free riders" who would subvert large-scale cooperation, and (5) a sensitivity to social punishment that can be used to stifle the expression of selfish impulses. Below I discuss potential neural substrates supporting each of these psychological adaptations. A model of the neurobiology of altruism is summarized in Fig. 17.1.

## Biases Toward Reciprocating Altruism

In relationships based on reciprocal exchange, there is of course an obvious temptation to accept but not reciprocate a favor. While this may be beneficial in the short term, it quite likely will not be beneficial in the long term because it will discourage the altruistic from granting future favors. Throughout the animal kingdom, the bias for immediate gratification is strong (Kagel et al., 1995) likely due to its adaptiveness when foraging. In some cases, this bias prevents us from establishing stable, cooperative relationships with each other. However, at least some of the time, humans are able to overcome these biases. How does the human brain accomplish this? Part of the answer seems to be that the short-term *social* reward associated with mutual cooperation can in some cases outweigh the short-term *material* rewards from cheating. That is, the subjective utility of mutual cooperation exceeds that of unilateral defection. fMRI studies of human subjects engaged in Prisoner's Dilemma (PD) or related trust games have shown that reciprocated cooperation is associated with activation of two brain regions involved in reward processing, the caudate nucleus and the orbitofrontal cortex (Delgado et al., 2005; Rilling et al., 2002, 2004) (Fig. 17.2). Moreover, the strength of response in the caudate predicts the degree of future cooperation (King-Casas et al., 2005; Rilling et al., 2002) suggesting that activation of this brain region positively reinforces cooperation. By rendering mutual cooperation immediately rewarding, evolution effectively removes the need to delay gratification. Although the material payoff from mutual cooperation may be realized down the road, the social payoff can be immediate. The areas that are activated by mutual cooperation are areas that receive dopamine projections from the midbrain, the "mesolimbic dopamine" system. This is an ancient system found in all primates that is involved in learning contingencies between actions and rewarding or punishing outcomes (O'Doherty, 2004). The system likely originally evolved to support efficient foraging (Panskepp, 1998) and retains that function in all primates but was apparently also exapted for reciprocal exchange in humans (see also Cloninger and Kedia, Chapter 5).

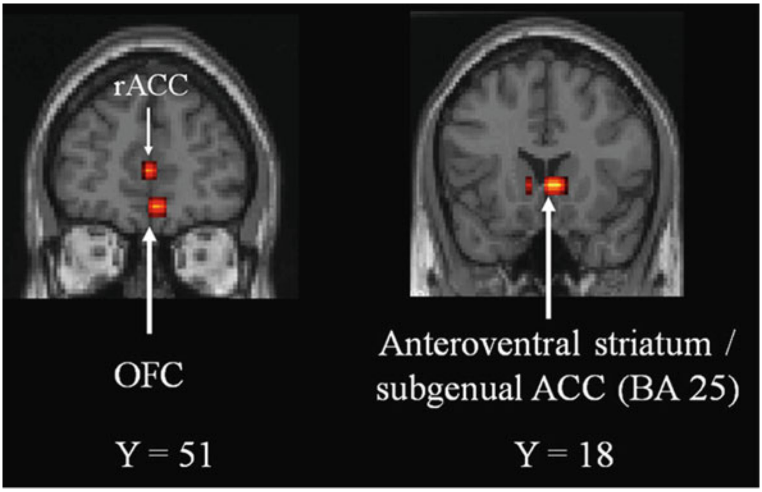


**Fig. 17.2** fMRI activation in ventral striatum and orbitofrontal cortex associated with mutual cooperation in the Prisoner's Dilemma game. From Rilling et al. (2002). Fig. 5a

The mesolimbic dopamine system may also be involved in altruism without the expectation of reciprocity. In recent studies, the neural correlates of altruistic behavior have been examined outside of reciprocal exchange, in tasks where players must decide whether to donate money to charitable organizations. In one study, the decision to voluntarily donate real money to actual charitable organizations was associated with activation in the ventral striatum, another mesolimbic dopamine system target involved in reward processing (Moll et al., 2006). In another study, subjects showing stronger ventral striatum activation to mandatory charity donations were more likely to voluntarily give to the charity when given a choice, whereas subjects showing stronger ventral striatum activation to payments to themselves were less likely to voluntarily donate to the charity (Harbaugh et al., 2007).

But, of course, there is variation in the extent to which people find altruism rewarding. While some people may cooperate for the "warm glow" it provides (Harbaugh et al., 2007), others may cooperate for strategic reasons. That is, they realize that they will benefit materially in the long run by enduring the short-term cost of behaving altruistically, and they consciously override impulses to cheat. Within the prefrontal cortex, the orbitofrontal cortex (OFC) is involved in emotionally guided decision-making (Bechara, 2004; Bechara et al., 2000), whereas the dorsolateral prefrontal cortex (DLPFC) is involved in the exertion of cognitive effort to overcome prepotent response tendencies (Miller and Cohen, 2001). In a recent fMRI study, most subjects activated OFC when choosing to cooperate and DLPFC when choosing to defect, suggesting that cooperation was the prepotent emotional response tendency and cognitive effort was required to override that tendency and defect. However, those subjects who scored highest on a measure of psychopathic personality showed the opposite pattern, that is, OFC activation when defecting and

DLPFC activation when cooperating. For these subjects, cognitive effort may have been required to override an emotional bias to defect (Rilling et al., 2007).

## Trust in the Brain

Of course, cooperation cannot be initiated or sustained without trust. How does the human brain allow us to trust others and overcome our fear of betrayal so that we choose the social risk of cooperation? Recent studies suggest that the neuropeptide oxytocin promotes trust in humans. Oxytocin (OT), which is synthesized in the hypothalamus, is released into the general circulation via the posterior pituitary where it promotes contraction of breast and uterine tissues during lactation and labor, respectively. However, oxytocin is also released into the brain where it functions as a neuropeptide. In rodents, central oxytocin is involved in the formation of social bonds (Young et al., 2005).

Neuropeptides, like OT, cross the blood–brain barrier after intranasal administration, bypassing the bloodstream (Born et al., 2002). This has made it possible to assess the effects of central OT levels on human brain and behavior. In normal subjects, central OT has been linked with increased trusting behavior in an interactive game (Kosfeld et al., 2005). In this two-player game, an "investor" is given an initial sum of money and has the option to transfer a portion of the sum to a "trustee," in which case the transferred amount is tripled. The trustee then has the option to back-transfer a portion of his sum to the investor, thereby reciprocating his trust. In one study, intranasal OT infusion increased the initial monetary transfer by the investor, a measure of trust (Kosfeld et al., 2005). Interestingly, intranasal OT did not increase risk-taking in a nonsocial task.

Intranasal OT administration has recently been combined with fMRI to assess the impact of OT on the neural response to fearful/threatening faces and scenes (Kirsch et al., 2005). The amygdala is a gray-matter nucleus within the medial temporal lobe that is highly responsive to dangerous or threatening stimuli (Dolan, 2000). Compared with placebo, OT decreased activation in the amygdala for both types of fearful stimuli. Elements of the previous two studies were combined in a recent study that imaged subjects with fMRI as they played a trust game either with or without OT treatment. Compared with placebo, OT treatment both increased trust and decreased amygdala activation during the decision-making portion of the game (Baumgartner et al., 2008). These results are consistent with evidence that OT reduces stress and anxiety (Heinrichs et al., 2003; McCarthy et al., 1996) and suggest a potential mechanism by which OT could increase trust by reducing the fear of betrayal (Fig. 17.1).

## Detecting and Avoiding Cooperation With Non-reciprocators

Psychological adaptations to trust and to reciprocate the trust of others constitute only a subset of the human adaptations that support altruism. Humans must also possess adaptations to avoid cooperation with non-reciprocators. It has been suggested that the human mind is uniquely specialized for detecting non-reciprocators or “cheaters” in reciprocal social exchange (Cosmides and Tooby, 2000). This notion is based on informed speculation of the evolutionary selective pressures that shaped our species (e.g., reciprocal food sharing), as well as empirical evidence that humans are better at reasoning about social exchange than other nonsocial rules (Cosmides and Tooby, 2000). Further evidence for this specialization is provided by the finding that people have enhanced memory for faces of others who are described as untrustworthy (Mealey et al., 1996; Chapter 19, this volume). This tendency to remember non-reciprocators may be related to a more generalized aversion to “free riders” (i.e., those who accept benefits without paying expected costs), as suggested by behavioral economics experiments in which people often choose to punish free riders, even if the punishment is personally costly (Fehr and Fischbacher, 2003; Fehr and Gachter, 2002).

As mentioned above, mutual cooperation in the PD game is associated with activation of the caudate nucleus. On the other hand, cooperation by the player combined with defection by the partner is associated with deactivation of the caudate nucleus (Rilling et al., 2002, 2004). Mesencephalic dopamine projections to the caudate are hypothesized to carry “teaching signals” that allow us to learn contingencies between our own responses and either rewarding or punishing outcomes and adjust behavior accordingly (Montague et al., 1996; O’Doherty, 2004; Schultz, 1997; Schulz et al., 1997). Thus, just as the activation within the caudate seems to positively reinforce cooperating with a reciprocating partner, deactivation may discourage cooperation with a non-reciprocating partner.

Cooperation by the player combined with defection by the partner is also associated with activation of the anterior insular cortex, which may be a neural correlate of an aversive response to free riding (Rilling et al., 2008) (Fig. 17.3). The

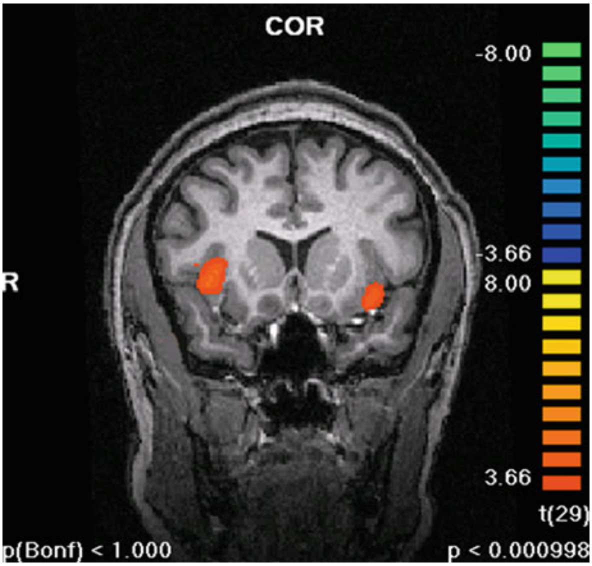


**Fig. 17.3** fMRI activation in the anterior insula in response to unreciprocated cooperation in the Prisoner’s Dilemma game. From Rilling et al. (2008). Fig. 7

anterior insula is involved in sensing the state of the viscera (e.g., heart, lungs, gut). It is activated in response to a variety of negative social interactions, from social exclusion (Eisenberger et al., 2003), to receiving an unfair offer in an Ultimatum Game (Sanfey et al., 2003), to watching a loved one receive a painful stimulus (Singer et al., 2004). Anterior insula is also responsive to physically painful stimuli and its activity is correlated with skin conductance responses (Critchley et al., 2000). These results and others suggest that the anterior insula is involved in mapping physiological states of the body, including pain, touch, and visceral sensations of autonomic arousal (Craig, 2002, 2003; Critchley, 2005). The right anterior insula, in particular, is thought to be a cortical station for interoception that may play a role in decision-making by instantiating valenced subjective feeling states (Damasio, 1994). Finally, recent fMRI data implicate right anterior insula in aversive conditioning (Seymour et al., 2004). Collectively, these findings suggest that the anterior insula may be involved in marking negative social interactions as aversive so that individuals learn to avoid such interactions in the future. Although the magnitude of activation in anterior insula does not by itself predict subsequent defection by the player in future interactions with the same non-reciprocating partner, correlated activity (i.e., functional connectivity) between anterior insula and lateral orbitofrontal cortex (OFC) does. This finding is consistent with evidence that lateral OFC is involved in the evaluation of punishing stimuli that may lead to behavioral changes (Kringelbach and Rolls, 2004) (Fig. 17.1).

Additional evidence with respect to brain regions that may be involved in cheater detection comes from the study of a brain-damaged patient who showed selective deficits in reasoning about social exchange (Stone et al., 2002). This patient suffered damage to orbitofrontal cortex, temporal pole (anterior tip of the temporal lobe), and amygdala, suggesting that these areas may be involved in detecting violations of social contracts.

## Motivation to Punish Free Riders

Although humans as a species are highly cooperative, there is significant heterogeneity in the cooperative tendencies among individuals, including some free riders who accept the benefits of public goods without paying the costs. Behavioral economics experiments suggest that large-scale cooperation depends on the willingness of at least some individuals to endure the costs of punishing free riders (Fehr and Fischbacher, 2003; Henrich and Henrich, 2006). How does the human brain mediate this so-called “altruistic punishment”? Two recent neuroimaging studies have shown that brain-reward regions, including the caudate nucleus and related structures in the ventral striatum, are activated when subjects successfully punish others who have previously treated them unfairly in a trust game or a PD game (de Quervain et al., 2004; Singer et al., 2006). In one study, the effect was observed for male but not female subjects, but among males, activation in reward areas in response to punishment of the non-reciprocator was correlated with self-reported desire for revenge (Singer et al., 2006). In the other study, subjects showing stronger activation of reward areas were willing to incur greater costs in order to punish the non-reciprocating partner (de Quervain et al., 2004). Thus, the motive to altruistically punish is correlated with and perhaps causally related to activation in brain-reward systems (Fig. 17.1).

## Sensitivity to Social Punishment

Both ethnographic evidence (Sober and Wilson, 1998) as well as experiments in behavioral economics have shown that some people will cooperate only under threat of punishment for not doing so (Fehr and Gachter, 2002). Thus, sensitivity to the threat of punishment is an important motive for cooperation in some people. In a recent fMRI study (Spitzer et al., 2007), subjects were imaged while playing two different games. In one game, which resembles a dictator game, subjects (player A) received a monetary endowment that they could distribute freely between themselves and another player (player B). In this game, player B is a passive recipient of player A's monetary transfer. In the other game, player B could choose to pay money to financially punish player A after having been informed of player A's decision. Player A transferred substantially more money to player B in the punishment compared with the non-punishment condition. Those subjects who showed the largest

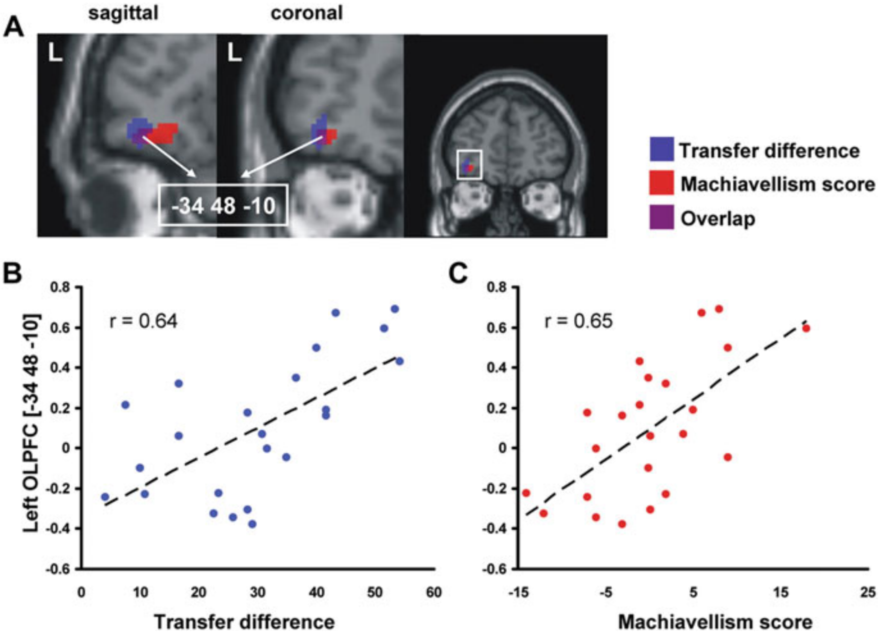


**Fig. 17.4** Lateral orbitofrontal cortex activity is correlated with the extent to which subjects adjust their altruistic behavior under threat of punishment. From Spitzer et al. (2007). Fig. 6

change in monetary transfer from the non-punishment to the punishment condition also showed the greatest increase in activation of the lateral orbitofrontal cortex across conditions (Fig. 17.4). As mentioned above, lateral OFC is involved in the evaluation of punishing stimuli that may lead to behavioral changes (Kringelbach and Rolls, 2004). This study suggests that lateral OFC motivates altruistic behavior in response to the threat of punishment (Fig. 17.1).

## Evolution of the Neural Substrates for Cooperation and Altruism

Although both the anterior insula and the caudate nucleus are involved in altruistic behavior, they are also involved in nonsocial decision making such as avoiding physically noxious stimuli and foraging, respectively. These neural systems likely initially evolved to support these more fundamental aspects of behavior. When social skills became more crucial with the evolution of primates, these systems may have been exapted for new functions such as detecting harmful social stimuli and learning when, and to whom, altruism should be dispensed. However, in the process of adapting these old systems to novel demands, they may well have been modified and social pressures may have left their imprint. The exact nature of the neurobiological adaptation that allows the human caudate nucleus and anterior insula to support and regulate altruistic social behavior is uncertain at this time due to limited comparative data but could relate to greater cortical and subcortical responsiveness to social stimuli that drives autonomic responses that are then sensed by the insula, as well as changes in the cortical inputs to the caudate.

## The Neurobiology of Cooperation in Social Mammals

Are the neural mechanisms supporting human reciprocal altruism discussed above relevant to explaining cooperation in nonhuman animals? Although reciprocal altruism appears to be uncommon in nonhuman animals, cooperation among nonrelatives does occur in some species of social mammals. In most cases, this cooperation takes the form of mutualism in which the benefits of cooperation are immediate and/or guaranteed rather than delayed and uncertain as they are in reciprocal altruism. This synchrony of costs and benefits means it is rarely possible to reap a benefit without paying a cost, and consequently selection pressure to deter cheating may have been weak. Still, it is possible that the mesolimbic dopamine system is involved in reinforcing mutualistic cooperation among nonhuman mammals, just as it is involved in supporting reciprocal altruism in humans. Given the synchrony of costs and benefits in mutualism, there may also be less need for trust in nonhuman cooperative relationships compared with human reciprocal altruism. However, just as OT appears to promote trust in human relationships, it is also the foundation for pair-bonds between unrelated adult male and female prairie voles (Young et al., 2005, see also, Chapter 18, this volume). Chimpanzee females will collectively punish unruly males that threaten group stability (Waal, 1996), and it is possible that this behavior, like human altruistic punishment, is motivated by activation of the mesolimbic dopamine system. To the extent that these males adjust their behavior in response to such punishment, this behavioral change may be motivated by activation in the lateral OFC, a brain region involved in the evaluation of punishing stimuli that may lead to behavioral changes. This is all pure speculation, however, until actual data come to bear on this question.

## Summary

Reciprocal altruism is much more common in humans than in other primates. Human reciprocal altruism may be dependent on prepotent emotional biases for cooperation, represented in the medial orbitofrontal cortex, combined with exaptations of both brain-reward systems to reinforce cooperation with reciprocators and the pain system to discourage cooperation with non-reciprocators. The neuropeptide oxytocin may also promote human cooperation by decreasing amygdala responses to potentially threatening stimuli, which may reduce the fear of betrayal and increase trust. Activation of the brain-reward systems also appear to be important for motivating altruistic punishment of free riders that can subvert large-scale cooperation, and the lateral orbitofrontal cortex is involved in responsiveness to altruistic punishment that motivates norm-abiding behavior. It remains to be seen whether some of these mechanisms also support cooperation among social mammals.

## References

Baumgartner T, Heinrichs M, Vonlanthen A, Fischbacher U, and Fehr E. 2008. Oxytocin shapes the neural circuitry of trust and trust adaptation in humans. Neuron 58(4):639–650.

Bechara A. 2004. The role of emotion in decision-making: evidence from neurological patients with orbitofrontal damage. [Review] [58 refs]. Brain & Cognit 55(1):30–40.

Bechara A, Damasio H, and Damasio AR. 2000. Emotion, decision making and the orbitofrontal cortex. Cerebral Cortex 10(3):295–307.

Born J, Lange T, Kern W, McGregor GP, Bickel U, and Fehm HL. 2002. Sniffing neuropeptides: a transnasal approach to the human brain. Nat Neurosci 5(6):514–516.

Clutton-Brock T. 2009a. Cooperation between non-kin in animal societies. Nature 462(7269): 51–57.

Clutton-Brock T. 2009b. Structure and function in mammalian societies. Philos Trans R Soc Lond B Biol Sci 364(1533):3229–3242.

Cosmides L, and Tooby J. 2000. The cognitive neuroscience of social reasoning. In: Gazzaniga MS (ed.). The new cognitive neurosciences. Champaign, IL: Massachusetts Institute of Technology, pp. 1259–1270.

Craig AD. 2002. How do you feel? Interoception: the sense of the physiological condition of the body. Nat Rev Neurosci 3(8):655–666.

Craig AD. 2003. Interoception: the sense of the physiological condition of the body. Curr Opin Neurobiol 13(4):500–505.

Creel S, and Creel NM. 2001. The African wild dog: behavior, ecology and conservation. Princeton, NJ: Princeton University Press, 360 pp.

Critchley H, Elliot R, Mathias C, and Dolan R. 2000. Neural activity relating to the generation and representation of galvanic skin conductance responses: a functional magnetic resonance imaging study. J Neurosci 20(8):3033–3040.

Critchley HD. 2005. Neural mechanisms of autonomic, affective, and cognitive integration. J Comp Neurol 493(1):154–166.

Damasio AR. 1994. Descartes' error: emotion, reason, and the human brain. New York: G.P. Putnam, xix, 312 pp.

Delgado MR, Frank RH, and Phelps EA. 2005. Perceptions of moral character modulate the neural systems of reward during the trust game. Nat Neurosci 8(11):1611–1618.

de Quervain DJ, Fischbacher U, Treyer V, Schellhammer M, Schnyder U, Buck A, and Fehr E. 2004. The neural basis of altruistic punishment. Science 305(5688):1254–1258.

Dolan RJ. 2000. Emotional processing in the human brain revealed through functional neuroimaging. In: Gazzaniga MS (ed.). The new cognitive neurosciences. Champaign, IL: MIT Press, pp. 1115–1131.

Eisenberger NI, Lieberman MD, and Williams KD. 2003. Does rejection hurt? An FMRI study of social exclusion. Science 302(5643):290–292.

Fehr E, and Fischbacher U. 2003. The nature of human altruism. Nature 425(6960):785–791.

Fehr E, and Gachter S. 2002. Altruistic punishment in humans. Nature 415(6868):137–140.

Harbaugh WT, Mayr U, and Burghart DR. 2007. Neural responses to taxation and voluntary giving reveal motives for charitable donations. Science 316(5831):1622–1625.

Heinrichs M, Baumgartner T, Kirschbaum C, and Ehlert U. 2003. Social support and oxytocin interact to suppress cortisol and subjective responses to psychosocial stress. Biol Psychiatry 54(12):1389–1398.

Henrich J, and Henrich N. 2006. Culture, evolution and the puzzle of human cooperation. Cognit Syst Res 7:220–245.

Kagel JH, Battalio RC, and Green L. 1995. Economic choice theory: an experimental analysis of animal behavior. Cambridge: Cambridge University Press.

King-Casas B, Tomlin D, Anen C, Camerer CF, Quartz SR, and Montague PR. 2005. Getting to know you: reputation and trust in a two-person economic exchange. Science 308:78–83.

Kirsch P, Esslinger C, Chen Q, Mier D, Lis S, Siddhanti S, Gruppe H, Mattay VS, Gallhofer B, and Meyer-Lindenberg A. 2005. Oxytocin modulates neural circuitry for social cognition and fear in humans. J Neurosci 25(49):11489–11493.

Kosfeld M, Heinrichs M, Zak PJ, Fischbacher U, and Fehr E. 2005. Oxytocin increases trust in humans. Nature 435(7042):673–676.

Kringelbach ML, and Rolls ET. 2004. The functional neuroanatomy of the human orbitofrontal cortex: evidence from neuroimaging and neuropsychology. Prog Neurobiol 72(5):341–372.

McCarthy MM, McDonald CH, Brooks PJ, and Goldman D. 1996. An anxiolytic action of oxytocin is enhanced by estrogen in the mouse. Physiol Behav 60(5):1209–1215.

Mealey L, Daood C, and Krage M. 1996. Enhanced memory for faces of cheaters. Ethol Sociobiol 17:119–128.

Miller E, and Cohen J. 2001. An integrative theory of prefrontal cortex function. Annu Rev Neurosci 24:167–202.

Moll J, Krueger F, Zahn R, Pardini M, de Oliveira-Souza R, and Grafman J. 2006. Human fronto-mesolimbic networks guide decisions about charitable donation. Proc Natl Acad Sci USA 103(42):15623–15628.

Montague PR, Dayan P, and Sejnowski TJ. 1996. A framework for mesencephalic dopamine systems based on predictive Hebbian learning. J Neurosci 16(5):1936–1947.

O'Doherty JP. 2004. Reward representations and reward-related learning in the human brain: insights from neuroimaging. Curr Opin Neurobiol 14(6):769–776.

Panskepp J. 1998. Affective neuroscience: the foundations of human and animal emotions. New York: Oxford University Press.

Ridley M. 1996. The origins of virtue. London: Viking, viii, 295 pp.

Rilling JK, Glenn AL, Jairam MR, Pagnoni G, Goldsmith DR, Elfenbein HA, and Lilienfeld SO. 2007. Neural correlates of social cooperation and non-cooperation as a function of psychopathy. Biol Psychiatry 61(11):1260–1271.

Rilling JK, Goldsmith DR, Glenn AL, Jairam MR, Elfenbein HA, Dagenais JE, Murdock CD, and Pagnoni G. 2008. The neural correlates of the affective response to unreciprocated cooperation. Neuropsychologia 46:1256–1266.

Rilling JK, Gutman DA, Zeh TR, Pagnoni G, Berns GS, and Kilts CD. 2002. A neural basis for social cooperation. Neuron 35(2):395–405.

Rilling JK, Sanfey AG, Aronson JA, Nystrom LE, and Cohen JD. 2004. Opposing BOLD responses to reciprocated and unreciprocted altruism in putative reward pathways. NeuroReport 15(16):2539–2543.

Sanfey AG, Rilling JK, Aronson JA, Nystrom LE, and Cohen JD. 2003. The neural basis of economic decision-making in the ultimatum game. Science 300(5626):1755–1758.

Schultz W. 1997. Dopamine neurons and their role in reward mechanisms. Curr Opin Neurobiol 7(2):191–197.

Schulz W, Dayan P, and Montague PR. 1997. A neural substrate of prediction and reward. Science 275:1593–1599.

Seymour B, O'Doherty JP, Dayan P, Koltzenburg M, Jones AK, Dolan RJ, Friston KJ, and Frackowiak RS. 2004. Temporal difference models describe higher-order learning in humans. Nature 429(6992):664–667.

Singer T, Seymour B, O'Doherty J, Kaube H, Dolan RJ, and Frith CD. 2004. Empathy for pain involves the affective but not sensory components of pain.[see comment]. Science 303(5661):1157–1162.

Singer T, Seymour B, O'Doherty JP, Stephan KE, Dolan RJ, and Frith CD. 2006. Empathic neural responses are modulated by the perceived fairness of others. Nature 439(7075):466–469.

Sober E, and Wilson DS. 1998. Unto others – the evolution and psychology of unselfish behavior. Cambridge, MA: Harvard University Press.

Spitzer M, Fischbacher U, Herrnberger B, Gron G, and Fehr E. 2007. The neural signature of social norm compliance. Neuron 56(1):185–196.

Stone VE, Cosmides L, Tooby J, Kroll N, and Knight RT. 2002. Selective impairment of reasoning about social exchange in a patient with bilateral limbic system damage. Proc Natl Acad Sci USA 99(17):11531–11536.

Trivers RL. 1971. The evolution of reciprocal altruism. Q Rev Biol 46:35–57.

Waal FD. 1996. Good natured: the origins of right and wrong in humans and other animals. Cambridge, MA: Harvard University Press, 296 pp.

Young LJ, Murphy Young AZ, and Hammock EA. 2005. Anatomy and neurochemistry of the pair bond. J Comp Neurol 493(1):51–57.

# Chapter 18
# Behavioral and Neuroendocrine Interactions in Affiliation

**Charles T. Snowdon**

Affiliations take many forms in the social relationships of both human and nonhuman primates. Which relationships are most important will vary as a function of the social structure and breeding system that is typical of a species and will also vary with life history stages within a species. For example, in species where males disperse and females remain, it is likely that the primary relationships (due to both genetic relatedness and social experience) will be between female kin with both mother–offspring and sister–sister relationships having a high priority. In species, where females disperse and males remain, there will be a strong affiliation between brothers as well as between mothers and offspring. In pair-bonded biparental and cooperatively breeding species, there is a strong affiliation or attachment between pair mates and between infants and their primary caregiver. For example, in experimental studies with biparental titi monkeys (*Callicebus moloch*), Mendoza and Mason (1986) have shown that when given a choice between mate and infant, the parents will choose each other and when given a choice between parents, infants will choose their fathers which have been the primary caregivers. In cooperatively breeding species such as the cotton-top tamarin (*Saguinus oedipus*), where fathers and older siblings provide substantial infant care through carrying and food transfers, infants who have become independent will, when frightened, preferentially seek the individual (father or older sibling) that had been most active in carrying and food transfers (Kostan and Snowdon, 2002).

Affiliative relationships may vary with life history stages. An infant's primary relationship will often be with its mother (though in species with biparental or cooperative care, it may be a father or sibling). As infants become independent of adult caregivers, primary affiliative relationships are likely to be established with other same-aged peers in species where multiple breeding females are present within the same group or with older siblings in species with only one breeding pair. Following puberty, individuals in multi-male, multi-female groups are likely to form affiliative relationships with same sex individuals with the intensity of the

---

C.T. Snowdon (✉)
Department of Psychology, University of Wisconsin, Madison, WI 53706, USA
e-mail: snowdon@wisc.edu

R.W. Sussman, C.R. Cloninger (eds.), *Origins of Altruism and Cooperation*,
Developments in Primatology: Progress and Prospects 36, DOI 10.1007/978-1-4419-9520-9_18,

relationships being greater in the non-dispersing sex. In species that form pair-bonds, a strong heterosexual relationship is likely with affiliation being the greatest in the initial stages of relationship formation and the lowest as the pair moves from courtship to parenthood where affiliation with infants will become important. These many social relationships, which change with life history, are sustained through a variety of proximate mechanisms both behavioral and neuroendocrine. This chapter reviews several of these mechanisms and are as follows: (1) social grooming, (2) non-conceptive sex, (3) social support and tolerance, (4) parenting with specific mechanisms that begin for males in some species even during their mates' pregnancies, and (5) cooperation, prosocial behavior, and teaching.

## Social Grooming

Social grooming plays an important role in maintaining social relationships with the most common finding that subordinate animals are more likely to groom more dominant animals than the reverse, presumably as an indicator of status since grooming is rewarding to the recipient (see below). Furthermore, Dunbar (1991) has argued that there is a direct relationship among group size, number of social interactions, brain size, and amount of grooming behavior.

Whereas these patterns of grooming are common in many terrestrial Old World primates, New World primates provide some interesting exceptions. First, there is a negative correlation among body size, group size, and amount of grooming (Snowdon and Cronin, 2009) with the smallest species living in the smallest groups [marmosets and tamarins grooming up to 21% of the day (Lazaro-Perea et al., 2004)] and the largest species living in the largest groups not grooming at all (*Brachyteles arachnoides* muriquis, Strier, 1992). Furthermore, there is evidence of grooming down the hierarchy in both capuchin monkeys (*Cebus apella*, Parr et al., 1997), common marmosets (*Callithrix jacchus*, Lazaro-Perea et al., 2004), and cotton-top tamarins (*Saguinus oedipus*, Ginther and Snowdon, 2009). In the cooperatively breeding marmosets and tamarins, breeding adults groom alloparents more than the reverse, and in cotton-top tamarins, the amount of grooming by a parent is directly related to the amount of infant care the recipient provided in the previous litter. Mothers groom most the alloparents that had carried most on the previous birth and fathers groom most those who had carried the least on the previous birth (Ginther and Snowdon, 2009). One explanation for these different responses by fathers versus mothers is that the carrying of mothers is reduced significantly with a single additional helper, whereas the workload of fathers (and paternal weight loss, Achenbach and Snowdon, 2002) is reduced linearly with each additional helper (Zahed et al., 2010). Thus, mothers may be rewarding those who provided the most help in a previous birth, while fathers are grooming to recruit additional helpers with the next birth.

In both wild common marmosets (Lazaro-Perea et al., 2004) and in captive cotton-top tamarins (Ziegler et al., 2004), breeding males groom their mates significantly more than they are groomed by their mates. However, Löttker et al.

(2007) found the opposite asymmetry in moustached tamarins (*Saguinus mystax*), with pregnant females grooming males more frequently. If grooming provides some sort of reward to the recipient, then a sexual asymmetry among pair-bonded species may reflect greater male investment in maintaining the relationship due to paternal uncertainty or of greater female investment to retain males for infant care.

The assumption is that being groomed provides some sort of reward. Grooming has been shown to release endogenous opioids in the brains of monkeys that have been groomed (Keverne et al., 1989), and work on the role of touch and massage in both rats and humans shows that these behaviors release the hormone oxytocin (Uvnäs-Moberg, 1998). Thus, there is a neuroendocrine basis for suggesting grooming is rewarding to recipients. The heart rate of recipients of grooming is also lowered in both pigtail macaques (*Macaca nemestrina*, Boccia et al., 1989) and rhesus macaques (*Macaca mulatta*, Aureli et al., 1999).

A recent study by Shutt et al. (2007) measured fecal hormonal samples from Barbary macaques (*Macaca sylvanus*) in relationship to grooming and found a converse effect, namely that glucocorticoid levels were lower in the animal doing the grooming than in the recipient. These results taken together suggest positive neuroendocrine effects for both the groomer and the recipient of grooming, supporting the hypotheses that grooming has a rewarding and calming function.

## Non-conceptive Sex

Many primates engage in sexual behavior at times when conception is not possible. Why should animals mate when conception cannot occur? In captive macaques one explanation relates to enclosure size. When females can move away from or escape a male, sexual behavior is frequently concentrated at the time of ovulation (Wallen, 1982). Female solicitation of sex and receptivity is controlled by ovarian hormones which may play a critical role in male–female affiliation in macaques. In one noteworthy study, several ovariectomized females lived in a large indoor–outdoor enclosure with several males. Over several years of observation, there were no observed social interactions between males and females. They behaved as separate species. Then one Friday the females were injected with ovarian hormones and by Monday morning when the researchers returned, the males and females were close together, engaging in mounts and grooming (Tannenbaum and Wallen, 1997). In this case affiliative behavior between sexes was initiated by female gonadal hormones.

However, there are many other examples in field and captive studies of primates where sexual activity extends well beyond a period of fertility. Thus, female chimpanzees and baboons have a conspicuous sexual swelling around the anogenital region that signals ovulation but is present for up to 2 weeks prior to ovulation. In a series of ingenuous studies, Bielert (1982) showed that swellings are estrogen dependent and that males are sexually aroused by the swellings, increasing masturbation rates as swelling increase in size; but the males do not show any sexual response even if housed in the same room as the female if unable to see her swelling. Females solicit mating from many different males throughout this period. The adaptive significance of this behavior for females living in multi-male, multi-female groups is that mating with many males confuses paternity, reduces threat of infanticide, and increases the likelihood that several males will support the female and her offspring. However, recent work using paternity testing has shown that male baboons preferentially display positive behaviors toward infants that they have sired (Alberts, 1999; Buchan et al., 2003) suggesting that the extended non-conceptive sex does not really confuse paternity.

In socially monogamous species where a strong relationship is formed between mates, non-conceptive sex is thought to also confuse male paternity. In this case, ovulation is concealed (it seems) and it was thought that by concealing ovulation, a specific male would have to stay with its mate for long periods of time and thus be available to the mate to help care for infants (Burley, 1979). However, a male could still benefit from mating with other females if he deserted his mate as soon as he could detect any signs of pregnancy, so the concealed ovulation of pair-bonded species must have some other function. If infant survival is dependent on male parental care, then the male should stay with the female regardless of whether the female conceals ovulation or not. Is ovulation truly concealed in socially monogamous primates?

We found that our captive cotton-top tamarins had a conception rate of 85% in the postpartum estrous, but we could find no visual or behavioral evidence of ovulation. Females do not menstruate, so there could be no way for a male to calculate when ovulation might occur. There was no change in the rate of scent marking or in the rate of male investigation of scent marks over the ovarian cycle. My long-time colleague and collaborator, Toni Ziegler, and I had a friendly argument. She thought that there had to be some cues to when ovulation occurred in order to explain the high rate of conception. I countered that all one needed to do was have sex at least once a day in order to ensure a high rate of conception. Ziegler devised a very clever experiment where scent marks were collected each day from an ovulating female who was unfamiliar to all of the test subjects. Each day the scent marks were introduced to pairs of animals where females were pregnant and, thus, not ovulating, and the behavior of the pair was observed. During the periovulatory period of the scent donor (the day before, the day of, and the day after ovulation determined by hormonal measures), the recipient pairs showed increased rates of male erection and increased mounting of each other. In contrast, there was no change in the rate of investigation of marks as a function of the ovulatory cycle (Ziegler et al., 1993). Thus, although ovulation was concealed to us as human observers, it was not at all concealed to the monkeys. A subsequent study on pygmy marmosets (*Cebuella pygmaea*) also found behavioral evidence that males could identify ovulation in their mates (Converse et al., 1995). Both marmoset and tamarin males can detect when ovulation occurred and the signal appeared to be through qualitative changes in scents in tamarins. But I was also correct. Paired tamarins mate an average of at least once a day throughout the ovulatory cycle and during pregnancy. So why is there so much non-conceptive sex in both pair-bonded primates and in baboons, chimpanzees and some other species?

In order to answer this question, I need to digress to consider some other species. One of the greatest stories in neuroendocrinology over the past two decades concerns the role of the neuropeptides, oxytocin, and arginine vasopressin in pair-bonding behavior. These classic studies looked at monogamous and polygamous species of a small rodent, the vole. Prairie voles are monogamous and form close pair-bonds and males not only defend a territory but also are active in caring for infants. Montane voles are polygamous and males neither defend territories nor do much with respect to infant care. Carter et al. (reviewed by Carter, 1998) showed that brain oxytocin receptors were activated in pair-bonded female prairie voles, and brain vasopressin receptors were activated in pair-bonded males. Injections of oxytocin to the brain of females would lead to formation of a paired relationship as much as natural courtship behavior and injections of an oxytocin antagonist would prevent a bond from occurring. Similar results were seen with vasopressin injections and vasopressin antagonists in male prairie voles.

What is the natural way in which a pair relationship develops in prairie voles? Voles spend a great deal of time mating when they first encounter one other. Copulations occur as often as every 10 or 15 min throughout the first 2 days of cohabitation and it appears to be after this period that brain oxytocin receptors are activated in females and brain vasopressin receptors are activated in males. But why so much sex? This extended period of sexual activity goes well beyond what would be needed for fertilization. Both hormones are known to be involved in social learning and memory. Voles maintain a preference for the partner with which they have copulated and/or experienced changes in brain neuropeptides suggesting that voles become conditioned to aspects of their mates (odors, vocalizations, visual cues) during sexual activity. This conditioning process may be important in identifying and staying with one's mate.

Similar processes may occur in humans. In some remarkable studies in Germany, Krüger et al. (e.g., Krüger et al., 2003) collected serum samples from men and women during both masturbation and coital sex and found a surge of oxytocin and another neuropeptide, prolactin, at the moment of orgasm. If orgasms lead to an increase in these peptides in humans and can also be conditioned to stimuli from one's mate, then humans may be experiencing a process that is not much different from prairie voles.

In cotton-top tamarins, we also saw a high rate of sexual and other affiliative behavior when pairs are first formed (Savage et al., 1988) and using a recently developed urinary oxytocin assay, we have found a great increase in oxytocin levels from pre-pairing baselines, when animals are paired (Snowdon et al., 2010). In collecting informal anecdotes from humans, it appears that sexual activity is similarly high at the start of a relationship, decreasing thereafter.

These results may also suggest an alternative interpretation of the extended mating periods seen in baboons and chimpanzees. If males in these species are able to identify their progeny, then females mating with multiple males may have little to do with paternity confusion to avoid infanticide. Rather, at the proximate level mating with multiple males may help females induce positive relationships with other group members. If a coherent group structure has benefits to members in terms of more efficient foraging, or better predator defense, then non-conceptive sex may function to reward other group members much as grooming was hypothesized to reward alloparents in cooperatively breeding species.

Non-conceptive sex may also function to restore a relationship that has been perturbed in some way. In several studies done for other purposes, we have noted an increase in non-conceptive sex following perturbations of the relationship. As noted above, when we transferred odors of a novel, ovulating female to a pair, we observed a significant increase in mounting relative to the rate seen to the odor of the same donor female when she was not ovulating (Ziegler et al., 1993). But the rate of mounting to the odors of a non-ovulating female was also significantly greater than baseline levels of mounting one' own mate. In another study involving odor transfers from reproductive, cycling females versus reproductively inhibited non-cycling females, there was again an increase in mounting as well as an eightfold increase in female solicitation behavior (Washabaugh and Snowdon, 1998). In another study we separated pairs for 30 min and found increased rates of vocalizations and agitation behavior during separation. On reunion, we observed an increase in mounting (Porter, 1994). Common to all of these examples is a social manipulation that might be viewed as threatening an established relationship. The increased sexual arousal (erections by males, solicitations by females) and increased mounting suggest that non-conceptive sex functions in established pairs to restore a relationship after some disruption. The well-known sexual responses of bonobos (*Pan paniscus*) to inter-individual or group tensions suggest a similar function of non-conceptive sex in a quite different species.

One of the most exciting results to emerge from the work on voles was the comparison between monogamous and polygamous species. Presumably a strong pair-bond is most important in a monogamous species where the female must depend on the male to assist with infant care, and the male before investing energy into infant care should be relatively confident about paternity. In the polygamous species where males do little, if any, infant care and males would have little, if any, paternal certainty, these mechanisms would have less value. So it is not surprising to find differences between monogamous and polygamous voles not only in levels of oxytocin and vasopressin but also in the distribution of receptors in the brain (see Carter, 1998 for review).

Similar results have been found in a related pair of rodent species studied by Marler et al. (Marler et al., 2003 for review). California mice (*Peromyscus californicus*) are not merely socially monogamous but genetically monogamous (Ribble, 1991). The white-footed mouse (*Peromyscus leucopus*) is polygamous. Male California mice actively defend territories and care for infants and they have much higher brain levels of arginine vasopressin than do white-footed mice with a different distribution of vasopressin activity in the brain. Cross-fostering studies between species show that male white-footed mice will acquire some of the aggressive and paternal behavior of California mice as well as a more similar brain distribution of vasopressin.

Between-species variation in levels of neuropeptides is exciting, but these demonstrations do not address an even more interesting question: Is there individual variation within a species? Can similar mechanisms be shown to be involved in regulating individual differences? Recent work on male prairie voles has found within-species polymorphisms in the promoter region of the arginine vasopressin 1-alpha receptor (*AVPR1a*) gene. A greater number of repeats in the promoter region are associated with greater affiliation and mate fidelity (Hammock and Young, 2005). Recently, a similar result has been reported for men (Walum et al., 2008). Three types of repeat polymorphisms on the *AVPR1A* gene were observed with one type, RS3, being negatively related to several measures of pair bonding. Males with one or more alleles carrying RS3 were rated as less bonded to their partners, more likely to have experience a marital crisis or threat of divorce and more likely to be cohabiting than married. Partners of these men reported lower levels of affectionate expression.

In pairs of cotton-top tamarins, we observed great variation in the amount of affiliative behavior. Some pairs had a high degree of affiliative behavior (contact, grooming, and non-conceptive sex), whereas other pairs had very low levels. We hypothesized that this variation in affiliation may be reflected in levels of prolactin and oxytocin as well. In an initial study, we measured levels of affiliation and urinary prolactin levels in female tamarins and found a close positive correlation between sexual and affiliative behavior and their prolactin levels. In a replication, we studied both males and females and found a similar correlation for each sex as well as between the mean values for a pair and affiliative and sexual behavior (Snowdon and Ziegler, 2007).

We have developed and validated a urinary oxytocin assay and studied pairs of tamarins with no offspring. We collected samples from males and females over a 3 week period to encompass the complete ovulatory cycle and we simultaneously observed a variety of social behaviors. Both oxytocin levels and affiliative behavior showed a 10-fold range of variation. We found significant positive correlations between oxytocin levels and affiliative behavior for males and females separately and when analyzed as pairs (Snowdon et al., 2010). We found no difference in mean oxytocin levels between male and female tamarins. In the related common marmoset, Wang et al. (1997) found no sex difference in the distribution of oxytocin immunoreactive cells in the brain, so it may be likely that in cooperatively breeding primates both sexes are equally responsive to oxytocin.

A multiple regression analysis of the components of affiliative behavior on oxytocin levels showed that amount of contact and grooming behavior explained a significant amount of variance in female oxytocin levels, whereas sexual activity explained a significant amount of variance in male oxytocin levels (Snowdon et al., 2010). Furthermore, in pairs with high oxytocin levels, females solicited sex more than in other pairs and males initiated bouts of huddling and grooming more than in other pairs. It is as though each mate is providing the behavior most needed by the other to maintain high oxytocin levels. There appear to be two different mechanisms that explain variation in oxytocin levels that differ by sex, but to the extent that oxytocin can serve as a proxy for relationship quality, the combination of grooming behavior and non-conceptive sex may be the proximate mechanisms jointly needed for maintaining positive relationships.

The amount of affiliative behavior may also directly affect reproductive success. Silva and Sousa (1997) studied sexually naïve common marmosets in newly formed relationships, and the pairs where a female conceived within 10 weeks after pairing exhibited significantly more affiliative behavior and behavioral coordination than the pairs that failed to conceive within 10 weeks.

Studies on humans also suggest a role for oxytocin in relationships. Women asked to recall a negative experience of loss or abandonment showed decreases in oxytocin levels that were proportional to the amount of negative emotions expressed (Turner et al., 1999). When engaging in affiliative cues, but not sexual cues, with their partners women had correlated increases in oxytocin levels (Gonzaga et al., 2006). These results are parallel to the findings on tamarins that affiliative cues are more important than sexual cues in female oxytocin levels. Parallel studies on men are needed. Grewen et al. (2005) did look at both sexes and reported higher oxytocin levels in relationships with strong partner support.

## Social Support and Tolerance

An alternative to direct affiliation through grooming or sexual behavior in pair-bonded species is social support and social tolerance in relationships not characterized by pair-bonds. Abbott et al. (2003) examined data on social support, rank differences, and cortisol levels in a variety of species ranging from cooperatively breeding marmosets and tamarins to rhesus macaques and baboons. In cooperatively breeding species, only one female is typically able to ovulate and breed within a group, creating a clear reproductive dominance, yet the reproductively suppressed females showed low levels of cortisol that were not different from those of the breeding adults (Ziegler et al., 1995). The highest levels of cortisol are seen in newly paired marmosets and tamarins when they begin to breed. In contrast, in baboons and macaques, there is clear evidence that subordinate animals have much higher cortisol levels. Abbott et al. (2003) argue that social support coupled with infrequent dominance displays lead to the low levels of cortisol seen in subordinate marmosets and tamarins.

As noted earlier, we have observed that breeding adults of both wild common marmosets and captive cotton-top tamarins groom subordinate group members more often than they are groomed in return (Lazaro-Perea et al., 2004; Ginther and Snowdon, 2009). Furthermore, we have observed a high degree of tolerance of subordinate male sexual behavior in tamarins. Unlike adult daughters, adult sons show no signs of reproductive suppression (Ginther et al., 2001) and exhibit levels of sexual activity as great as reproductive males, but they direct sexual behavior to brothers, sisters, and even mothers. Yet, even in the extreme case of sexual behavior toward the breeding female, we see no evidence of aggression from breeding males or females. A son who has just attempted a mount with his mother is 95 times more likely to be groomed by a parent than to receive aggression. This extraordinary tolerance of sexual activity by adult sons may be an expression of tolerance that functions to retain the infant-carrying services of subordinate animals (Ginther and Snowdon, in preparation). Supporting this idea of tolerance between fathers and sons, an analysis by Price and McGrew (1991) of which types of departures from monogamy were stable in groups of captive cotton-top tamarins showed that only father–son polyandry led to stable groups with successful reproduction. Baker et al. (1999) found that father and son pairs of common marmosets lived together and shared copulation with an unrelated female without any aggression.

At the opposite extreme of the primate world is the mountain gorilla (*Gorilla berengei berengei*). Long thought to live in harems dominated by a single silverback male, many groups have two or more silverback males. Hormonal sampling revealed clear differences in testosterone levels between the dominant and subordinate silverback male but no differences in cortisol (which was low in both dominant and subordinate males, Robbins and Czekala, 1997). Behavioral relationships between adult males are characterized by extremely low levels of aggression and high levels of social tolerance, even to the extent of both males copulating with the same female within a short time of each other (Robbins, 1999). Paternity analyses of 48 gorillas indicated that the dominant male sired 85% of the individuals, whereas the subordinate male sired 15% (Bradley et al., 2005). That both males are able to sire offspring in the same group while showing tolerance, but not aggression, provides another example of tolerance.

Analyses of long-term records of mountain gorillas, at the Karisoke Research Station in Rwanda, indicate that a subordinate male has greater potential reproductive success by remaining in the group compared with males seeking reproductive opportunities elsewhere and that the sons of dominant males are more likely to mate successfully if they grow up in a group with multiple silverback males (Robbins, 1995). Furthermore, although infanticide has been observed in mountain gorilla groups with a single male when the male dies, infanticide has never been observed in groups with multiple adult males. Thus, by exhibiting tolerant rather than aggressive relationships, silverback male mountain gorillas benefit proximally from low levels of stress and ultimately from attaining greater reproductive success.

## Parenting

Parenting can be considered as a special case of affiliation, and although all mammalian mothers must exhibit some form of affiliative relationship with their infants, the involvement and even attachment of other family members with infants are of special interest. We rarely think of mammalian males as having relationships with infants, so, when they do, their behavior and the mechanisms leading to that behavior are of considerable interest.

For a long time, it was difficult to find specific mechanisms for maternal care since birth is characterized by a drop in maternal estrogen and progesterone levels. Prolactin, which is involved in preparing the mammary glands for milk production, has been shown to be a critical hormone for the behavioral control of infant care as well (reviewed by Rosenblatt, 1990). The production of prolactin is stimulated by the high levels of estrogen that are present during pregnancy. In addition, the hormone oxytocin which is involved in uterine contractions and the milk let-down reflex in nursing is also stimulated by estrogen (Sprangers et al., 1989; Ochedalski et al., 2007) and oxytocin stimulates maternal behavior in virgin females (Pederson & Prange, 1979).

Estrogen also stimulates the growth of neurons in the hippocampus, an area important to spatial learning and memory as well as stress regulation (Woolley and McEwen, 1992, 1993). Following on these results, Kinsley et al. found that primiparous and multiparous mother rats had better performance on a spatial maze task than females with no maternal experience (Kinsley et al., 1999) and that motherhood reversed the cognitive decline seen with aging compared with age-matched virgin controls (Gatewood et al., 2005). The brains of multiparous females had significantly less amyloid precursor protein known to be involved in Alzheimer's disease in humans. Multiparous mothers were more able to multi-task and showed more exploratory behavior and less fear of novelty than did virgin controls (Love et al., 2005). Oxytocin has been proposed as a mediator of the increased spatial learning seen in mothers (Tomizawa et al., 2003).

Much less is known about the paternal brain than the maternal brain, but several interesting parallels emerge in recent work. The California mouse (*Peromyscus californicus*) is one of the few mammals known to have genetic as well as social monogamy. Male California mice also showed increased prolactin levels after infant birth (Gubernick and Nelson, 1989) and experienced male California mice, but not pup-exposed males of a polygamous species, showed increased neuronal growth in the hippocampus (Franssen et al., 2009), and male California mice showed greater oxytocin immunoreactivity in brain areas related to paternal care than polygamous mice (Everette et al., 2006, 2007).

Testosterone has been thought to be involved in aggressive behavior leading to the Demonic Male hypothesis of Wrangham and Peterson (1996). In monogamous males that exhibit a high degree of paternal care, it would be logical to expect low levels of testosterone and one could hypothesize that removing testosterone might make a male even more to nurture its infants. However, when Trainor and Marler (2001) castrated male California mice, they found a reduction in paternal care. Castrated males were poorer at parenting than intact males. How could this be? Trainor and Marler reasoned that testosterone might be converted to estrogen in paternal males and when they blocked the enzyme that converts testosterone to estrogen in gonadally intact males, they observed a disruption of paternal behavior. When estrogen was given to castrated males they showed high-quality paternal care (Trainor and Marler, 2002). Thus, testosterone appears to be an important hormone in male paternal care and does not necessarily lead to demonic males.

Many parallels have been observed in cooperatively breeding marmosets and tamarins. Kozorovitskiy et al. (2006) reported dendritic changes and increases in arginine vasopressin receptors in the prefrontal cortex of male marmosets with extensive paternal experience. The prefrontal cortex in humans is activated by stimuli from one's own infant and is the location for receptors of many of the affiliative hormones such as vasopressin, prolactin, and oxytocin. Male marmosets also have elevated prolactin levels especially when they have been recently carrying infants. Dixson and George (1982) first reported this increased prolactin and Mota et al. (2006) subsequently replicated the study with both fathers and alloparents, reporting increased prolactin levels in both types of males immediately after carrying infants. Mota et al. (2006) also reported no differences in basal prolactin levels prior to birth compared with levels obtained when males were not carrying infants after birth suggesting that elevated prolactin is a direct response to infant carrying. Roberts et al. (2001b) also found increased prolactin levels in subadult marmosets after they carried infants. Roberts et al. (2001a) manipulated prolactin levels by injecting bromocriptine to subadult animals and found some disruption of infant care. However, Almond et al. (2006) gave a different prolactin blocker (cabergoline) to paternally experienced male marmosets and found no effect on male infant care. Their only finding was that males showed greater interest in infants when injected with the prolactin blocker.

There are several differences between the studies—experienced fathers versus subadults, two different blocking agents, and an experimental test with unrelated infants versus observations of fathers in natural situations. But one intriguing possible explanation is that for males without infant care experience, prolactin may be a necessary stimulus for infant care whereas for experienced fathers, prolactin is no longer needed to initiate infant care, but serves to reward fathers for care. In this case the fathers in the Almond et al. (2006) study may be seeking additional infant contact to make up for the missing prolactin reward. (Remember that prolactin levels increase in humans at orgasm suggesting a potential reward function.)

Fathers experience other neuroendocrine and behavioral changes. When common marmoset males were presented with the odor of a novel ovulating female, many males showed increased erections and increased sniffing and licking at the scent compared to a vehicle control odor. Blood samples were collected 30 min after the stimulus presentation and in many males there was a significant increase in testosterone. There was considerable individual variation, but when males were categorized by whether they were fathers or not, none of the fathers showed any interest in the odor and none showed increases in testosterone levels. The entire effect was due to the response of non-fathers (Ziegler et al., 2005). Experienced fathers and non-fathers were tested with odors of infants versus vehicle control with a blood sample taken just 20 min after stimulus presentation. Testosterone levels in fathers decreased significantly after encountering an infant's odor whereas there was no change in hormonal levels in control males (Prudom et al., 2008). Thus, something about the experience of fatherhood changes the father's neuroendocrine responses to odor cues from novel, ovulating females and to odors from infants.

Marmoset fathers also show great interest in infants whether their own or someone else's. It is difficult to examine directly the behavior of fathers in the context of a family group since other group members often compete to carry infants and fathers generally reduce infant care with increased number of alloparents. To study paternal interest in infants more directly, Zahed et al. (2008) created a test chamber where males could be tested with infant stimuli separately from the rest of the family. Fathers were tested with their own infant or an unrelated infant present and also tested with vocalizations of their own and an unrelated infant. Strikingly, father responded equally to their own infants and to novel infants, but the novel infant rejected all attempts by the male to pick it up. Fathers also did not distinguish between the calls of their own versus strange infants. In contrast, when parentally inexperienced males were tested with a strange infant or a vocalization, they showed relatively little interest compared with fathers (Zahed et al., 2008). Thus, fatherhood also affects the responsiveness of a male to infant cues.

Both common marmoset males and cotton-top tamarin males show weight gain during their mate's pregnancy that is out of phase with maternal weight gain meaning that males are not just eating when their mates are eating (Ziegler et al., 2006). This raises the question of how males "know" that their mates are pregnant. As noted above, female hormones change throughout pregnancy leading to the production of hormones critical for nursing and other infant care, but are there changes in male hormones during pregnancy and, if so, what triggers these hormonal changes? Many of the effects of fatherhood described above have compared males with no paternal experience with males that have been fathers multiple times. Are there differences between first-time fathers and experienced fathers?

We monitored hormones in cotton-top tamarin males through urine samples and therefore could not get fine detail on whether prolactin levels were elevated transiently as a result of carrying infants. However, like Mota et al. (2006) we not only found that pre-partum prolactin levels in males did not differ from post-partum levels but also found a positive correlation between prolactin concentration and the number of births a male had been involved with (Ziegler et al., 1996). Furthermore, male prolactin levels prior to birth were as high as those of nursing mothers when nursing. Taken together, the results suggest that male hormone levels may be changing prior to birth and that there may be differences between experienced and first-time fathers.

We followed 10 pairs of tamarins throughout their mate's pregnancy: half with multiple previous pregnancies and half which were first-time parents. There were clear differences between the two groups with hormonal patterns of experienced fathers beginning to change in mid-pregnancy, whereas hormones in first-time fathers did not change until the last month before birth (Ziegler et al., 2004). Experienced fathers had higher levels of testosterone, estrone, and cortisol in the last month of pregnancy than first-time fathers, and experienced fathers had higher levels of prolactin in all months except the month prior to birth when both experienced and first-time fathers had high levels. We also made behavioral observations on the pairs over the pregnancy and saw little affiliative behavior in the experienced pair. However, in the month prior to birth, first-time parents showed a significant increase in sexual and affiliative behavior, suggesting that these affiliative interactions may have been important in increasing the first-time father's prolactin levels.

However, we still need to explain the changes in hormones in experienced fathers. We examined female hormone levels to see if we could identify a potential cue. Midway through pregnancy, all mothers whether experienced or first time showed a significant peak in excretion of glucocorticoids, and in experienced fathers, but not first-time fathers, there was an increase in glucocorticoids within a week of the female excretion. Thus, changes in female excretion of glucocorticoids may be the trigger for the hormonal changes that subsequently occur in experienced fathers (Ziegler et al., 2004).

Where do the maternal glucocorticoids come from? One intriguing possibility is that the fetal adrenal gland becomes active in mid-pregnancy and a mother would benefit from clearing these excess glucocorticoids from her body. If this is the case, then it is the fetus working through the mother's body that is providing the signal to prepare the father's hormones for parental care.

However, in this study, there were two possible confounds. The experience of mothers co-varied with that of fathers and many experienced parents had recent infants to care for during the pregnancy. To control for both of these confounds, we paired experienced fathers with first-time mothers with no infants present and we replicated the original results with experienced fathers. First-time mothers showed the mid-gestation peak in glucocorticoids and their experienced mates immediately responded with changes in their hormones (Almond et al., 2008).

To summarize, parental care is a critical form of affiliative care for mammalian females as well as for males in biparental and cooperatively breeding species. Similar hormonal and neural changes occur in both sexes with fathers appearing to anticipate infant births with endocrine changes occurring during pregnancy. In both California mice and tamarins, testosterone appears to play an important role in paternal care likely through being converted to estrogens, which in turn stimulate the production of prolactin and oxytocin. In first-time pairs of tamarins, the hormonal changes do not occur until the end of pregnancy at a time when sexual and affiliative behaviors increase. But experienced fathers appear sensitive to changes in female urinary glucocorticoids, likely produced by the fetus. It is not clear whether prolactin is a necessary hormone for inducing paternal care or whether it serves to reward fathers for carrying infants, or both. Parental experience may play an important role in understanding the role of prolactin. Fatherhood changes male brains in similar ways to how motherhood changes female brains, and neuroendocrine responses to cues from novel females and from infants work differently in fathers versus non-fathers serving as a potential proximate mechanism to maintain mate fidelity and responsiveness to infants.

So far I have considered parenting from the perspective of parents, but infants are also an important factor. We examined the care infants received and, across a wide variation in group size and in parental experience, the infants received an equal amount of care—both nurturing and rejecting. One consequence of multiple caregivers is the reduction of variation of what infants experience (Washabaugh et al., 2002). And infants develop attachments to the individuals who provided the most infant care. Kostan and Snowdon (2002) recorded which family members were most involved in carrying infants and in transferring food to them and then when these infants were independent juveniles, we presented a brief threatening stimulus (a standard test of attachment). In all cases, the infants ran to be close to the individual that had spent the most time with that infant. In no case was the mother involved.

The primary affiliative relationship of juveniles was established with the one who provide them as infants with the greatest affiliation.

## Cooperation, Donation, and Teaching

There have been several recent studies examining variation in cooperative behavior in nonhuman primates. Experimental studies of cooperation seek whether animals will jointly work to solve a problem that cannot be solved by one animal alone. Typically this involves the use of an apparatus to obtain food where two animals must work together simultaneously in order to obtain food. Early studies were on chimpanzees (*Pan troglodytes*) and orangutans and reported that cooperative problem solving occurred but typically with a dominant individual coercing a subordinate with the dominant individual receiving more than 90% of the rewards (Chalmeau, 1994; Chalmeau et al., 1997a).

Research with capuchin monkeys led to ambiguous results, with one research group finding no evidence of cooperative behavior, suggesting that any solutions occurring were accidental due to the attraction of both individuals toward food (Chalmeau et al., 1997b; Visalberghi et al., 2000), whereas Mendres and de Waal (2000) found that capuchin monkeys would cooperate to obtain a food reward. In the latter study, capuchin monkeys appeared to understand the role of the partner since they would not attempt to solve the problem when the partner was not present and not visible. Coussi-Korbel and Fragaszy (1995) have argued that the social dynamics of a species or population will have an effect on social learning and cooperative activities. In species with high levels of competition and aggression, there will be low levels of social tolerance and, therefore, slower rates of social learning and reduced cooperative behavior. Conversely, the reverse would be true in species with high degrees of social tolerance and behavioral coordination. Indeed, research on chimpanzees illustrates that they perform better in social situations where competition is involved (Hare and Tomasello, 2004), whereas the more socially tolerant congeneric bonobo (*Pan paniscus*) performed more successfully in cooperative tasks than chimpanzees (Hare et al., 2007).

Cooperatively breeding species should be among the best performers in cooperative tests since they have a high degree of social tolerance as well as coordination of behavior in order to share duties of infant care, food locating, and vigilance (Snowdon, 1996). Indeed cotton-top tamarins rapidly acquired cooperative behavior with an apparatus that required simultaneous pulling of trays to obtain food (Cronin et al., 2005). When one animal was separated, the other animal still showed interest in the apparatus but attempted to solve the task at a significantly lower rate indicating an understanding of the need of the partner to solve the task. In the original task, both individuals received food rewards simultaneously. In subsequent studies, the animals still performed at a high rate even when only one food reward was available (Cronin and Snowdon, 2008). Successful performance decreased from 99% to 75% when only one animal at a time received all of the rewards on a single day in alternation with the other animal receiving all the rewards. Pairs sustained reciprocal behavior even with up to 11 days elapsing between test sessions. In a final study, food was placed adjacent to one individual but rolled down a ramp to the other individual. Over 10 sessions, cooperative behavior was maintained by the animal receiving no food. The overall performance of 99% on two-reward sessions and 75% on one-reward session contrasts with the non-cooperatively breeding capuchin monkey results of 75% on two reward trials and only 38% on one-reward trials. Even though some capuchin monkeys can solve the cooperative task, they do not perform as well as cooperatively breeding tamarins.

Another way to examine prosocial behavior such as cooperation is to see if one animal will voluntarily donate food to another, both when there is no additional cost to the donor and when the donor receives no reward. Using the first paradigm, Silk et al. (2005) and Jensen et al. (2006) found that chimpanzees would not preferentially provide food for a conspecific even when there was food for the actor as well. In a follow-up study using a more stringent paradigm where the potential donor receives nothing and only the partner is rewarded, Vonk et al. (2008) found no evidence of donation. In contrast, Warneken and Tomasello (2006) did find evidence of altruistic behavior in chimpanzees comparable to that of young children when the tasks did not involve food. Perhaps chimpanzees are so distracted by food that they can express altruistic behavior only in situations that do not involve food.

Burkart et al. (2007) reasoned that cooperatively breeding species would be more likely to show prosocial or donation behavior than other species and they found that common marmosets would readily pull a tray that delivered food only to a partner with no reward for the actor. At the same time, we designed a virtually identical study with cotton-top tamarins using the same rationale. We tested both the paradigm where an animal could donate food to its mate while receiving food itself as well as the more stringent test of having only a single reward for the partner. Surprisingly, despite having a similar apparatus, similar training, and similar testing techniques, we found that cotton-top tamarins would not preferentially donate food to their mates (Cronin et al., 2009). Further support for the lack of prosocial behavior comes from the finding that tamarins were even less likely to donate food when the partner gave food vocalizations or reached toward the food (Cronin et al., 2009).

It is difficult to account for the contradictory results between marmosets and tamarins, especially when the training and testing paradigms were so similar. There may be something different between the two species that is not captured by the variable of cooperative breeding or there may have been environmental differences. For example, the tamarins were tested in home cages where they could do many other activities, whereas marmosets were tested in smaller, more confining test cages.

Temporal dynamics may also affect when and how donation behavior is observed. Cronin et al. (2010) developed a paradigm using the same tray-pulling apparatus as Cronin et al. (2009) but with a single tray. One tamarin pulled the tray to provide food for itself as well as to its mate for 5 min. Roles were immediately reversed, and the recipient could now pull the tray but only the mate received food. A negative condition consisted of placing a block on the tray movement so that food was visible to both animals but neither could receive food, and then roles were reversed. A nonsocial control consisted of having both animals receive rewards, but then instead of reversing roles, the previous donor was moved elsewhere and the previous recipient had an empty cage. In the first 100 s after role reversal, tamarins presented food to their mate significantly more often after having received food than not having received food, but they also pulled just as often after a positive experience when there was no recipient in the adjacent cage. The tamarins did not show reciprocity but rather initially reacted positively independent of whether a recipient was present or not. However, by the last 100 s of the 5-min test, tamarins, regardless of whether they had a positive or negative experience with the mate, donated food equally often to the mate and significantly more than in the nonsocial condition. The dynamics of donation changed with time, but eventually tamarins demonstrated prosocial behavior without requiring reciprocity.

What mechanisms can sustain cooperation and donation behavior? Perhaps donation and exchange of cooperative behavior simply engender good feelings and do not require much cognitive ability (as in the first part of the Cronin et al., 2010 study). Studies of rats by Rutte and Taborsky (2007, 2008) found that rats will maintain what they call “generalized reciprocity.” If a rat has recently experienced an interaction with another rat in which it has received a reward, it will then act to provide a reward to the individual rat that had provided a reward previously. Rutte and Taborsky argue that being the recipient of something good may engender good feelings that are simply transferred to the next interaction.

What is the biological source of feeling good? Recent studies in humans suggest that oxytocin is associated with generosity in humans (Zak et al., 2007) and that oxytocin also increases trust in humans as evidenced by performance on games involving cooperation and trust to maximize rewards (Kosfeld et al., 2005; Zak et al., 2005; Chapter 17, this volume). Thus, if being the recipient of a gift leads to increased oxytocin which in turn makes one more generous and trusting, we can imagine a scenario whereby altruistic behavior can be sustained without requiring the positing of any complex cognitive mechanisms. The role of oxytocin increasing trust compares with the results reported earlier on how grooming and non-conceptive sex increase oxytocin levels suggesting that a variety of socially administered rewards serve to increase trust and well-being between individuals.

Teaching represents another example of altruistic or prosocial behavior. Caro and Hauser (1992) have provided an operational definition of teaching behavior that requires some specific behavior directed toward another that incurs a cost toward the animal performing the behavior that leads to long-term change in the behavior of the observer. Teaching is more than simple social learning which can occur through observation alone since teaching requires some directed action on the part of another.

King (1994) has observed that in most nonhuman primates, mothers do not teach young about foraging skills or what foods to select. The infant observes the mother closely, but there is no direct action by the mother to improve the performance of the infant. King suggests that the only nonhuman primates to show teaching are the marmosets and tamarins. In these species, it is commonly observed that an adult will offer food or tolerate scrounging from an infant (Brown et al., 2004). In a longitudinal study of food transfers in cotton-top tamarins, Joyce and Snowdon (2007) found that adults initially offered food to infants, but as the infants became older, the adults tolerated food transfers less. Adults made a specific vocalization that was observed only in the context of food transfers, and food transfers with infants were successful only when the adults vocalized. Adults began food transfers significantly sooner with twin infants than with singletons suggesting a greater cost to nursing twins. Furthermore, infants who received food transfers at an earlier age were feeding independently significantly sooner than infants with food transfers beginning at a later age (Joyce and Snowdon, 2007). Thus, food transfers may be a form of teaching since adults provide specific cues to infants; sharing food is costly for adults and infant behavior changes as a function of the age of onset and intensity of adult food transfers.

This is not an artifact of captivity. Rapaport (2006) studying golden lion tamarins (*Leontopithecus rosalia*) found that whereas juveniles could readily eat fruit on their own, they were much less successful foraging for insects. She documented a high level of food vocalizations and food transfers of insect food toward juveniles that decreased with the age of the juveniles. Furthermore, she documented (Rapaport and Ruiz-Miranda, 2002, 2006) several cases of scaffolding behavior where an animal would give food vocalizations but not offer any food when the juvenile approached. The juvenile searched in the proximity and found an insect nearby. So adult tamarins do not simply provide food transfers to infants and juveniles, but appear to systematically provide less assistance to their young as they develop skills. Cooperatively breeding meerkats also demonstrate teaching behavior by adults stunning potentially harmful prey before transferring them to the young (Thornton and McAuliffe, 2006).

We have found similar results in a captive experimental study of cotton-top tamarins (Humle and Snowdon, 2008). We developed an apparatus from which food could be obtained through one of two methods and trained one parent in each family group with one of the methods. Juvenile tamarins (aged 25–36 weeks) were then tested one twin with each parent. Most of the adult demonstrators gave the infant food transfer vocalizations during the tests, even though their young had been feeding independently for several months. Ironically, the most successful juvenile learners were the ones who received transferred food least often. Once a juvenile successfully solved the problem, the adult demonstrators vocalized and engaged in food transfers significantly less often. The results parallel the field results of Rapaport. Adult tamarins reinstated food transfers with juveniles during a novel foraging task and they ceased food transfers as soon as the juvenile was successful by itself. When we replicated the same task with adults, we found no evidence of food transfers but most adults learned the task more readily than the juveniles and with shorter amounts of direct observation (Dillis et al., 2010). Taken together, these results suggest that tamarins adjust food transfers and accompanying vocalizations according to the skill level of their companions, a rudimentary form of “theory of mind”.

These results on tamarins contrast sharply with a parallel study on ant-dipping behavior in chimpanzees at Bossou in Guinea. Even though driver ants can inflict considerable pain when they bite, mother chimpanzees gave no evidence of assisting their infants and juveniles as they learned to ant-dip (Humle et al., 2009). In this case, chimpanzees must learn difficult foraging skills on their own with no assistance from a parent.

## Summary and Conclusions

In this chapter, I have examined the behavioral and neuroendocrine mechanisms involved in a variety of affiliative interactions. Grooming and other physical contact are obvious in a wide variety of social relationships and can induce neuroendocrine changes such as increased endogenous opioids and oxytocin levels, reduced levels of glucocorticoids and reduced heart rate. Together the physiological changes induced by grooming activate brain reward systems and induce calming behavior. Furthermore, the act of grooming may itself bring benefits to the groomer as well as the groomee.

Non-conceptive sex is seen in species with many different social systems. Although non-conceptive sex is often thought to function primarily to confuse paternity, the finding that males of socially monogamous species are able to detect ovulation and still engage in frequent non-conceptive sex suggests other functions must be involved. The findings that levels of the neuropeptides prolactin and oxytocin are elevated at orgasm in men and women suggest that non-conceptive sex may function to reward partners, and thus be critical in forming and maintaining relationships. Increased sexual behavior in response to social perturbations in tamarins suggests that non-conceptive sex may also play an important role in restoring relationship equilibrium between mates. Basal oxytocin and prolactin levels are directly related to the amount of affiliative behavior seen in tamarin pairs with variation in male oxytocin levels being explained best by sexual activity and variation in females being explained best by contact and grooming behavior.

Social tolerance is a less active form of affiliative behavior, but subordinate individuals in species with high social tolerance have significantly lower levels of stress hormones than subordinates in species with low levels of tolerance.

Parenting is a special form of affiliative behavior but because maternal care is obligatory to all mammals, there has been relatively little attention to maternal care as a specific form of affiliation. However, since care by fathers and alloparents is often not as obligatory as maternal care is, the mechanism leading to male infant care is of interest. Fatherhood significantly changes the brain and neuroendocrine system, with increased dendritic growth and vasopressin receptors in the prefrontal cortex, a lack of testosterone response to odors from novel females and a decreased testosterone response to scents of infants compared with non-fathers. Experienced fathers respond avidly to infant cues and do not appear to discriminate between their own infants and unrelated infants.

Fathers show hormonal changes prior to the birth of infants with experienced fathers showing the changes sooner than first-time fathers. Experienced fathers appear to begin a cascade of hormonal changes within a week of the pregnant female excreting increased glucocorticoids, likely from the activation of the fetal adrenal gland, making it likely that the fetus is changing the hormones of its father to prepare him for infant care. This appears to be a learned response since first-time fathers do not respond to the increased glucocorticoid levels. However, first-time parents showed a significant increase in grooming, contact, and sexual behavior in the month before birth suggesting that an increase in affiliation might lead to hormonal changes in first-time fathers.

Testosterone, often thought to be involved exclusively in aggressive behavior is also necessary for male parental care. Some of the testosterone is metabolized into estrogen which in turn is critical to stimulate prolactin and oxytocin. Thus, testosterone plays a critical role in the affiliative and nurturing behaviors of infant care.

Species differ greatly in their ability to display cooperative and altruistic behavior. Those species that are less aggressive show more social tolerance, and more coordination of social behavior appears more likely to exhibit cooperative behavior and to donate resources to others. It is possible that prosocial exchanges lead to changes in hormones like oxytocin, producing good feelings that can be conditioned to specific partners or can lead to an overall increase in generosity.

Teaching behavior is rare among most nonhuman primates even under conditions of risk to the infant, but it is clearly evident from cooperatively breeding species and from golden lion tamarins, cotton-top tamarins, and meerkats that adults adjust their teaching to the skill level of their offspring.

Affiliative and altruistic behaviors now pose many interesting questions and deserve to be studied as much as competition, dominance, and aggression have been studied historically. Affiliative and altruistic behaviors play an important role in group cohesion and infant development. We are just beginning to understand the sources of variation in affiliative and altruistic behavior as well as the neural and hormonal mechanisms involved. But understanding the behavioral and neuroendocrine mechanisms of affiliation is an important task for future research.

**Acknowledgments** The author's research was supported by USPHS Grants MH029775 and MH035215, by the University of Wisconsin Graduate School Research Committee, and by a Hilldale Professorship. I thank Katherine A. Cronin for her suggestions and for her critical review of the chapter.

## References

Abbott, D. H., Keverne, E. B., Bercovitch, F. B., Shively, C. A., Mendoza, S. P., Saltzmann, W., Snowdon, C. T., Ziegler, T. E., Banjevic, M., Garland, T., Jr., & Sapolsky, R. M. (2003). Are subordinates always stressed: A comparative analysis of rank differences in cortisol levels among primates? *Hormones and Behavior*, 43: 67–82.

Achenbach, G. G. & Snowdon, C. T. (2002). Costs of caregiving: Weight loss in captive adult male cotton-top tamarins (*Saguinus oedipus*) following the birth of infants. *International Journal of Primatology*, 23: 179–189.

Alberts, S. C. (1999). Paternal kin discrimination in wild baboons. *Proceedings of the Royal Society of London, Series B*, 266: 1501–1506.

Almond, R. E A., Brown, G. R., & Keverne, E. B. (2006). Suppression of prolactin does not reduce infant care by parentally experienced common marmosets (*Callithrix jacchus*). *Hormones and Behavior*, 49: 673–680.

Almond, R. E. A., Ziegler, T. E., & Snowdon, C. T. (2008). Changes in prolactin and glucocorticoid levels in cotton-top tamarin fathers during their mate's pregnancy: The effect of infants and paternal experience. *American Journal of Primatology*, 70: 560–565.

Aureli, F., Preston, S. D., & deWaal, F. B. M. (1999). Heart rate responses to social interactions in free-moving rhesus macaques (*Macaca mulatta*): A pilot study. *Journal of Comparative Psychology*, 113: 59–65.

Baker, J. V., Abbott, D. H., & Saltzman, W. A. (1999). Social determinants of reproductive failure in male common marmosets housed in their natal family. *Animal Behaviour*, 58: 501–513.

Bielert, C. (1982). Experimental examination of baboon (*Papio ursinus*) sex stimuli. In Snowdon, C. T., Brown, C. H., & Petersen, M. R. (eds.), *Primate Communication*, pp. 373–95. New York: Cambridge University Press.

Boccia, M. L., Reite, M., & Laudenslager, M. (1989). On the physiology of grooming in a pigtail macaque (*Macaca nemestrina*). *Physiology and Behavior*, 45: 667–670.

Bradley, B. J., Robbins, M.., Williamson, E. A., Steklis, H. D., Steklis, N. G., Eckhardt, B., Boesch, C., & Vigilant, L. (2005). Mountain gorilla tug-of-war: Silverbacks have limited control over reproduction in multimale groups. *Proceedings of the National Academy of Sciences*, 102: 9418–9423.

Brown, G. R., Almond, R. E. A., & van Bergen, Y. (2004). Begging, stealing, and offering: Food transfers in nonhuman primates. *Advances in the Study of Behavior*, 34: 265–295.

Buchan, J. C., Alberts, S. C., Silk, J. B., & Altmann, J. (2003). True paternal care in a multi-male, primate society, *Nature*, 425: 179–181.

Burkart, J. M., Fehr, E., Efferson, C., & van Schaik, C. P. (2007). Other-regarding preferences in a non-human primate: Common marmosets provision food altruistically. *Proceedings of the National Academy of Sciences USA*, 104: 19762–19766.

Burley, N. (1979). The evolution of concealed ovulation. *American Naturalist*, 114: 835–858.

Caro, T. M. & Hauser, M. D. (1992). Is there teaching in nonhuman animals? *Quarterly Review of Biology*, 67: 151–174.

Carter, C. S. (1998). Neuroendocrine perspectives on social attachment and love. *Psychoneuroendocrinology*, 23: 779–818.

Chalmeau, R. (1994). Do chimpanzees cooperate in a learning task? *Primates*, 35: 385–392.

Chalmeau, R., Lardeux, K., Brandibas, P., & Gallo, A. (1997a). Cooperative problem solving by orangutans (*Pongo pygmaeus*). *International Journal of Primatology*, 18: 23–32.

Chalmeau, R., Visalberghi, E., & Gallo, A. (1997b). Capuchin monkeys, C*ebus apella*, fail to understand a cooperative task. *Animal Behaviour*, 54: 1215–1225.

Converse, L. J., Carlson, A. A., Ziegler, T. E., & Snowdon, C. T. (1995). Communication of ovulatory state to mates by female pygmy marmosets (*Cebuella pygmaea*). *Animal Behaviour*, 49: 615–621.

Coussi-Korbel, S. & Fragaszy, D. M. (1995). On the relation between social dynamics and social learning. *Animal Behaviour*, 50: 1441–1453.

Cronin, K. A., Kurian, A. V., & Snowdon, C. T. (2005). Cooperative problem solving in a cooperatively-breeding primate, the cotton-top tamarin (*Saguinus oedipus*). *Animal Behaviour*, 69: 133–142.

Cronin, K. A., Schroeder, K. K., Rothwell, E. D., Silk, J. A., & Snowdon, C. T. (2009). Cooperatively breeding cottontop tamarins (*Saguinus oedipus*) do not preferentially donate rewards to their long-term mates. *Journal of Comparative Psychology*, 123: 231–241.

Cronin, K. A., Schroeder, K. K., & Snowdon, C. T. (2010). Prosocial behavior emerges independent of reciprocity in cottontop tamarins. *Proceedings of the Royal Society, London, Series B*. Published on line, July 14, 2010.

Cronin, K. A. & Snowdon, C. T. (2008). The effects of unequal reward distributions on cooperative problem solving by cottontop tamarins (*Saguinus oedipus*). *Animal Behaviour*, 75: 245–257.

Dillis, C., Humle, T., & Snowdon, C. T. (2010). Socially biased learning among adult cottontop tamarins (*Saguinus oedipus*). *American Journal of Primatology*, 72: 287–295.

Dixson, A. F. & George, L. (1982). Prolactin and parental behavior in a male New World primate. *Nature*, 299: 551–553.

Dunbar, R. I. M. (1991). Functional significance of grooming in primates. *Folia Primatologica*, 57: 121–131.

Everette, A., Fleming, D., Higgins, T., Tu, K., Bardi, M., Kinsley, C. H., & Lambert, K. G. (2007). *Paternal Experience Enhances Behavioral and Neurobiological Responsivity Associated with Affiliative and Nurturing Responses*. Rio de Janeiro: International Behavioral Neuroscience Society.

Everette, A., Tu, K. Rima, B., Major, J., Conway, A. F., Kinsley, C. H., & Lambert, K. G. (2006). *Plasticity of Paternal Responsiveness in Two Peromyscus Species*. Whistler, BC: International Behavioral Neuroscience Society.

Franssen, C. L., Karsner, S., Tu, E., Hyer, M., & Lambert, K. G. (2009). *Neuroplasticity in Two Congeneric Species*. Boston, MA: Society for Integrative and Comparative Biology.

Gatewood, J. D., Morgan, M. D., Eaion, M., NcNamara, I. M., Stevens, L. F., Macbeth, H A., Meyers, E. A. A., Lomas, L. M., Kozub, F. J., Lambert, K. G., & Kinsley, C. H. (2005). Motherhood mitigates aging-related deficits in learning and memory. *Brain Research Bulletin*, 66: 91–98.

Ginther, A. J. & Snowdon, C. T. (2009). Expectant parents groom adult sons according to previous alloparenting in a cooperatively breeding primate. *Animal Behaviour*, 78: 287–297.

Ginther, A. J., Ziegler, T. E., & Snowdon, C. T. (2001). Reproductive biology of captive male cotton-top tamarin monkeys as a function of social environment. *Animal Behaviour*, 61: 65–78.

Gonzaga, G. C., Turner, R. A., Keltner, D, Campos, B., & Altemus, M. (2006). Romantic love and sexual desire in close relationships. *Emotion*, 6: 163–179.

Grewen, K. M., Girdler, S. S., Amico, J., & Light, K. C. (2005). Effect of partner support on resting oxytocin, cortisol norepinephrine and blood pressure before and after warm partner contact. *Psychosomatic Medicine*, 67: 531–538.

Gubernick, D. J. & Nelson, R. A. (1989). Prolactin and paternal behavior in the biparental California mouse (*Peromyscus californicus*). *Hormones and Behavior*, 23: 203–210.

Hammock, E. A. D. & Young, L. J. (2005). Microsatellite instability generates diversity in brain and sociobehavioral traits. *Science*, 308: 1630–1634.

Hare, B., Melis, A. P., Woods, V., Hastings, S., & Wrangham, R. (2007). Tolerance allows bonobos to outperform chimpanzees on a cooperative task. *Current Biology*, 17: 619–623.

Hare, B. & Tomasello, M. (2004). Chimpanzees are more skilful in competitive than in cooperative cognitive tasks. *Animal Behaviour*, 68: 571–581.

Humle, T. & Snowdon, C. T. (2008). Socially biased learning in the acquisition of a complex foraging task in juvenile cottontop tamarins (*Saguinus oedipus*). *Animal Behaviour*, 75: 267–277.

Humle, T., Snowdon, C. T., & Matsuzawa, T. (2009). Social influences on the acquisition of ant dipping among the wild chimpanzees (*Pan troglodytes verus*) of Bossou, Guinea, West Africa. *Animal Cognition*, 12: S37–S48.

Jensen, K., Hare, B., Call, J., & Tomasello, M. (2006). What's in it for me? Self-regard precludes altruism and spite in chimpanzees. *Proceedings of the Royal Society of London. Series B*, 273: 1013–1021.

Joyce, S. M. & Snowdon, C. T. (2007). Developmental changes in food transfers in cotton-top tamarins (*Saguinus oedipus*). *American Journal of Primatology*, 28: 257–270.

Keverne, E. B., Martensz, N. D., & Tuite, B. (1989). Beta-endorphin concentrations in cerebrospinal fluid of monkeys as influenced by grooming relationships. *Psychoneuroendocrinology*, 14: 155–161.

King, B. J. (1994). *The Information Continuum: The Evolution of Information Transfer in Monkeys Apes and Hominids*. Santa Fe: School for American Research.

Kinsley, C. H., Madonia, L., Gifford, G. W., Tureski, K., Griffin, G. R., Lowry, C., Williams, J., Collins, J. McLearie, H., & Lambert, K. G. (1999). Motherhood improves learning and memory, *Nature*, 402: 137–138.

Kosfeld, M., Heinrichs, M., Zak, P. J., Fischbacher, U., & Fehr, E. (2005). Oxytocin increases trust in humans. *Nature*, 435: 673–676.

Kostan, K. M. & Snowdon, C. T. (2002). Attachment and social preferences in cooperatively-breeding cotton-top tamarins. *American Journal of Primatology*, 57: 131–139.

Kozorovitskiy, Y, Hughes, M., Lee, K., & Gould, E. (2006). Fatherhood affects dendritic spines and vasopressin V1a receptors in primate prefrontal cortex, *Nature Neuroscience*, 9: 1094–1095.

Krüger, T. H. C., Haake, P. Chereath, D., Knapp, W., Janssen, O. E., Exton, M. S., Schedlovsky, M., & Hartmann, U. (2003). Specificity of the neuroendocrine response to orgasm during sexual arousal in men. *Journal of Endocrinology*, 177: 57–64.

Lazaro-Perea, C., Arruda, M. F., & Snowdon, C. T. (2004). Grooming as reward? Social functions of grooming in cooperatively breeding marmosets. *Animal Behaviour*, 67: 627–636.

Löttker, P., Huck, M., Zinner, D. P., & Heymann, E. W. (2007). Grooming relationships between breeding females and adult group members in cooperatively breeding moustached tamarins (*Saguinus mystax*). *American Journal of Primatology*, 69: 1159–1172.

Love, G., Torrey, N., McNamara, I., Morgan, M., Banks, M. Hester, N. W., Glasper, E. R., deVries, A. C., Kinsley, C. H., & Lambert, K. G. (2005). Maternal experience produces long lasing behavioral modification in the rat. *Behavioral Neuroscience*, 119: 1084–1096.

Marler, C. A., Bester-Meredith, J. K., & Trainor, B. C. (2003). Paternal behavior and aggression: Endocrine mechanisms and nongenomic transmission of behavior. In Slater, P. J. B., Rosenblatt, J. S., Snowdon, C. T., & Roper, T. J. (eds.), *Advances in the Study of Behavior*, Vol. 32, pp. 263–323. San Diego: Academic Press.

Mendoza, S. P. & Mason, W. A. (1986). Parental division of labour and differentiation of attachments in a monogamous primate (*Callicebus moloch*), *Animal Behaviour*, 34: 1136–1147.

Mendres, K. A. & de Waal, F. B. M. (2000). Capuchins do cooperate: The advantage of an intuitive task. *Animal Behaviour*, 60: 523–529.

Mota, M. T. S., Franci, C. R., & Sousa, M. B. C. (2006). Hormonal changes related to paternal and alloparental care in common marmosets (*Callithrix jacchus*). *Hormones and Behavior*, 49: 293–302.

Ochedalski, T., Subburaju, S., Wynn, P. C., & Aguliera, G. (2007). Interactions between oestogen and oxytocin on hypothalamic-pituitary-adrenal axis activity. *Journal of Neuroendocrinology*, 19: 189–197.

Parr, L. A., Matheson, M. D., Bernstein, I. S., & de Waal, F. B. M. (1997). Grooming down the hierarchy in captive brown capuchin monkeys. *Animal Behaviour*, 54: 361–367.

Pedersen, C. A. & Prange, A. J., Jr. (1979). Induction of maternal behavior in virgin rats after intracerebroventricular administration of oxytocin. *Proceedings of the National Academy of Sciences, USA*, 76: 6661–6665.

Porter, T. A. (1994). The development and maintenance of heterosexual pair associations in cotton-top tamarins (*Saguinus oedipus oedipus*) Unpublished Ph.D. dissertation, University of Wisconsin, Madison.

Price, A. C. & McGrew, W. C. (1991). Departures from monogamy in colonies of captive cotton-top tamarins. *Folia Primatologica*, 57: 16–27.

Prudom, S. L., Broz, C. A., Schultz-Darken, N., Ferris, C. T. Snowdon, C. T., & Ziegler, T. E. (2008). Exposure to infant scent lowers serum testosterone in father common marmosets, (*Callithrix jacchus*). *Biology Letters*, 4: 603–605.

Rapaport, L. G. (2006). Provisioning in wild golden lion tamarins (*Leontopithecus rosalia*) Benefits to omnivorous young. *Behavioral Ecology*, 17: 212–221.

Rapaport, L. G. & Ruiz-Miranda, C. R. (2002). Tutoring in wild golden lion tamarins. *International Journal of Primatology*, 23: 1063–1070.

Rapaport, L. G. & Ruiz-Miranda, C. R. (2006). Ontogeny of provisioning in two populations of wild golden lion tamarins (*Leontopithecus rosalia*). *Behavioral Ecology and Sociobiology*, 60: 724–735.

Ribble, D. O. (1991). The monogamous mating system of *Peromyscus californicus* as revealed by DNA fingerprinting. *Behavioral Ecology and Sociobiology*, 29: 161–166.

Robbins, M. M. (1995). A demographic analysis of male life history and social structure in mountain gorillas, *Behaviour*, 132: 21–47.

Robbins, M. M. (1999). Mating patterns in multimale groups of mountain gorillas. *Animal Behaviour*, 57: 1013–1020.

Robbins, M. M. & Czekala, N. M. (1997). A preliminary investigation of urinary testosterone and cortisol levels in wild male mountain gorillas. *American Journal of Primatology*, 43: 51–64.

Roberts, R. L., Jenkins, K. T., Lawler, T., Jr., Wegner, F. H., & Newman, J. D. (2001b). Bromocryptine administration lowers serum prolactin and disrupts parental responsiveness in common marmosets (*Callithrix j. jacchus*) *Hormones and Behavior*, 39: 106–112.

Roberts, R. L. Jenkins, K. T., Lawler, T., Wegner, F. H., Norcross, J. L., Bernhards, D. E., & Newman, J. D. (2001a) Prolactin levels are elevated after infant carrying in parentally inexperienced common marmosets, *Physiology and Behavior*, 72: 713–720.

Rosenblatt, J. S. (1990). Landmarks in the physiological study of maternal behavior with special reference to the rat. In Krasnegor, N. A. & Bridges, R. S. (eds.), *Mammalian Parenting*, pp. 40–60, Oxford: Oxford University Press.

Rutte, C. & Taborsky, M. (2007). Generalized reciprocity in rats. *Public Library of Science*, 5: 1421–1425.

Rutte, C. & Taborsky, M. (2008). The influence of social experience on cooperative behaviour of rats (*Rattus norvegicus*): Direct vs. generalised reciprocity. *Behavioral Ecology and Sociobiology*, 62: 499–505.

Savage, A., Ziegler, T. E., & Snowdon, C. T. (1988). Sociosexual development, pairbond formation and mechanisms of fertility suppression in female cotton-top tamarins (*Saguinus oedipus oedipus*). *American Journal of Primatology*, 14: 345–359.

Shutt, K. MacLarnon, A., Heistermann, M., & Semple, S. (2007). Grooming in Barbary macaques: Better to give than to receive? *Biology Letters*, 3: 231–233.

Silk, J. B., Brosnan, S. F., Vonk, J., Henrich, J., Povinelli, D. J., Richardson, A. S., et al. (2005). Chimpanzees are indifferent to the welfare of unrelated group members. *Nature*, 437: 1357–1359.

Silva, H. P. A. & Sousa, M. B. C. (1997). The pairbond formation and its role in the stimulation of reproductive function in female common marmosets (*Callithrix jacchus*). *International Journal of Primatology*, 18: 387–400.

Snowdon, C. T. (1996). Parental care in cooperatively breeding species. In Rosenblatt, J. S. & Snowdon, C. T. (eds.), *Parental Care: Evolution, Mechanisms and Adaptive Significance*, pp. 643–689. San Diego: Academic Press.

Snowdon, C. T. & Cronin, K. A. (2009). Comparative cognition and neuroscience, In Berntsen, G. & Cacioppo, J. (eds.), *Handbook of Behavioral Neuroscience*, pp. 30–55. New York: Wiley.

Snowdon, C. T., Pieper, B. A., Boe, C. Y., Cronin, K. A., Kurian, A. V., & Ziegler, T. E. (2010). Variation in oxytocin is related to variation in affiliative behavior in monogamous pairbonded tamarins *Hormones and Behavior*, published on-line June 28, 2010.

Snowdon, C. T. & Ziegler, T. E. (2007). Growing up cooperatively: Family processes and infant development in marmosets and tamarins. *Journal of Developmental Processes*, 2: 40–66.

Sprangers, S. A., Brenne, R. M., & Bethea, C, L. (1989). Estrogen and progestin receptor immonocytochemistry in lactotropes versus gonadotropes of monkey pituitary cell cultures. *Endocrinology*, 124: 1462–1470.

Strier, K. B. (1992). *Faces in the Forest*. New York: Oxford University Press.

Tannenbaum, P. L. & Wallen, K. (1997). Sexually initiated affiliation facilitates rhesus monkey integration. *Annals of the New York Academy of Science*, 807: 578–582.

Thornton, A. & McAuliffe, K. (2006). Teaching in wild meerkats. *Science*, 313: 227–229.

Tomizawa, K., Iga, N., Lu, Y., Moriwaki, A., Matsushita, M., Li, S., Miyamoto, O., Itano, T., & Matsui, H. (2003). Oxytocin improves long lasting spatial memory during motherhood through MAP kinase cascade. *Nature Neuroscience*, 6: 384–390.

Trainor, B. C. & Marler, C. A. (2001). Testosterone, paternal behavior, and aggression in the monogamous California mouse, *Peromyscus californicus*. *Hormones and Behavior*, 40: 32–42.

Trainor, B. C. & Marler, C. A. (2002). Testosterone promotes paternal behaviour in a monogamous mammal via conversion to oestrogen. *Proceedings of the Royal Society of London Series B*, 269: 823–829.

Turner, R. A., Altemus, M., Enos, T., Coopeer, B., & McGuinness, T. (1999). Preliminary research on plasma oxytocin in normally cycling women: Investigating emotion and interpersonal distress. *Psychiatry*, 62: 97–113.

Uvnäs-Moberg, K. (1998). Oxytocin may mediate the benefits of positive social interactions and emotions. *Psychoneuroendocrinology*, 23: 819–835.

Visalberghi, E., Pellegrini Quarantotti, B., & Tranchida, F. (2000). Solving a cooperation task without taking into account the partner's behavior: The case of capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, 114: 297–301.

Vonk, J., Brosnan, S. F., Silk, J. B., Henrich, J., Richardson, A. S., Lambeth, S. P., et al. (2008). Chimpanzees do not take advantage of very low cost opportunities to deliver food to unrelated group members. *Animal Behaviour*, 75: 1757–1770.

Wallen, K. (1982). Influence of female hormonal state on sexial behavior varies with space for social interaction. *Science*, 217: 375–377.

Walum, H., Westberg, L., Henningsson, S., Neiderhiser, J. M., Reiss, D., Igl, W., Ganiban, J. M., Spotts, E. L., Pedersen, N. L., Erikssin, E., & Lichtenstein, P. (2008). Genetic variation in the vasopressin receptor 1A gene (*AVPR1A*) associates with pair-bonding behavior in humans. *Proceedings of the Natioanl Academy of Science*, 105: 14153–14156.

Wang, Z., Moody, K. , Newman, J. D., & Inselm T. R. (1997). Vasopressin and oxytocin immunoreactive neurons and fibers in the forebrain of male and female common marmosets (*Callithrix jacchus*). *Synapse*, 27: 14–25.

Warneken, F., & Tomasello, M. (2006). Altruistic helping in human infants and young chimpanzees. *Science*, 311: 1301–1303.

Washabaugh, K. & Snowdon, C. T. (1998). Chemical communication of reproductive status in female cotton-top tamarins (*Saguinus o. oedipus*). *American Journal of Primatology*, 45: 337–349.

Washabaugh, K. F., Ziegler, T. E., & Snowdon, C. T. (2002). Variations in care for cotton-top tamarin (*Saguinus oedipus*) infants as a function of parental experience and group size. *Animal Behaviour*, 63: 1163–1174.

Woolley, C. S. & McEwen, B. S. (1992). Estradiol mediates fluctuation in hippocampal synapse density during the estrous cycle of the adult. *Journal of Neuroscience*, 12: 2549–2554.

Woolley, C. S. & McEwen, B. S. (1993). Role of estradiol and progesterone in the regulation of hippocampal spine density during the estrous cycle in the rat. *Journal of Comparative Neurology*, 336: 293–306.

Wrangham, R. & Peterson, D. (1996). *Demonic Males: Apes and the Origin of Human Violence*. Boston: Houghton Mifflin.

Zahed, S. K., Kurian, A. V., & Snowdon, C. T. (2010). Social dynamics and individual plasticity of infant care behavior in cooperatively breeding cotton-top tamarins. *American Journal of Primatology*, 72: 296–306.

Zahed, S. R., Prudom, S. L., Snowdon, C. T., & Ziegler, T. E. (2008). Male parenting and response to infant stimuli in the common marmoset (*Callithrix jacchus*). *American Journal of Primatology*, 70: 84–92.

Zak, P. J., Kurzban, R., & Matzner, W. T. (2005). Oxytocin is associated with human trustworthiness. *Hormones and Behaviour*, 48: 522–527.

Zak, P. J., Stanton, A. A., & Ahmadi, S. (2007). Oxytocin increases generosity in humans. *Public Library of Science, 2*(11): E1128.

Ziegler, T. E., Epple, G., Snowdon, C. T., Porter, T. A., Belcher, A., & Kuederling, I. (1993). Detection of the chemical signals of ovulation in the cotton-top tamarin, *Saguinus oedipus, Animal Behaviour*, 45: 313–322.

Ziegler, T. E., Prudom, S. L., Schultz-Darken, N. J., Kurian, A. V., & Snowdon, C. T. (2006). Pregnancy weight gain: Marmoset and tamarin dads show it too. *Biological Letters of the Royal Society*, 2: 181–183.

Ziegler, T. E., Scheffler, G., & Snowdon, C. T. (1995). The relationship of cortisol levels to social environment and reproductive functioning in female cotton-top tamarins, *Saguinus oedipus, Hormones and Behavior*, 29: 407–424.

Ziegler, T. E., Schultz-Darken, N. J., Scott, J. J., Snowdon, C. T., & Ferris, C. F. (2005). Neuroendocrine response to female ovulatory odors depends upon social condition in male common marmosets, *Callithrix jacchus. Hormones and Behavior*, 47: 56–64.

Ziegler, T. E., Washabaugh, K. F., & Snowdon, C. T. (2004). Responsiveness of expectant male cotton-top tamarins, *Saguinus oedipus*, to mate's pregnancy. *Hormones and Behavior*, 45: 84–92.

Ziegler, T. E., Wegner, F. H., & Snowdon, C. T. (1996). A hormonal role for male parental care in a New World primate, the cotton-top tamarin (*Saguinus oedipus*). *Hormones and Behavior*, 30: 287–297.

# Chapter 19
# Early Social Experience and the Ontogenesis of Emotion Regulatory Behavior in Children

**Seth D. Pollak**

Emotions are complex processes that organisms use to evaluate their environments, rapidly assess the significance of environmental changes, and adjust their behaviors. Over the course of (normative) development, these processes interact seamlessly and rapidly, affording successful adaptation to a variety of demands. Yet, problems in emotional functioning can lead to pervasive problems in mental and physical health. A central assumption in the study of human emotion is that we are born with certain basic, normative emotions (at least those referred to in Western cultures by words such as *anger*, *sadness*, *fear*, *disgust*, and *happiness*) and that some rudimentary neural circuitry for emotion is preconfigured in the human brain. But increasingly, the role of social experience in configuring human brain function has shed new light on the emergence of emotional behavior. The issue of how adverse social experiences alter and shape children's social and emotional development has become center-stage for the exploration of the relative contributions of nature and nurture in child development. Our research has examined the ways in which children's developing biology is shaped in a manner that may be adaptive to their immediate environment, but confers risk for a host of negative developmental outcomes. Such an approach raises issues about the role of social factors in the construction of typically observed as well as statistically deviant behaviors. Current research is examining the ways in which environmental experiences influence the complex sets of neural circuitry underlying emotional behaviors. One way to address these questions is to focus on the development of children, rodents, and nonhuman primates who receive poor or inadequate parental care; each species allows exploration of a different level of analysis. Maltreatment of human children is notoriously difficult to define, measure, and investigate empirically. Nevertheless, this phenomenon has provided an important forum for investigating the role of environmental stress, individual differences, and developmental factors in the ontogenesis of social behavior. In this article, I begin by reviewing the kinds of emotion-regulatory problems experienced by maltreated children that appear to reflect alterations in underlying

---

S.D. Pollak (✉)
Department of Psychology, University of Wisconsin, Madison, WI 53706-1696, USA
e-mail: spollak@wisc.edu

R.W. Sussman, C.R. Cloninger (eds.), *Origins of Altruism and Cooperation*,
Developments in Primatology: Progress and Prospects 36, DOI 10.1007/978-1-4419-9520-9_19,

biological processes. The second half of this chapter focuses on the neurodevelopmental mechanisms that may account for how early experience influences affective processes. Our initial investigations underscored how these groups of children develop sets of behavioral problems that are specific to the features of their social environment (Pollak et al., 2005; Pollak, 2008). More recent research from our group, employing neurobiological metrics such as electrophysiological, neuroimaging, and neuroendocrine indices, has assayed potential neurobiological mediators of these social difficulties.

## Neurobiological Consequences of Child Maltreatment

Maltreated children experience high rates of physical and mental health problems including conduct disorders/aggression, depression, anxiety, and substance abuse; they also lag behind their peers in social skills (Mulvihill, 2005). Not surprisingly, child abuse co-occurs with a host of genetic and environmental risk factors that affect child, parent, and family functioning. It is thus difficult to evaluate where to place the occurrence of child maltreatment in the causal chain leading to behavioral problems. Experiments with nonhuman animals have provided the opportunity for careful modeling of the effects of inadequate nurturance, leading to studies of the neuroanatomical and neurophysiological substrates of emotion processing that are not feasible with humans.

Generalizations about the biological processes underlying emotional behaviors across species require caution for a number of reasons. Animal models do not always mimic human emotional disorders; brain development, structure, and function are not identical across species; there are chromosomal differences between species; and the actual behaviors exhibited by parents and the way these behaviors are received and experienced by offspring are not identical across species. But there are phenomena that do occur across species—such as poor or inadequate parental nurturance—that provide critical clues about the biological effects of child abuse. Indeed, the developmental outcomes of infant maltreatment among nonhuman primates are strikingly similar to those reported in maltreated children (Sanchez et al., 2007).

It is possible that heritable factors that co-occur with maltreatment, rather than maltreatment per se, are responsible for the behavioral difficulties observed in children. As in humans, physical abuse in rhesus monkeys has a high prevalence in some family lineages, suggesting inter-generational transmission. However, evidence from rhesus cross-fostering studies (in which infants are raised by unrelated surrogates) suggests that behavioral problems observed in monkeys are due to the postnatal experience of maltreatment rather than to genetic heritability (Maestripieri, 2005). Consistent with this view, behavioral and molecular genetic analyses support the view that the experience of abuse has a causal role in the emergence of behavioral problems in maltreated children. Current data are consistent with the position that genetic risk, in combination with early traumatic experiences, dramatically increases the likelihood of children developing mental health problems (Kim-Cohen et al., 2007).

The early experience of maltreatment appears to establish developmental trajectories of risk. One recent report revealed that individuals who were abused earlier in life demonstrated higher levels of anxiety and depression in adulthood, whereas individuals who were older at the time of the maltreatment were more likely to evince symptoms associated with aggression and substance abuse (Kaplow & Widom, 2007). To excavate the developmental processes associated with early life stress, it is also necessary to examine patterns of emotional behavior that may appear before the onset of psychological disorders. Thus, the phenomenon of early stress in the form of child maltreatment now figures prominently in considerations of the relative contributions of nature and nurture in development, and has focused attention on the neural mechanisms through which social experiences influence emotional functioning.

## Mechanisms Underlying Altered Emotion Regulation in Maltreated Children

### *Cognitive Processing Mechanisms*

A critical question concerns how early experiences relate to the wide range of health and behavioral outcomes associated with child maltreatment. One current hypothesis is that children's early experience alters sensory thresholds in ways that undermine effective regulation of emotion. Consistent with this view, when abused children performed a task that required them to distinguish faces that had been morphed to produce a continuum on which each face differed in signal intensity, abused children displayed enhanced perceptual sensitivity to angry facial cues. Unlike non-abused children, abused children judged ambiguous facial expressions (blends of two emotions) as "angry." Yet abused children's processing of other facial expressions was generally similar to that of non-maltreated children (Pollak & Kistler, 2002). These findings are consistent with the view that infants and children adjust or tune their pre-existing perceptual mechanisms to process aspects of their environments that have become salient through learning from their social experiences (see Fig. 19.1).

This acquired salience of certain emotional signals undermines abused children's attentional control. Non-maltreated children and adults attend to happy, fearful, and angry faces similarly. However, physically abused children display relative increases in brain electrical activity when actively searching for angry faces, and show rapid orienting to, as well as delayed disengagement from, anger cues. The degree of children's attentional differences correlates with both the magnitude of abuse the child endured and the child's degree of anxiety symptoms (Shackman et al., 2007). This point is illustrated in Fig. 19.2, which shows how physically abused children

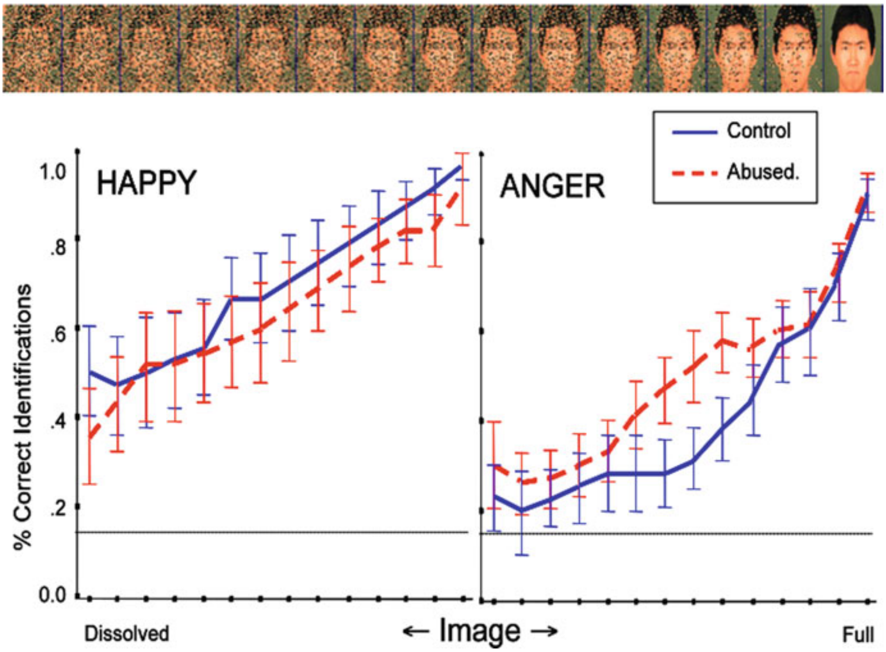


**Fig. 19.1** Abused children's accuracy at identifying happy (*left graph*) or angry (*right graph*) faces at progressive levels of image clarity compared to that of controls. Abused children's accuracy is shown in *red*; controls are shown in *blue*. The figure depicts children's accuracy as the image came into focus (the angry-face example is shown at *top*) with 95% confidence intervals around each group's mean

automatically attend to threatening cues at the expense of more contextually relevant information.

The critical point about these studies is that while it is adaptive for salient environmental stimuli to elicit attention, successful self-regulation requires flexibility and control over these processes. We suspect that failure of regulatory capacities is a proximal link between early experience and abused children's troubles, and makes what is adaptive within an abusive environment maladaptive in more normative social settings. Physically abused children's processing abnormalities appear to be specific to anger rather than being general information-processing deficits. It is thus unlikely that these effects are secondary to more global aspects of deprivation such as poverty, poor nutrition, or inadequate health care.

Neglected children also have difficulties differentiating between and responding to expressions of emotion and formulating selective attachments to caregivers (Wismer Fries et al., 2005). These social and emotional difficulties may reflect neuropsychological difficulties due to alterations in brain maturation (Prasad et al., 2005). Indeed, impaired cognitive functioning in monkeys reared in isolation is associated with decreased white matter in parietal and prefrontal cortices as well as

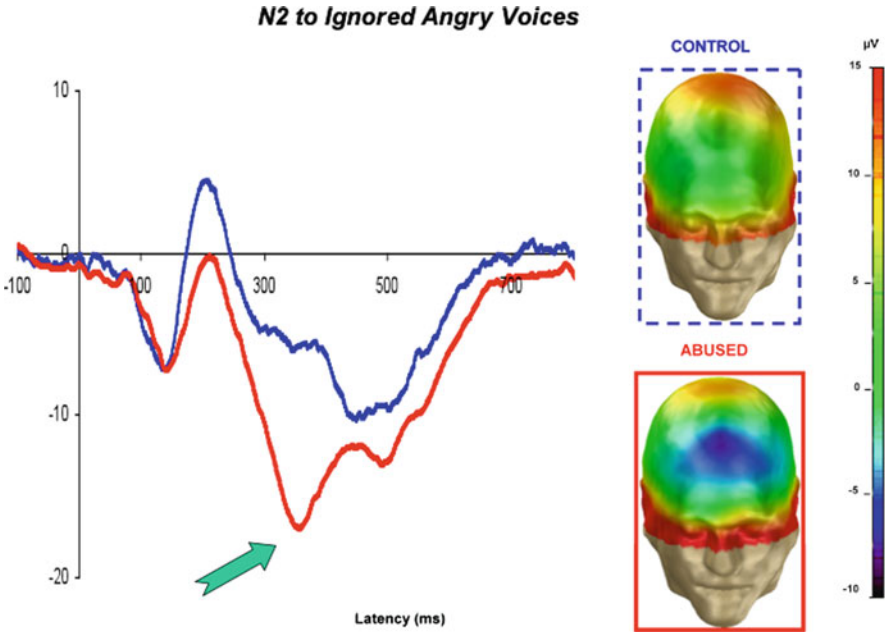


**Fig. 19.2** N2 response of the event-related potential (recorded from electrodes at the frontal region of the scalp) for children who were instructed to attend to emotional faces while ignoring angry voices. N2 is associated with inhibitory control and conflict resolution. As indicated by the *arrow*, abused children (*red line*) showed a larger N2 when trying to suppress their responses to angry voices that were irrelevant to the task than did controls (*blue line*). Topographic maps for control (*top*) and abused (*bottom*) children are presented alongside the waveforms and illustrate the general location of the inhibitory effect. The magnitude of this effect was related to the severity of the abuse children received

alterations in the development of hormone receptors that underlie fearful and anxious behaviors (Sanchez et al., 2007). A recent brain-imaging study of children with maltreatment-related PTSD revealed smaller sized regions such as the prefrontal cortex and right temporal lobe in comparison to sociodemographically matched controls; these effects suggest that early stress may delay brain development (Tupler & De Bellis, 2006). Future studies using prospective high-risk designs may be able to rule out the possibility that these brain differences reflect a vulnerability to the effects of, rather than the result of, maltreatment.

One recent study (Pollak et al., 2005) examined attention regulation in physically abused preschoolers presented with interpersonal hostility, a situation that predicts abuse in these children's home environments. Autonomic measures such as heart rate and skin conductance were measured in abused and non-abused children while they overheard two unfamiliar adults engage in an argument. The abused children maintained a state of anticipatory monitoring of the environment, from the time the actors began expressing anger throughout the entire experiment—even after the actors had reconciled. This response was quite distinct from that of the non-maltreated children in the study; they showed initial arousal to the expression of anger but were better able to regulate their responses once they determined that it was not personally relevant to them. This lack of regulatory control over emotion processing is likely to guide children's social behavior in ways that are maladaptive.

## *Stress Regulatory Mechanisms*

Studies of nonhuman animals have long provided evidence that adverse parental care shapes the development of the neural systems believed to underlie emotional problems. Perhaps the most frequently examined system is the limbic hypothalamic pituitary adrenal axis (L-HPA). The L-HPA axis is one of the threat response systems that is particularly open to modification by experience during early life. The L-HPA system mediates neuroendocrine responses to stress, resulting in the release of steroid hormones from the adrenal gland. These hormones, glucocorticoids, affect a broad array of problems experienced by abused children, including energy mobilization, immune responses, arousal, and cognition. In a recent study, we found that a high degree or severity of neglect experienced by children was associated with long-term regulatory problems of the stress-responsive system (Fries et al., 2008). Not surprisingly, alterations in pituitary and adrenal function have been associated with illnesses common among previously abused individuals, including depression, anxiety, post-traumatic stress disorder (PTSD), fibromyalgia, hypertension, and immune system suppression.

In addition to stress hormones, other neuroactive peptides such as arginine vasopressin and oxytocin are emerging as important regulators of stress responses and critical mediators of affiliative behaviors and social recognition and memory. Oxytocin, for example, plays a critical role mediating affiliative behaviors such as maternal attachment and social bonding; it also reduces anxiety and HPA axis responses to stress. The effects of maltreatment experiences on oxytocin neural circuits have been recently confirmed in humans as well, as demonstrated by evidence that children who experienced severe early neglect showed lower levels of salivary oxytocin reactivity compared with controls (Fries et al., 2005). Similarly, women with histories of childhood maltreatment had lower cerebrospinal fluid levels of oxytocin than did controls (Heim et al., 2006). The study with children and the one with adults both suggested that the functioning of the oxytocin system was correlated with severity of maltreatment experienced by the individual. Reduced oxytocin activity could have a detrimental effect on affiliative behaviors and stress regulation in individuals who experienced early adversity.

Another way to evaluate brain plasticity is through the immune system, which must learn to respond to environmental pathogens encountered after an individual is born. Indeed, early life stress appears to have continued effects over development, with individuals continuing to show poor immune competence—a long-term reflection of heightened stress—years after stress has ended. For example, monkeys with high levels of maternal rejection show high inflammatory markers and low concentrations of serotonin (Sanchez et al., 2007). Similarly, adults who retrospectively recall maltreatment show sustained effects on immunity in a pattern (altered B- and cytotoxic C-cell numbers and inflammatory markers such as C-reactive protein) consistent with psychological states of physiological arousal (Danese et al., 2007).

### *Neuroanatomical Mechanisms*

A related neural system of relevance to abused children's emotion regulation is the circuitry of the amygdala, implicated in threat responses. Hariri et al. (2002) used functional magnetic resonance imaging (fMRI) to directly explore the relationship between a common regulatory variant in the serotonin transporter gene (*5-HTTLPR*) and emotional behavior in adults. Subjects performed a simple perceptual processing task involving the matching of fearful and angry human facial expressions. People carrying the less efficient *5-HTTLPR* short allele exhibited increased amygdala activity in comparison to subjects homozygous for the long allele. Thus, increased anxiety and fearfulness may reflect the hyper-responsiveness of the amygdala to relevant environmental stimuli. In rhesus monkeys, high rates of maternal rejection, which co-occur with infant maltreatment, affect the development of brain serotonergic systems, resulting in increased anxiety (Maestripieri et al., 2006).

Consistent findings are emerging in studies of abused children. Maltreated children with the *5-HTTLPR* short allele and little social support had high levels of depression. However, maltreated children with the same genotype and similar levels of maltreatment but who had access to social support from adults showed minimal depressive symptoms (Kaufman et al., 2004). These findings are consistent with research in adults showing that *5-HTTLPR* variation moderates the development of depression after stress and suggest that negative outcomes may be modified by environmental factors that confer risk for or protection from psychological disorders.

## Conclusions and Future Directions

The phenomenon of child abuse has been of interest to clinicians, educators, and public policy leaders for decades because of the clear associations between child abuse and poor mental and physical health outcomes. Contemporary research has cast important light on specific mechanisms that are responsible for the social and health risks seen in maltreated children. Drawing from neurophysiologically precise nonhuman primate studies, it appears that the modulatory role of hormonal and neurotransmitter systems may help explain risk to maltreated children. Because of their regulatory role in reactivity to threat, the prefrontal cortex and infralimbic regions appear to be central candidates for explaining the ways in which experience-dependent fine-tuning of attention, learning, emotion, and memory systems affect emotion regulation.

Important directions for future research include prospective longitudinal studies in humans that can determine whether the neurobiological correlates of early adversity are enduring long-term changes, whether short-term responses to early stress serve as risk factors for the onset of other stressors or developmental problems, and how early effects on brain and behavior may be reversed or remediated. In addition, a better understanding of how treatments work will also inform understanding of basic emotion processes in children. Developmentally informed models of the links between early experience and subsequent behavior will also require more detailed specification about how behavioral outcomes relate to variations in children's experiences, including variations in the nature, severity, and duration of stressors, as well as more fine-grained examination of the ages at which children experienced them.

Understanding the processes through which early social experience affects child development increases the likelihood of developing effective prevention and intervention programs. Studying children who have experienced atypical emotion-learning environments, such as maltreated children, also yields valuable knowledge about fundamental issues in psychological science. These include a focus on the neural circuitry and neurobiological regulation of emotion and their subsequent implications for behavior, as well as understanding adaptations and sequelae of chronic social stress exposure on affective neural circuits—especially during periods of rapid neurobiological change during which the brain may be particularly sensitive to contextual or environmental influences. Because existing data have not rendered it possible to reach firm conclusions about whether emotion is innate, we have examined the development of emotion among children whose environments have differed in important ways from a species-typical care giving environment. The general principle behind these studies is that examining the ways in which the aberrant environments influence biobehavioral development may highlight the nature of the learning mechanisms underlying emotion. Studying this question across species and across typically and atypically developing populations of children may highlight learning mechanisms that may not be obvious when emotional development is unfettered. Ongoing research in this area is focusing on defining and specifying ways in which the environment creates long-term effects on brain and behavior, including potential corrective experiences that might foster recovery of competencies and promote health.

**Acknowledgments** This work was supported by the National Institute of Mental Health through grant numbers R01-MH61285 and R01-MH68858.

## References

Danese, A., Pariante, C.M., Caspi, A., Taylor, A., & Poulton, R. (2007). Childhood maltreatment predicts adult inflammation in a life-course study. *Proceedings of the National Academy of Sciences, USA, 104*, 1319–1324.

Hariri, A.R., Mattay, V.S., Tessitore, A., Kolachana, B., Fera, F., Goldman, D., et al. (2002). Serotonin transporter genetic variation and the response of the human amygdala. *Science, 297*, 400.

Heim, C., Newport, D.J., Mletzko, T., Miller, A.H., Young, L.J., & Nemeroff, C.B. (2006). Decreased cerebrospinal fluid oxytocin concentrations associated with childhood maltreatment in adult women. *Developmental Psychobiology Abstract, 48*, 603–630.

Kaplow, J.B., & Widom, C.S. (2007). Age of onset of child maltreatment predicts long-term mental health outcomes. *Journal of Abnormal Psychology, 116*, 176–187.

Kaufman, J., Yang, B.-Z., Douglas-Palumberi, H., Houshyar, S., Lipschitz, D., Krystal, J.H., & Gelernter, J. (2004). Social supports and serotonin transporter gene moderate depression in maltreated children. *Proceedings of the National Academy of Sciences, USA, 101*, 17316–17321.

Kim-Cohen, J., Caspi, A., Taylor, A., Williams, B., Newcombe, R., Craig, I.W., & Moffitt, T.E. (2007). MAOA, early adversity, and gene-environment interaction predicting children′s mental health: New evidence and a meta-analysis. *Molecular Psychiatry, 11*, 903–913.

Maestripieri, D. (2005). Early experience affects the intergenerational transmission of infant abuse in rhesus monkeys. *Proceedings of the National Academy of Sciences, USA, 102*, 9726–9729.

Maestripieri, D., McCormack, K., Lindell, S.G., Higley, J.D., & Sanchez, M.M. (2006). Influence of parenting style on the offspring′s behavior and CSF monoamine metabolite levels in cross-fostered and noncrossfostered female rhesus macaques. *Behavioural Brain Research, 175*, 90–95.

Mulvihill, D. (2005). The health impact of childhood trauma: An interdisciplinary review, 1997–2003. *Issues in Comprehensive Pediatric Nursing, 28*, 115–136.

Pollak, S.D., (2008). Mechanisms linking early experience and the emergence of emotions: Illustrations from the study of maltreated children. *Current Directions in Psychological Science, 17*, 370–375.

Pollak, S.D., & Kistler, D.J. (2002). Early experience is associated with the development of categorical representations for facial expressions of emotion. *Proceedings of the National Academy of Sciences, USA, 99*, 9072–9076.

Pollak, S.D., Vardi, S., Bechner, A.M.P., & Curtin, J.J. (2005). Physically abused children′s regulation of attention in response to hostility. *Child Development, 76*, 968–977.

Prasad, M.R., Kramer, L.A., & Ewing-Cobbs, L. (2005). Cognitive and neuroimaging findings in physically abused preschoolers. *Archives of Disease in Childhood, 90*, 82–85.

Sanchez, M.M., Alagbe, O., Felger, J.C., Zhang, J., Graff, A.E., Grand, A.P., et al. (2007). Activated p38 MAPK is associated with decreased CSF 5-HIAA and increased maternal rejection during infancy in rhesus monkeys. *Molecular Psychiatry, 12*, 895–897.

Shackman, J.E., Shackman, A.J., & Pollak, S.D. (2007). Physical abuse amplifies attention to threat and increases anxiety in children. *Emotion, 7*, 838–852.

Tupler, L.A., & De Bellis, M.D. (2006). Segmented hippocampal volume in children and adolescents with posttraumatic stress disorder. *Biological Psychiatry, 59*, 523–529.

Wismer Fries, A.B., Shirtcliff, E.A., & Pollak, S.D. (2008). Neuroendocrine dysregulation following early social deprivation in children. *Developmental Psychobiology, 50*(6), 588–599.

Wismer Fries, A.B., Zigler, T., Kurian, J., Jacoris, S., & Pollak, S.D. (2005). Early experience in humans is associated with changes in neuro-peptides critical for regulating social behaviour. *Proceedings of the National Academy of Sciences, USA, 102*, 17237–17240.

# Part V

# Human Altruism and Cooperation: Needs and the Promotion of Well-Being in Modern Life

## Chapter 20

# Human Altruism and Cooperation: Needs and the Promotion of Well-Being in Modern Life: Introduction Part V

**Juan E. Mezzich**

The remarkable journey that this volume represents on the exploration of the origins of altruism and cooperation reaches its last station, one that is eminently human. Altruism may be seen as the unselfish concern for or devotion to the welfare of others. Cooperation involves joint activity for a common purpose or benefit. Together, these concepts denote high forms of prosocial behavior and illustrate forms of positive health or well-being (Cloninger, 2004; Cloninger & Zohar, 2011; Mezzich, 2005).

A brief analysis of the scope and implications of the above health concepts may be helpful for understanding their bases better and advancing their fulfillment.

Despite the conventional modern emphasis on pathology or ill health, the World Health Organization (1946) has affirmed since its establishment that health is a state of full physical, emotional, and social well-being and not merely the absence of disease or infirmity. The growing recognition of the importance of specific and unspecific prevention and health promotion makes this definition of health not only tenable but also compelling.

A reasonable theoretical framework for understanding health may involve several levels of analysis, that is, not only the traditional biological, psychological, and social frames (Engel, 1977) but also the cultural and spiritual (Fabrega, 1975; Cox et al., 2007). This is also in line with the existential perspectives of Ortega y Gasset, *I am I and my circumstance*. This *circumstance* may include both cross-sectional and historical perspectives and be multidimensional along the lines mentioned above.

A fundamental set of considerations for understanding health and advancing health care involve human relationships. As documented well by Finset (2010) and Van Dulmen et al. (2007), clinical communication can be enhanced when it is engaging, empathetic, and informative. This speaks of the importance of attending to human needs and concerns and not merely managing a disease.

---

J.E. Mezzich (✉)
International Center for Mental Health, Mount Sinai School of Medicine, New York University, New York, NY 10029, USA
e-mail: juanmezzich@aol.com

R.W. Sussman, C.R. Cloninger (eds.), *Origins of Altruism and Cooperation*,
Developments in Primatology: Progress and Prospects 36, DOI 10.1007/978-1-4419-9520-9_20,

Empowering persons to assume responsibility for their own health (beyond the responsibilities of society in their various forms) is emerging as strategically crucial for dealing with the growing epidemics of chronic diseases. Empowering is also ethically compelling as related to respect for the person's autonomy (Christodoulou, 2010). Another important aspect of clinical communication is respect for the person's dignity. This is a fundamental ethical imperative regardless of the person's condition or level of health.

Also emerging as a crucial clinical strategy is the establishment of effective partnerships at all relevant levels. Concerning health professionals, this usually involves an interdisciplinary team approach. This requires a high degree of communication and an attitude of cooperation among professionals of various specialties and disciplines. Most crucial is the partnership among clinicians, the patient, and the patient's family. This is not only essential in regular clinical work but also valuable for organizational purposes, as exemplified by *trialogues* among professionals, service users, and relatives (Amering, 2010). In connection to fundamental clinical processes, the abovementioned partnerships find expression in conceptualizing and organizing diagnosis as shared understanding and treatment planning as shared commitment (Fulford, 2010).

Many of the concepts and procedures outlined in this brief chapter find an umbrella in the initiative on *person-centered medicine* cultivated since 2008 through annual Geneva Conferences organized by the International Network for Person-centered Medicine in collaboration with the World Medical Association, the World Organization of Family Doctors, the World Health Organization and 20 other international health institutions. It places the person as the center and goal of health care. Its purposes may be summarized as promoting a medicine *of* the person (of the totality of the person's health, including its ill and positive aspects), *for* the person (promoting the fulfillment of the person's life project), *by* the person (with clinicians extending themselves as full human beings, well grounded on science and with high ethical aspirations), and *with* the person (working respectfully, in collaboration, and in an empowering manner through a partnership of patient, family, and clinicians) (Mezzich et al., 2009).

David Hay in the first chapter in this book section examines altruism and spirituality as aspects of relational consciousness. This relational consciousness is posited as a quasi biological basis of the higher attributes. As such, this article represents a bridge between biological substrate and altruism. Contraposed to related consciousness is individualism, which Hay perceives as product of European circumstance and inimical to both altruism and spirituality.

Kevin Cloninger authored the second chapter, "Hope rekindled: Well-being, humanism and education" cogently projecting the book arguments to the broad field of human development and learning. Building on Western civilization examples, he posits that educating people has always involved helping them to attain well-being. Furthermore, he argues that in education we need to work toward the cultivation of the whole person, quite consistently with the proposals advanced earlier in this introduction.

Lauren Munsch and Helen Herrman address in the third chapter promoting well-being in health care. They note that cooperative behaviors are fundamental to health and well functioning in individuals and populations, that the prevailing disease-based medicine often sees human beings as little more than faulty machines that need repair, and that such medicine usually fails to focus on the whole person and how the person may have a healthy and happy life. They plea for new approaches to personal health and public health seeking to promote the full development of human potential.

In the final chapter, Dan Blazer proposes moving beyond the nature–nurture distinction. To this effect, he discusses the value of transdisciplinary research to understand the social, behavioral, and genetic factors interacting to influence health.

The findings and arguments formulated in this volume on the origins of cooperative behavior have been amplified in this section with special reference to human perspectives. Emerging person-centered approaches to health and health care and the four extensive chapters in this part have clarified the cruciality and scope of cooperative and other positive behaviors for the survival and flourishing of human beings.

## References

Amering M (2010): Trialogue and exercise in communication between consumers, carers and professional mental health workers beyond role stereotypes. International Journal of Integrated Care 10 Supplement: e014.

Christodoulou G (2010): Moral theories and medicine for the person. International Journal of Integrated Care 10 Supplement: e018.

Cloninger CR (2004): Feeling Good: The Science of Well-being. New York, Oxford University Press.

Cloninger CR, Zohar AH (2011): Personality and the perception of health and happiness. Journal of Affective Disorders 128: 24–32.

Cox J, Campbell AV, Fulford KWM (2007): Medicine of the Person: Faith, Science and Values in Health Care Provision. London, Jessica Kingsley.

Engel GL (1977): The need for a new medical model: A challenge for biomedicine. Science 196: 129–36.

Fabrega H (1975): The need for an ethnomedical science. Science 189: 969–975.

Finset A (2010): Research on person-centred clinical care. Journal of Evaluation in Clinical Practice 17: 384–386.

Fulford KWM (2010): Bringing together values-based and evidence-based medicine: UK department of health: Initiatives in the “personalization” of care. Journal of Evaluation in Clinical Practice 17: 341–343.

Mezzich JE (2005): Positive health: Conceptual place, dimensions and implications. Psychopathology 38: 177–179.

Mezzich JE, Snaedal J, Van Weel C, Heath I (2009): The international network for person-centred medicine: Background and first steps. World Medical Journal 55: 104–107.

van Dulmen S, Sluijs E, van Dijk L, de Ridder D, Heerdink R, Bensing J (2007): Patient adherence to medical treatment: A review of reviews. BMC Health Service Research 7: 55.

World Health Organization (1946): WHO Constitution. Geneva, Author.

# Chapter 21
# Altruism as an Aspect of Relational Consciousness and How Culture Inhibits It

**David Hay**

> *Avarice, envy, pride,*
> *Three fatal sparks, have set the hearts of all*
> *On Fire. – Dante Alighieri, The Divine Comedy (1314)*[1]
>
> *No man is an island, entire of itself. . .any man's death diminishes me, because I am involved in mankind; and therefore never send to know for whom the bell tolls; it tolls for thee. – John Donne Devotions upon Emergent Occasions (1624)*[2]
>
> *It is not from the benevolence of the butcher, the brewer or the baker that we expect our dinner, but from their regard to their own interest. We address ourselves, not to their humanity but to their self-love, and never talk to them of our necessities but of their advantages. – Adam Smith The Wealth of Nations (1776)*[3]
>
> *The point is, ladies and gentleman, that greed – for lack of a better word – is good. Greed is right. Greed works. Greed clarifies, cuts through, and captures the essence of the evolutionary spirit. – Gordon Gecko in Wall Street (1987)*[4]
>
> *We have to fight uphill to rediscover the obvious, to counteract the layers of suppression of the modern moral consciousness. It's a difficult thing to do. – Charles Taylor Sources of the Self (1992)*[5]

---

[1] Translation by Henry Francis Cary. Currently available in an edition published in 2006 by Hard Press, Lenox, MA.

[2] In, *Devotions upon Emergent Occasions/Death's Duel*, Vintage Books, 1999.

[3] See Penguin Classics Edition (edited by Andrew Skinner), p. 119.

[4] Starring Michael Douglas in the role of Gordon Gecko. Directed by Oliver Stone, written by Stanley Weiser and Oliver Stone. First shown in 1987.

[5] *Sources of the Self: the Making of the Modern Identity*, Cambridge University Press, 1992.

D. Hay (✉)
Department of Divinity and Religious Studies, School of Divinity, History and Philosophy,
King's College, University of Aberdeen, Aberdeen AB24 3UB, UK
e-mail: j.d.hay@abdn.ac.uk

R.W. Sussman, C.R. Cloninger (eds.), *Origins of Altruism and Cooperation*,
Developments in Primatology: Progress and Prospects 36, DOI 10.1007/978-1-4419-9520-9_21,

## Introduction

The concept of *relational consciousness* emerged during an investigation of the plausibility of the hypothesis that Darwinian natural selection underlies the cultural phenomenon of religion. This conjecture originated with Sir Alister Hardy FRS, who was the Head of the Zoology Department in Oxford University between 1946 and 1961 and founder in 1969 of the Religious Experience Research Unit, originally based in Manchester College Oxford.[6] Hardy's initiative is not well known in the United States, so I will begin with some background information as a preliminary to clarifying my own hypothesis about the connection of relational consciousness with altruism.

When Hardy came up to Oxford in 1914 to read zoology he ran headlong into controversy, for his appointed tutor was Julian Huxley, the grandson of Charles Darwin's most powerful advocate, T.H. Huxley. Hardy wrote in his unpublished autobiography about the disturbance he felt when he encountered the conflict between Darwin's ideas and the religion of his boyhood. He was troubled because of his conviction that Darwin was right but that somehow (and at the time he did not know how) this did not entail the discarding of his spiritual experience as nothing more than a delusion. His discomfort led him at the age of 18 to make a solemn vow to work at resolving the clash, a commitment he maintained throughout his career as an orthodox student of organic evolution and a passionate but unorthodox religious believer.

Shortly after his retirement from his Chair in Oxford, Hardy was invited to give the Gifford Lectures[7] in Aberdeen University. It was there, during the sessions of 1963–64 and 1964–65, that he gave the first detailed account of his biological interpretation of religion. In his view, as part of the process of consciously investigating their environment, our prehistoric ancestors discovered their relationship to a transcendent dimension of reality akin to that described by the poet Wordsworth, in his *Lines written above Tintern Abbey*:

> I have felt
> A presence that disturbs me with the joy
> Of elevated thoughts; a sense sublime
> Of something far more deeply interfused,
> Whose dwelling is the light of setting suns,
> And the round ocean, and the living air,
> And the blue sky, and in the mind of man,
> A motion and a spirit, that impels
> All thinking things, all objects of all thought,
> And rolls through all things.[8]

---

[6] Renamed The Religious Experience Research Centre, the Unit is now based in the University of Wales at Lampeter. See the website: http://www.alisterhardyreligiousexperience.co.uk.

[7] The lectures were published in two volumes, the first concerning evolution entitled *The Living Stream,* appeared in 1965, and the second, on the biological basis of religion, entitled *The Divine Flame,* came out in 1966, both published in London by Collins.

[8] From, 'Lines composed a few miles above Tintern Abbey, on revisiting the banks of the Wye during a tour. July 13, 1798' See *Collected Poems* published by Wordsworth Editions Ltd. in 1994.

Hardy had in mind a biological endowment that is not a construction of culture, though from his perspective, discourse about this form of consciousness is universally manifested, primarily but not exclusively, in the world's religions. As an orthodox Darwinian, he claimed that the reason for the natural selection of this predisposition is that it has survival value for the individual. My work over the past 30 years has been concerned with testing the resilience of Hardy's hypothesis, and on that basis I will expound an argument to show the following:

(1) Altruism is the outcome of a process of natural selection during organic evolution and, along with spiritual awareness, is a facet of relational consciousness.
(2) A sequence of historical events unique to Europe has culminated in the socially constructed suppression of relational consciousness. Consequently, altruism has become problematic, along with ethics and religion, in societies strongly influenced by post-Enlightenment European thought.

## Part I: Relational Consciousness as the Biological Basis of Altruism

### *Research Leading to the Concept of Relational Consciousness*

Hardy's view of the religious impulse as a human universal might seem implausible, for when he first put forward his proposal, formal religious adherence had already been in steep decline in most of Western Europe for many years. Currently, statistics show that in the United Kingdom less than 8% of the population are regular attendees at a religious service.[9] It is therefore important to note the distinction between adherence to a formal religion and personal spiritual awareness.

In contrast to church attendance figures, national surveys of reports of spiritual experience suggest that a large majority of adults in Britain claim such awareness and the proportion has increased over time. Between 1987 and 2000, there was at least a 60% rise in report of spiritual experience (from 48% to 76% of the adult population), as measured by a device developed by Hay and Heald,[10] whilst over approximately the same period, regular church attendance fell by more than 20%.[11] Judging from data gathered by the European Study of Values (ESV),[12] there is a

---

[9] See Peter Brierley's report *Religious Trends No. 1: 1999/2000*, London: Christian Research Association, 2000. For an account of the decline of the religious institutions in the UK, consult Steve Bruce's provocatively titled book, *God is Dead*, published by Blackwell in 2002. See also, Callum Brown, *The Death of Christian Britain*, published by Routledge in 2001.

[10] See, David Hay and Gordon Heald, 'Religion is good for you' *New Society*, 17 April. 1987; also, David Hay and Kate Hunt's *The Spirituality of People who don't go to Church.* Final Report, Adult Spirituality Project: Nottingham University, 2000.

[11] Brierley, op. cit.

[12] Lambert, Y. (2004). 'A turning point in religious evolution in Europe', *Journal of Contemporary Religion*, 19(1), 29–45.

similar pattern of formal religious decline and increasing report of spiritual experience in much of Western Europe. The same phenomenon has been reported for Australia.[13] Even in the United States, which most obviously bucks the trend of institutional decline in Western countries, the work of Zinnbauer et al.[14] suggests that there are parallels.

## Focusing on the Nature of Spiritual Experience

Even if the proportion of people reporting spiritual experience is very high, as in the United Kingdom,[15] a substantial minority still deny that they have ever encountered such awareness. If Hardy's hypothesis is correct, then we need to explain the shortfall. As a first step, let us take it that like any other primordial competence, spiritual awareness can be interpreted in numerous ways, determined by the culture to which the experient belongs [a parallel might be found in language, where Chomsky suggests the existence of a biologically inbuilt Language Acquisition Device (LAD), upon which is constructed the multitude of human languages]. In a secularised culture, this primordium would not disappear but be labelled according to non-religious criteria sufficiently plausible to be accepted by the individual. Assuming for heuristic purposes that this is so, an investigator can proceed to look directly at reports of experience, with a view to disclosing something of the substantive nature of the primordium.

In response to this requirement, and as part of a more general investigation of the nature of contemporary spiritual experience, I set up the *Children's Spirituality Project* in the United Kingdom during the mid-1990s. I reasoned that in a culture highly critical of religion, the place to find spiritual experience most easily must be amongst children because they have not yet assimilated the sceptical canons of the adult world. We chose to study the spiritual lives of 6-year-old and 10-year-old children in primary schools in two large industrial cities in England, Nottingham and Birmingham. Prior to our research, there had been some studies of children's spirituality, based in Europe and North America, where the terminology through which spirituality has traditionally been expressed is overwhelmingly Christian. If Hardy is right, such an assumption may be excluding – spiritual awareness should

---

[13] See David Tacey, *The Spirituality Revolution: the emergence of contemporary spirituality*, Hove and New York: Brunner-Routledge, 2004 (see also Poll, 1983).

[14] See Bryan Zinnbauer et al. 'Religion and Spirituality: Unfuzzying the fuzzy.' *Journal for the Scientific Study of Religion*, 76(4), 1997, 549–564. I should add that, at the time Hardy was writing, the distinction between 'religion' and 'spirituality' was not as clear as it is today and he himself was inclined to confuse the two.

[15] Data from surveys of reports of experience are summarised and commented upon in my book *Religious Experience Today: studying the facts*, published by Cassell in 1990. See also Hay (1994, 2006, 2007); Hay and Morisy (1978, 1985); Hay with Nye (2006); Hay and Socha (2005). '"The biology of God": what is the current status of Hardy's hypothesis?' *International Journal for the Psychology of Religion*, 4(1), 1–23. There are complex problems concerning comparability of data in a field where definitions of the subject matter are diverse. In a short chapter, there is not space to cover this question adequately. For more detail, see, D. Hay, 'Asking questions about religious experience', *Religion*, 18, 1988, 217–229.

be species-wide and affect all of us, whether or not we have religious beliefs. How in such circumstances does one recognize spirituality in a secularized culture? We needed to devise a research procedure that would allow us to leap over boundaries created by cultural construction.

At first, we attempted to produce a formal definition of spirituality by setting up a seminar group of theologians, philosophers, and other specialists on the spiritual life. The seminar was a failure. There were profound disagreements between the experts about the subject under discussion. Furthermore, the language they were using was remote from the world of the child, partly not only because of its technical nature but also because in Britain religious language is alien to many children. Nevertheless, whilst the seminar group could not agree on a definition, all of them said that they recognised spiritual experience when they came across it and could specify examples of the kinds of circumstances that were conducive to it.

Following that hint, we decided to focus our research on certain practical situations rather than theoretical definitions. We identified three types of commonplace situation where, if there is such a thing as spiritual experience, it will be likely to manifest itself. At the time, we were thinking about children, but as the categories evolved, we realised that they applied to children and adults alike.

*Awareness of the here-and-now*: The Edinburgh psychologist of early childhood, Margaret Donaldson, reminds us that babies under 18 months or so appear to have no memory of an extended past stretching out behind them. Nor, apart from the briefest anticipations, do they appear to have any conception of the future. Donaldson talks about this ‘here-and-now’ awareness as the ‘point mode’. She identifies it as the most basic mode of the mind’s operation and as such it continues to have prominence in children even when they have partially achieved the ‘line mode’; that is, the ability to focus on the ‘there and then’ of the past and future.[16] This immediacy of awareness also lies at the heart of meditation and contemplative prayer. It is celebrated and taken to very high levels of sophistication in the practical life of religious cultures, both East and West. In the Christian tradition, this is most obviously seen in the practice of contemplation and those approaches to prayer that stress awareness of the presence of God in all things. The 18th-century French Jesuit, Jean Pierre de Caussade, speaks directly of the ‘sacrament of the present moment’,

> We are well instructed only by the words God speaks to us personally. It is not by reading or historical study that we become wise in the science of God: such methods alone produce but a vain, confused and self-inflating science. What instructs us is what happens from moment to moment. . .[17]

To summarise, at the same time as the ‘point mode’ is the object of widespread and sophisticated religious interest, it is also universally available in childhood.

*Awareness of mystery*: There are aspects of our life experience that are *in principle* incomprehensible and about which we feel we can say nothing. To take the

---

[16] See her book *Human Minds* published in London by Allen Lane at the Penguin Press in 1992.

[17] In *Self Abandonment to Divine Providence* (trans. Algar Thorold), London: Burns Oates, 1933.

mystery that obsesses many a person lying sleepless in the middle of the night, why is there something rather than nothing? Another way mystery is brought to our attention is in occasional feelings of disorientation. ‘Isn’t life strange’, we sometimes say, to which an appropriate reply might be ‘Compared with what?’ For young children, the distinction between the commonplace and the profound may not yet have any meaning. Their sense of mystery can be awakened by down-to-earth and familiar phenomena, simple events such as the appearance of a flame when a match is struck, or when a light comes on at the flick of a switch, or when the operation of a tap produces water. In adult life, technical explanations learned in school obscure the underlying question of *Being* to the extent that it is forgotten, as pointed out by Martin Heidegger in *Sein und Zeit*.[18] I suggest that children’s perceptions of mystery, in situations where from an adult perspective there is a simple explanation, arise from as profound an experience as those of the contemplative philosopher or the theologian.

*Awareness of Value*: Feeling is a measure of what we value. Those things that matter to us most are associated with feeling at its most profound. As someone trained in the methods of empirical science, I know that the supposed objectivity of scientists is in fact driven by feeling, related to sensed meaning. Children readily express their ideas of worth or value in the intensity of their everyday experience of delight or desolation. Much of this is connected with the endless curiosity and meaning making of children. The following adult example seems to me to put explicitly what is implicit in childhood and is drawn from the archive of the Religious Experience Research Centre:

> One day years ago, I went for a walk in the fields with my dog. My mind suddenly started thinking about the beauty around me, and I considered the marvellous order and timing of the growth of each flower, herb and the abundance of all the visible growth going on around. I remember thinking ’Here is mind’. Then we had to get over a stile and suddenly I was confronted with a bramble bush which was absolutely laden with black glistening fruit. And the impact of that, linked with my former reasoning, gave me a great feeling of ecstasy. For a few moments I really did feel at one with the Universe or the Creative Power we recognize. I know it was a feeling of oneness with something outside myself, and also within. I must have been confronted with the source of all being, whatever one should call it. I have often told my friends about it, though it seems too sacred to talk about. The experience has never been forgotten. It was quite electric and quite unsought.

There is much more in this quotation than the logical deductions of natural theology. It is an expression of spirituality in which the person, perhaps consciously, uses some of the language of natural theology to refer to direct intuitive knowing but does not wish to relate it to conventional religion. Children of course are filled with intuitive longing to know. Questions are raised which are essentially spiritual: Who am I? Where do I belong? What is my purpose? To whom or what am I connected or responsible? These apparently cognitive signs of spiritual activity are in many cases

---

[18] Published by Basil Blackwell as *Being and Time*, (trans. John Macquarrie & Edward Robinson) in Oxford in 1962.

the secondary products of spiritual stirrings found in *awareness sensing, mystery sensing and value sensing.*

## Talking with Children About Spirituality

My then doctoral student Rebecca Nye spent many hours talking with children individually, gently introducing the areas of our interest, yet without the use of religious language unless it appeared spontaneously. To avoid being directive in that way, she stimulated conversation with a set of photographs of children in situations akin to the three categories mentioned above:

- a little girl sitting gazing into the fire in the dark of the evening
- a small boy sitting on his bed and looking out of the window at a star-filled night
- a girl crying as she looks at her dead pet gerbil in its cage
- a boy looking skywards with his hands spread out after dropping his packed lunch onto a wet pavement
- a boy standing in a school yard alone, with bowed head and apparently ignored by other children.

Rebecca asked the children questions like, 'What do you suppose the girl is thinking as she gazes into the fire?', or 'what is the boy thinking about as he looks up at the stars?' The children's replies showed that they were projecting themselves into the situation and offering their personal thoughts and experiences.

All the children with whom Rebecca spoke, without exception, had a spiritual dimension to their experience, and over a 1000 pages of transcribed research conversations resulted. Rebecca undertook a computer-assisted analysis of the units of meaning in the text, using the NUDIST program,[19] a forerunner of IN VIVO. The purpose was to use the program's technical speed in producing a hierarchically organized tree of meanings, to see if it was possible to identify an overall word or phrase which drew together what was common to all the spiritual talk of the children. After Rebecca's extremely laborious line-by-line analysis, the phrase that increasingly dominated her awareness as she examined the data was *relational consciousness*. By this we mean,

> *a generalised awareness of intimate relationship to reality, whether other people, the environment, to the depths of ones' self or to God.*

At first this finding disconcerted us because we had a preconception of spiritual practice as an isolated, private matter, and I thought we had scriptural warranty for it (cf. In the Gospels: 'When you pray, go to your private room and shut the door'; in the *Bhagavad-Gita*: 'Let the yogi find a secret place in the forest'; etc.) On thinking more deeply about the question, the primary purpose of physical privacy became clear; it is to cut down the tendency to be distracted from the 'point mode' – looking

---

[19] See the *User's Guide for QSR.NUD*IST* published by Sage software SCOLARI in 1996.

directly at one's relationship with immediate reality – by the temptation to posture or display oneself.

### Empirical Evidence of the Biological Basis of Altruism

I suggest that relational consciousness is the primordial, inbuilt precursor of publicly expressed (and hence socially constructed) spirituality. It is thus a biological reality and, as I will explain below, it is the immediate source of altruism. I thus dissent from the modern repudiation of spiritual experience as delusory. The latter view originates as a corollary of Ludwig Feuerbach's claim that religious belief is the result of a projection, as discussed in *The Essence of Christianity,* first published in 1841.[20] In his *Lectures on the Essence of Religion* given in Heidelberg and published in1851,[21] Feuerbach dismisses claims to religious experience as due to ignorance and stupidity, asserting that there is no 'organ of religious experience':

> We should be more justified in assuming the existence of a specific organ of superstition. Religion, that is, the belief in gods, in spirits, in so-called higher invisible beings who rule over man, has been said to be as innate in man as his other senses. Translated into the language of honesty and reason, this would only mean that . . .superstition is innate in man. But the source and strength of superstition are the power of ignorance and stupidity[22]

During the past decade, empirical evidence has begun to accumulate that contradicts Feuerbach's assertion. Two areas of investigation are proving to be particularly interesting, neither of them available to the science of Feuerbach's day. I have in mind the use of twin studies to discriminate between genetically and environmentally mediated features of living organisms and the development of scanning devices to investigate metabolic changes in soft tissue, especially in the field of neurology.

*Twin studies* have been used for many years in distinguishing human characteristics that are inherited from those that are acquired from the environment. The methodology has only recently been applied to the study of spirituality, presumably because the dominance of Feuerbach's assumptions made it seem a redundant exercise. The work of Lindon Eaves at the Virginia Institute for Psychiatric and Behavioral Genetics is particularly interesting, especially the report published in 1999 on research done in cooperation with Katherine Kirk and Nicholas Martin at the University of Queensland.[23] The team examined more than 2,200 pairs of identical and non-identical twins. In assessing spiritual awareness, they were able to use a measure of self-transcendence devised by Robert Cloninger as one of the character

---

[20] See the translation by George Eliot and with an introduction by Karl Barth, published in New York by Harper Torchbooks in 1957.

[21] Translated by Ralph Manheim and published in New York by Harper & Row in 1967.

[22] *Lectures on the Essence of Religion.* Op. cit. pp. 219–221. Kant makes a similar assertion in *Religion Within the Limits of Reason Alone*, published in 1793. See the 1960 edition (trans. Theodore M Greene & Hoyt H. Hudson) published in New York by Harper & Row, p. 163.

[23] See Katherine Kirk et al. 'Self-transcendence as a measure of spirituality in a sample of older Australia twins', *Twin Research*, 2(2), 1999, 81–87.

dimensions in his Temperament and Character Inventory.[24] The twins also answered questions about church attendance. The researchers found that whilst churchgoing had much more to do with upbringing than heredity, spiritual awareness was significantly linked to genetic inheritance, thus supporting Alister Hardy's contention that it is biologically inbuilt. In a more recent twin study in Japan, Juko Ando et al.[25] have made a similar finding in relation to spiritual awareness, suggesting that biology transcends East/West cultural differences.

*Scanning devices* that can photograph events taking place in soft tissue in living organisms have been applied to the study of spiritual experience only in very recent years. One of the more thoughtful applications of this technology is by the head of the Nuclear Medicine Department in the University of Pennsylvania, Andrew Newberg. Newberg used a SPECT scanner to measure the changes in blood flow in the brain in volunteers as they practised the most characteristic religious activity, prayer or meditation. He began by studying experts in Tibetan Buddhist meditation and later repeated the investigation with Franciscan nuns who were proficient in centring prayer.[26] In both cases, there were numerous alterations throughout the brain but two stood out. In deep meditation and prayer, the flow of blood reduces in the left posterior parietal lobe of the cerebral cortex (the back of the brain). This is the part of the cerebrum that makes us aware of where the boundary of our body lies, or 'where I stop and the rest of the world starts'. At the same time, the flow of blood increases bilaterally in the parts of the frontal lobes that are concerned with awareness. The combined effect is to lose the distinction between the praying individual and their surroundings at the same time as raising the general level of awareness.

First reported by Newberg et al. in 2001, this is a remarkable finding, for the physiological data closely complement the subjective accounts of mystical experience available in many religious traditions, including Christianity. More recently still, in 2006, Mario Beauregard and Vincent Paquette[27] at the University of Montreal published the data from a parallel study of a group of Carmelite nuns, using an MRI scanner, which works on a different principle from the SPECT scanner. Their research methodology was also different from that used by Newberg. Nevertheless, they obtained results that appear to complement Newberg's

---

[24] For a review of this measure, see C.R. Cloninger et al. *The Temperament and Character Inventory: A guide to its development and use.* St Louis, Missouri, Washington University Center for Psychology of Personality, 1994. To understand Cloninger's perspective, I have also consulted his book *Feeling Good: The Science of Wellbeing*, published by Oxford University Press in 2004.

[25] Consult, Juko Ando et al. 'Genetic and Environmental Structure of Cloninger's Temperament and Character Dimensions', *Journal of Personality Disorders*, 18(4), 2004, 379–393.

[26] See Andrew Newberg et al. 'W*hy God Won't Go Away: Brain Science and the Biology of Belief*', New York: Ballantine Books, 2001.

[27] See, Mario Beauregard and Vincent Paquette, 'Neural correlates of a mystical experience in Carmelite nuns', *Neuroscience Letters* Volume 405, Issue 3, 25 September 2006, pp. 186–190.

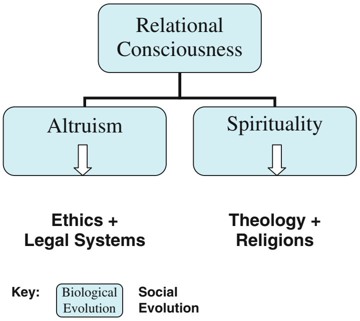


**Fig. 21.1** The biological origin of altruism and spirituality in relational consciousness and the sociocultural evolution of ethics, law, theology, and religion

findings. On this interpretation, relational consciousness highlights the aspect of reality through which we realise that we are immersed in a continuum, part and parcel of the whole.

According to this model (Fig. 21.1) altruism and spirituality have the same origin, in relational consciousness. A new awareness of the singularity of reality brings with it the realisation that I am much closer to other people, the environment and God than I had originally thought. In relation to other people and the environment, I discover in myself an obligation to care for them, even to the point of self-sacrifice, perhaps equivalent to Emmanuel Levinas' account of ethics as 'first philosophy'.[28] Levinas is implying that before all extended discourse – religious, scientific, philosophical – there is a discovery of absolute obligation to the other and I take it that this is especially clear when we are in the point mode. As discussed in Zygmunt Bauman's *Postmodern Ethics*,[29] the primordial nature of this obligation manifests itself in my encounter with a single other but is potentially at odds with ethical and legal obligation to the community, which is a cultural matter and, consequently, socially constructed. Bauman illustrates this conflict with a story from the *Talmud*:

> Ulla bar Koshev was wanted by the government. He fled for asylum to Rabbi Joshua ben Levi at Lod. The government forces came and surrounded the town. They said: 'If you do not surrender him to us, we will destroy the town'. Rabbi Joshua went up to Ulla bar Koshev and persuaded him to give himself up. Elijah used to appear to Rabbi Joshua, but from that moment on he ceased to do so. Rabbi Joshua fasted many days, and finally Elijah revealed himself to him. 'Am I supposed to appear to informers?' he asked. Rabbi Joshua said: 'I followed the law'. Elijah retorted: 'But is the law for saints?'[30]

The well-being of the individual on whom I gaze *and* the totality both matter to me because I am more than an isolated, self-preoccupied billiard ball, bumping into the rest of reality (Monroe, 1996). Spiritual insight has a physiological component that reveals to me that I am an intimately connected part of the whole. This may

---

[28] See for example, Chapter 5, 'Ethics as first philosophy', in Seán Hand (ed.) *The Levinas Reader*, published by Blackwell in Oxford in 1989.

[29] See *Postmodern Ethics* published by Blackwell in Oxford in 1993.

[30] Ibid. p. 81.

occur not only in the course of a disciplined life of meditation or contemplative prayer but also, as the empirical data demonstrate, very commonly in secularized cultures via spontaneous religious or spiritual experience (Selznick, 1992). One important corollary is that religion (as opposed to spirituality) and altruism are independent of one another, that is, it is possible to be spiritually aware without being religious and religious without being spiritually aware (Preus, 1987). The model thus transcends a familiar argument about the link between ethics and religion. There is, or should be, a link between the two. However, people without religious belief are not necessarily out of touch with their relational consciousness and therefore have in them the same possibility of truly altruistic behaviour, though they will not attribute it to a religious source.

## Part II: Why Altruism is Problematic in Western Culture

### *European Individualism in Conflict with Relational Consciousness*

The research that I have been discussing provides evidence in support of the notion of spirituality and altruism as facets of a biologically inbuilt primordium, both of which are traditionally associated with religion. Since relational consciousness is, on that reading, a human universal, why do ethics and religion seem so problematic in those parts of the world most strongly influenced by European culture? Only the other day a friend of mine was wondering sadly why words like 'virtue' and 'self-sacrifice' sounded so weak to him. In addition, what is it about European history that has made it a special case in terms of the criticism of religion?[31]

One of the severest contemporary opponents of religion in the United Kingdom is a former student in Alister Hardy's department, the zoologist Richard Dawkins (1976, 1986). His book *The God Delusion* was at the top of the non-fiction best-seller list in the United Kingdom for many months after its publication in 2006 and other hostile commentators have also been remarkably successful. Their current prominence is plausibly attributable to widespread anxiety following spectacular atrocities directed at Western targets, carried out by terrorists claiming to represent Islam and also concern over Christian fundamentalist attacks on scientific freedom (cf. attempts to ban the discussion of Darwinism in schools).

However, it is important to remember that criticism of religion is not a phenomenon that began in 2006 (Buckley, 1987). It is still something of a shock to read the opening aphorism of Blaise Pascal's defence of religion, the *Pensées*, first published in 1657:[32]

> Men despise religion; they hate it, and fear it may be true.

---

[31] See especially Grace Davie's *Europe: The Exceptional Case; parameters of faith in the modern world*, published in London by Darton, Longman & Todd in 2002.

[32] Republished in Penguin Classics, 2003.

That sentence could have been written yesterday. Pascal was pondering the state of religion in 17th century France, where the process of secularization was already under way. The late Bryan Wilson, who was head of the Sociology Department in Oxford (and incidentally an adviser to the Religious Experience Research Unit), was one of the leading exponents of classical secularization theory,[33] asserting that as the organisation of society becomes more rational, the religious institutions increasingly lose power and influence. At first assumed to be equivalent to something like a universal law, secularization is nowadays recognized to be particularly applicable to those regions of the world that have been influenced by the thought associated with the Enlightenment. A particular aspect of the ideology inherited from the Enlightenment stands out immediately as at odds with relational consciousness, and that is Individualism. Returning for a moment to Fig. 21.1, it can be seen that the promotion of Individualism threatens not only relational consciousness but also altruism, spirituality and socially derived institutions including ethical and legal systems and religious institutions.

## *Five Stages in the Development of European Individualism*

Europeans seem to have invented an extreme form of individualism – in a way that appears not to be duplicated in any other culture.[34] My hypothesis is that in achieving social dominance it comes into conflict with our biologically inbuilt altruism. As such, the development of individualism is an illustration of a form of cultural evolution identified by William Durham in his book on *Co Evolution*[35] as damaging to the survival chances of a community. In what follows, my intention is to justify this claim by unpacking some of the factors lying behind the rise of Individualism and, via its undermining of relational consciousness, its damaging effect on altruism. Individualism has extremely complex roots in history[36] and since we Westerners are ourselves immersed in this history, its assumptions are likely to be hidden from us. Nevertheless it is possible to identify five major steps in its social evolution. Each

---

[33] See Wilson's book *Religion in Secular Society*, published in London in 1966 by C.A. Watts.

[34] The atheism of Advaita in India, or in Theravada Buddhism might be cited as evidence to contradict my thesis, but these forms of atheism are in fact intra-religious. They are aspects of a debate about the nature of transcendence and as such are akin to certain mystical movements in Christianity, for example, the near monism of someone like the fourteenth-century Dominican mystic, Meister Eckhart.

[35] See, Chapter 7 in W.H. Durham, *Co Evolution: Genes, Culture and Human Diversity* published by Stanford University Press in 1991.

[36] There are many texts on this theme. Possibly the best introduction because he gives a systematic overview of its many dimensions is Stephen Lukes' *Individualism* published in the series *Key Concepts in the Social Sciences* by Basil Blackwell, in 1973. See also, Colin Morris *The Discovery of the Individual, 1050–1200*, published by SPCK in London in 1972; and Louis Dumont, *Essays on Individualism*, published by Chicago University Press in 1986; also Aaron Gurevich, who disagrees with Morris' claim that individualism appeared in the 12th century. See his *The Origins of European Individualism*, published by Blackwell in 1995.

of these steps has an ambivalent quality, that is to say, each is accompanied by both apparent gains and losses for our humanity.

## *Stage One: Coming to Think of Myself as 'I'*

Some students of the origins of language argue that the skills necessary for the manufacture of stone tools imply being able to speak. If so, then this might apply to the human species *Homo habilis*, whose fossil remains in East Africa have been dated to two million years ago or more.[37] Estimates that are more conservative confine language to our own species, *Homo sapiens*, in which case it cannot have its origins much before 200,000 years ago. Either way, the effect of language on the construction of the self is longstanding and universal, affecting all members of our own species.

Animals without language, although they are sensitive to their surroundings and relate to them in a knowing way, give at best only rather ambivalent indications of self-awareness.[38] Whilst they quite clearly have a memory, they lack the verbal apparatus for reflecting upon their memories or for considering the fact of their own existence. Consequently, they live almost entirely in the here-and-now of the immediate events around them, immersed in an unbroken continuum that includes themselves. The distinction between self and other, though it is acted out in the way animals manipulate their environment, is never clearly articulated. We saw earlier that the same is true of young infants. Adult observers of infants' behaviour can see quite easily that they operate in ways that implicitly recognize a distinction between self and other.[39] Putting it grammatically, they discriminate behaviourally between subject and object but have little or no conscious awareness of the difference between the two. They are thus behaviourally strongly in touch with relational consciousness.

With the coming of language, a radical change occurs and by the age of 18 months, most healthy toddlers clearly and easily articulate the subject–object difference. When we are able to name the things around us, it makes them stand out in contrast to their surroundings and we can also reflect on them remotely, at other times and in other places.[40] One of the most prominent objects that an infant learns about through language is its self, a fact that is drawn attention to constantly by the

---

[37] For further information on these questions see the articles by Terrence Deacon on 'Biological aspects of language' (pp. 128–133) and C.B. Stringer on 'Evolution of early humans' (pp. 241–251) in *The Cambridge Encyclopaedia of Human Evolution,* (edited by Steve Jones, Robert Martin and David Pilbeam), Cambridge University Press, 1994.

[38] The question of the self-awareness of other animals is hotly disputed. It is discussed at length in Marc Bekoff et al. (eds.) *The Cognitive Animal*, Cambridge, MA: The MIT Press, 2002.

[39] See for example Nagy, E. & Molnar, P. (2004). '*Homo imitans* or *Homo provocans*? Human imprinting model of neonatal imitation'. *Infant Behavior and Development*, 27, 54–63.

[40] For a popular discussion of the effect of language on self-awareness, see John McCrone *The Ape that Spoke: Language and the Evolution of the Human Mind*, London: Picador, 1990.

parents when they teach the baby to say ‘You’, ‘Me’ and ‘I’. When ‘I’ becomes an object of consciousness, it can be thought about in the same way as any other object. ‘I’ begin to build up a set of memories and anticipations that make up a life history and in the process, I become an individual. Nevertheless, it is important not to lose sight of the fact that the process of individualisation is not done in isolation; it is always done in the context of a culture and in intimate relationship to others.

## *Stage Two: Learning to Read and Write*

Compared to the span of existence of the human species, literacy arrived almost yesterday. Most people for most of human history have been illiterate and this was true until little more than a century ago even in the industrialised West. For example, in Britain, it was not until the passing of the 1870 Education Act that a concerted effort was made to eliminate illiteracy – a task that is not yet complete. Human consciousness has therefore evolved over many millennia in the absence of the ability to read and write. In a fundamental way, becoming literate is a revolutionary move away from the longstanding natural and universal human condition.

Such a radical change is bound to have large-scale cognitive effects and these were first fully investigated by the Russian psychologist Alexander Luria. During the 1930s, the Soviet government under the leadership of Stalin decreed the forced collectivisation of agriculture throughout the vast republic. The decree was combined with a vigorous effort to teach the peasantry to read and write, for literacy was necessary if they were to be able to manage the complex work of the collective farms. Luria took the opportunity to study how the shift to literacy affected hitherto illiterate peasants living in a group of remote mountain villages and pasturelands in Uzbekistan and Kyrgyzstan.

In summary, Luria[41] showed that, compared with people who could read and write, the thinking of illiterates is much more tied to the immediate situation (i.e. the here-and-now) than to abstract reflections on the past and future. This meant that intellectual tasks that were elementary for literate people, for example simple classification, were difficult or impossible for them. In one of Łuria’s experiments, semi-educated and only recently literate collective farm activists were easily able to sort skeins of wool in terms of category, shades of blue, red, yellow and so on. On the other hand, illiterate peasant women who, as expert embroiderers, were perfectly well aware of subtle variations of colour, when asked to classify a set of wools into shades of brown, would say things like ‘It can’t be done, they’re not at all alike; this is like calf’s dung, this is like a peach.’ Similarly, most men failed to complete simple syllogisms, such as: In the North, all bears are white. Novaya Zemlya is in

---

[41] See Luria’s book *Cognitive Development: Its Cultural and Social Foundations.* (trans. Martin Lopez-Morillas and Lynn Solotaroff; ed. Michael Cole), Harvard University Press, 1976. Because of difficulties with Stalinist censorship, these findings were not published in the Soviet Union until the decade of the 1970s.

the North. What colour are the bears there? Many of the men were unable to give the correct answer, saying things like, ‘How should I know, I’ve never been to the North. I’ve seen a black bear.’ More crucially, people also seemed not to have much conception of themselves as individuals and when invited to describe themselves, suggested to Luria et al. that they should ask someone else to answer for them.

Luria realized that such responses were due, not to lack of intelligence, but to the structure imposed on thought by illiteracy. Literacy continues the process of individualisation initiated by the ability to speak but with much greater impact. Literacy extends memory, permits us to classify and to generalize and gives us the ability to move in our imagination out of the concrete here-and-now and into lengthy abstraction. Above all, literacy opens the possibility of a private world and the ability to have a uniquely personal point of view, limited only by the size of one’s library. In an important sense, literacy opens the door to personal freedom.

Complex modern society would be unable to operate without the skills that become possible with the ability to read and write. However, the construction of a vast private world also potentially creates blindness to our relationship with the here-and-now. Along with this loss, there is the likelihood of deterioration in our immediate sense of belonging to and being continuous with the surrounding community. In those traditional religious societies that are literate (Jews, Christians and Muslims are after all, ‘People of the Book’), this weakness is recognized and strategies have been created to counteract the loss of immediacy. Each of these cultures has developed a highly sophisticated set of practical exercises that help people to enter more and more deeply into holistic awareness of the here-and-now. I mean of course the skills of contemplative prayer (raising the heart and mind to God now, in this moment) or silent meditation (e.g. maintaining awareness of the act of breathing) currently being investigated by Newberg et al.. These practices are undertaken by the faithful as a structured routine, often attended to several times each day. Ultimately the aim is to remain in this state of alertness permanently, or as St Paul put it, to pray without ceasing.

## *Stage Three: Abandoning the Holistic Perspective*

What happens to consciousness though, when these strategies for staying in touch holistically are largely ignored, or abandoned altogether, as is more often than not the case in contemporary Western society? This constitutes the third step towards the ideology of individualism. As literacy becomes more and more widespread, it is more difficult, less natural, for people to enter the here-and-now awareness that is commonplace amongst members of primary oral cultures.[42] One effect on those

---

[42] One only has to think of the way that reading and writing dominate our everyday lives, now added to by the ubiquity of the Internet and the World Wide Web, to begin to see that the mode of action of our consciousness is very different from that of our non-literate forebears. See, for example, John L. Locke’s (1998) book, *Why we Don’t Talk to Each Other any More: the Devoicing of Society*.

who are highly literate is the increasing probability that they will acquire a disembodied, theoretical consciousness of the self, withdrawn from engagement in the surrounding environment.

The legacy in academic circles, perhaps especially in the field of empirical science in which I was educated, is an admiration for detached objectivity as a necessary professional stance. Like every other beginner in the laboratory, I learned that the inconstant and emotionally labile 'me' never puts water in a test tube. In writing up experiments, 'it was noted' that 'water was placed in a test tube' by an abstract, clinically detached being who had nothing to do with the scruffy bunch of schoolboys occupying the classroom. This cult gave the false impression that human factors like hesitancy, error and free-floating imagination did not enter into the properly conducted research act. Taken far enough, training in detachment can include a distancing from other people and a loss of awareness of one's own emotional state. Intellectuals are notorious for 'living in their heads', cut off from emotion, sometimes to the detriment of their health.[43]

Many suggestions have been made about both the timing and the historical and political aspects of this growing sense of personal isolation. The 19th-century Swiss historian, Jacob Burckhardt, was one of the first to suggest a specific period in which individualism began to become dominant in European history. In his pioneering study *The Civilisation of the Renaissance in Italy*,[44] he identified the emergence of the 'free person' as occurring first in Italy, pre-eminently in renaissance Florence. Another suggested source of individualism is the Protestant branch of the Christian religion. Max Weber famously claimed that Protestantism, especially in its Calvinist form, created an inner isolation in the believer sufficiently powerful to change the entire economic and political structure of the countries of the Reformation during the 16th century. Calvin's emphasis on the doctrine of predestination faces anyone who takes this belief seriously with an unprecedented inner loneliness:

> No one could help him. No priest, for the chosen one can understand the word of God only in his own heart. No sacraments, for though the sacraments had been ordained by God for the increase of His glory, and must hence be scrupulously observed, they are not a means to the attainment of grace, but only the subjective *externa subsidia* of faith. No Church, for though it was held that *extra ecclesiam nulla salus* in the sense that whoever kept away from the true Church could never belong to God's chosen band, nevertheless the membership of the external Church included the doomed... Finally, even no God. For even Christ had died only for the elect ...[45]

---

[43] Note for instance the experience of the psychotherapist Eugene Gendlin (1981, 1997), when encountering academically high-flying clients in his Chicago consulting rooms. Gendlin comments on the disconcerting fact that he was unable to help many of them to explore their immediate emotional difficulties because they were isolated from the felt sense of their bodies. Too good a training in academic detachment had crippled them. See also the related arguments from the neurologist Antonio Damasio (1994, 2000) on the importance of the body in relation to emotion and consciousness.

[44] Republished in Penguin Classics in 2004.

[45] See, *The Protestant Ethic and the Spirit of Capitalism*, (translated by Talcott Parsons), London: George Allen & Unwin, 1930: p. 104. Pastoral need led to the mitigation of the doctrine and it

The mere appearance of goodness is no guarantee since anyone can make a public pretence of virtue whilst being inwardly corrupt. Therefore, a robust doctrine of predestination encourages not only endless self-questioning, as Weber remarked, but also suspicion of the motives of others. A belief in predestination was not limited to Calvinism; it also appeared in certain 17th century forms of Catholicism, especially Jansenism.[46] In his essay *Of Charity and Self Love* written in 1674, Pierre Nicole, Jansenist priest and friend of Blaise Pascal, explains how impersonation of virtue can be so accurate that it deceives everyone; hence, it is not wise to trust anyone. It is deeply incongruous that a religious doctrine should have the effect of encouraging the erosion of the relational consciousness that underpins spirituality.

The idea of 'man alone' also gained currency in 17th century Europe through the influence of the two dominant and contrasting philosophical perspectives of that period. Two archetypal representatives are the idealist Descartes and the materialist Thomas Hobbes. In the case of Descartes, his decision to make the *Cogito* ('*I think*, therefore I am') the rock on which to build his philosophy had a devastating effect on the plausibility of relational consciousness. In the words of the Scottish 20th-century philosopher John Macmurray,

> ... the adoption of the 'I think' as the centre of reference and starting-point of [...] philosophy makes it formally impossible to do justice to religious experience. For thought is inherently private; and any philosophy which takes its stand on the primacy of thought, which defines the Self as the Thinker, is committed formally to an extreme logical individualism. It is necessarily egocentric.[47]

Thomas Hobbes' materialism was probably even more influential than Descartes' philosophy in promoting individualism. Hobbes was born in 1588 and lived through what historians see as one of the most violent periods of turmoil in European history. In particular, the Thirty Years War ravaged the continent throughout his early adult life. It is perhaps no surprise that he had a sceptical attitude towards the possibility of human benevolence. Most scholars believe he was a secret atheist at a time when publicly declared atheism would put a person in considerable personal danger.[48]

His materialist interpretation of human nature led him to the view that, in the state of nature, life is a warfare of all against all. If we cooperate with other people, it is only because we see these interactions as in our interest (in this sense, he was a

---

became accepted that one plausible sign of election was material prosperity in this life. Weber's (often-disputed) contention was that this belief encouraged the growth of capitalism in Europe.

[46] The teaching of Cornelius Jansen, which split the Roman Catholic Church in France in the mid-17th century. Jansen emphasised the belief that individuals can do nothing to assure their own salvation, all is due to divine grace. Jansenism was centred on the abbey of Port Royal and Pascal was its most prominent lay supporter. The Jansenists were excommunicated in 1719.

[47] See *The Self as Agent.* (with an introduction by Stanley M. Harrison), London: Faber & Faber, 1995, p. 71.

[48] See David Berman's fascinating thesis on hidden atheism in, *A History of Atheism in Britain: From Hobbes to Russell*, London & New York: Routledge, 1990.

precursor of modern biological theorists of reciprocal altruism and kin selection).[49] His assumption that each of us is in a struggle for power against everyone else is based on a materialist metaphysics stating that 'minds never meet, that ideas are never really shared and that each of us is always and finally isolated from every other individual'.[50] According to his most celebrated aphorism, life in the state of nature is 'solitary, nasty, brutish and short'.

People who have not read Hobbes are not always aware of the extreme violence he uses to describe the natural state of human society – totally at odds with the insights provided by relational consciousness. Thus,

> All men in the state of nature have a desire and will to hurt.[51]

In his masterwork *Leviathan*, Hobbes makes explicit the brutality that people unleash upon each other in such a state:

> I put for a generall inclination of all mankind, a perpetuall and restlesse desire of Power after power, that ceaseth onely in Death... The way of one Competitor, to the attaining of his desire, is to kill, subdue, supplant, or repell the other.[52]

Hence the need for *Leviathan*, a Sovereign to subdue the anarchy and who himself gains that position through acts of terror or outright warfare:

> The attaining to this Soveraigne Power, is by two ways. One, by Natural force; as when a man maketh his children to submit themselves, and their children to his government, as being able to destroy them if they refuse; or by warre subdueth his enemies to his will, giving them their lives on that condition.[53]

## *Stage Four: Individualism Seen as the Pivot of the Market Economy*

The unbridled savagery that Hobbes loads onto human nature is of much more than antiquarian interest. The Canadian economic historian Brough Macpherson asserted that Hobbes' account of society continues to dictate the organisation of the modern bureaucratic state. It is based, in Macpherson's phrase, on the doctrine of 'possessive individualism'.[54] The picture of human beings that Hobbes came up with was not simply the result of his free-ranging scholarly reflection. It was conditioned by

---

[49] For an overview of scientific approaches to altruism theory, see Lee Alan Dugatkin, *The Altruism Equation: Seven scientists search for the origins of goodness*, Princeton University Press, 2006.

[50] In, Jean Hampton, *Hobbes and the Social Contract Tradition.* Cambridge University Press, 1988, p. 9.

[51] In, *Philosophical Rudiments concerning Government and Society*, Ch. 1, Section 4, 25–26, (quoted in MacPherson 1962a: p. 44).

[52] *Leviathan* (edited with an introduction by C.B. Macpherson), London: Penguin Classics, 1985.

[53] Ibid, p. 228.

[54] C.B. Macpherson, *The Political Theory of Possessive Individualism*, Oxford University Press, 1962.

the social order in which Hobbes was living, that is to say, 17th-century bourgeois society at the point where market forces first began to take on a dominant role. This is the fourth and most crucial step in the construction of European individualism because of its powerful economic impact.

Selfishness was not invented in the 17th century. What was new was the legitimation it gained at that point in time. Selfishness has come to be seen as not merely acceptable but as a necessary expedient in the search for economic and political stability. The impassioned speech on behalf of 'greed as good' by the reptilian financier Gordon Gecko in the film *Wall Street* takes its justification from this belief. In his essay *The Passions and the Interests*,[55] the economic historian Albert Hirschman meditates on the remarkable metamorphosis of the mediaeval sin of avarice into a necessary economic virtue. Dante's *Divine Comedy*, completed at the beginning of the 14th century, had envisioned sins of avarice as sufficient to consign their perpetrator to the fourth level of Hell. By the end of the 18th century, avarice had been seen by economists as a virtue.

Hirschman traces the evolution of this transformation in the first place to,

> . . . a feeling [that] arose in the Renaissance and became firm conviction during the seventeenth century that moralizing philosophy and religious precept could no longer be trusted with restraining the destructive passions of men.[56]

Hobbes' initial solution, the advocacy of the straightforward repression of uncontrolled passion, came to be seen as inadequate. His pessimism about human motivation was not sufficiently responded to by the mere existence of a sovereign power. Who can predict if the sovereign will truly guard the peace of society, when in reality he may himself be a cruel despot, heedless of the cries of the oppressed, or merely weak?

According to Hirschman, the answer that emerged was to harness one of the passions against the others. The key to this solution, according to a whole series of 17th- and 18th-century thinkers, was the unquenchable desire for personal gain. The term that came to be used for this particular lust for possessions and which sanitized and set it apart from the others was 'interests':

> Because of the semantic drift of the term 'interests', the opposition between interests and passions could also mean and convey a different thought, much more startling in view of traditional values: namely, that one set of passions, hitherto variously known as greed, avarice, or love of lucre, could be usefully employed to oppose and bridle such other passions as ambition, lust for power, or sexual lust.[57]

The effect of this semantic drift is important because throughout the 17th century, outside the field of economic and political writing, ordinary popular tracts on

---

[55] *The Passions and the Interests: Political Arguments for Capitalism before its Triumph* was first published by Princeton University Press in 1977, and republished as a Twentieth Anniversary Edition with an foreword by Amartya Sen.

[56] Hirschman, Op. Cit. p. 14.

[57] Ibid, p. 40.

virtue continued to refer to avarice as one of the most repulsive of sins. On the other hand, its synonym, 'interest', achieved a steadily enhanced status as the 'countervailing' passion. Finally, says Hirschman, it took on such a mantle of virtue, that in certain respects it was seen as more admirable, certainly more socially useful, than unselfishness. Thus in 1767, the Scottish economist Sir James Steuart could argue that in economic matters, self-interest is to be preferred to traditional virtue *especially* a meddling concern for the public interest:

> ...were a people to become quite disinterested: there would be no possibility of governing them. Everyone might consider the interest of his country in a different light, and many might join in the ruin of it, by endeavoring to promote its advantages. (quoted in Hirschman).[58]

The point was, as Steuart's colleague David Hume had also said of desire for gain, that it is a universal passion that operates at all times, in all places and upon everybody. It is thus much more predictable than other passions such as lust or revenge, which operate sporadically and are directed towards particular people. The very constancy of avarice had made it a virtue. Most famously, because of his influence on all subsequent economic thinking, in *The Wealth of Nations*, published in 1776,[59] the Scottish philosopher Adam Smith gave a financial rather than a political or moral justification for the unrestricted pursuit of personal gain.[60] Individualist philosophy (whether materialist or idealist) and the promotion of self-interest as the necessary basis for a stable market economy were mutually and powerfully reinforcing. They could not fail to be severely damaging to any trust in relational consciousness, and hence to altruism. But beyond the four steps leading up to this point, there is a fifth and final step to go.

## *Stage Five: Relational Consciousness Totally Repudiated*

I mentioned Ludwig Feuerbach earlier. One might feel that Feuerbach's repudiation of religion was as extreme as it is possible to get. Not so. His opinion was to be violently rejected as incomplete atheism by Max Stirner,[61] a member of the neo-Hegelian group in Berlin to which Marx and Engels had once belonged. With Stirner, we see the final abandonment of any notion of relational consciousness, for

---

[58] Ibid. p. 50.

[59] Currently available in the two volume Penguin edition, with an introduction and notes by Andrew Skinner, published in 1999.

[60] A distinction must be made between Smith's account of the way things are in capitalist society and his personal view of ethics. Smith's moral philosophy is expounded in *The Theory of Moral Sentiments* (1759) published seventeen years before *The Wealth of Nations*. He has much to say of 'sympathy', which suggests that it is not remote from relational consciousness. The apparent ethical disjunction between the two works has led to much discussion. It must be added that Smith's rhetoric, particularly in the later chapters of *The Wealth of Nations* frequently makes clear his distaste for some of the situations he is describing (See Muller, 1993).

[61] Pseudonym of Johann Caspar Schmidt.

he preached absolute egotism. Stirner concurred with the rejection of a relationship with God as fantasy but felt that Feuerbach was a sentimentalist who had failed to see the full implications of his discovery. Feuerbach, though a convinced atheist, continued to hold to the moral ideals advocated by Christianity. To Stirner, such ideals were also projections, not different in kind from belief in God. For him all ideals and moral laws, without exception, are simply religion by another name since they imply an imaginary and enslaving obligation beyond the self.

Published in 1845, 4 years after Feuerbach's *Essence of Christianity*, Stirner's only major work is *The Ego and Its Own.*[62] Of all atheist writings, Stirner's is the most thoroughgoing in its uncompromising rejection of every philosophical, religious and political ideal, seen as nothing more than the depreciation of the individual:

> Away. . .. with every concern that is not altogether my concern! You think that at least the 'good cause' must be my concern? What's good? What's bad? Why I myself am my concern, and I am neither good nor bad. Neither has meaning for me. The divine is God's concern: the human, man's. My concern is neither the divine nor the human, not the true, good, just, free etc, but is – unique, as I am unique. Nothing is more to me than myself![63]

And, reminiscent of Hobbes,

> For me you are nothing but my food, even as I am fed upon and turned to use by you. We have only one relation to each other, that of *usableness,* of utility, of use.[64]

Stirner's biographer R.W.K Paterson[65] comments,

> Whether owing to a failure of nerve, or to some basic astigmatism, the Feuerbachs and the Bauers[66] had all stopped short of the crucial point; at the last moment they had admitted the presence of some transcendental object in the scheme of things – not indeed a 'God' in the sense of a personal deity, but a 'Humanity', or a 'Society' or a 'Morality', all of which were as fictitious, and as autocratic in their claims upon the individual concrete human being, as any personal God had ever been; and thus the programme of atheism still remained to be carried through to its conclusion. . . ..[67]

And with a brutality fully equal to Hobbes,

> *Nothing*, not even the primordial obligations not to lie, steal, kill etc. can induce the self-possessed egotist to take any step that is not in the fullest accord with his own distinct interests as he himself determines them . . .. . .[68]

---

[62] Translated by Steven Byington, with an introduction by Sydney Parker. Published in London by Rebel Press in 1993.

[63] Ibid, p. 5.

[64] Ibid, pp. 296–297. His lover in Berlin left him in disgust, accusing him appropriately enough of being totally self-centred. She eventually entered religious life and died in a convent in London.

[65] *The Nihilistic Egoist Max Stirner*, published for the University of Hull by Oxford University Press in 1971.

[66] Bruno Bauer, another member of the Young Hegelian group in Berlin and a former theologian.

[67] Ibid p. 31.

[68] Ibid p. 263.

Paterson sums up:

> Stirner's contribution to the German religious debate of the 1840s was to bring the whole debate to a momentary and stupefied halt. The full consequences of thoroughgoing atheism were now disclosed for all to see.[69]

Remarkably, Stirner's hero, the isolated self-sufficient individual, had already been identified and attacked ferociously. He was none other than the unencumbered entrepreneurial fat cat who is still with us today in plentiful supply. He is,

> .... an individual separated from the community, withdrawn into himself, wholly preoccupied with his private interest and acting in accordance with his private caprice... [for him] the only bond between men is natural necessity, need, and private interest.[70]

Stirner's extreme individualism put into stark and uncompromising words what had been developing as an increasingly powerful but muffled and disinfected assumption over the previous two centuries. Individualism encourages the complete suppression of relational consciousness and a consequent leeching away of ethical relationships between the members of our modern commercial society. Once transcendence is abandoned (either belief in God or the kind of transcendental equivalent advocated by Feuerbach), morality becomes entirely subservient to what is financially prudent. In practice, Hobbes had already dispensed with all purposes apart from those that ensure the smooth working of the marketplace.[71] The binding obligation that remains in possessive market societies is to make sure the market does not collapse through financial mismanagement. In this circumstance, the difference between moral obligation and what is financially prudent becomes insignificant.

Where financial prudence is the arbiter of conduct, politeness and care for the other person become suspect as no more than a manoeuvre, an optional extra to smooth the path of a financial transaction. In other words, it is spiritually corrupt. Martin Buber makes the same point in his comments on Stirner:

> Responsibility presupposes one who addresses me primarily, that is, from a realm independent of myself, and to whom I am answerable. He addresses me about something that he has entrusted to me and that I am bound to take care of loyally. He addresses me from his trust and I respond in my loyalty or refuse to respond in my disloyalty, or I have fallen into disloyalty and wrestle free of it by the loyalty of the response......... Where no primary address and claim can touch me, for everything is "My property", responsibility has become a phantom. ....[72]

---

[69] Ibid p. 197.

[70] Karl Marx quoted in Michael Walzer (1990). 'The communitarian critique of liberalism', *Political Theory*, 18(1), 6–23.

[71] Hobbes may have dispensed with religion, but it would be interesting to investigate the theological complexion of his early upbringing. He certainly encountered Calvinist opinions when he was a student at Magdalen Hall in Oxford and this may have encouraged in him a belief in the natural depravity of the species. When he discarded religious belief in his maturity, he would then have been left with depravity, now deprived of saving grace.

[72] See *Between Man and Man* (trans. Ronald Gregor Smith), London: Fontana, 1961, p. 64.

The difficulty for Stirner is that he has entirely lost touch with relational consciousness; hence, altruism is incredible to him. For Buber, he is a sociopath:

> He simply does not know what of elemental reality lies between life and life, he does not know the mysteries of address and answer, claim and disclaim, word and response. . .[73]

## Concluding Evaluative Remarks

Stirner and Hobbes between them bracket a period in European history when individualism led to the progressive and cumulative discrediting of a fundamental aspect of our biological make-up, relational consciousness, one major facet of which is altruism. The recent findings from twin studies and the use of scanning devices give a degree of confidence to the assertion that Feuerbach was mistaken in his dismissal of spiritual experience. It is a dismissal that has been the default position for critics of religion over the past 150 years, and it continues to be almost axiomatic in sceptical rhetoric.

Neither of the types of finding exemplified above gets a mention in *The God Delusion*. Though he never discusses the hypothesis of his old professor, Richard Dawkins is aware that a physiological basis cannot be dismissed as easily as Feuerbach claimed. He responds by offering a radically modified hypothesis to explain spiritual experience, drawing his ideas from the fascinating biological speculations of the anthropologist Pascal Boyer[74] and the somewhat similar views of the American anthropologist Scott Atran (Atran and Norenzayan, 2004; Atran, 2002). They move away from Feuerbach's outright denial of the biological reality underlying religion and accept that religious beliefs had survival value in the past and therefore were selected during the process of evolution. Whether such beliefs are thought, by those who hold this view, to be merely the result of social evolution, or have a deeper biological basis is not entirely clear, but in any case, Dawkins interprets this as a fortunate accident. That is to say, cognitive adaptations that have evolved for other purposes just happen to be available for the construction of what were once socially useful, but mistaken, religious ideas. Since we now 'know' that these ideas are delusory, they cease to have a function and become instead the source of fanaticisms and social divisions.

This is where Hardy and secular critics like Dawkins would certainly part company and where, in my view, Hardy's hypothesis is the more plausible. Dawkins' argument is flawed because it assumes as axiomatic that religious belief is erroneous and therefore he chooses to explain away the biological realities as accidental. That is to prejudge the issue within the sceptical canons of the European Enlightenment and to contort improperly the scientific method of which in other respects Dawkins

---

[73] Ibid, p. 66.

[74] Boyer's interesting ideas are a development of his anthropological field work in West Africa. A highly readable account of his views is contained in his book *Religion Explained: the evolutionary origins of religious thought*, published in New York by Basic Books in 2001.

is such an eminent defender. Science bases itself on empirical data and, following Occam's razor, seeks the most straightforward and simplest interpretation of the facts. In this case, it is to say that there appears to be a transcendent dimension to human experience, universally found, associated with specific physiological states, and commonly but not exclusively associated with religious belief systems.

The resolution of this debate is of more than academic interest since it has a bearing on a large group of social problems that arguably we have inherited from the Enlightenment. Several of the most important of these are comprehensively documented for the United States in Robert Putnam's study, *Bowling Alone*.[75] He provides statistics that show a collapse since the 1960s across almost all social behaviour. The loss of what Putnam calls 'social capital' and I identify as natural altruism is graphically illustrated in the contemporary urban environment: the ubiquitous deployment of the paraphernalia of surveillance (cameras, electronic tracking devices, alarm systems, databases) to discourage crime. At the same time, there is a considerable volume of recent legislation designed to protect innocent and vulnerable people from exploitation either sexually or economically. No doubt such laws are needed, but they help to perpetuate and sediment a view of society as unfriendly and untrustworthy. They are a totalitarian means of controlling a society in which altruism has become suspect and virtue a fraud.

The history that I have outlined explains why it is of no surprise that altruism is suspect in modern society, and with it, there are many doubts about the plausibility of religion. Nevertheless, the empirical evidence suggests that in investigating altruism we are examining a biological constant that is not a meme acted upon by social evolution or a delusion. The fact that human decency and mutual trust continue to be widespread is evidence of its resilience, even though severely constricted in its range by the straitjacket of individualism. Furthermore, since individualism is a socially constructed ideology, there is always the possibility of deconstruction.

## References

Alighieri, D. (1314/2006). *The Divine Comedy*, Lenox, MA: Hard Press.

Ando, J., et al. (2004). 'Genetic and environmental structure of Cloninger's temperament and character dimensions', *Journal of Personality Disorders*, 18(4), 379–393.

Atran, S. (2002). *In Gods We Trust: The Evolutionary Landscape of Religion*, New York: Oxford University Press.

Atran, S. & Norenzayan, A. (2004). 'Religion's evolutionary landscape: Counterintuition, commitment, compassion, communion', *Behavioral and Brain Sciences* 27(6): 713–730.

Bauman, Z. (1993). *Postmodern Ethics*, Oxford: Blackwell.

Beauregard, M. & Paquette, V. (2006). 'Neural correlates of a mystical experience in Carmelite nuns', *Neuroscience Letters*, 405(3): 186–190.

Bekoff, M., et al. (eds.). (2002). *The Cognitive Animal*, Cambridge, MA: The MIT Press.

Berman, D. (1990). *A History of Atheism in Britain: From Hobbes to Russell*, London and New York: Routledge.

---

[75] See, *Bowling Alone: The Collapse and Revival of American Community*, New York: Simon & Schuster, 2000.

Boyer, P. (2001). *Religion Explained: The Evolutionary Origins of Religious Thought*, New York: Basic Books.

Brierley, P. (2000). *Religious Trends No. 1: 1999/2000*, London: Christian Research Association.

Brown, C. (2001). *The Death of Christian Britain: Understanding Secularisation 1800–2000*, London and New York: Routledge.

Bruce, S. (2002). *God is Dead: Secularization in the West*, Oxford: Blackwell Publishers.

Buber, M. (1961). *Between Man and Man* (trans. Ronald Gregor Smith), London: Fontana.

Buckley, M. (1987). *At the Origins of Modern Atheism*, New Haven and London: Yale University Press.

Burckhardt, J. (1860/2004). *The Civilisation of the Renaissance in Italy*, London: Penguin Classics.

Caussade, J-P. de (1933). *Self Abandonment to Divine Providence* (trans. Algar Thorold), London: Burns Oates.

Cloninger, C.R. (2004). *Feeling Good: The Science of Wellbeing*, Oxford: Oxford University Press.

Cloninger, C.R. et al. (1994). *The Temperament and Character Inventory: A guide to its development and use.* St Louis, MO: Washington University Center for Psychobiology of Personality.

Damasio, A. (1994). *Descartes' Error: Emotion, Reason and the Human Brain*, New York: Putnam

Damasio, A. (2000). *The Feeling of What Happens: Body, Emotion and the Making of Consciousness*, London: Vintage Books.

Dawkins, R. (1976). *The Selfish Gene*, Oxford: Oxford University Press.

Dawkins, R. (1986). *The Blind Watchmaker*, London: Longman Scientific and Technical.

Donne, John (1623/1999). *Devotions upon Emergent Occasions/Death's Duel*, New York: Vintage Books.

Dugatkin, L.E. (2006). *The Altruism Equation: Seven Scientists Search for the Origins of Goodness*, Princeton, NJ: Princeton University Press.

Dumont, L. (1986). *Essays on Individualism,* Chicago, IL: Chicago University Press.

Feuerbach, L. (1841/1957). *The Essence of Christianity* (trans. George Eliot & intro. Karl Barth), New York: Harper Torchbooks.

Feuerbach, L. (1851/1967). *Lectures on the Essence of Religion* (trans. Ralph Manheim), New York: Harper & Row.

Gendlin, E. (1997). *Experiencing and the Creation of Meaning*. Chicago: Northwestern University Press.

Gendlin, E. (1981). *Focusing*. Second Edition. New York: Bantam Books.

Gurevich, A. (1995). *The Origins of European Individualism*, Oxford: Blackwell.

Hampton, J. (1988). *Hobbes and the Social Contract Tradition*, Cambridge: Cambridge University Press.

Hand, S. (ed.). (1989). *The Levinas Reader*, Oxford: Blackwell.

Hardy, A. (1965). *The Living Stream*, London: Collins.

Hardy, A. (1966). *The Divine Flame,* London: Collins.

Hay, D. (1988). 'Asking questions about religious experience', *Religion*, 18, 217–229.

Hay, D. (1990). *Religious Experience Today: Studying the Facts*, London: Cassell.

Hay, D. (1994). ' "The biology of God": What is the current status of Hardy's hypothesis?' *International Journal for the Psychology of Religion*, 4(1), 1–23.

Hay, D. (2006). *Something There: The Biology of the Human Spirit*, London: Darton, Longman & Todd.

Hay, D. (2007). *Why Spirituality is Difficult for Westerners*, Exeter: Imprint Academic.

Hay, D. & Hunt, K. (2000). *The Spirituality of People who Don't Go to Church.* Final Report, Adult Spirituality Project: Nottingham University.

Hay, D. & Morisy, A. (1978). 'Reports of ecstatic, paranormal or religious experience in Great Britain and the United States: A comparison of trends.' *Journal for the Scientific Study of Religion*, 17(3), 255–268.

Hay, D. & Morisy, A. (1985). 'Secular society/Religious meanings: A contemporary paradox', *Review of Religious Research*, 26, 213–227.

Hay, D. with Nye, R. (Rev. edn.). (2006). *The Spirit of the Child,* London: Jessica Kingsley Publishers.

Hay, D. & Socha, P.M. (2005). ‘Spirituality as a natural phenomenon: Bringing biological and psychological perspectives together’, *Zygon*, 49(3), 589–612.

Heidegger, M. (1927/1962). *Being and Time* (trans. John Macquarrie & Edward Robinson), Oxford: Basil Blackwell.

Hirschman, A. (1997). *The Passions and the Interests: Political Arguments for Capitalism before its Triumph* (foreword by Amartya Sen), Princeton, NJ: Princeton University Press.

Hobbes, T. (1651/1962a). *Philosophical Rudiments concerning Government and Society*, Ch. 1, Section 4, 25–26 (quoted in MacPherson).

Hobbes, T. (1651/1962b). *Leviathan* (ed. and intro. by C.B. Macpherson), London: Penguin Classics.

Kant, E. (1793/1960). *Religion Within the Limits of Reason Alone* (trans. Theodore M. Greene & Hoyt H. Hudson), New York: Harper & Row,

Kirk, K., Martin, N., & Eaves, L. (1999). ‘Self-transcendence as a measure of spirituality in a sample of older Australia twins’, *Twin Research*, 2(2), 81–87.

Lambert, Y. (2004). ‘A turning point in religious evolution in Europe’, *Journal of Contemporary Religion*, 19(1), 29–45.

Locke, J.L. (1998). *Why we Don’t Talk to Each Other any More: The Devoicing of Society*, New York: Simon and Schuster.

Lukes, S. (1973). *Individualism*, Oxford: Basil Blackwell.

Luria, A. (1976). *Cognitive Development: Its Cultural and Social Foundations* (trans. Martin Lopez-Morillas & Lynn Solotaroff; ed. Michael Cole), Cambridge, MA: Harvard University Press.

Macmurray, J. (1957/1995). *The Self as Agent* (intro. Stanley M. Harrison), London: Faber & Faber.

Macpherson, C.B. (1962). *The Political Theory of Possessive Individualism*, Oxford: Oxford University Press

McCrone, J. (1990). *The Ape that Spoke: Language and the Evolution of the Human Mind*, London: Picador.

Monroe, K.R. (1996). *The Heart of Altruism: Perceptions of a Common Humanity*, Princeton, NJ: Princeton University Press.

Morris, C. (1972). *The Discovery of the Individual, 1050–1200*, London: SPCK.

Muller, J.Z. (1993). *Adam Smith I His Time and Ours: Designing the Decent Society*. New York: The Free Press.

Nagy, E. & Molnar, P. (2004). ‘Homo imitans or Homo provocans? Human imprinting model of neonatal imitation’. *Infant Behavior and Development*, 27, 54–63.

Newberg, A., d’Aquili, E., & Rause, W. (2001). *Why God Won’t Go Away: Brain Science and the Biology of Belief*, New York: Ballantine Books.

Pascal, B. (~1660/1961). *Pensées* (trans. J.M. Cohen), London: Penguin Classics.

Paterson, R.W.K. (1971). *The Nihilistic Egoist Max Stirner* (published for the University of Hull), Oxford: Oxford University Press.

Poll, M. (1983). ‘Unpublished poll of reports of religious experience in Australia.’

Preus, S. (1987). *Explaining Religion: Criticism and Theory from Bodin to Freud*, New Haven, CT & London: Yale University Press.

Putnam, R. (2000). *Bowling Alone: The Collapse and Revival of American Community*, New York: Simon & Schuster.

QSR.NUD*IST (1996). *User’s Guide*, London: Sage/SCOLARI

Selznick, P. (1992). *The Moral Commonwealth: Social Theory and the Promise of Community*, Berkeley, CA: University of California Press.

Smith, A. (1759/2000). *The Theory of Moral Sentiments*, Amherst, New York: Prometheus Books.

Smith, A. (1999). *The Wealth of Nations* (2 Vols.) (intro. Andrew Skinner), London: Penguin Books.

Stirner, M. (1845/1993). *The Ego and His* Own (trans. Steven Byington; intro. Sydney Parker), London: Rebel Press.

Stringer, C.B. (1994). ‘Evolution of early humans’, *The Cambridge Encyclopaedia of Human Evolution,* (eds. Steve Jones, Robert Martin and David Pilbeam), Cambridge: Cambridge University Press, pp. 241–251.

Tacey, D. (2004). *The Spirituality Revolution: The emergence of contemporary spirituality*, Hove and New York: Brunner-Routledge.

Taylor, C. (1989). *Sources of the Self: The Making of the Modern Identity*, Cambridge: Cambridge University Press.

Walzer, M. (1990). ‘The communitarian critique of liberalism’, *Political Theory*, 18(1), 6–23.

Weber, M. (1930). *The Protestant Ethic and the Spirit of Capitalism* (trans. Talcott Parsons), London: George Allen & Unwin.

Wilson, B. (1966). *Religion in Secular Society*, London: C.A. Watts.

Wordsworth, W. (1994). *Collected Poems*, Ware: Wordsworth Editions Ltd.

Zinnbauer, B.J., Pargament, K., et al. (1997). ‘Religion and Spirituality: Unfuzzying the fuzzy.’ *Journal for the Scientific Study of Religion*, 76(4), 549–564.

# Chapter 22
# Hope Rekindled: Well-Being, Humanism, and Education

**Kevin Cloninger**

## Introduction and Rationale

There is a powerful lesson to be learned from this book. Science and scientific advancement are both influenced by our subjectivity. The Heisenberg uncertainty principle already demonstrated how much we can influence an experiment, but in the social sciences our subjectivity can influence things differently. Subjectivity is both a strength and a weakness as it leads us to pay attention to some data and ignore others. An innovator may see something in a set of data that has long escaped the attention of others. On the contrary, we may consistently ignore information that contradicts long-held beliefs or traditions. This is the real challenge of scientific innovation. We must strive to see beyond our self-imposed limitations. Much like a human being, the field of science is never completely immune from the problems of subjectivity such as bias and prejudice.

However inconvenient this fact may be, sometimes on basis of very little evidence, powerful theories are constructed that have wide ramifications for our perceptions in the scientific community (and consequently a deep impact on society and culture). The "Man the Hunter" theory is a perfect example of this fact. I have been asked to write a chapter in this book because this is as true in the field of anthropology as it is in field of education and the practices of schools. In point of fact, the education we offer our children depends in no small part on our views of human potential, psychology, and the purposes of learning. For example, on an epistemological level, if a teacher, administrator, or superintendent believes that students minds are a *tabula rasa* (a blank slate), then they will structure schools or classrooms very differently from someone who holds a constructivist position. Similarly, an educator who believes that human beings are by nature violent may see school as a civilizing force, whereas someone who views students as autonomous democratic citizens may seek to maximize the freedom of those citizens who must be trusted with difficult decisions. In the everyday practices of school, however, little if any

---

K. Cloninger (✉)
Anthropedia Foundation, 1033 Corporate Square Drive, St. Louis, MO 63132, USA
e-mail: kcloninger@anthropedia.org; www.anthropedia.org

R.W. Sussman, C.R. Cloninger (eds.), *Origins of Altruism and Cooperation*,
Developments in Primatology: Progress and Prospects 36, DOI 10.1007/978-1-4419-9520-9_22,

consideration is given to what views of human nature, psychology, and learning are guiding our schools (Cohen, 2006; Eisner, 2005; Spring, 2007). This is despite the fact that such views have a deep impact on the practices of schools. These problems are further exacerbated by our attempts to measure the "success" of students. Standardized achievement tests may be excellent measures of certain forms of learning, but are they really the best way to measure all the learning of a child? What does it tell us about the relationships in the classroom or the love between a student and her/his teacher? What do they tell us about their maturity or their character? What do they say about a child's mental or physical health? Achievement testing while excellent in its very limited domain is hardly adequate to measure the full development of a child. And yet, public discussion about schools frequently centers around scores on standardized testing and the economic repercussions of schools. Politicians from both ends of the political spectrum capitalize on this fact to tell us that, "Our schools are no longer competitive in the global economy," or "Kids don't read and write as well as they used to."

What will perhaps come as a surprise to the reader is that such concerns and fears are not at all new in the history of public education. Many of the educational reforms made during the 1980s embodied in documents like *A Nation at Risk*, preyed upon public fears and took advantage of a *Manufactured Crisis* (Berliner and Biddle, 1995). In further evidence of this historical reality let's take a look at a quote from John Dewey written in 1904:

> Consider the wave by which a new study is introduced into the curriculum. *Someone feels that the school system of his town is falling behind the times.* There are *rumors of great progress* in education making elsewhere. Something new and important has been introduced; education is being revolutionized by it; the school superintendent, or members of the board of education, become somewhat uneasy; the matter is taken up by individuals or clubs; pressure is brought to bear on the managers of the school system; letters are written to the newspapers; the editor himself is appealed to use his great power to advance the cause of progress; editorials appear; finally the school board ordains that on and after a certain date the particular new branch—be it nature study, industrial drawing, cooking, manual training, or whatever—shall be taught in the public schools. The victory is won, and everybody—unless it be some already overburdened and distracted teacher—congratulates everybody else that such advanced steps are taken. The next year, or possibly the next month, there comes *an outcry that children do not write or spell or figure as well as they used to*; that they cannot do the necessary work in the upper grades, or in the high school, because of lack of ready command of the necessary tools of study. We are told that *they are not prepared for business, because their spelling is so poor, their work in addition and multiplication so slow and inaccurate, their handwriting so fearfully and wonderfully made.* Some zealous soul writes on the school board takes up this matter; the newspapers are again heard from; investigations are set on foot; and *the edict goes forth that there must be more drill in the fundamentals of writing, spelling, and number.* (Dewey, 1904, pp. 14–15, *emphasis added*)

It is staggering to see the same rhetoric used in modern school reform debates described in school reform efforts in 1904! Viewed in this light, it is self-evident that the need for reform in schools goes well beyond tinkering with techniques and standards in math, science, or any other subject. In this chapter, I will argue that we need to work toward the cultivation of the whole person, which is far more than a technique. It involves the cultivation of different climate in the schools. Abstract knowledge is not an end in and of itself. It is a means to an end, which to my mind is the development of the full potential of an individual human being. As it is obvious that the problems we have now are not new, this chapter will turn to history to help elucidate the relationship between well-being and education. Before I do that, I need to clarify what I mean by well-being.

## Definitions of Well-Being and Their Relevance to Education

There are few pursuits that captivate all cultures. The search for happiness is a notable exception. There is just one small catch—like our conception of the "good life," happiness means different things to different people at different times. An oft-quoted passage of Aristotle's *Nicomachean Ethics* alludes to this fact:

> As far as its name [*the good*] goes, most people virtually agree, since both the many and the cultivated call it happiness, and suppose that living well and doing well are the same as being happy. But they disagree about what happiness is, and the many do not give the same answer as the wise. (1095a17–21, *Italics added*)[1]

So we find ourselves in a predicament. A fundamental human aim, the search for happiness, is sometimes shrouded in confusion and acrimonious debate. In fact, at certain points in history the importance of well-being for society and individuals has been overlooked entirely—a subject we will return to later. Still, while there is no universally agreed upon definition, there are some consistently recurring ideas. For example, some would associate happiness with pleasure or wealth, while others would associate it with good fortune and physical health. A general distinction can be drawn between hedonistic conceptions of well-being and eudaimonistic conceptions (Cloninger, 2004; Ryff & Singer, 2008). The former looks at positive and negative emotions, while the latter emphasizes positive functioning and virtue. Such debates began long ago and can be traced back at least as far back as the Ancient Greek Civilization, particularly in the writings of Homer, Plato, and Aristotle (Cahn & Vitrano, 2008; Cloninger, 2004; McMahon, 2002, 2006; Ryff & Singer, 2008; Seligman & Csikszentmihalyi, 2000). In contemporary times, advances in the fields of psychology, psychiatry, and medicine have led to a reexamination of these age old questions using the tools of modern science (Argyle, 2001; Aspinwall & Staudinger, 2003; Cloninger, 2004, 2006a; Csikszentmihalyi, 2000; Deci & Ryan, 2008; Diener & Suh, 2000; Diener et al., 1999; Hird, 2003; Huppert et al., 2005; McMahon, 2006; Peterson & Seligman, 2004; RM Ryan & Deci, 2001; Richard Ryan et al., 2008; Ryff & Singer, 1998; Seligman & Csikszentmihalyi, 2000; Veenhoven, 2007). This new Science of Well-Being explores the principles and practices that help people live a healthy and happy life. Using a scientific idiom, the Science of Well-Being circumvents the aforementioned debates by examining the question empirically. What, in other words, does it take to cultivate lasting well-being? This chapter, in keeping with research, will rely upon an operational

---

[1] Trans. by Terence Irwin, Hackett Publishing Co., 1985

definition of well-being; that is, a state of positive functioning, psychological health, happiness, and satisfaction with life, which comes about through a harmonious relationship between and among the various aspects of a person[2] and the cultural and social context in which the person lives.

There is a growing body of educational theory on the subject of schools and well-being that draws on these recent scientific advances (Cohen, 2006; Konu & Rimpelä, 2002; Noddings, 2003, 2006; Spring, 2007). In other papers (Cloninger, 2005, 2006b, 2008), I have used the Science of Well-Being to elucidate educational practice and theory. Rather than rehash those ideas here, it is the purpose of this chapter to explore, historically, the importance of humanism's emphasis on well-being in education and society. I do this to draw a line between historically humanist periods and our present moment. As we will see each time that important world events led to major advances in art and science, human beings had to learn how to adapt in order to survive and live well. History teaches us that we can never have a fixed set of rules for living or for education, but must be constantly adapting ourselves to changing context. Globalization, climate change, the ecological crisis, the economic crisis, and the threat of nuclear war are once again calling on us to adapt. The development of an altruistic life is not only desirable now but also necessary if we hope to see our way through our uncertain times. This chapter is organized in two parts. In the first part, I will lay out an argument for why it is imperative that schools focus on well-being by looking to psychology, anthropology, and curriculum theory. In the second part, I will look at specific historical examples to illustrate how educational theory has addressed well-being in the past and draw out the lessons that might help us to address well-being once again.

## Part 1: The Door to Humankind

It is my contention that schools—and more broadly speaking, the education we receive—hold the keys to helping human beings express their full human potential. Our education provides the sustenance necessary for the seeds of our humanity to blossom. Unfortunately, schools are not presently focused on this flowering. It is no secret that schools are primarily focused on preparing children for the global economy (Ayers et al., 1998; Cohen, 2006; Cuban, 2004; Cuban & Shipps, 2000; Eisner, 2005; Kohn & Shannon, 2002; Noddings, 1992; Spring, 2007). Despite the fact that we know that well-being has not increased as a result of our material and technological advances (Cloninger, 2004; Diener et al., 1999; Myers & Diener, 1996), there is an implicit assumption that the best way to prepare our children for the world is to prepare them to get and keep a job. Certainly this is an important ingredient of a good education, but it is not sufficient in and of itself. While our global economy and

---

[2] Cloninger (2004) discusses at great length the importance of a harmonious relationship among the three aspects of the person—body, thoughts, and psyche—for the development of well-being. He also relates this to the development of societal well-being as do Hermann et al. (2005).

systems of communication have become increasingly complex (e.g., globalization, TV, and the internet), the resulting explosion of information has led us to lose sight of the fundamental purpose of the transmission of knowledge, which is to equip a person with the knowledge and necessary tools to help him or her live well.

Helping our children to learn how to live well through pedagogy is not a new idea; in fact it is as old as education itself. Scientists studying human origins point out that cultural transmission by means of pedagogy is one of the defining features of *Homo sapiens*. Premack and Premack (1996) explore this idea:

> Pedagogy, the teaching of one individual by another, appears to be a biological novelty, an activity largely confined to humans. . .Pedagogy is not a neutral achievement: it permits the evolution of culture and the possibility of history—that sequence of changes through which a species passes while remaining biologically stable. These changes are cultural changes, each stage incorporating important aspects of the past. The means for preserving and transforming culture are primarily pedagogical. The more rapid the social changes the more they are dependent upon pedagogy. (p. 302)

From the very dawn of humanity, the tools necessary to live have been transmitted from one generation to the next through pedagogy. The use of language, the creation of tools, and even social understanding itself has been created and then transmitted to human progeny (Bruner, 1977, 1996; Olson, 2003; Premack & Premack, 1996; Tomasello, 1999). Premack and Premack (1996) point out that while the rudiments of pedagogy are present in other species, they differ in kind and complexity. They argue that because humans display a greater degree of variation (within-species) of intelligence there is a greater need for education. In fact, the type of giftedness we see in the human species is more dramatic than that found in other members of the animal kingdom (Cloninger, 2004; Cloninger, 2005; Premack & Premack, 1996). Pedagogy in its fullest form is something we find confined to the human species.

At its core, pedagogy's function is to enable the survival of the species and, consequently, to teach humanity how to live well. As knowledge and technology have expanded, education has become more complex and increasingly institutionalized. However, the foundation of education remains the same: e*ducating people has always been about helping them attain well-being*. Knowledge about learning how to survive, how to eat better, to suffer less, to engage in aesthetic study of art and culture, to learn how to think better, even to learn how to read and write helps an individual cultivate well-being.

In the information age, there has been a dramatic increase in the amount of knowledge and our access to it. Today the problem is understanding what is worth transmitting. Currently, when children attend schools they *do not* feel they are learning about well-being[3] (Cohen, 2006; Eisner, 2002; Freire, 1993; Noddings, 1992, 2003, 2006; Ruyter, 2004; Spring, 2007). Writing 500 years ago, Michel de

---

[3] As I stated earlier, this chapter will not discuss the practicalities of educating for well-being. I have addressed the subject in other papers (Cloninger, 2005, 2006b, 2008).

Montaigne, a French philosopher and essayist made a similar point in his essay on the education of children:

> The son of the house is seeking book-learning not to make money (for so abject an end is unworthy of the grace and favour of the Muses and anyway has other aims and depends on others) nor for external advantages, but rather for those which are truly his own, those which inwardly enrich and adorn him. Since I would prefer that he turned out to be an able man not an erudite one, I would wish you to be careful to select as guide for him a tutor with a **well-formed rather than a well-filled brain.** Let both be looked for, but place character and intelligence before knowledge; and let him carry out his responsibilities in a new way.[4] (Montaigne, 1991, pp. 168–169; **emphasis added**.)

When Montaigne spoke of a well-formed brain, he meant a person who not only had plenty of information or knowledge (well-filled) but also someone who had a well-constructed sense of the knowledge they possess and an ability to put it into action, "an able man, not an erudite one." The essence of knowledge—well-being—is currently being lost in the shuffle. *There is a lack of connection to practical and active tools and dispositions that can lead one to greater well-being.* We need to provide children with tools and understanding in all the domains of human experience—sexual, material, emotional, cultural, and spiritual. Preparing students for the global economy may provide some tools at a material level, but practically ignores every other level. Any learning at the other levels is incidental, not necessarily rejected, but not deliberately included. This is only sustainable for so long.

The Science of Well-Being contends that to properly foster well-being, to give people tools to cultivate well-being, we must address bodily aspects, mental aspects, and spiritual aspects in the person. There is obviously considerable overlap across these various aspects. Nonetheless, it is useful to consider each of these three aspects independently, remembering that they are interrelated. Physical health, coordination, bodily awareness, nutrition, and hygiene help students to understand the proper functioning of the body. Study of all forms, literacy, subject-matter study, disciplinary knowledge, and meta-cognition (thinking about thinking) can help students to understand the proper functioning of their thoughts. However, what are frequently overlooked are the spiritual components of well-being. We can help individuals to increase their spiritual sensitivity by contemplating the significance of life, the nature of the self, their intuitions, and the ethical dimensions of reality. By this I do not mean religious education or the indoctrination of children with religious ideology. Rather, a serious theory of education based on well-being must provide students with tools to exercise all three aspects of the human being, one of which is spiritual

---

[4] Montaigne continues: Teachers are for ever bawling into our ears as though pouring knowledge down through a funnel: our task is merely to repeat what we have been told. I would want our tutor to put that right: as soon as the mind in his charge allows it, he should make it show its fettle by appreciating and selecting *things*—and by distinguishing between them; the tutor should sometimes prepare the way for the boy, sometimes let him do it all on his own. . .Socrates and then Archesilaus used to make their students speak first; they spoke afterwards. . .[For those who want to learn, the obstacle can often be the authority of those who teach.]

in nature. In this manner, education can serve its vital function: the transmission of well-being.

## Part 2: A Brief History of Well-Being in Education

It is unfortunate that schools have lost sight of this aim in education, but it is not the first time that we have lost sight of the connection between well-being and education (and I fear it will not be the last!). History can be instructive, therefore, in helping us to identify the processes and mechanisms necessary to reintegrate learning and well-being. With this in mind, there are two major points I hope to impress upon the reader in what follows. First, throughout history there have been individuals and theories that have helped remind our civilization of the importance of well-being. The essence of the transmission of knowledge, namely well-being, has been forgotten, rediscovered, and then forgotten again only to be rediscovered at a later time. That is, rather than being a novel problem in the history of human civilization, the current amnesia has plagued us on and off from the very beginning of our existence. In education, we can point out that at each major period of rapid expansion of human knowledge, well-being is often brought out of neglect. Individuals and theoretical perspectives evolve in order to face the challenge and remind us of the importance of well-being in cultural advancement. This leads me to my second major point, namely that at each major sociological and historical shift in human history, there has been a corresponding shift in the social sciences and philosophy. In particular, our views of human nature, psychology, and the purposes of education have changed. I am not the first to allude to the dialectical relationship between social events, the social sciences, and philosophy (Hegel, 1991; Kuhn, 1996; King, 1986; Whitehead, 1967). Each time there is a sociological shift all of the social sciences have adapted to it. Sometimes this sociological shift is a theory. Sometimes it is an event like a war or a pandemic, other times it is a social movement.

As I pointed out above, in every period of rapid expansion of human knowledge and culture, there has always been both people and theories to help us go back to the origin and essence of the transmission of knowledge: well-being (Cloninger, 2004; Greer & Lewis, 1992; Hegel, 1991). This pattern can be easily identified by perusing surveys of Western Civilization (Greer & Lewis, 1992; Hegel, 1991; Proctor, 1998). What is often overlooked, however, is that each of these movements can be considered as one single connecting thread through Western history.[5] That is, they do

---

[5] Each period of expansion made direct reference to proceeding periods of expansion. During the Renaissance, literally translated as "the rebirth," there was a deliberate study of Greek, Roman, and Egyptian Civilization. Similarly many of the great minds during the Enlightenment, like Voltaire and Diderot, studied the works of the Renaissance, the Ancient Greeks and Romans, the Middle Eastern thinkers of the Golden Age of Islam, and the works and ideas of the Hebrew and Christian bibles.

not occur in a vacuum; each of these periods of expanding knowledge was fertilized with seeds from previous periods.

Cloninger (2004) has described this movement in philosophy and referred to it as "positive philosophy." The word "positive" denotes the constructive contribution these individuals have made to civilization. We can see examples of this phenomenon in ancient Egypt, in the Middle East during the Golden age of Islam, even during the Renaissance in Europe.[6] Each major period of expansion of knowledge witnessed movements that tried to reconnect modern times with the wisdom of times immemorial. Martin Luther King Jr., in his last speech before his death, described this phenomenon:

> As you know, if I were standing at the beginning of time, with the possibility of general and panoramic view of the whole human history up to now, and the Almighty said to me, "Martin Luther King, which age would you like to live in?"—I would take my mental flight by Egypt through, or rather across the Red Sea, through the wilderness on toward the promised land. And in spite of its magnificence, I wouldn't stop there. I would move on by Greece, and take my mind to Mount Olympus. And I would see Plato, Aristotle, Socrates, Euripides and Aristophanes assembled around the Parthenon as they discussed the great and eternal issues of reality. But I wouldn't stop there. I would go on, even to the great heyday of the Roman Empire [. . .] But I wouldn't stop there. I would even come up to the day of the Renaissance, and get a quick picture of all that the Renaissance did for the cultural and esthetic life of man. But I wouldn't stop there [. . .] Strangely enough, I would turn to the Almighty, and say, "If you would allow me to live just a few years in the second half of the twentieth century, I will be happy." Now that's a strange statement to make, because the world is all messed up. The nation is sick. Trouble in the land. Confusion all around. That's a strange statement. But I know, somehow, that only when it is dark enough, can you see the stars. (Martin Luther King, 1986, pp. 279–280)

In this quote, King outlines the major influences on his own thinking about the civil rights struggle, from history. He clearly identifies many of the previous periods of rapid expansion of knowledge: ancient Egypt and the ancient Greeks, the Roman Empire and the Renaissance. More importantly, King sensed that there was another period of expansion of knowledge beginning at the end of the 20th century. As we have already discussed, our world has fundamentally transformed in the last 50 or 60 years. After the world wars, we witnessed a tremendous change in the world economy (e.g., globalization) and concomitantly our communication systems have also fundamentally transformed. In a very meaningful sense, a new global economy began to develop after the two great wars (Spring, 2007; Stromberg, 1953). The communication systems of this new economy have also led to great changes. The power of TV, cell phones, internet, computers, and other technologies have changed the shape and tenor of our societies. As a result of a sociological shift—the global economy, the rise of the information age, and the transformation of communications

---

[6] I am well aware that I am focusing solely on Western Civilization. The movements I have described are not strictly European, however they are all generally considered "western." I am not implying that this phenomenon does not take place in other regions of the world and in no way do I mean disrespect or disregard for those cultures. While I am confident that this phenomenon is relevant to all cultures and all peoples, I am not familiar enough with other civilizations (e.g., Eastern Civilization or Native Americans Cultures) to use them as exemplars of the theory.

systems—the social sciences will, and indeed must, adapt, so that children can be "well-formed," not simply "well-filled," and as a result, in a state of well-being.

Up to now I have only spoken abstractly about periods of expansion. We will now turn to two concrete examples, the Renaissance and the Enlightenment. There are many parallels that can be drawn between these periods and our own, so it is useful to consider. In the excerpt of his visionary and prophetic speech earlier in this chapter, Martin Luther King described all the periods of human history he would have liked to have lived through. Each of these periods of time was the result of rapid expansion of human knowledge where the social and cultural development of civilization was evident and clearly focused on well-being. These periods can be contrasted with periods of obscurantism, like the Middle Ages or the periods during the two great world wars, where there was wide-scale opposition to the free dissemination and spread of knowledge.[7] Roessler and Miklos describe this phenomenon during World War I:

> The most direct intervention in the lives of the citizens was the imposition of conscription, which served to add hundreds of thousands to the numbers of soldiers already present in the standing armies of 1914. Further civilians experienced restrictions far beyond economic regulation. The free flow of ideas which had expanded during the nineteenth century, was now severely limited. Governments faced the challenge of maintaining morale among their populations during the protracted struggle, and they used all the techniques and media available to them to take advantage of mass literacy. Propaganda and censorship shaped messages that demonized opponents and sustained the emotional enthusiasm required to endure privations and casualties. (Roessler & Miklos, 2003, p. 246)

This marked change in the free flow of ideas and knowledge through society tends to have a depressing or dulling effect on society. Subsequent periods of expansion of knowledge help counter this depressing influence in society and its thoughts by reinvigorating the diffusion of knowledge. Like, for example, during the Renaissance in Florence:

> The spirit of humanism could not be confined to literature and philosophy, and as early as the fourteenth century it burst forth splendidly in the visual arts. It appeared first, as one might expect, in Italy—in Florence, the capital of humanism, which remained for some two hundred years the leading center of European art. Few places on Earth, over a comparable period, can match the city's output of painting, sculpture, and architecture. (Greer & Lewis, 1992, p. 329)

---

[7] I am neither implying that periods of expansion of knowledge are perfection or absolute harmony across civilization nor am I implying that periods of obscurantism are periods of total shadow. Our historical descriptions of these periods of expansion and obscurantism merely serve to characterize the overall ambience of the world during these periods of history. At an individual level, this may or may not manifest. Indeed during the Middle Ages, there were still great cultural and social achievements, but the overall ambience of the world was quite depressed. People were barely affected by these cultural advances and instead subject to wide-scale oppression by both church and state (Greer & Lewis, 1992). Barzun (2000, pp. 47–48) discusses the fuzzy boundaries to which I refer. Indeed the Renaissance has been considered by some to have begun in the end of Middle Ages. Nonetheless, considering the broad strokes I am making in this chapter, I do not wish to belabor the point and thrust the reader into the controversy. That is, it goes without saying that no period of time is without some expansion and obscurantism. Viewed from afar however, some periods had more or less expansion, and, consequently, more or less obscurantism.

The expansion of knowledge in the art, culture, and education of Florence helped to counterbalance the dulling effects of the lack of free flow of knowledge during the Middle Ages. This understanding can help to explain why periods of expansion are characterized as a time of light or clarity (Renaissance, Enlightenment, etc.), whereas periods of obscurantism are generally characterized as shadowy or dark times (e.g., the Dark Ages). It is during these periods of expansion that both people and theories come about to help humanity remember the importance of well-being and the positive aspects of human nature (Barzun, 2000; Greer & Lewis, 1992; Martin Luther King, 1986; Proctor, 1998; Roessler & Miklos, 2003; Whitehead, 1967). Each of these periods of time represents periods of success and prosperity in many different spheres: economic, political, cultural, etc.; indeed, in such conditions times are ripe for transformative ideas.

A good example of the general conditions during these periods can be seen during the Renaissance in Italy. Greer and Lewis explain:

> So exciting were the fresh ideas about human affairs that some observers felt civilization itself was being "reborn." In fact, some historians later used the word "Renaissance" (rebirth) to describe the era as a whole…its core was an upsurge of humanism. (1992, p. 318)

Many have argued that the fountainhead of this "rebirth" was Francesco Petrarch, the father of humanism. Petrarch, inspired by Cicero, began to study the *humanitatis,* or the qualities that make us uniquely human like wisdom and virtue. During the Middle Ages, universities used Scholasticism as their primary pedagogical framework, a method of study that employed Aristotelian logic and an emphasis on dialectical reasoning (Barzun, 2000; Greer & Lewis, 1992). Petrarch criticized the Scholastics for being too concerned with technique and method; he believed that for most Scholastics the method became an end in itself (Barzun, 2000; Greer & Lewis, 1992; Proctor, 1998). Petrarch found the lack of meaning and depth in the Academy of his time distasteful and set out to reinvigorate one of Cicero's dearest concepts, *studia humanitatis*, a study that helps us understand virtue and what it is to be human. (Proctor, 1998). By studying the qualities of mind and spirit that make us human—*humanitatis*—we could contemplate virtue and the depths of the self, and in so doing, this knowledge would make us happier and morally better people. Petrarch argued that the study of method, Aristotelian logic, and the natural sciences—while useful as a means to an end—could never be an end in and of themselves unless they helped people to look inward, understand the self, and to cultivate an inner state of well-being (Proctor, 1998).

These ideas clearly ran counter to many of the Christian teachings of the Middle Ages which accepted the doctrine of "original sin" and the natural human sinfulness (Barzun, 2000; Greer & Lewis, 1992). According to humanism, people could, through their own efforts, raise themselves up and live the good life, which meant a life that was pleasing to the senses, the intellect, and man's aesthetic capacities. For Petrarch, this was much more than mere study. Proctor describes Petrarch's approach well,

> But Petrarch, unlike many who later taught and practiced the "humanities" as a career, was not a professional classicist. There was no divorce between his literary studies and his life. His scholarship was so personally motivated that one hesitates to call it scholarship at all, because of the connotations of personal detachment and disinterest associated with that word today. Petrarch was driven to study classical antiquity because he was driven to study himself. (Proctor, 1998, p. 26)

For Petrarch, humanism was a way of life and a way of understanding the self; it was not simply academic. With his dedication to the classical worldview, Petrarch provided much more than influence on the Renaissance, he provided a paradigm for all those who would follow him in his rebirth: Boccaccio, Bruni, Leonardo da Vinci, Donatello, Michelangelo, Botticelli, Veronese, Ficino, Valla, Mirandola, Brunelleschi, Erasmus, Van Eyck, Montaigne, and so many others. Humanism was the fruit of Petrarch's understanding of previous periods of expansion of knowledge. Indeed, we can see how, as a result of sociological and historical shifts during Petrarch's time, there was a corresponding modification of views of human nature, views of development, and views of how to educate people to help them express their latent human potential. Petrarch's life and works galvanized all of these elements and returned their focus to well-being. These changes, Greer and Lewis (1992) point out, came about because of changes in culture:

> Interest in the classics had not altogether disappeared during the Middle Ages [. . .] Before the fourteenth century, however, there had been little to equal the enthusiasm of Renaissance scholars for Classical writing. It was in those works that they caught their "new" vision of humanity. Moved by this vision, they searched eagerly for ancient documents and developed a deep respect for the literary culture of antiquity. Their enthusiasm was not caused primarily by dramatic finds of "new" documents; it resulted, rather, from a quickening change in the European *state of mind.* (p. 319)

This shift in consciousness led to an expansion of knowledge and an eager search for whatever documents could be discovered. At the same time, this increased access to knowledge of antiquity catalyzed an unprecedented flourishing of art, music, literature, science, and mathematics. It also led to the advent of new technologies like Gutenburg's printing press, movable type, and the gear. All of this led to the close of the Middle Ages, and the dawn of the "modern" era (Barzun, 2000; Greer & Lewis, 1992; Proctor, 1998). Indeed, we can see just how modern Petrarch's criticisms of the Scholasticism of his day are since they could be applied just as easily to modern education at any level, a subject I will return to later in this literature review. What is important for the reader to take away from this discussion is that each period of expansion of knowledge has led to dramatic shifts in views of human nature, human development, and human learning, as well as views of education. Greer explains the changes in educational thought:

> This new body of knowledge challenged traditional patterns of education and thought. Along with new social forces and the rising secular spirit, it set off a revolution in European schooling. Medieval education had been almost exclusively by and for the clergy [. . .] for medieval Europe as a whole, religion remained the focus of higher learning. The *trivium* and *quadrivium* centered on scriptural texts, the writings of Church Fathers, and the logic of Aristotle. The Italian humanists made up the first substantial body of *secular* (non-religious) scholars in Europe. Most of them were sons of the middle class or nobility and had no

> connection with the clergy. Nor had they any use for the tiresome scholasticism that still dominated education; in fact, they regarded it as irrelevant to the new society. In Greek and Roman literature they saw the means of providing students with a truly *liberal* education. (Greer & Lewis, 1992, p. 322)

Here we see how sociological shifts lead to changes in the views of human nature, which in turn lead to changes in views of development, learning, and the purposes of education. The spirit of the Renaissance was focused not on authority and preserving traditions but on a revolutionary new "liberal" spirit. The history books often make this distinction between religious and secular knowledge, marking the change in emphasis that occurs in the Renaissance, but this only speaks to part of the paradigm shift. In humanism, rather, we see a shift from reliance on authoritative knowledge and dogma to a belief in the potential of the human spirit of its own accord to find true knowledge (Barzun, 2000; Greer & Lewis, 1992; Proctor, 1998). Notice that both worldviews acknowledge something sacred or spiritual. That said, prior to the Renaissance, there was an implicit assumption that the human being was defiled or inadequate—unworthy of the divine—and after the Renaissance, thinkers would find something divine in the human being in and of itself. In this way, one can see how views of human nature lead to changes in social theory. Indeed, this evolution is unending. Our views of human nature and the nature of existence must continuously evolve as our understanding of the world, the self, and the being deepen. It is not surprising to see how the Renaissance itself would engender further evolutions in the 17th and 18th centuries after the bloody times of the Reformation. Many argue, in fact, that the Renaissance helped pave the way for the coming of the scientific revolution that would lead to the Enlightenment (Proctor, 1998).[8]

The 17th century is perhaps most famous for its explosive revolution in science. This explosion could be seen in the form of changes in our descriptions of the natural world, the creation of better and more accurate scientific instruments, and the development of mathematics that allowed for more complex calculations allowing scientists to make detailed predictions and descriptions of nature (Roessler & Miklos, 2003; Whitehead, 1967). The work of Bacon, Descartes, Galileo, Copernicus, and Newton exemplify these changes:

> While Bacon and Descartes devised methodologies based on observation and analysis, others were already employing these techniques using new instruments in their study of astronomy and physics. Johann Kepler (1571–1630) and Galieo Galilei (1564–1642) tested the validity of the Copernican hypothesis, which held that the Sun rather than the Earth was the center of the universe, and investigated planetary and terrestrial motion [. . .] It

---

[8] Proctor (1998, p. 23) said it this way, "In fact, one could even argue that the *studia humanitatis* prepared the way for the Scientific Revolution by providing a program of studies and a philosophy of education which helped people adjust to the dichotomies of a postclassical universe centuries before Galileo and Descartes theorized them." Whitehead (1967) adds, "Leonardo also illustrated the theory which I was advancing in my last lecture, that the rise of naturalistic art was an important ingredient in the formation of our scientific mentality [. . .] The practice of naturalistic art is more akin to the practice of physics, chemistry and biology than is the practice of law" (p. 43).

> remained for Isaac Newton (1642–1727) to provide the synthesis and mathematical explanation of motion that suggested that the whole material universe could be understood using the scientific method. (Roessler & Miklos, 2003, p. 3)

The ensuing development of scientific knowledge, as well as its transformation of society and culture, has been called the "scientific revolution" by some historians (Greer & Lewis, 1992; Shapin, 1998). Although there is controversy regarding the exact dates of the period, as well as the origins, causes, debates, and results of the "revolution," there is little doubt that something new and profound took place during this period of time (Greer & Lewis, 1992; Shapin, 1998). In Greer and Lewis's (1992) words,"The scientific revolution of the seventeenth century produced a radically different *view of the universe* and a new *mode of thinking*" (p. 410). Whitehead (1967) stated this quite eloquently in his *Science and the Modern World*:

> [. . .] this quiet growth of science has practically recoloured our mentality so that modes of thought which in former times were exceptional are now broadly spread through the educated world. This new colouring of ways of thought had been proceeding slowly for many ages in the European peoples. At last it issued in the rapid development of science; and has thereby strengthened itself by its most obvious application. The new mentality is more important even than the new science and the new technology. It has altered the metaphysical presuppositions and the imaginative contents of our minds; so that now the old stimuli provoke a new response. (p. 2)

The fundamental transformations in human knowledge and their methods of discovery ushered in a new era in our view of the universe and the self. Take, for example, the Copernican heliocentric universe. It not only changed our vision of the universe (that is, earth is not the center of the galaxy) but also led to a revision of our metaphysical assumptions. Sandra Bermann, in *The Sonnet Over Time* (1988, p. 12), points out that rather than egocentrism, the belief that the earth was in the center of the universe placed it *furthest away from God*—a wasteland, of a sort, which had profound metaphysical consequences (the belief of a distant, cold, disappointed God, for example). The revision of this belief had a far more dramatic effect on spirituality than we often think insofar as it brought man and God closer in the human imagination and in theology.

This and many other discoveries, some rediscovered from previous periods of expansion of knowledge, led to a fundamental shift in human consciousness. Continuing his description of the flourishing of scientific ideas in the 17th century, Whitehead states:

> The crowded stage of this hundred years is indicated by the coincidences which mark its literary annals. At its dawn Bacon's *Advancement of Learning* and Cervantes' *Don Quixote* were published in the same year (1605), as though the epoch would introduce itself with a forward and a backward glance. The first quarto edition of *Hamlet* appeared in the preceding year, and a slightly variant edition in the same year. Finally Shakespeare and Cervantes died on the same day, April 23, 1616. In the spring of this same year Harvey is believed to have first expounded his theory of the circulation of blood in a course of lectures before the College of Physicians in London. Newton was born in the year that Galileo died (1642), exactly one hundred years after the publication of Copernicus' *De Revolutionibus*. One year earlier Descartes published his *Meditationes* and two years later his *Principia Philosophiae*.

> There simply was not time for the century to space out nicely its notable events concerning men of genius.

The 17th century was truly a prolific time, with many great minds helping to engender a new day in the history of humanity. This period of expansion of knowledge, like many others, was a period of great convergence—convergence of people and consequent spiritual, cultural, social, and intellectual achievements. The scientific revolution was only the beginning of the social and cultural changes.

The Age of Enlightenment was the name given to the influence of the ideas of the scientific revolution on the ideas, values, and attitudes of society. The work of the scientists—or "natural philosophers"—of the 17th century like Newton and other thinkers like Montaigne, Spinoza, and Locke had led to a new confidence and belief in reason, natural law, and progress (Barzun, 2000; Greer & Lewis, 1992; Montaigne, 1991; Roessler & Miklos, 2003; Spinoza, 1994; Whitehead, 1967). At the same time, the thinkers of the Enlightenment believed that if, through reason, humanity could discover the natural laws that governed existence, then surely these laws could be applied to improve society. Let me state for the reader, so as to avoid confusion, that this is not a tacit approval of oppressive colonialist practices. It was, I believe, a misappropriation of Enlightenment ideas that led to the violent oppression of non-European states with these ideas. They hoped "the application of the study of everything" would lead to justice (which does not include violence, oppression, or a sense of cultural superiority) and eventually a state of unending progress (Roessler & Miklos, 2003).

Roessler and Miklos (2003) describe the individuals who spread the news of the Enlightenment:

> The eighteenth-century intellectuals to whom the spread of Enlightenment ideas is attributed were the French philosophes. Few possessed extensive academic credentials. Many were journalists, publicists, freelancers, even economic and political reformers. Their goal was not the development of systems of thought for the purpose of investigating ultimate questions of existence. Rather, like the thinkers of the Renaissance, they placed man at the center of intellectual activity and sought to understand the complexities of the world in which they lived [. . .] They turned their attention to problems arising from economics, justice, education, religion, and politics. In so doing, policies and institutions were scrutinized in the confidence that natural laws could be discovered and used to implement constructive reforms. Such activities soon brought them into conflict with authority, with the result that the intellectual freedom needed to realize their objectives was hindered by censorship and defensive measures taken by church and state in most European countries. (Roessler & Miklos, 2003, p. 6)

Such confidence in natural law had come about because of the strength of the scientific revolution and the "light" that Enlightenment thinkers believed was being shed on man and the cosmos. The leaders of the *philosophes* were indisputably François Marie Arouet (Voltaire) (1694–1778), Baron de Montesquieu (1689–1755), and Denis Diderot (1717–1784), who avoided being imprisoned or killed by diffusing their messages *in cognito* through subtleties, satires, and double entendres in the content of their novels and plays, as well as through their histories, dictionaries, and encyclopedias (Roessler & Miklos, 2003). Their message was indeed very powerful and far-reaching. Its ideas sparked two revolutions: one in America and one in France. Among the most important Enlightenment ideas were the belief in life, liberty, and the pursuit of happiness, the belief that all men are created equal, the belief that a just law governed society, and the belief in a separation of church and state.

Like Petrarch during the Renaissance, Voltaire's name became synonymous with the Enlightenment itself (Barzun, 2000; Greer & Lewis, 1992; Roessler & Miklos, 2003). He was a controversial figure because he was a satirist and a staunch critic of all faulty or superstitious thinking. His writings brought him many problems. He was exiled from Paris at the age of 21 when he insulted a regent, which was compounded when a published attack was attributed to him later on that year and he was sent to the Bastille for 11 months and then banished again (Roessler & Miklos, 2003). However, perhaps this was for the best, for in response to another insult he made to a nobleman he embarked on a 3-year voluntary exile to England. Upon his return, he published his first acknowledged contribution to the Enlightenment, *Letters on the English* (1773) (Roessler & Miklos, 2003). Voltaire, more than most philosophers and thinkers of our past, was a man of action. Like Petrarch, his affinity for the Enlightenment was not a vain speculation,[9] but a way of life. For example, he not only spoke about science but also conducted experiments in chemistry and physics with Marquise Emilie du Chatelet[10] at her chateau near the Lorraine border in France. When Voltaire spoke at length about the importance of tolerance in his *Treatises on Toleration*, it was not mere philosophic reverie, but the result of taking up the cause of Jean Calas, a Protestant who had been wrongly convicted and tortured to death for the murder of his son (Roessler & Miklos, 2003; Voltaire, 1994). Roessler and Miklos highlight Voltaire's penchant for action:

> Supporters of Jean Calas maintained he was guilty only of attempting to cover up the son's suicide to prevent public scandal and financial ruin. Voltaire launched a campaign to reopen the case, lending not only his pen and finances to the cause but requesting funds from foreign heads of state. He highlighted the case as an atrocious example of religious fanaticism, part of a long history of Christian intolerance and persecution encompassing Catholic and

---

[9] As the reader is probably familiar, Voltaire spent a great deal of energy criticizing philosophers for what he considered to be useless, "vain," speculation about the nature of existence. It was not that he denied the legitimacy of existential questions, but because he believed that human thought and the mind could never adequately encapsulate the problems many philosophers dwelled upon. To him, it was more important to focus on making a concrete difference in people's lives. For example, he harshly chastised Rousseau and his philosophy as being hypocritical. Voltaire thought it unconscionable, for example, that while Rousseau spoke at length about the natural state of men and our distortion of their natural goodness during childhood that he kept his four children in an orphanage because he felt it was counterproductive to his work. Such hypocrisy was the very thing Voltaire spent his entire life fighting against.

[10] The Marquise Emilie du Chatelet (1706–1749), being a woman, was restricted from engaging in academic activities and publishing, but she nonetheless translated Newton's *Principia Mathematica* into French and published several treatise on Physics and systematic thought (Roessler & Miklos, 2003). Voltaire and Chatelet were intimate intellectual and romantic companions until her death in 1749. Voltaire was said to have remarked that "Chatelet was a brilliant man whose only fault was being a woman."

> Protestant faiths alike. Four years after the initial trial, the king's council proclaimed Jean Calas innocent. Voltaire's famous cry of "crush the infamous thing" arose from the tribulations of the Calas affair. Despite his strong stand, Voltaire did see value in religion and retained belief in God. (Roessler & Miklos, 2003, p. 10)

Voltaire's active philosophy often makes him go unnoticed as a philosopher. Nonetheless, as his deeds show, he was a tireless advocate of people and of the ideas he supported during the Enlightenment. He also helped provide a direct connection between the ideas of the times and the general well-being and welfare of the people around him. This period of expansion of knowledge exposes the same dialectic among sociological conditions, philosophy, and the social sciences. In this case, it led to the creation of what we recognize as modern social science. Many others followed Voltaire in the ensuing 100 years: Rousseau, Diderot, Montesquieu, Alambert, d'Holbach, but equally Mary Astell, Christine McCauley, Mary Wollstonecraft, and the German Idealists like Kant and Hegel, and the countless others who gave themselves to the movement of the Enlightenment which emanated from France (Barzun, 2000; Greer & Lewis, 1992; Roessler & Miklos, 2003).

The resulting shifts in views of human nature and human development during the Enlightenment, just as we have seen during the Renaissance, led to shifts in views of the nature and purpose of education. Once the Enlightenment was in full swing, there was a felt need to disseminate the new knowledge to the public (Greer & Lewis, 1992; Roessler & Miklos, 2003). This discussion and dissemination of "enlightened" ideas took place in many different contexts in Europe, most prominently in salons, academies, and Masonic lodges of the 18th century (Roessler & Miklos, 2003). Salons were places where the social and cultural elite, as well as intellectuals from all over Europe, could come together and exchange new ideas. In addition to the salons, the academies that were created during the Enlightenment helped to encourage the diffusion of knowledge throughout European society. Roessler and Miklos (2003) explain:

> In addition, through the learned academies, eighteenth-century ideas reached a wider audience. The most prominent were institutions that had been established in national capitals such as the French Academy of Sciences, the Royal Society of London, and the Berlin Academy. However, the number of these institutions increased markedly throughout the century, particularly in France, where there were academies in more than thirty provincial cities. These academies promoted intellectual activity by providing an institution where people interested in science and philosophy could gather regularly for discussion, debate, and lectures. Unlike the universities, which with few exceptions remained enclaves of established thought and doctrine, the academies encouraged the exploration of new ideas and began to contribute to a climate favorable to a wide range of reforms. (2003, pp. 19–20)

These academies allowed people to continue to learn about the new ideas of the Enlightenment, and like the salons, they provided opportunities for networking and the publication of ideas that had direct social interest. Lastly, the Masonic lodge provided a third formal institution that made possible a wider diffusion of Enlightenment ideas possible. Roessler and Miklos (2003, p. 20) tell us that,

> [t]his fraternal organization of the Freemasons probably originated out of seventeenth-century stonemasons' guilds, but a century later in England, the order aimed to bring people together around a set of universal religious beliefs that cut across conflicting dogmas and diverse socioeconomic backgrounds. The ideas of the early Enlightenment, which valued tolerance, reason, and progress, were welcomed, and Masonic organizations spread across Europe and North America. Although practices and beliefs were not uniform from one Masonic lodge to another, their humanitarian and educational activities made them effective organizations for spreading the messages of the Enlightenment.

So it was through salons, academies, freemasonry, and (believe it or not) coffee-shops, that Enlightenment views of human nature, human psychology, and human development found an educational expression in society (Roessler & Miklos, 2003).

These historical periods—the Renaissance and the Enlightenment—demonstrate the relationship between sociological shifts and the social sciences and philosophy. In each period, we see how shifts in society lead to changes in views of human nature, psychology, and purposes of education. In fact, both the Renaissance and the Enlightenment were periods characterized by a marked interest in education of both adults and children. In both periods, humanism flourished and was the guiding force behind education and other social initiatives (Barzun, 2000; Greer & Lewis, 1992; Locke, 1983; Montaigne, 1991; Proctor, 1998; Roessler & Miklos, 2003). Indeed, the term *humanism* itself comes about from Cicero's view of education, which was reinvigorated during the Renaissance and then put into action once again during the Enlightenment.

Some modern curriculum theorists like Hirsch (1999) and Ravitch (2000) would have us believe that appropriate content will create the sort of enlightened minds we had during these periods of expansion, but clearly this misses the point of these movements. The subject matter of the Renaissance and the Enlightenment was merely the vehicle of something much larger. It was a vehicle for the inner development of humanity, or *humanitatis,* as Cicero might have said. The words themselves are unimportant if they do not convey that spirit. It is this spirit that can lead a student of any age to well-being. If we were forced to choose an adequate curriculum, clearly we might be well-served by studying Ancient Greece and Rome where many of the eternal ideas of humanity were discussed, but this alone will not suffice. In fact, one of the biggest challenges currently facing us in this period of rapid expansion of human knowledge is finding a new idiom, a new manner of expression of the spirit behind all cultural and human advancement, one that is capable of reaching a far more diverse audience than the middle and upper class Europeans who resonate with the Western ideas I have discussed. I am not suggesting that we solidify a curriculum that is unable to reach the students of our times, but we must choose a course of study that is informed by theory drawn from the enduring lessons of history. The revolutionary spirit of transformation seen during both the Renaissance and the Enlightenment is universal because its principles, its spirit, transcends cultural bounds. It is the same spirit that catalyzed the civil rights movement of the 1950s, for example, Gandhi's salt march, the abolition of slavery, and, perhaps even more broadly, American democracy.

Unfortunately, however, the last time there was a clear emphasis on this universal spirit of well-being in education was during the Enlightenment. During this time, a great deal of light was shed on the need to transform our social institutions and rid our society of superstition and intolerance. It was considered self-evident to all theorists in the Enlightenment that the best education would be that which led to happiness and well-being. Take for example, John Locke in his work entitled *Some Thoughts Concerning Education* written in 1693, stated, "A SOUND mind in a sound body, is a short but full description of a happy state in this world: he that has these two, has little more to wish for; and he that wants either of them, will be but little the better for any thing else" (Locke, 1983). During the Renaissance, Leonardo Bruni (a disciple of Petrarch) made it clear—in a letter to a young lady whose education came in his stead—that the purpose of the *studia humanitatis* was for self-perfection leading one to wisdom, virtue, and inevitably well-being (Proctor, 1998). Much like Montaigne, whose treatise on education and a well-formed mind we discussed earlier, Bruni urged his student to treat her education like nourishment for the soul:

> It is a matter of food for the soul, with which the mind is fed and nourished. And just as those who care about their stomachs do not pour just any kind of food into them, so one who wants to preserve the integrity of his mind will not permit it just any reading whatsoever. (Proctor, 1998, p. 6)

During the Renaissance and the Enlightenment it was clear that our education, our "formation" as it was sometimes called, must help create an ordered or "well-formed" mind that led one to well-being. I am not arguing that content does not matter, but my argument should not be read to mean that we need to use the classics in instruction either. Clearly there are some works from classical times or traditional education that may be more or less suited to this. However, the essential piece, far beyond simple content considerations, is that we need to ensure that the information that is ingested or studied can help lead us toward well-being. In other words, the pedagogy, the institutional approach, as well as the awareness of the teachers and students are paramount to fostering well-being.

While the pursuit of happiness found its way into our declaration of independence, it has not permeated all of our social institutions. One need not look very deeply into the history of American education to understand that it has rarely if ever been focused on our well-being (Bruner, 1996; Cremin, 1988; Kliebard, 2004; Olson, 2003). Our schools have adapted to the "information age" by placing different forms of technologies in schools; they have tried to prepare children to work in the global marketplace, but they have not considered how to adapt our education to bring well-being and happiness to a new generation of humanity: a generation who is consumer driven, consumption oriented, and who spend most of their day basking in the light of their TV or their computer. Moreover, as theorists in curriculum are well aware, the power of the global economic considerations has tended to trump the importance and power of the politicians, theoreticians, and social theorists in making educational decisions. That is, in our day, the intellectual has been relegated to the back-seat or confined to an "ivory tower." Unlike the intellectuals of Petrarch and Voltaire's day who were actively engaged in social decisions, the intellectuals of our time have been shut out and drowned out by the deafening noise of those who think that shouting is the best and only way to win an argument. At this moment in time, the stakes are too high to let this noise guide our social and educational policies.

## Conclusion

One can reflect on the dramatic irony of the fact that the two World Wars were waged on French and Italian soil. The battlegrounds of the potent forces of obscurantism (i.e., Nationalism, Fascism, and Nazism) are coincidentally the places where the last two great expansions of knowledge took place. More than cultural traditions and a sense of human heritage were lost as a result of the two World Wars. What has also been lost—in the wake of the unprecedented horrors of the Holocaust—is a sense that collectively—we as humanity—are progressing toward a better, brighter future. Along with this loss of faith in our common humanity, we have ceased believing in the intrinsic goodness of our being. What has been lost is neither technological nor something that can be addressed in schools by reencouraging the studies of the humanities or ensuring that children perform better on standardized tests. What has been lost is a sense of our place in the universe and our self-awareness. Not until the seeds of humanity are once again nourished by love, truth, and hope can we even dream of recreating what Hitler, Mussolini, and the fascists of the world took away from us during the World Wars. The world still lives in their shadows and today we must dare to light a small candle. "You can light a candle in the darkness," Mohandas Gandhi once said, "but you can never light the darkness in the light." It is encouraging to see that those who helped bring to our attention the beginning of this new period of expansion, Gandhi and Martin Luther King Jr., had this awareness. For when we despair in trying to rekindle this humanistic awareness, it helps to remember Gandhi's resonant words, "When I despair, I remember that all throughout history the way of truth and love has always prevailed. There may be tyrants and assassins, and for a time they may seem invincible, but in the end they always fall."

## References

Argyle, M. (2001). *The Psychology of Happiness* (2nd ed.). New York: Taylor & Francis Inc.

Aspinwall, L. G., & Staudinger, U. M. (Eds.). (2003). *A Psychology of Human Strengths: Fundamental Questions and Future Directions for a Positive Psychology*. Washington, DC: American Psychological Association.

Ayers, W., Hunt, J., & Quinn, T. (1998). *Teaching for Social Justice. A Democracy and Education Reader*. New York: New Press.

Barzun, J. (2000). *From Dawn to Decadence: 500 Years of Western Cultural Life*. New York: Harper Collins.

Berliner, D. C., & Biddle, B. J. (1995) *The Manufactured Crisis: Myths, Fraud, and the Attack on America's Public Schools.* New York: Perseus Books.

Bermann, S. L. (1988). *Sonnet over Time: A Study in the Sonnets of Petrarch, Shakespeare, and Baudelaire*. Chapel Hill, NC: University of North Carolina.

Bruner, J. (1977). *The Process of Education*. Cambridge: Harvard University Press.

Bruner, J. (1996). *The Culture of Education*. Cambridge: Harvard University Press.

Cahn, S. M., & Vitrano, C. (Eds.). (2008). *Happiness: Classic and Contemporary Readings in Philosophy*. New York: Oxford University Press.

Cloninger, C. R. (2004). *Feeling Good: The Science of Well-Being*. New York: Oxford University Press.

Cloninger, C. R. (2006a). The science of well-being: An integrated approach to mental health and its disorders. *World Psychiatry, 5*(2), 71–76.

Cloninger, K. (2005). The science of well-being: A new way to understand the gifted. In N. L. Hafenstein, B. Kutrumbos, & J. Delisle (Eds.), *Perspectives in Gifted Education: Complexities of Emotional Development, Spirituality and Hope* (Vol. 3, pp. 76–115). Denver: Institute for the Development of Gifted Education, Ricks Center for Gifted Children.

Cloninger, K. (2006b). Making intuition practical: A new theoretical framework for education. *Curriculum and Teaching Dialogue, 8*(1), 15–28.

Cloninger, K. (2008). Giving beyond care: An exploration of love in the classroom. *Curriculum and Teaching Dialogue, 10*(1 and 2), 193–211.

Cohen, J. (2006). Social, emotional, ethical, and academic education: Creating a climate for learning, participation in democracy, and well-being. *Harvard Educational Review, 76*(2).

Cremin, L. (1988). *American Education: The Metropolitan Experience 1876–1980*. New York: Harper and Row.

Csikszentmihalyi, M. (2000). Positive psychology: The emerging paradigm. *North American Montessori Teachers' Association Journal, 25*(2), 4–25.

Cuban, L. (2004). *The Blackboard and the Bottom Line: Why Schools Can't Be Businesses*. Cambridge, MA: Harvard University Press.

Cuban, L., & Shipps, D. (2000). *Reconstructing the Common Good in Education: Coping with Intractable American Dilemmas*. Palo Alto, CA: Stanford University Press.

Deci, E., & Ryan, R. (2008). Hedonia, Eudaimonia, and well-being: An introduction. *Journal of Happiness Studies, 9*, 1–11.

Dewey, J. (1904). *The Educational Situation*. Chicago: The University of Chicago Press.

Diener, E., & Suh, E. M. (2000). *Subjective Well-Being Across Cultures*. Cambridge, MA: MIT Press.

Diener, E., Suh, E. M., Lucas, R., & Smith, H. E. (1999). Subjective well-being: Three decades of progress. *Psychological Bulletin, 125*, 276–302.

Eisner, E. (2002). What can education learn from the arts about the practice of education. *Journal of Curriculum and Supervision, 18*(1), 4–16.

Eisner, E. (2005). Education learning from the arts. In *Reimagining Schools: The selected works of Elliott W. Eisner* (pp. 205–215). New York: Routledge.

Freire, P. (1993). *Pedagogy of the Oppressed*. New York: Continuum International.

Greer, T. H., & Lewis, G. (1992). *A Brief History of the Western World* (6th ed.). New York: Harcourt Brace Jovanovich College Publishers.

Hegel, G. (1991). *The Philosophy of History* (J. Sibree, Trans.). Amherst: Prometheus Books.

Herrman, H., Saxena, S., & Moodie, R. (2005). *Promoting Mental Health: Concepts, Emerging Evidence, Practice*. Geneva, Switzerland: World Health Organization.

Hird, S. (2003). *Individual Well-Being: A Report for the Scottish Executive and Scottish Neighbourhood Statistics*: NHS Health Scotland.

Hirsch, E. D., Jr. (1999). *The Schools We Need And Why We Don't Have Them*. New York: Anchor Books.

Huppert, F. A., Baylis, N., & Keverne, B. (2005). *The Science of Well-Being*. New York: Oxford University Press.

King, M. L. (1986). *A Testament of Hope: The Essential Writings of Martin Luther King Jr*. New York: Harpercollins.

Kliebard, H. (2004). *The Struggle for the American Curriculum: 1893–1958* (Third Edition ed.). New York: RoutledgeFalmer.

Kohn, A., & Shannon, P. (Eds.). (2002). *Education, Inc.: Turning Learning into a Business* (Revised ed.). Portsmouth, NH: Heinemann.

Konu, A., & Rimpelä, M. (2002). Well-being in schools: A conceptual model. *Health Promotion International, 17*(1), 79–89.

Kuhn, T. S. (1996). *The Structure of Scientific Revolutions* (3rd ed.). Chicago: University of Chicago Press.

Locke, J. (1983). *Some Thoughts Concerning Education*. Oxford: Oxford University Press.

McMahon, D. (2002, Winter 2002–2003). Developing happiness. *Correspondence: An international Review of Culture and Society, 10*.

McMahon, D. (2006). *Happiness: A History*. New York: Atlantic Monthly Press.

Montaigne, M. (1991). *The Essays of Michel de Montaigne*. London: Allen Lane.

Myers, D. G., & Diener, E. (1996). The pursuit of happiness. *Scientific American, 274*(5), 70–72.

Noddings, N. (1992). *The Challenge to Care in Schools: An Alternative Approach to Education. Advances in Contemporary Educational Thought, Volume 8*. New York: Teachers College Press.

Noddings, N. (2003). *Happiness and Education*. Cambridge: Cambridge University Press.

Noddings, N. (2006). Educating whole people: A response to Jonathan Cohen. *Harvard Educational Review, 76*(2).

Olson, D. R. (2003). *Psychological Theory and Educational Reform: How School Remakes Mind and Society*. New York: Cambridge University Press.

Peterson, C., & Seligman, M. E. P. (2004). *Character Strengths and Virtues: A Handbook and Classification*. New York: Oxford University Press.

Premack, D., & Premack, A. J. (1996). Why animals lack pedagogy and some cultures have more of it than others. In D. R. Olson & Torrance, N. (Eds.), *The handbook of education and human development* (pp. 302–323). Cambridge, MA: Blackwell.

Proctor, R. (1998). *Defining the Humanities: How Rediscovering a Tradition Can Improve Our Schools*. Bloomington: Indiana University Press.

Ravitch, D. (2000). *Left Back: A Century of Failed School Reforms*. New York: Simon and Schuster.

Roesslor, S., & Miklos, R. (2003). *Europe, 1715–1919: from Enlightenment to World War*. Oxford: Rowman and Littlefield.

Ruyter, D. J. D. (2004). Pottering in the garden? On human flourishing and education. *British Journal of Educational Studies, 52*(4), 377–389.

Ryan, R., & Deci, E. (2001). On happiness and human potentials: A review of research on hedonic and eudaimonic wellbeing. *Annual Review of Psychology, 52*, 141–166.

Ryan, R., Huta, V., & Deci, E. (2008). Living well: A self-determination theory perspective on eudaimonia. *Journal of Happiness Studies, 9*, 139–170.

Ryff, C., & Singer, B. (1998). The Contours of positive human health. *Psychological Inquiry, 9*, 1–28.

Ryff, C., & Singer, B. (2008). Know thyself and become what you are: A eudaimonic approach to psychological well-being. *Journal of Happiness Studies, 9*(1), 13–19.

Seligman, M. E. P., & Csikszentmihalyi, M. (2000). Positive psychology: An introduction. *American Psychologist, 55*, 5–14.

Shapin, S. (1998). *The Scientific Revolution*. Chicago: University of Chicago Press.

Spinoza, B. D. (1994). In E. Curley (Ed.), *A Spinoza Reader: The Ethics and Other Works*. Princeton: Princeton University Press.

Spring, J. (2007). *A New Paradigm for Global School Systems: Education for a Long and Happy Life*. Philadelphia: Lawrence Erlbaum Associates.

Stromberg, R. N. (1953). American business and the approach of war 1935–1941. *The Journal of Economic History, 30*(1), 58–78.

Tomasello, M. (1999). *The Cultural Origins of Human Cognition*. Cambridge, MA: Harvard University Press.

Veenhoven, R. (2007). World database of happiness. Retrieved 6/18/07: http://worlddatabaseofhappiness.eur.nl/.

Voltaire. (1994). *A Treatise on Toleration and Other Essays* (J. McCabe, Trans.). Amherst, NY: Prometheus Books.

Whitehead, A. N. (1967). *Science and the Modern World*. New York: The Free Press.

# Chapter 23
# Promoting Well-Being in Health Care

**Lauren E. Munsch and Helen Herrman**

## Introduction

The conference on “Man the Hunted: Sociality, Altruism, and Well-Being,” brought together research from a number of domains to examine and challenge a prevailing assumption among anthropologists studying primate behavior and human origins, namely that early human beings were savage, violent hunters who exhibited little, if any, cooperation or prosocial behavior beyond what was necessary for basic survival. This view has many implications for our understanding of human nature. In this chapter, we examine and note the further challenges to this assumption from the viewpoint of research in modern medicine and health care. From this viewpoint, we now understand that cooperative and nonviolent behaviors are fundamental to the health and well-functioning of individuals and the population as a whole.

We also note that while research and theory have moved solidly in this direction, mainstream approaches to health care in many countries are characteristically restricted by a biomedical view of disease and its cure. In the biomedical view, a human being is little more than a faulty machine that must be repaired. The strict biomedical approach fails to focus on the whole person and how he or she may live a healthy and happy life. At the same time, an approach to health care and public health that integrates the social with the biological and psychological dimensions of human life is fundamental to improving the well-being of the individual and the good health of a population.

Recent reports on the social determinants of health (Marmot, 2007; Marmot et al., 2008; Wilkinson, 2005) clarify the understanding that the main drivers of health lie outside the health care system. This accords with the modern definition of the integrated nature of health as inclusive of physical, mental, and social well-being. Health and well-being cannot be achieved without attention to living and working conditions, human rights and equality, and a supportive social environment. Efforts to work in this way are undermined by the same pessimistic views of the person

---

L.E. Munsch (✉)
Anthropedia Foundation, Mt. Sinai School of Medicine, New York, NY 10029-6574, USA
e-mail: lmunsch@gmail.com

R.W. Sussman, C.R. Cloninger (eds.), *Origins of Altruism and Cooperation*,
Developments in Primatology: Progress and Prospects 36, DOI 10.1007/978-1-4419-9520-9_23,

that confound anthropologists studying human origins. This chapter will discuss a framework for action at individual and population levels that moves beyond this reductive model.

Mainstream health care is focused on the treatment and cure of acute problems. Although there is increasing pressure to consider seriously the management of chronic disease and the promotion of well-being while living with an illness or disability, problems arise because of the nature and timing of the interventions. Medical interventions most often occur when illnesses are too serious to cure and the cost is high. The focus of the system often means that the chance of enhancing or maintaining quality of life is low. Health care professionals and organizations need now to do much more in partnership with others in the community to prevent disease and promote long-term well-being. Restrictions in access, financing, professional training, and organization allow little time or resource for methods such as personalized care, lifestyle counseling, health education and support, and education of the family and other caregivers.

In this chapter, we discuss the nature of well-being, the relationship between health and well-being, factors influencing individual and population health, and practical strategies to promote well-being in health care. Well-being can be promoted on at least two levels: by means of a broad bio-psycho-social approach to health care (Engel, 1977) and by considering a population approach to health promotion.

## From Human Being to Well-Being

In early Greek thought, sophists and physicians claimed it is “not possible for anyone to know medicine who does not know what the human being is and how the human being was made and constructed, and that whoever would cure men properly, must learn this in the first place” (Hippocrates, 2005). In the same vein, it is evident that to understand *well-being*, it is necessary to first have a clear understanding of the *human being*.

Historically, notions of the human being ranged from those who supposed that the human being was composed of the four elements earth, air, fire, and water, to philosophers who explored the aspects of the human being as body, thought, and soul. Common to all viewpoints is regard for the human being as a composite of corporeal, intellectual, and spiritual aspects. However, the perception and treatment of these aspects over time were simplified and separated into distinct functions of the human. This is particularly evident in the modern philosophical movement beginning with Rene Descartes (1596–1650). With the “Cartesian split,” the mind and spirit became the focus of religious leaders, and scientists regarded the body separately. The reductionist movement that shaped the scientific field during the 17th and 18th centuries fostered our modern tendency to consider the mind and body distinctly and to keep separate the notions of physical and mental health. It also contributes to the failure to integrate social aspects of life and illness when considering clinical care or public health. Here, too, we find a powerful theory based on scant evidence that sees the human being as essentially split. The person is considered split in body and mind, individual and social, well-being and disease. As we will see later, this split has been called into question as research has shown that individuals who are more prosocial (i.e., higher in character development) and socially integrated are healthier and happier (Cloninger, 2004). Furthermore, basic science and clinical research in areas such as neuroendocrinology, neuroimmunology, and psychophysiology have begun to define the complex relationships between the mind, body, and social context, and the importance of understanding the human being as an integrated whole. Research has demonstrated that the various aspects of a human being (body, thoughts, psyche) are distinguishable, yet they do not operate separately (Solomon, 1987).

Well-being in this context refers to an integrated and harmonious relationship among a person's body, thoughts, psyche, and surrounding environment. Well-being is more than the absence of pain, disorder, and illness; it is the positive functioning and coherence that arrive when an individual fulfills his or her potential in each aspect of being.

## Relationship Between Health and Well-Being

The World Health Organization (WHO) defines health as "a state of complete physical, mental, and social well-being and not merely the absence of disease." Mental health is further defined by the WHO as "a state of well-being in which the individual realizes his or her own abilities, can cope with the normal stresses of life, can work productively and fruitfully, and is able to contribute to his or her community" (Herrman and Jané-Llopis, 2005:2).

While these definitions are widely quoted, their association and application in clinical practice are limited. Around the world, health is most commonly considered an absence of disease, and the goal of illness treatment is eliminating the disease rather than restoring the person to a state of well-being. Treatments that aim to eliminate the disease are usually limited in their ability to foster health, as defined by the WHO, when they fail to address the entire person in his or her social context. As social conditions and population demographics in many parts of the world change and become more complex, patterns of health and disease evolve and the need for review becomes more urgent. For example, the chronic disease burden is growing in many low-income countries that are still beset by old and new infectious diseases. Statistics from health organizations worldwide describe a rise in depression, obesity, and other lifestyle-related and stress-related disorders. An effective response requires changes in health care delivery and a broad view of the influences on public health.

According to the WHO, depression is the fourth leading contributor to the global burden of disease (measured as the sum of years of potential life lost due to premature mortality and the years of productive life lost due to disability). It is projected to become the second leading cause of disability for all ages and both sexes, by the year 2020. Additionally, the WHO reports that at least 80% of premature deaths from cardiovascular disease and strokes could be prevented through a healthy diet, regular physical activity, and by avoiding the use of tobacco. In developing countries, smoking is responsible for more than 80% of all lung cancers. Lung cancer from tobacco use is the single largest preventable cause of cancer in the world. Psychosocial distress is the single most common reason for consulting a doctor, and the largest class of prescription medications is given for psychoactive drugs or painkillers to help people cope with depression, anxiety, sleeplessness, and pain (Wilkinson, 2005). It is estimated that the tendency to experience and communicate psychological distress in the form of physical symptoms and to seek medical help is the primary problem for 30–40% of medical patients, and increases medical utilization and cost in the United States (Fava and Sonino, 2008). Additionally, the world is facing two extreme problems: over-nutrition and under-nutrition. In the United States and similar countries, the increased consumption of fats, preservatives, sweeteners, and highly processed foods is producing new health risks. A growing body of evidence demonstrates the inadequacies of a biomedical model for improving individual and social health. This highlights the need to consider different approaches to health promotion and maintenance.

## The Biopsychosocial Approach to Health Care

More than 30 years ago, George L. Engel understood the limitations of a biomedical model for health care when he proposed a biopsychosocial (BPS) approach to promoting health and treating illness (Engel, 1977). The BPS approach views illness as a result of interacting mechanisms at the biological, psychological, and social levels, and it acknowledges that all have a significant role in health and illness (Engel, 1977). The BPS model considers the individual, his/her body, and his/her surrounding environment as essential components of the total system (Fava and Sonino, 2008). Traditionally, the *bio* aspect of the model referred to the activities and mechanisms of the human at a cellular, tissue, biochemical, and physiological level. The *psycho* aspect included factors such as the behaviors, emotions, and thoughts of a person. Today, there is also growing evidence that the *psycho* aspect of the BPS model includes the spiritual aspect of human beings, namely the *psyche*, “an immaterial intelligent aspect of human beings that leads them to contemplate and search for what is beyond their individual existence and for elevated things like truth, beauty, and love” (Cloninger, 2004). The *social* aspect of the BPS model takes into consideration the surrounding environment as well as the social conditions of the person. Studies in the Science of Well-Being and research in social science and public health shed light on how each of these aspects relate to health and illness, thereby providing a basis to understand better the determinants of health and well-being (Blazer, 2005).

## Determinants of Well-Being

Whereas disease prevention focuses on the cause of disease, the promotion of health and well-being is concerned with the determinants of health and the factors underlying the positive functioning of physical (body), mental (mind), and social health (Herrman et al., 2008). A focus on positive functioning of the whole person in harmony with their social environment can help physicians prevent illness and increase well-being as well as treat disease. Over the last century, research has greatly increased the understanding of the biological factors contributing to disease and health promotion. Studies in psychiatry, psychology, neuroscience, anthropology and other social sciences (like that presented at the conference) have increased our understanding of the psychological and social determinants of health and well-being. To elucidate an integrative view of the person and work on fostering health and well-being, it is essential to understand the determinants of health.

### *Biological Determinants of Health*

Biological factors fundamentally contribute to health and can be classified as either endogenous or exogenous. Endogenous biological determinants include genetic heritage; physiology, metabolism, and mechanisms of homeostasis; cell signaling; and the immunity that is passively acquired from maternal antibodies passed across the placenta or transmitted via maternal milk. A person’s genetic heritage influences their responses to inborn and environmental challenges. DNA composition determines a person’s blood group, tendency to develop errors of metabolism, inherent immunity to different types of infection, and susceptibility to different types of cancer, mental illness, allergies, diabetes, and many other conditions.

Exogenous biological determinants of health are the other living things with which humans interact and factors that have a direct influence on biological functions, such as diet, exercise, and medications. The most significant exogenous factors are microorganisms. Microorganisms contribute to both the positive and negative functioning of the body. The human body depends on certain microorganisms to assimilate foods and to break down complex chemicals into simpler components in our intestines. To maintain good health, people rely on healthy symbiotic relationships with innumerable microorganisms. Microorganisms can also cause pathological processes or diseases and provoke immune defensive reactions. A person′s immunologic defenses are also influenced by his or her nutritional status.

Poorly nourished, protein-starved, and vitamin-deprived individuals mount ineffective immune defense mechanisms and are therefore more vulnerable to serious infection by invading pathogenic organisms.

## *Psychological Determinants of Health*

The psychological determinants of health can be understood in terms of various theories and schema of personality. One prominent and useful schema, the Temperament and Character Inventory (TCI), describes character traits, including Self-Directedness (i.e., responsible, purposeful, resourceful), Cooperativeness (i.e., tolerant, helpful, compassionate), and Self-Transcendence (i.e., intuitive, judicious, spiritual). In general, high scorers in all three character traits have frequent positive emotions (i.e., happy, joyful, satisfied, optimistic) and infrequent negative emotions (i.e., anxious, sad, angry, pessimistic) (Cloninger, 2004). The ability of an individual to be resourceful, purposeful, goal directed, controlled, and aware of his psychological attachments and dependences is a strong positive predictor of health (Cloninger, 2004). Low TCI Self-Directedness is a strong indicator of vulnerability to major depressive disorders (Farmer, 2003). TCI Self-Directedness is also a predictor of rapid and stable response to both antidepressants and CBT (Cloninger, 2000).

Psychological methods to improve well-being can be understood as working on the development of the three branches of mental self-government that can be measured as character traits in the TCI (Cloninger, 1993, 1997). These character traits can be exercised and developed by interventions that encourage a sense of hope and mastery for Self-Directedness, kindness and forgiveness for Cooperativeness, and awareness and meaning that go beyond oneself for Self-Transcendence. Encouragement of problem solving leads to increases in autonomy and the sense of personal mastery, which all facilitate greater hope and well-being in ways that are common in effective psychotherapies.

Human spirituality is an essential factor in helping people cope with challenges and discover joy in life. Interestingly, the word *psychiatry* is derived from Greek and literally means, “the healing of the psyche.” *Psyche* is the Greek word for soul or spirit, which is the immaterial but intelligent aspect of the consciousness of a human being. Discovering spiritual meaning through self-transcendent values reduces relapse and improves well-being in randomized controlled trials of patients with depression, schizophrenia, and terminal diseases (Cloninger, 2006). Additional evidence demonstrates that CBT can be augmented with an added focus on existential issues, such as self-acceptance and finding meaning in coping with challenges and suffering. Meaning is often realized by encountering someone or something that is valued, acting with purpose in the service of others, or developing attitudes such as compassion and kindness (Cloninger, 2006).

Many scientists, philosophers, and artists of the past, in dealing with the nature of being, have pointed out that human consciousness is characterized by a capacity for self-awareness, creative gifts that are innate but neither inherited nor acquired, and free choices that are not fully determined by past experience (Cloninger, 2006). Growth in self-awareness, listening to the psyche, and freedom of choice are key factors underlying the development of well-being (Cloninger, 2004).

## *Social Determinants of Health*

As disease patterns are changing and people in many countries are living longer, there is an increasing necessity to understand the complete picture of health and illness. In the last 25 years, research in the social sciences has increased awareness of the social factors contributing to health and the importance of promoting population health for the development of complete well-being (Table 23.1).

## *Natural Environment*

At both the micro and macro level, the natural environment influences the health of an individual and a population. Natural disasters, changes in infectious disease patterns, and even gradual shifts in ecology all have effects on local food yields, the supply of fresh water, sanitation, the vitality of ecosystems, and the loss of livelihood. These environmental factors have an effect on modulating serious illnesses such as infectious diseases and malnutrition. Climate change and air pollution are influenced strongly by human activity and increasingly pose serious risks to health.

## *Human Rights and Gender Equality*

The differential status between men and women in almost every society is one of the most pervasive and entrenched inequities. The disempowerment and disadvantage of women are exemplified at many levels including the sanctioned violation of women; social conduct that rewards violence against women; restrictions of physical mobility and pleasure; unequal access to and control over property, inheritance, and assets; and unequal participation of women in political institutions.

## *Socioeconomic Status and Social Equity*

Health inequities result from unequal distribution of power and resources. Evidence demonstrates that the lower an individual's socioeconomic position, the worse his or her health is likely to be (Marmot, 2007; Velupillai et al., 2008). Relative socioeconomic disadvantage in any community is associated with increases in chronic disease risk factors and physical disorders, such as cardiovascular disease, infections due to immune down-regulation, lung cancer from increased smoking, accidents, and risk-taking behavior. In the United States, income level predicts mortality.

**Table 23.1** Social determinants of health and actions to promote population health

| Aspect | Level | Determinants | Action |
|---|---|---|---|
| Social | Coherence | Cooperative behavior among governmental and non-governmental organizations, civil society, trade unions, political parties, public health organizations, health professionals, educators, sociologists, anthropologists | Multi-level/Multi-sector integration and action |
| | Spiritual | Freedom of choice, autonomy and authenticity in spiritual practice | Community action to foster interfaith tolerance, respect, and nonviolence |
| | Culture/communication | Education, expression, and cultural upbringing | Access to early and continuing education, cultural development, policy to promote freedom of speech, positive media initiatives |
| | Social Relationships | Safety, security, comfort, early childhood development, cooperative behavior | Good urban–local governance to improve social protection from violence and discrimination, development of safe nurturing environments |
| | Socioeconomic | Access to basic requisites for a decent life, living and working conditions, quality and accessibility of social and health care services | Improve social equity through employment, improved living and working conditions, and equal distribution of resources and power |
| | Ethics | Respect for human life and human rights | Promote woman and human rights, civil liberties, sexual responsibility |
| | Natural environment | Extreme weather events, natural disasters, infectious disease patterns | Ecological awareness and education, disaster preparedness |

Additionally, unemployed people have higher mortality rates than those employed (Mittelmark et al., 2005).

The health status for all in a population is related to income differences within rich countries but not to those between them. Health and social problems are worse in more unequal countries (Wilkinson and Pickett, 2009, see Fig. 23.1). For example, higher levels of socioeconomic inequity in a society are correlated with

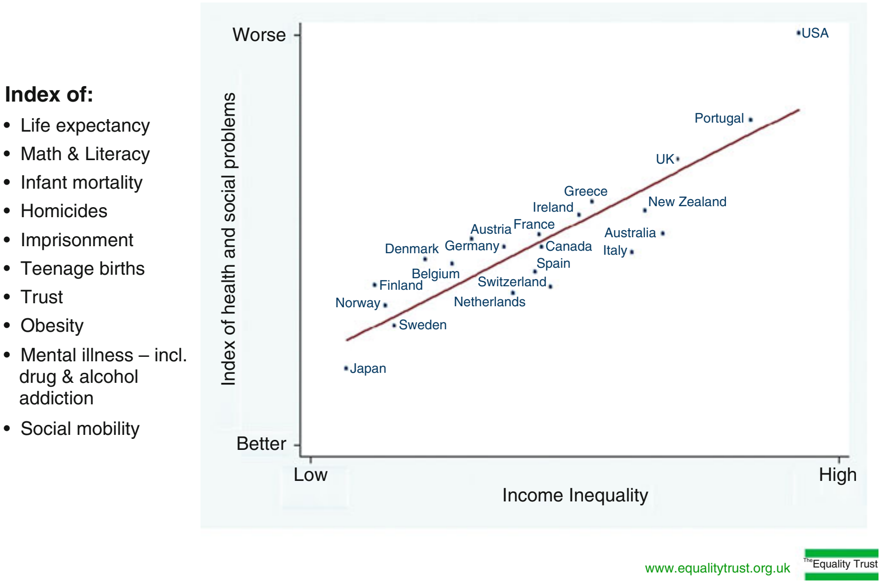


**Fig. 23.1** Health and social problems are worse in more unequal countries. *Source:* Wilkinson and Pickett, *The Spirit Level* (2009)

increased rates of mental disorders such as depression, anxiety, and drug abuse, and increases in social threats, including violence and homicide.

## *Living and Working Conditions*

Living and working conditions have important consequences for health. Poor sanitation, crowd, and inadequate ventilation are associated with respiratory infections, asthma, lead poisoning, meningitis, accidents, injuries, and poor mental health (Mittelmark et al., 2005). Additionally, work related injuries and illness—such as skin and respiratory disorders, postural problems, and psychological stress from exposure to toxic substances, unsafe machinery, and poor ergonomic conditions—are serious threats to health.

## *Social Relationships*

Social relationships and social connectedness influence health. Relationships and connections with others influence attitudes, behaviors, and habits that affect health. Social support from family and friends is important to help cope with and manage illness on a material level (i.e., helping patients with transportation to the doctor, helping with medications, paying bills) and to provide the psychological support needed to endure hardship. There is extensive evidence that social isolation and social stress lead to poor health, while social participation enhances health (Mittelmark et al., 2005).

### *Early Childhood Development*

Early childhood development is an important social determinant of health. A child's early development has a significant influence on brain development (Marmot, 2007). Positively stimulating environments cause an increased number of connections to form in the brain and the child demonstrates improved physical development, emotional and social development, and an increased capacity for self-expression and the capacity to acquire knowledge (Marmot, 2007; Chapter 19, this volume). Recent investigations have focused on studying the plasticity (i.e., biochemical changes at the cellular level) of the emotional circuitry in the brain and have begun to identify factors that increase the capacity to regulate negative emotion and decrease the duration of negative affect once it appears. Laboratory studies in rats suggest that early environment can have significant effects on the central circuitry of emotion. In these studies, mother rats that use more licking, grooming, and nursing with their newborn babies have offspring that behave with lower responsiveness to stress than others later in life. This results from changes in the way genes are expressed (Davidson, 2004).

### *Education*

Formal and informal education is a critical factor affecting health. Worldwide, there is a clear gradient demonstrating that people with higher levels of education have better health than those with less education. In Russia, there are increasing differences in life expectancy by level of education among both men and women. Evidence from Sweden demonstrates that adults with a PhD have lower mortality than those with a Master's degree or other professional qualification (Marmot, 2007). Additionally, an increase in education level improves the health of both women and their children (Mittelmark et al., 2005).

## Understanding Individual and Population Well-Being as a Whole

While it is important to consider each of these groups of health determinants individually, it is also crucial to recognize that the determinants of health interact with each other over the course of life, so that the health of any individual is the outcome of a complex summation of two factors—proximal and distal. If we observe the factors that influence our health at each level of being, then it is clear that physical, mental, and social health are each influenced by interactions between the biological, psychological, and social determinants of health (Table 23.2). Furthermore, the

**Table 23.2** The unity of well-being: determinants of physical, mental, and social well-being

| Structure and function of human beings | Physical well-being (Body) | Mental well-being (Mind) | Social well-being (Social context) |
|---|---|---|---|
| Unity | Level of integration of physical, mental, and social health at and between each level of human development | Level of maturity and integration of physical, mental, and social health at and between each level of human development | Level of maturity and integration of physical, mental, and social health at and between each level of human development |
| Spiritual | Degree of temperance and moderation | Level of self-awareness, self-transcendence, listening to psyche, comprehension of elevated notions (love, hope, faith) | Degree of freedom to practice, gather, worship |
| Cultural/ communicative | Ability of self-expression | Ability to reason, analyze, observe and understand oneself—mindfulness | Education, freedom of speech, freedom to gather and organize, freedom of press, cultural endowments |
| Emotional | Ability to form bonds and social attachments, tendency toward addictions, history of traumatic memories | Level of cooperativeness, coping skills, presence of positive emotion | Social relationships and support networks, social protection, degree of freedom from discrimination and violence, early childhood development |
| Material | Access to basic requisites for decent life, lifestyle (sleep, exercise, diet) | Degree of self-directed character development: resourcefulness, purposefulness, self-sufficiency | Degree of social equity, living and working conditions, availability and access to good transport, social security, social services |
| Sexual | Corporeal hygiene, sexual practices, choice of partner, living conditions | Basic trust and respect, sexual education, social taboos, early childhood experiences | Degree of freedom and empowerment of women, gender equality |
| Biological | DNA, genetic comportment, physiology, homeostasis, gene–environment interactions, fetal development, metabolic conditions, physical condition | Nervous system, plasticity in underlying brain circuitry, neural substrates, psycho-neuro-immuno-endocrine functioning | Environmental conditions: presence or absence of plagues, viruses, parasites, predators, environmental changes, heat waves, availability of resources, natural disasters, sanitation |

BPS model helps us to understand the positive functioning and dysfunction of both individual and population health. The BPS model demonstrates the importance of the role of an individual's social context in the development and maintenance of health (Fig. 23.2); the BPS model also demonstrates that the health of the people is an important input in the productivity and flourishing of a society (Fig. 23.3).

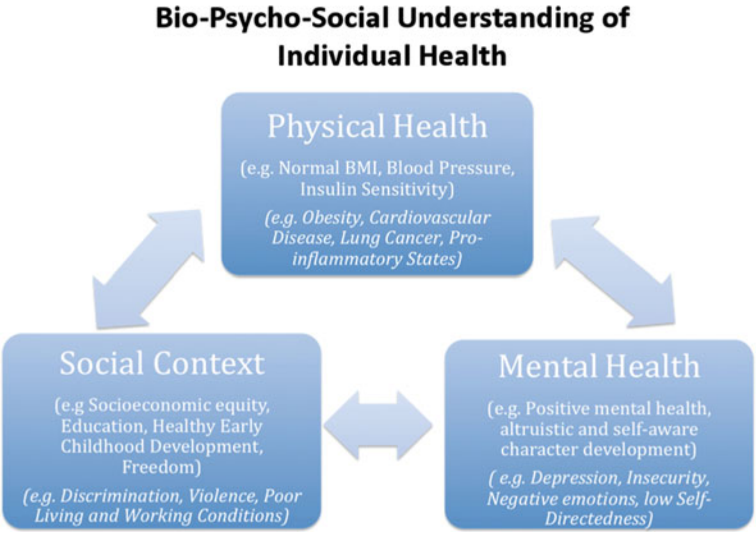


**Fig. 23.2** BPS approach to understanding the positive and *negative* feedback cycles in the development of individual health

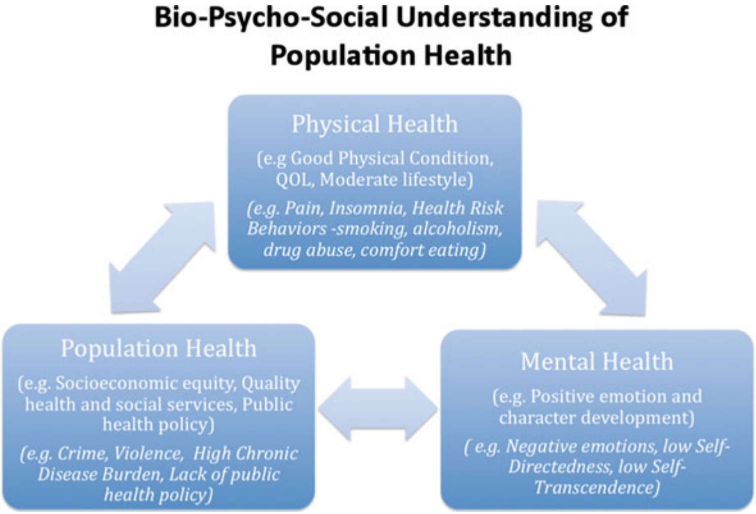


**Fig. 23.3** BPS approach to understanding the positive and *negative* feedback cycles in the development of population health

Understanding the complex interactions within a person and between the person and their social environment reveals the poverty of perspectives and theories that do not take into account the full range of human functioning and well-being.

Research shows that bio-psycho-social factors affect health by triggering bio-psycho-social stress responses. Psychosocial stress can affect physical health through interactions among the nervous, immune, and endocrine systems, as well as by influencing human behavior and lifestyle. Stress suppresses the immune system, which increases vulnerability to infections. Stress also contributes to cardiovascular disease, digestive disorders, and cancer (Reiche, 2004; Sheps, 2001). Depression is the single best predictor of subsequent cardiac events in those with coronary artery disease (Wassertheil-Smoller et al., 1996). Stress also leads to increased propensity for engaging in health risk behaviors, which contribute to physical illness, such as lung cancer from smoking, liver disease from drinking, and accidents from drinking and drug abuse (Marmot, 2007).

There are also reciprocal influences between the mental health of an individual and the health of a society. Social distress as measured by social inequity affects the mental health of individuals and can lead to increases in depression, life dissatisfaction, anxiety, and apathy, which in turn cause decreased motivation, efficiency, and productivity (Wilkinson, 2005). Psychosocial stress is the most common cause of sickness-related absences (Wilkinson, 2005).

Positive mental health contributes to improved quality of life and efficiency, as well as to society's effective functioning and to the stimulation of the economy (Herrman et al., 2008). Physical health also enables people to participate in society, with positive consequences for economic performance (Marmot, 2007).

The positive and negative feedback cycles influencing health make it clear that physical, mental, and social health cannot be separated and that we need to look at the system as a whole. Disparaging views of the human being as savage by nature are a serious obstacle to appreciating the full spectrum of human functioning and these feedback cycles.

## Strategies for Promoting Well-Being in Health Care

Policies and practices that support the full development of human health and well-being require that all concerned see beyond this nihilistic thinking. Social inequities in a population affect health at a micro and macro level, and we now have to consider how to take social action in order to promote health. Promoting well-being in health care happens within and outside the scope of medicine. Social conditions are usually, but not always, influenced by factors operating above and beyond the individual. The key to change is to encourage healthy lifestyles, growth in character development and self-awareness, and social equity and coherence through a multi-sector/multi-level approach. We can also apply the BPS determinants of health to our understanding of the function of human beings in their daily life in order to develop a framework to begin promoting population health.

## Biological Level: Medication, Cerebral Plasticity, Disease Control

Health can be improved at a biological level with policy and practice focused on preventive health care and increasing the accessibility of medicines and vaccinations. Increasing knowledge of the environmental factors affecting health, improving ecological awareness, and encouraging individuals and nations to engage in ecologically sustainable practices also benefit individual and population health (Marmot, 2007). Additionally, the protection of the environment and the conservation of natural resources are fundamental to a socio-ecological approach to health. Access to clean water is an essential provision. Lack of access to clean water is responsible for severe adverse health outcomes. Urban development efforts should focus on ensuring the availability of this key health asset for the population.

## Gender and Sexual Level: Hygiene, Information, Equal Rights

The WHO Global Burden of Disease Study identified sexual behavior as one of the six major causes of morbidity and mortality. Education on sexuality and safe sex practices is important to health. Since many parents and caregivers are not themselves educated properly, it is important for local governments and public schools to incorporate sexual education into their curriculum. Education should focus on helping people develop an understanding of their sexuality and safe sexual practices. Additionally, collective social action to develop policy that ensures the empowerment of woman to enjoy the same social freedoms as men is essential to the foundation of social health. This is fundamental to ensuring that women have healthy experiences as children and develop self-confidence and self-esteem as adults.

## Material Level: Lifestyle, Resourcefulness, Social Equity

People need the basic necessities of life, autonomy, and collective social action to give a voice in decision making processes in order to reduce social inequality and improve well-being (Marmot, 2007). Empowering the population through employment, policies to improve living and working conditions, and increased access to health care services and education will facilitate a greater distribution of resources across social sectors and provide people with the freedom to live the lives they value.

Improving local governance to increase the availability of resources and services such as welfare, public transportation, and childcare is a key to reducing the burden of disease and improving physical and mental well-being. There are numerous reasons for this. First, the accessibility and availability of services and resources reduce individual stress and decrease the tendency to develop addictive behaviors that are harmful to health. It also improves the individual's ability to develop a more balanced lifestyle, access higher quality food, and find personal time for self-care.

## Emotional Level: Attachment, Cooperative Behavior, and Social Relationships

A key determinant of psychological resilience is the balanced development of all three branches of character and positive emotion. Encouraging healthy early childhood development through the cultivation of intimate social bonds and exposure to safe enriching environments and positive sentiments will greatly contribute to long-term health and well-being (Marmot, 2007). Additional work in psychology should focus on helping patients develop positive emotion. In the treatment of patients with recurrent depression, work on positive emotions in addition to CBT alone lowered relapse and recurrence rates in 40 people with recurrent depression lasting 2 years (25% versus 80%) (Cloninger, 2006).

Improving policy, legislation, and local governance to protect people from discrimination and violence are essential for health. Greater physical comfort, safety, and security decrease anxiety among people and encourage cooperative behavior, which is important to the development of positive emotions and life satisfaction. Without cooperation and prosocial attitudes, human health and well-being are incomplete and transitory. Friendly and supportive international relationships are also important for population health. Governance and policy that promote strong social networks, as well as nonviolent and cooperative relationships between people also improve population health.

## Communication: Expression, Intellect, and Culture

An individual's ability to understand and express himself or herself is unique to humans and important to health. First, physicians depend on what people tell them about their experiences in order to begin to develop impressions and opinions (Engel, 1977). Additionally, effective psychologically therapeutic interventions often involve both moderate emotional expression and cognitive reappraisal. Cognitive Behavior Therapy (CBT) and various dynamic therapies are effective treatments for mental disorders. CBT augmented with exercises to develop awareness of positive emotions, mindfulness, or spiritual meaning further increases well-being (Cloninger, 2006). Additionally, encouraging increased awareness and appreciation of beauty, love, and life through art, culture, and positive philosophy helps reduce feelings of isolation and increases self-understanding (Cloninger, 2004).

Cultural efforts to encourage freedom of expression, an increased awareness of relevant social issues, the development of the arts, media targeted at increasing awareness of healthy lifestyles, and enrichment education will improve individual and population health on a global level.

## Spiritual Level: Temperance, Self-Awareness, and Nonviolence

There are a number of different ways to encourage growth in self-awareness. Many studies show the potential for meditation and relaxation techniques to help elevate thoughts and increase self-awareness. Two concrete exercises individuals can practice to grow in self-awareness include the "Silence of the Mind" meditation and "Union in Nature" (Cloninger, 2006). Additionally, structured explorations of one's own personality, cognitive states, and positive philosophy can help individuals gain greater awareness of their predispositions and unquestioned beliefs. Although this list is by no means comprehensive, it helps give an idea of the practical works that can be done to help individuals grow in self-awareness. As individuals grow in self-awareness, they are able to exert greater levels of self-restraint and habitual moderation concerning their appetites and passions. This in turn allows them to control unhealthy behaviors and positively influence their physical health. Social policies and community action to encourage spiritual tolerance and autonomy can contribute to the positive functioning of both individual and social health.

## Unity Level: Integration, Coherence, Multi-level, Multi-sector Action

Improving individual and public health requires action on the social determinants of health through non-health sectors, as well as through the conduct and organization of health care. The WHO Commission on the Social Determinants of Health identifies coherence as the key determinant to multi-level, multi-sector action on improving population health. Multiple social conditions and environments—including a person's home, work, school, neighborhood, and health care system—all expose individuals to different risk factors to health. Improving social well-being is a multi-stakeholder process involving cooperation among government and non-government organizations, civil society, trade unions, political parties, public health organizations, health professionals, educators, sociologists, anthropologists (Marmot, 2007), and service users and their families.

Additional goals to promote public health include the following:

1. Educating health care professionals about the relationship among physical, mental, and social health.
2. Developing and providing personal and professional educational resources, complementary therapies, and self-evaluation tools that help people develop growth in character development and self-awareness.

3. Reducing the relapse and onset of disorders by encouraging health care models that emphasize integrative, preventative, and person-centered care.
4. Demonstrating the effectiveness of integrative health care in clinical practice through both observation and evaluation using QOL, personality, and affect scales.

Clinical treatments and services, and population or public health strategies, each needs to consider the biological, psychological, and social determinants of health in order to influence population health and well-being.

## Conclusion

A rich body of evidence demonstrates that the healthy functioning of a human being and society depends largely on socially cooperative and nonviolent behavior. Exploring the bio-psycho-social determinants of health reveals a positive feedback cycle between the different domains and further challenges the idea that humans are savage and uncooperative by nature. The framework described in this chapter should prove useful in consolidating and finding new approaches to health care and public health that seek to foster the full development of human potential, whatever human nature may be.

## References

Blazer, D. (2005) *The Age of Melancholy: Major Depression and Its Social Origins*. New York: Taylor and Francis Group.

Cloninger, C. R. (2000) A practical way to diagnosis personality disorder: A proposal. *J Pers Disord*, 14, 99–108.

Cloninger, C. R. (2004) *Feeling Good: The Science of Well-Being*. New York: Oxford University Press, Inc.

Cloninger, C. R. (2006) The science of well-being: An integrated approach to mental health and its disorders. *World Psychiatry*, 5, 71–76.

Cloninger, C. R., Svrakic, D. M., & Przybeck, T. R. (1993) A psychobiological model of temperament and character. *Arch Gen Psychiatry*, 50, 975–990.

Cloninger, C. R., Svrakic, N. M., & Svrakic, D. M. (1997) Role of personality self-organization in development of mental order and disorder. *Dev Psychopathol*, 9, 881–906.

Davidson, R. J. (2004) Well-being and affective style: Neural substrates and biobehavioural correlates. *Philos Trans R Soc Lond B Biol Sci*, 359, 1395–1411.

Engel, G. L. (1977) The need for a new medical model: A challenge for biomedicine. *Science*, 196, 129–136.

Farmer, A., Mahmood, A., Redman, K., Harris, T., Sadler, S., & Mcguffin, P. (2003) A sib-pair study of the temperament and character inventory scales in major depression. *Arch Gen Psychiatry*, 60, 490–496.

Fava, G. A. & Sonino, N. (2008) The biopsychosocial model thirty years later. *Psychother Psychosom*, 77, 1–2.

Herrman, H., & Jané-Llopis, E. (2005) Mental health promotion in public health. *Promot Educ*, (Suppl 2), 42–47, 63, 69.

Herrman, H., Moodie, R., & Saxena, S. R. (2008) Mental health promotion. In: K. Heggenhougen & S. Quah (eds.), *International Encyclopedia of Public Health*, Vol. 4. San Diego, CA: Academic.

Hippocrates, translated by Mark John Schiefsky (2005) *Hippocrates on Ancient Medicine*, Boston: Brill, Inc.

Marmot, M. (2007) Achieving health equity: From root causes to fair outcomes. *Lancet*, 370, 1153–1163.

Marmot, M., Friel, S., Bell, R., et al. (2008) Commission on Social Determinants of Health. Closing the gap in a generation: health equity through action on the social determinants of health. *Lancet*, 372, 1661–1669.

Mittelmark, M. B., Puska, P., O'Byrne, D., & Tang, K. C. (2005) Health promotion: A sketch of the landscape. In: H. Herrman, S. Saxena, & R. Moodie (eds.), *Promoting Mental Health: Concepts, Emerging Evidence, Practice*, pp. 189–202. Geneva: World Health Organization.

Reiche, E. M., Nunes, S. O., & Morimoto, H. K. (2004) Stress, depression, the immune system, and cancer. *Lancet Oncol*, 5, 617–625.

Sheps, D. S. & Sheffield, D. (2001) Depression, anxiety, and the cardiovascular system: The cardiologist's perspective. *J Clin Psychiatry*, 62(Suppl 8), 12–16; discussion 17–18.

Solomon, G. F. (1987) Psychoneuroimmunology: Interactions between central nervous system and immune system. *J Neurosci Res*, 18, 1–9.

Velupillai, Y. N., Packard, C. J., Batty, G. D., Bezlyak, V., Burns, H., Cavanagh, J., Deans, K., Ford, I., Mcginty, A., Millar, K., Sattar, N., Shiels, P., & Tannahill, C. (2008) Psychological, social and biological determinants of ill health (pSoBid): Study protocol of a population-based study. *BMC Public Health*, 8, 126.

Wassertheil-Smoller, S., Applegate, W. B., Berge, K., Chang, C. J., Davis, B. R., Grimm, R., Kostis, J., Pressel, S., & Schron, E. (1996) Change in depression as a precursor of cardiovascular events. SHEP cooperative research group (Systolic Hypertension in the elderly). *Arch Intern Med*, 156, 553–561.

Wilkinson, R. G. (2005) *The Impact of Inequality: How to Make Sick Societies Healthier*. New York, NY: The New Press.

Wilkinson, R. & Pickett, K. (2009) *The Spirit Level: Why More Equal Societies Almost Always Do Better.* London: Allen Lane.

# Chapter 24
# Moving Beyond the Nature/Nurture Distinction: Promotion of Transdisciplinary Research

## (Overview of the Institute of Medicine Report on Genes, Behavior, and the Social Environment)

**Dan G. Blazer**

## Introduction

Some may wonder as to the relevance of a chapter on transdisciplinary research in a book devoted to "Man the Hunted: Sociality, Altruism, and Well-being." Though focused on a common theme, namely the evolution and nature of cooperation and "altruism" in social-living animals, the conference from which this volume is derived begs for such an approach. First, scholars from various backgrounds informed this topic with specific studies, both from primate and human studies, provided evidence of the primacy of cooperation. These studies ranged from observational to interventional and from observations of cooperative social activity to explorations of the neural mechanisms which underlie cooperation. Second, the premise of the conference itself is cooperation, and cooperation is something from which science at the advent of this new millennium requires. Science practiced in silos just does not work today.

The author of this chapter was the chair of an Institute of Medicine committee which addressed cooperation in science. Specifically, our task was to facilitate bridging one of the most well-known controversies in biological science—the nature/nurture controversy (Ridley, 2003). I will describe the background and the outcome of the deliberations of this conference below.

Great hope has emerged that the well-being of humankind will be enhanced by the genomic revolution. The most ardent supporters of this revolution even go so far as to implicitly suggest that genes alone determined our health, and the manipulation of genetic factors will be the royal road to well-being and increased life

---

The concept for this chapter is drawn extensively from the Institute of Medicine report: Hernandez LM, Blazer DG: Genes, Behavior, and the Social Environment: Moving Beyond the Nature/Nurture Debate. Washington, DC, The National Academies Press, 2006

D.G. Blazer (✉)
Departments of Psychiatry and Behavioral Sciences and Community & Family Medicine,
Duke University Medical Center, Durham, NC 27710, USA
e-mail: blaze001@mc.duke.edu

R.W. Sussman, C.R. Cloninger (eds.), *Origins of Altruism and Cooperation*,
Developments in Primatology: Progress and Prospects 36, DOI 10.1007/978-1-4419-9520-9_24,

expectancy. (Weissman, 1889; Nusslein-Volhard, 2006) Of course, most recognize that this deterministic focus upon genes alone ignores many of the advances in health and well-being over the past 100 years. (Ridley, 2003) Yet, how investigators are to study and how the public is to think about the integration of genes with factors such as behavior, the social environment, and even spirituality remain in large part unknown? In this presentation, I will provide an overview of the Institute of Medicine report, *Genes, Behavior, and the Social Environment* (Hernandez and Blazer, 2006).

## *Statement of Task*

In 2005, the National Institutes of Health, Office of Behavioral and Social Sciences Research, in conjunction with the National Human Genome Research Institute and the National Institute of General Medical Sciences, requested that the Institute of Medicine undertake a study to examine the state of the science on gene–environment interactions that affect health, with a focus on the social environment. The goal of this study was to identify approaches and strategies to strengthen the integration of social, behavioral, and genetic research and to consider the relevant training and infrastructure needs. In this chapter, I (as chair of the committee) will review the background and recommendations of this committee report "Genes, Behavior, and the Social Environment: Moving Beyond the Nature/Nurture Debate" (Hernandez and Blazer, 2006). Given the pregnant implications of the current conference on "Man the Hunted: Sociality, Altruism, and Well-being" this presentation may appear on the surface sterile. Nevertheless, I believe the findings and recommendations of the committee are most relevant to a scientific understanding of the important topics discussed at this conference.

## *Public Health Within the Context of Genes, Behavior, and the Social Environment*

During the past 20 years, great attention has been directed toward the Human Genome Project (International Human Genome Sequencing Consortium, 2001). The mapping of the genome and the identification of an ever-increasing number of genetic "markers" for either resistance or susceptibility to disease and effective versus not effective use of medications in individuals have opened the door for what many are describing as "personalized medicine." For example, complications from the use of Coumadin are among the most frequent causes of emergency room visits and hospitalizations. Some individuals can take Coumadin, a blood thinner, with few problems. Others, however, react with poor control and subsequent episodes of bleeding that are quite dangerous. We have learned that a genetic marker can identify individuals who exhibit a propensity for problems with Coumadin via a test that is relatively inexpensive (Gage et al., 2004).

The implementation of this test into routine clinical practice (for many general medical patients are taking Coumadin) could dramatically reduce the adverse effects from Coumadin, significantly increase the well-being of individuals taking the drug, and reduce medical costs. Yet, even a superficial examination of this finding assumes that social factors (such as educating clinicians) and behavioral factors (such as the willingness of clinicians to order these genetic test and the willingness of patients to accept the test, not to mention close monitoring of their Coumadin levels) are essential if this genomic advance is to be realized in clinical practice.

Prior to the genomic revolution, great strides were made in reducing diseases and improving the health and well-being of individuals and populations. Public health measures, such as sanitation, improved hygiene, and vaccines all lead to major reductions in mortality and morbidity (Turnock, 2001). Focus upon hazards in the workplace reduces injuries and leads to better health for workers (Institute of Medicine, 2003). In addition, much evidence has emerged which indicate that behavioral factors, such as smoking, diet, and alcohol use are among the most important determinants of health and well-being (Berkman and Kawachi, 2000). Finally, social factors such as socioeconomic status and social support are known to contribute significantly to the health and well-being of individuals (Blazer, 1982; Chapter 23, this volume).

In addition, we are gaining increased knowledge of the interaction of genetic and socio-environmental factors. For example, we have found "evidence of a gene-by-environment interaction, in which an individual's response to environmental insults is moderated by his or her genetic makeup" (Caspi et al., 2003). We know that tobacco use, obesity, and physical inactivity are the most preventable causes of morbidity and mortality in the United States. On the surface, these appear to be purely behavioral and therefore determined solely by the will of the individual. However, we have learned that some behaviors, such as smoking cessation, result in part from genetic factors (Sullivan and Kendler, 1999).

Even concepts such as altruism and spirituality involve genes and environment. In evolutionary biology, an organism is said to behave altruistically when its behavior benefits other organisms, at a cost to itself. The costs and benefits are measured in terms of *reproductive fitness* or expected number of offspring. This biological notion of altruism is not identical to the everyday concept. For most humans, an action would only be called "altruistic," if it was done with the conscious intention of helping another. Therefore, for humans, we might expect a gene–environment interaction to greatly influence the expression of altruism (Zalta, 2009).

Though the presence of a so-called "God gene" is hotly debated, there is little debate that spirituality is significantly influenced by hereditary predisposition. For example, Kirk, Eaves, and Marin found no strong correlations between self-transcendence and any measure of psychological or physical health (Kirk et al., 1999). In contrast, additive genetic effects were found to be important in influencing self-transcendence, with heritability estimates of 0.37 and 0.41 for men and women, respectively. Again, however, the environment can significantly influence genetic predisposition. For example, Alcoholic's Anonymous employs social and behavioral interventions, specifically the 12-step program. This program may very well augment the genetic predisposition to spirituality for an underlying predisposition to the spiritual definitely enhances the success of 12-step programs. Genes, behavior, and the social environment are intricately related and mutually dependent upon one another. The nature/nurture debate (Is it the gene or the environment?) is a debate beyond which we must move. It is both.

An ecological model provides the appropriate framework for assessing the impact on health by interactions among social, behavioral, and genetic factors. "An ecological model assumes that health and well-being are affected by interaction among multiple determinants including topology, behavior, and the environment. Interaction unfolds over the life course of individuals, families, and communities, and evidence is emerging that societal-level factors are critical to understanding and improving the health of the public" (Institute of Medicine, 2003).

## *The Social Environment*

Our committee, along with our National Institute of Health sponsors, defined social environment as the relationships among people both as individuals and in societies. The term was not designed in a way that included environmental conditions, such as global warming and toxic waste, even though these factors significantly impact human well-being. We chose to emphasize certain variables of the social environment that have high potential for research about interactions, both because there is a large body of evidence that examines the impact of these variables on health and because there exists well-established and well-accepted measures for the investigation of these variables. These variables include socioeconomic status, race/ethnicity, social networks/social support, and the psychosocial work environment. The influence of social and cultural variables on health must encompass dimensions of both time (that is, the impact may be more important and critical stages in the life course and must account for the effects of cumulative exposure) as well as place (multiple levels of exposure).

## *Genetic Factors*

Genetic factors include not only Mendelian patterns of disease inheritance but also the more common genetic susceptibility to disease as the consequence of the joint effects of many genes, each with small to moderate effects, and often with interaction among themselves and the environment. No discussion of genetic factors can dismiss the importance of epigenetic phenomena. Epigenesis originated as a term to describe the process in embryonic development that transforms the undifferentiated cells in newly fertilized eggs into a complex, multi-tissue organism (Jaenisch and Bird, 2003). Today, it is used to represent, in particular, the specific molecular mechanisms by which cells differentiate, age, change metabolic functions, or even transform, for example, from normal to cancerous cells. The most well-known mechanism for the epigenetic regulation of cell phenotypes is DNA methylation, which turns off a gene or genes' region (Jaenisch and Bird, 2003). Of importance for this report, environmental factors such as infection and diet (but possibly social factors as well) are known to affect gene methylation. Therefore, the environment can directly influence gene expression itself at the level of the gene, not just modify a predetermined expression of the gene.

### *Behavior*

Our use of the term "behavior" includes two components. First are observable behaviors that influence health, including smoking, drinking, drug use, diet, and exercise. Such factors are referred to as risk or protective factors. The second component includes certain psychological characteristics, such as cognitive and emotional function and resilience.

### *Interaction*

The complex interaction among genes, behavior, and the social environment requires work at many levels. First, as suggested above, a life-course perspective must be embraced. "As a concept, a life course is defined as a sequence of socially defined events and roles that the individual enacts over time" (Giele and Elder, 1998). "These events and roles do not necessarily proceed in a given sequence but rather constitute the sum total of the person's actual experience." Thus the concept of life course implies age-differentiated social phenomena distinct from uniform life-cycle states and the life span. Animal models are essential in understanding further how social systems regulate physiologic systems and genetic functions as well as vice versa. Understanding these complex interactions requires research designs and analyses that are statistically sophisticated, especially in the exploration of genetic environment interactions (see below).

## Transdisciplinary Research

Perhaps the most important recommendation made by our committee was that a new type of investigator would be needed in the future, an investigator trained in transdisciplinary methods. To facilitate a cohort of such investigators, a number of infrastructure supports would be required, including education and incentives as well as rewards.

Transdisciplinary research involves broadly constituted teams of researchers who work across disciplines in the development of emerging research questions which cannot be answered by traditional research approaches (Institute of Medicine, 2003). While interdisciplinary research focuses on answering a question of mutual concern to those of various disciplines, multidisciplinary research involves research on questions of both mutual and separate interests to participating investigators. In contrast, transdisciplinary research "implies the conception of research questions that transcend the individual departments or specialized knowledge bases because they are intended to solve research questions that are, by definition, beyond the purview of the individual disciplines" (Institute of Medicine, 2003). The practical implication of such an approach is that the disciplines will no longer function like "silos" that exists side-by-side, deeply rooted in their respective traditions. Rather, these disciplines will involve more broadly constituted and integrated "teams."

Our committee recognized, however, that developing teams of scientists who can engage in and conduct the necessary transdisciplinary research present several practical difficulties. For example, researchers from different disciplines must be able to understand and value one another's language, concepts, and methods. In addition, sources of data that support such transdisciplinary efforts must be developed and enhanced (for example, adding genetic markers to epidemiologic studies). Our preparation of investigators currently tends to force individuals into ever more restrictive and narrowly focused activities in contrast to the need of transdisciplinary investigations. In addition, faculty members within the institution's traditional departments do not have the knowledge and skill that are needed to engage in transdisciplinary research or teaching.

## Recommendations of the Committee

Our first recommendation (and a recommendation which we believe to be the most important) is that the National Institutes Health should develop requests for applications to study the impact on health of interactions among social, behavioral, and genetic factors with an emphasis upon their interactive pathways. To accomplish this task, genuine collaboration of social, behavioral, and genetic scientists in transdisciplinary teams is essential. Yet, this is an extremely broad task. To assist in narrowing this task, our committee recommended that key variables be the focus of our efforts in the near future. Key social variables recommended included educational attainment, income and wealth, occupational status, social networks/social support, and work conditions.

As with social variables, we have studied over many years a plethora of behavioral and psychological variables. Our committee suggested a focus upon the following: tobacco/alcohol/drug use, eating behavior, physical activity, temperament, perceived stress and coping (as distinguished from actual stressors in the environment), perceived social support (as distinguished from actual social support), emotional state, and motivation. Many behaviors in which individuals engage are risky or protective of health. Yet, these behaviors interact with genetic and social variables. For example, smoking clearly has an adverse effect upon health. Yet, we know that genetic factors contribute to the propensity to smoke (such as phenotypes related to nicotine addiction) and that social factors may contribute as well. For example, campaigns in the public media focusing upon the dangers of smoking have been shown to decrease the frequency of smoking.

A key factor in studying gene–environment interactions of risky health behaviors is intermediate phenotypes. Intermediate phenotypes are traits or outcome measures that mediate the effects of gene–environment influence on risky behaviors. These measures are more proximal to the biological determinants of the risky behaviors themselves, and therefore, they can be assessed with greater experimental control in human models. For example, when we consider tobacco use, laboratory-based intermediate phenotypes have included individual differences in the rewarding value and tolerance of nicotine, in cognitive and autonomic effects, and the effects of nicotine deprivation.

Key genetic variables (again a plethora of such variables are available) include DNA sequence variation, structural chromosomal changes, gene expression, epigenetic modifications, and downstream targets of gene expression. Most genes likely serve different functions at different times in different environments. For this reason, we must be able to measure and evaluate differential gene expression. To accomplish this task, we recommended that further development of technologies is necessary to study molecular systems that interact with social and behavioral variables. Therefore, researchers should use genomic, transcriptomic, proteomic, metabonomic, and other high-dimensional molecular approaches to discover new constellations of genetic factors, biomarkers, and mediating systems through which interactions with the social environment and behavior influence health.

To truly explore gene–behavior–social environment interactions, diverse groups and settings must be employed. Context or culture of course influences health outcomes. For example, the frequency of menopausal symptoms varies significantly across cultures. In addition, despite the dramatic similarity of the genome across the entire world, different subgroups may have different genetic backgrounds that can influence health. For example, Tay-Sachs disease is relatively common among Ashkenazi Jews (Merryweather-Clarke et al., 2000). In addition, for this research to be generalized, findings must be applicable beyond a small population. For this reason, the committee recommended that research efforts ensure an inclusion of diverse groups and settings. In addition, efforts should be made to ensure that the findings of these investigations are validated by replication in independent studies, translated to patient-oriented research, conducted and applied in the context of public health, and used to design preventive and therapeutic approaches.

Animal models provide an ideal opportunity for exploring gene–environment interactions. For example, animal models can be controlled, standardized, or manipulated more than human studies. They allow for invasive examination not possible in humans. The short reproductive cycles and life spans are invaluable for developmental studies. An example of such studies is the implementation of social isolation, which can be accomplished by housing animals individually instead of in small groups (McClintock et al., 2005). Such isolation has been used as a stressor. We know from epidemiologic studies of humans that social isolation is associated with increased morbidity and mortality. The committee therefore recommended that animal models be implemented to study the interactions among social, behavioral, and genetic factors and their interactive pathways.

When studying gene, behavioral, and social factors, an understanding of the interaction among these factors is critical. For example, the interaction of genotype with social/behavioral factors may occur in a number of ways. The impact of social/behavioral factors on disease onset may be modified by the direct influence of genotype on the social/behavioral risk factor (that is, the genotype increases the expression of the risk factor). A second possibility is that the genotype intervenes between social/behavioral risk factors and disease (that is, the genotype exacerbates or inhibits the effect of the risk factor). A third possibility is that the social/behavioral risk factor exacerbates the effect of the genotype upon the disease. A fourth possibility is that both the genotype and the risk factors are required to increase the risk for the disease. Finally, the genotype and risk factors each effects risk, such that the combined effects can be either additive or nonadditive.

Statistical tests have been used for decades to study interaction. Yet, these tests for interaction are dependent on the measurement scale used. For this reason, measurement scales should be chosen for these investigations based on a theoretical model for disease causation that is more closely tied to biology. The committee therefore recommended that studies should be based on interaction on a conceptual framework, and rather simply the testing of the statistical model and the scales used for assessment should be specified clearly. The statistical measure of interactions is complex and therefore should not be undertaken lightly.

As noted above, the most important recommendation of the committee, given the complexity of gene–behavioral–social interactions described above, is the necessity for training a new generation of investigators who are skilled in transdisciplinary investigation. Given the burgeoning investigations and findings across multiple relevant disciplines, disciplines which often progress in relative isolation from one another, the scientific training of young investigators is filled with many gaps. We recommended that specific training be developed in transdisciplinary investigation, not simply encouraging established investigators from existing disciplines to work on interdisciplinary teams.

Understanding how social, behavioral, and genetic factors interact to influence health is not a short-term effort. Understanding requires the following: collaborative, transdisciplinary investigation; investigations conducted in diverse groups and settings; comprehensive, predictive models and modeling strategies; investigative designs that can be used to test for interactions; new statistical software for implementing such tests; and a cadre of investigators trained in the conduct of transdisciplinary research.

## References

Berkman, L. & Kawachi, I. 2000. *Social Epidemiology*. New York: Oxford University Press.

Blazer, D. 1982. Social support and mortality in an elderly community population. *American Journal of Epidemiology*, 115, 684–694.

Caspi, A., Sugden, K., Moffitt, T., Taylor, A., Craig, I., Harrington, H., McClay, J., Mill, J., Martin, J., Braithwaite, A., & Poulton, R. 2003. Influence of life stress on depression: Moderation by a polymorphism in the 5-HTT gene. *Science*, 301, 386–389.

Gage, B., Eby, C., Milligan, P., Banet, G., Duncan, J., & Mcleod, H. 2004. Use of pharmacogenetics and clinical factors to predict the maintenance dose of warfarin. *Thrombocyte Haemostasis*, 91, 87–94.

Giele, J. & Elder, G. 1998. *Methods of Life Course Research: Qualitative and Quantitative Approaches*. New York: Sage.

Hernandez, L. & Blazer, D. 2006. *Genes, Behavior, and the Social Environment: Moving Beyond the Nature/Nurture Debate*. Washington, DC: The National Academies Press.

Institute of Medicine. 2003. *The Future of Public's Health*. Washington, DC: National Academies Press.

International Human Genome Sequencing Consortium. 2001. Initial sequencing and analysis of the human genome. *Nature*, 409, 860–921.

Jaenisch, R. & Bird, A. 2003. Epigenetic regulation of gene expression: How the genome integrates intrinsic and environmental signals. *Nature Genetics*, 33(Suppl), 245–254.

Kirk, K., Eaves, L., & Martin, N. 1999. Self transcendence as a measure of spirituality in a sample of older Australian adults. *Twins Research*, 2, 81–87.

McClintock, M., Conzen, S., Gehlert, S., Masi, C., & Olopade, F. 2005. Mammary cancer and social iteractions: Identifying multiple environments that regulate gene expression throughout the life span. *Journals of Gerontology:Series B*, 60B, 32–41.

Merryweather-Clarke, A., Pointon, J., Jounolle, A., Rochette, J., & Robson, K. 2000. Geography of HFC C282Y and H63D mutations. *Genetic Testing*, 4, 183–198.

Nusslein-Volhard, C. 2006. *Coming to Life: How Genes Drive Development,* Carlesbad, CA: Kales Press.

Ridley, M. 2003. *Nature via Nurture*. New York: Harper Collins.

Sullivan, P. & Kendler, K. 1999. The genetic epidemiology of smoking. *Nocotine and Tobacco Research*, 1(Suppl 2), S51–S57.

Turnock, B. 2001. *Public Health: What It Is and How It Works*. Gaithersburg, MD: Aspen Publishers.

Weissman, A. 1889. *Essays on Heredity*. London: Oxford University Press.

Zalta E. (ed.). 2009. *Biological Altruism: Stanford Encycopedia of Philosophy* [Online]. http://plato.stanford.edu/entries/altruism-biological/ [Accessed].

# Index

Note: The letters “f” and “t” refer to figures and tables in the text.

R.W. Sussman, C.R. Cloninger (eds.), *Origins of Altruism and Cooperation*,
Developments in Primatology: Progress and Prospects 36, DOI 10.1007/978-1-4419-9520-9,