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An Introduction to *The Evolution* of *Mind*

Why We Developed This Book

STEVEN W. GANGESTAD JEFFRY A. SIMPSON

In the history of ideas, Darwin's theory of evolution through natural selection stands as one of most awe inspiring. His ideas profoundly changed the way scientists understand and appreciate the biological world. As Theodosius Dobzhansky (1973) once quipped, ever since Darwin, "nothing in biology makes sense except in the light of evolution" (p. 125). Just as influential, however, have been the theory's implications for how we, as human beings, understand ourselves. According to modern evolutionary biology, modern-day *Homo sapiens* represent merely a pixel of a present-day snapshot of the recurrent stream of replication, variation, and selection that began over 3 billion years ago. This stream, which all humans are a part of, operates according to certain principles. And these principles can divulge a great deal about who we are.

Despite being a formative influence on the emerging science of psychology in the late 1800s, evolutionary biology did little to shape the social and behavioral sciences for nearly a century after Darwin's death. The ethologists Tinbergen, Lorenz, and von Frisch, of course, reminded psychologists that animals, including humans, were shaped by selection pressures to adapt to their natural environments and that, accordingly, much can be learned via careful observation of behavior in natural habitats. But ethological theory itself was not deeply informed by evolutionary biology at that point in time.

This fact was largely a reflection of the state of affairs within biology, not within psychology. For the first half of the 20th century, the major theoretical task in evolutionary biology was to complete the grand synthesis of Darwinism and Mendelism. Evolutionary genetics, in fact, enjoyed great progress during this period. With a few notable exceptions (e.g., Cole, 1954; Lack, 1966), however, evolutionary biologists had not turned their attention to developing broad theories of how selection might have shaped the phenotypes of organisms, including how organisms evolved to interact with both their physical environments and with one another.

When theorists eventually turned their attention to this task in the 1960s and 1970s, they discovered that many of the phenotypes of interest happened to be behavioral in nature. Examples included how organisms are shaped to relate to kin, how they are shaped to reproduce; the general nature of their lifecourses, how the sexes relate to one another, and how cooperation can evolve and be sustained. The optimality and game theoretic approaches developed during these decades quickly generated a multitude of new theories that remain foundational in evolutionary biology today, such as life history theory, parental investment theory, parent-offspring conflict theory, sperm competition theory, the concept of reciprocal altruism, optimal foraging theory, and sex allocation theory. In 1975, Edward O. Wilson's Sociobiology promised a "new synthesis" of the life and social sciences based on some of these new principles. Debates over precisely how these principles could be applied to understand human behavior quickly ensued. Within a decade, several promising alternative approaches were founded, including human behavioral ecology (e.g., Chagnon & Irons, 1979), gene-culture coevolutionary approaches (e.g., Boyd & Richerson, 1985), and evolutionary psychology (Tooby & Cosmides, 1989).

During the last two decades, the study of the evolutionary foundations of human nature has grown at an exponential rate. In fact, it is now a booming interdisciplinary scientific enterprise, one that sits at the cutting edge of the social and behavioral sciences.

Textbooks and handbooks often chronicle the emergence of new fields. Although not one textbook on evolutionary psychology was on the market a decade ago, today textbooks on human evolution abound. Within the past 10 years, a dozen new textbooks touting different evolutionary perspectives have appeared, including Buss's Evolutionary Psychology: The New Science of the Mind (1999), Gaulin and McBurney's Psychology: An Evolutionary Approach (2001), Cartwright's Evolution and Human Behavior (2000), Barrett, Dunbar, and Lycett's Human Evolutionary Psychology (2002), and Palmer and Palmer's Evolutionary Psychology: The Ultimate Origins of Human Behavior (2002), to name a few. These textbooks provide excellent introductions to the field and the major topics within it. In addition, several major handbooks have been or will soon be published, including edited volumes by Buss (2005), Crawford and Krebs (1998), and Dunbar and Barrett (2007).

Precisely because of the profound implications that evolutionary biology holds for understanding human nature, the new evolutionary behavioral sciences have also inspired popular press books. Authors such as Steven Pinker (*The Language Instinct*, 1994; *How the Mind Works*, 1997; *The Blank Slate*, 2003), Robert Wright (*The Moral Animal*, 1994), Frank Sulloway (*Born to Rebel*, 1996), Sarah Hrdy (*Mother Nature*, 1999), Geoffrey Miller (*The Mating Mind*, 2000), and Matt Ridley (*The Red Queen*, 1993; *The Origins of Virtue*, 1996; *Nature via Nurture*, 2003) have all written influential works. Moreover, Dawkin's *The Selfish Gene* (1976) and Dennett's *Darwin's Dangerous Idea* (1995) remain among the most widely read treatises on the foundations of evolutionary biology.

Needless to say, evolutionary approaches to understanding human behavior have also been criticized. Wilson's Sociobiology (1975), for example, was castigated by some evolutionary biologists, most notably Stephen Jay Gould and Richard Lewontin (1979). Evolutionary psychology has also been criticized for similar reasons. Some criticism expresses fear that evolutionary approaches serve right-wing agendas. Other criticism has been directed at the adaptationist approach in evolutionary biology (see Gould & Lewontin, 1979). The former criticisms hold little water; many evolutionary theorists, such as John Maynard Smith and Robert Trivers, publicly endorse liberal social and political views. Many of the latter criticisms regarding the adaptationist approach have been addressed (see Alcock, 2001, for a review). Thus, although human evolutionary behavioral science has hardly won over all critics, many behavioral scientists are open to hearing and learning more about the insights into human nature that evolutionary biology has to offer. As a result, the most important debates today do not center on whether evolutionary approaches can offer deeper insights into human nature and behavior, but on which approaches might offer the most significant insights. One purpose of this book is to foster effective clarification and resolution of the most important debates and controversies.

THEORETICAL APPROACHES IN HUMAN EVOLUTIONARY BEHAVIORAL SCIENCE

Four main perspectives can be identified in human evolutionary behavioral science (Laland & Brown, 2002). They include human sociobiology and three counterreactions to sociobiology that address genetic evolution—human evolutionary ecology, evolutionary psychology, and gene–culture coevolution. We briefly describe, compare, and contrast the major tenets of each approach below.

Human Sociobiology

Wilson's *Sociobiology* (1975) brought together many breakthroughs in evolutionary theory that occurred in the 1960s and 1970s, especially Hamilton's (1964) notion of inclusive fitness, the gene's-eye view championed by Hamilton (1964) and Williams (1966), life-history theory, four major theories introduced by Trivers (1971, 1972, 1974; Trivers & Willard, 1973), and the evolutionary economic strategy of modeling selection pressures on phenotypes through analysis of their fitness benefits and costs. The first six chapters of *Sociobiology* laid out these ideas. The remainder of the book applied them to the behavior of organisms within various taxa—with the final chapter focusing on humans. Shortly thereafter, Wilson (1978) published *On Human Nature*, which expanded the ideas sketched out in that final chapter on humans.

Perhaps the most lasting influence of Sociobiology was Wilson's (1975) declaration that a new evolutionary perspective on the behavior of animals had emerged, one that was based on the new "gene's-eye view" and rigorous modeling of selection pressures on behavioral phenotypes. The ideas presented in his first six chapters, followed by additional theoretical developments rooted in kindred evolutionary economic modeling (e.g., optimal foraging theory, sex allocation theory, evolutionary game theory) soon transformed the way biologists thought about and studied animal behavior. The focus of ethologists on naturalistic observation and the identification of behavioral "fixed action patterns" was replaced by the focus of behavioral ecologists on behavioral function in response to selection pressures, the approach that currently defines the study of animal behavior (see Krebs & Davies, 1997). With an intellectual heritage indebted to the ideas and perspective captured in Wilson's 1975 book, some current animal behavioral ecologists still refer to themselves as sociobiologists (e.g., Alcock, 2001), and a leading journal in the field is entitled Behavioral Ecology and Sociobiology.

Wilson's (1978) writings on human behavior, however, spawned few direct intellectual descendants of his approach. Most of his ideas were highly speculative and not well documented, especially with respect to humans. Much of his evidence was anecdotal, and he neglected to review and incorporate relevant theory and data from various fields in the social and behavioral sciences. To complicate matters, Wilson adopted a hereditarian stance; that is, he wrote of genes "for" particular behaviors, implying that behavior itself is inherited and relatively insensitive to environmental influences. For these reasons, most major approaches in human evolutionary behavioral science today fashion themselves as reactions largely *against* sociobiology.

Human Behavioral Ecology

By the 1970s, several anthropologists had become attracted to new adaptationist ideas in evolutionary biology. In addition to primatologists such as Irven DeVore (who worked at Harvard with Wilson and Trivers) and Jane Lancaster, the individuals included Napoleon Chagnon, William Irons, and Kristen Hawkes. Anthropologists were struck by the variability of behavior across cultures. People in different groups eat different foods, spend differing amounts of time hunting or fishing, have different customs involving sexual relations and marriage, divide tasks between men and women differently, and raise children differently. Wilson's hereditarian sociobiological approach failed to offer sufficient explanations for this variability. The emerging animal behavioral ecology approach did, however. Behavioral ecologists wanted to understand differences in behavior across species as different adaptive solutions to problems posed by the varying ecologies in which different species reside. They did so by modeling and measuring selection on phenotypes imposed by particular local ecologies. Human behavioral ecologists (also known as evolutionary or Darwinian anthropologists) began to apply this approach to account for variation within and between human populations. In different ecological settings, different behavioral strategies for tasks such as foraging, mating, parental investment, and childrearing were found to optimize reproductive success (e.g., Smith & Winterhalder, 1992). Accordingly, behavioral ecologists wanted to know whether actual variations in these domains both within and between different cultures reflected variations in optimal strategies.

To address these questions, human behavioral ecologists developed theoretical tools and research strategies similar to those used by animal behavioral ecologists. Specifically, they developed quantitative models to identify which kinds of behavior tend to be optimal in promoting reproductive fitness within a given ecology. For instance, what allocation of time to hunting in a particular group tends to maximize net calorie gain? To derive optima when testing these models, researchers must estimate parameters within the model with actual data, such as the rate of return per unit time as a function of hunting, gathering roots, picking fruits, and so on. In some instances, this might include estimating the rate of actual reproduction as a function of a particular behavior. Human behavioral ecologists then measure actual performance (e.g., the actual amount of time spent hunting) and compare it to the estimated optimum. If a discrepancy exists, they usually refine the model by taking into account benefits or costs not specified in the initial optimality model, such as considering the benefits of obtaining mates through hunting success in addition to the benefits of energy capture.

Human behavioral ecologists seldom focus on the proximate mechanisms through which people make optima decisions. In this regard, they are similar to animal behavioral ecologists. Empirical success reflects understanding the function of a behavior in terms of a rigorous selection model. Precisely how an animal achieves optimal behavior through a psychological process tends to be of little concern to most behavioral ecologists. Instead, human behavioral ecologists assume that individuals in different groups behave differently because they facultatively, flexibly, and adaptively adjust their behavior in response to the particular contingencies imposed by certain environments. In that sense, they differ from most animal behavioral ecologists. Although animal behavioral ecologists recognize that individuals in species may have evolved to enact different strategies in different circumstances (e.g., to adjust clutch size in response to changes in resource abundance), cross-species differences are typically presumed to reflect differences in gene pools. Evolutionary psychologists, on the other hand, seek to specify the precise proximate psychological mechanisms through which individuals facultatively adjust their behavior.

Evolutionary Psychology

In the late 1980s, two synergistic events led to the emergence of what is now known as evolutionary psychology. First, anthropologist Donald Symons (1987, 1990) and the team of anthropologist John Tooby and psychologist Leda Cosmides critiqued the "adaptivist" orientation in human behavioral ecology and claimed that a truly adaptationist approach was needed. Second, Tooby and Cosmides (1989, 1990, 1992) developed a metatheory for an adaptationist approach.

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Darwinism, Symons (1987) argued, offers a historical explanation for the evolution of phenotypic traits. Some of these traits, namely, specific adaptations, were favored by natural selection for their reproductive benefits. Other traits, called "by-products," were not directly selected, but were incidental effects of selection for other adaptive features. A Darwinian approach applied to understanding human behavior, therefore, must shed light on the nature of adaptations that were recurrently favored in ancestral environments, as evidenced by their phenotypic design. Human behavioral ecologists, Symons charged, do not study adaptations. Rather, they study adaptiveness; their approach asks whether behaviors themselves (e.g., polyandry, bridewealth, matrilineal inheritance) are adaptive. But behaviors themselves, Symons argued, are not aspects of phenotypic design; they are merely outputs of design that interact with specific environmental inputs. Some behaviors may be adaptive but are not the product of actual adaptations. Behaviors that are not adaptive but are the product of adaptations may be fairly common (Tooby & Cosmides, 1990).

Symons (1987) illustrated the difference between adaptiveness and adaptation with a familiar example, taste preferences. People prefer foods high in sugar and fat. These preferences most likely reflect adaptations to a hunter-gatherer existence in which calories were limited and humans had to be motivated to find and consume energy-rich foods. In modern societies, of course, calories are not restricted and, hence, these preferences contribute to unhealthy, maladaptive dietary habits. An adaptationist approach asks whether the preferences themselves were selected historically and, if so, for what benefits? An adaptivist approach, by comparison, focuses only on whether the behavior itself is *currently* adaptive. The former approach is truly Darwinian, according to Symons; the latter approach is not.

Tooby and Cosmides (1990, 1992) then proposed a specific version of psychological adaptationism, which has become the primary approach identified with evolutionary psychology. Psychological adaptations can be described at multiple levels of analysis. One can, for instance, ask what brain features could have been selected to give rise to particular forms of adaptive behavior. Cosmides and Tooby suggested that the most useful level of description from a functional perspective is the *cognitive* one. This level addresses questions about *which* cues in ancestral environments (i.e., which recurrent cues in the environments in which the adaptation was selected) are processed to generate *which* specific cognitive, emotional, or behavioral responses. Precise description should specify the particular computational procedures (or "Darwinian algorithms") that mediate information available in the environment as it leads to the response. Cosmides's (1989) "cheater detection algorithm" is one paradigmatic example of how theories about psychological adaptations can be derived, developed, and tested.

Evolutionary psychologists also focus on "adaptive problems," circumstances in ancestral environments in which an adaptation arose and for which the adaptation offers a solution. Taste preferences for sugar and fat, for example, solved the adaptive problem to obtain and consume energyrich food sources. Adaptive problems, therefore, are a common way in which evolutionary psychologists discuss ancestral (rather than current) selection pressures. Adaptive problems in past environments should have been numerous (problems associated with foraging, mating, kin recognition, alliance formation, etc.). Different problems should have demanded different solutions. According to Tooby and Cosmides (1992), a "general problem solver" cannot proficiently solve different kinds of problems. Accordingly, most evolutionary psychologists believe that psychological adaptations are functionally specialized in nature and diverse in number, each one having been designed to solve a particular ancestral adaptive problem. In the parlance of Tooby and Cosmides, an adaptationist approach anticipates that psychological architecture should be characterized by "massive modularity." In other words, the mind should have evolved to have many specialized information-processing procedures (algorithms), each one dedicated to detecting and solving a particular adaptive problem.

In the early 1990s, debates between human behavioral ecologists and evolutionary psychologists began. More recently, the evolutionary psychology approach has also been criticized by developmental scientists. Before discussing these debates, we turn to the third major response to sociobiology, the gene–culture coevolutionary approach.

The Gene-Culture Coevolutionary Approach

In his widely-acclaimed book *The Selfish Gene*, Richard Dawkins (1976) proposed that just as genes evolve via differential replication, ideas also undergo a Darwinian-like selection process. Ideas are passed from individual to individual, from one mind to another. Some ideas, however, more effectively "replicate" themselves in new minds (i.e., they are more effectively transmitted across individuals), spreading rapidly and becoming popular. Dawkins coined the term "meme" (shortened from *mimeme*, the Greek root of "imitation") to refer to the unit of replication in the evolution of ideas. These notions gave rise to the science of memetics, which examines the processes through which memes spread and are maintained. The differen-

tial spread of ideas, practices, and norms, according to this viewpoint, explains cultural evolution.

According to this perspective, selection operates on two systems of "inherited" information: one system based on the replication of genes (genetic evolution), and the other based on the replication of ideas (cultural evolution). In classic work, Boyd and Richerson (1985) have shown that population genetic mathematical models developed for genetic evolution also model parallel processes of cultural evolution. This perspective is called *dual inheritance theory*.

The two systems of inheritance, however, do not evolve independently. Lumsden and Wilson (1981) and Cavilli-Svorza and Feldman (1981) recognized that the way in which cultural information is transmitted and evolves depends on human development and learning, with genes playing a role in each. Genetic evolution, therefore, affects cultural evolution. But cultural evolution can also affect genetic evolution, in that cultural innovation changes the selective environments of genes, stimulating genetic evolution. Cavilli-Svorza and Feldman labeled this approach *gene–culture coevolutionary theory*, a term now applied to other major theories within this approach (e.g., Boyd & Richerson, 1985; see also Laland & Brown, 2002).

Gene–culture evolutionary models have several interesting implications. First, they predict that some behaviors or beliefs selected against at the genetic level can be strongly culturally selected and, hence, spread. Because of this process, "maladaptive" behavior or beliefs can and do culturally evolve. One example is the common belief that effective birth control should be used to regulate and suppress fertility. At a superficial level, this observation appears to be similar to the claim of evolutionary psychologists that, in the modern world, some behaviors may be maladaptive. At a deeper level, however, it is very different. Evolutionary psychologists contend that maladaptive behavior often is a result of modern environments not matching ancestral ones; in ancestral environments, currently maladaptive behaviors (e.g., eating energy-rich foods) would have been adaptive. Gene–culture coevolutionary theorists, in contrast, contend that some behaviors or beliefs that *are not and would never have been adaptive* (e.g., using effective birth control) may nonetheless evolve via cultural selection.

Second, transmission processes may cause group practices that have evolved through cultural selection to persist even when substantial changes in the environment are operating on *genetic* variants. This possibility is inconsistent with most human behavioral ecology approaches. Strong forms of behavior ecology, for instance, claim that changes in behaviors that are adaptive in certain ecologies should *produce* behavioral change. Third, cultural evolution can operate via group selection. Williams (1966) argued that only under highly restrictive conditions should genetically based adaptations evolve if they are good for the group but detrimental to individual fitness (e.g., the tendency to warn others about a predator, calling perhaps lethal attention to oneself). The rate at which groups become extinct would have to be substantial to cause group selection on genetic variation between groups to counteract selection on individuals to act in their best self-interest within groups (cf. Sober & Wilson, 1998). Boyd and Richerson (1985) suggest that group selection may, however, operate to cause *cultural* evolution. Accordingly, cultural selection may create and maintain substantial variation across groups relative to within-group variation due to enforcement of and conformity to norms or tendencies to copy others. The differential success of groups, then, may cause substantial "spread" of cultural practices that foster group success if successful groups produce descendant splinter groups that adopt similar practices.

MAJOR DEBATES IN HUMAN EVOLUTIONARY BEHAVIORAL SCIENCE

The Adaptationist versus Adaptivist Debates

Following major critiques by Symons (1987, 1990) and Tooby and Cosmides (1990, 1992), the behavioral ecologists responded. A vigorous debate—known as the evolutionary anthropology versus evolutionary psychology debate—ensued. Indeed, one entire issue of the journal *Ethology and Sociobiology* (1990) was dedicated to it.

This debate centered on several questions and issues. First, what is the appropriate level of analysis for studying the outcomes of evolutionary processes? Evolutionary psychologists argued it should be psychological adaptations. Evolutionary anthropologists, on the other hand, defended their focus on behavior. Behaviors do, of course, qualify as "phenotypes" of organisms, and they are subjected to selection pressures. Although psychological adaptationary anthropologists argued that there are advantages to keeping description at the level of direct observation rather than risking incorrect inferences about unseen, underlying psychological adaptations.

Second, what is the nature of psychological outcomes produced by selection? Evolutionary psychologists argued that selection should have produced many specialized psychological adaptations, each designed to solve an important and specific ancestral problem. In addition, these adaptations should be virtually universal. Behavioral ecologists, in contrast, accentuated the flexibility of human behavior. However, they typically did not try to specify or study the psychological mechanisms responsible for generating different behaviors, which is central to the mission of evolutionary psychology. Behavioral ecologists emphasized the ability of humans to generate novel solutions to adaptive problems, which they believe casts doubt on evolutionary psychologists' assumptions that adaptations are modular and specialized.

Third, is there any utility to examining *current* fitness outcomes or adaptiveness to test evolutionary theories? Evolutionary psychologists have argued that there is not, stating that selection relevant to understanding current adaptations and behavior has already occurred in our ancestral past. Current adaptiveness (or selection) is irrelevant (Thornhill, 1997). Organisms ought to be viewed as "adaptation executers," not "fitness maximizers." Historically shaped adaptations that guide current behavior, whether adaptive or not, can be inferred by examining the design of organisms today. Behavioral ecologists have countered this point by contending that evolutionary psychologists assume that modern environments have changed in crucial ways from ancestral environments. However, current environments may not have changed as much as some evolutionary psychologists believe, particularly in the more traditional cultures that behavioral ecologists often study.

Fourth, what should explanations of the evolution of human behavior look like? Evolutionary psychologists have argued that these explanations should focus on the specific kinds of adaptive problems in ancestral environments that current adaptations were designed to solve. Human behavioral ecologists have countered that evolutionary psychologists' treatment of selection pressures tends to be oversimplified. Organisms undoubtedly face trade-offs when solving adaptive problems. The effort put into solving one problem may detract from effort that could be put into solving other problems. As a result, according to behavioral ecologists, organisms *are* selected to maximize fitness, at least within the constraints of specific trade-offs. In so doing, organisms must compromise solutions to any one adaptive problem. Human behavioral ecologists also have claimed that only through explicit optimality modeling can one appreciate how organisms are shaped by selection. Evolutionary psychologists, they have noted, rarely use mathematical optimality modeling to test their speculations.

During these debates, each side has occasionally caricatured the other in an overly critical light, or has presented an oversimplified, monolithic view of the other's positions. Many human behavioral ecologists, for instance, recognize that modern environments are different in significant ways from ancestral ones, meaning that some adaptations that are "mismatched" to current environments could be the source of certain maladaptive behaviors (e.g., Smith, Borgerhoff Mulder, & Hill, 2001). Some behavioral ecologists also acknowledge specialized design in certain domains (e.g., Kaplan, Hill, Lancaster, & Hurtado, 2000). By the same token, some evolutionary psychologists not only recognize but have also written about human capacities to innovate, although most have claimed that these capacities are adaptations specialized for innovation per se (e.g., Tooby & Cosmides, 2000). Other evolutionary psychologists have also written on how humans should respond "flexibly" to different ecologies, resulting in the sort of ecology-dependent variation that behavioral ecologists emphasize (e.g., Gangestad & Simpson, 2000). Still other evolutionary psychologists have started to employ optimality and game theoretical models, though most note that the selection pressures being modeled are relevant to explaining current adaptations shaped by similar ancestral selection pressures (see DeScioli & Kurzban, Chapter 13, this volume; Kaplan & Gangestad, Chapter 12, this volume). Attempts to resolve these debates are likely to proceed more quickly and in more fruitful directions if participants appreciate both the subtleties and the variations that exist within different theoretical vantage points.

Tensions with Gene-Culture Coevolutionary Theory

Whereas debates between behavioral ecologists and evolutionary psychologists have at times been vociferous, gene–culture coevolutionary theorists have more quietly criticized other approaches. These theorists contend that practices, beliefs, and norms can and do persist via cultural selection despite significant changes in local ecologies. Contrary to the expectations of behavioral ecologists, these components of culture may not track ecology (see Richerson & Boyd, 2005). Moreover, although evolutionary psychologists acknowledge that transmission of information and cultural practices are important evolved outcomes in humans, gene–culture coevolutionary theorists complain that most evolutionary psychologists do not sufficiently recognize either the extent to which cultural transmission and selection can generate maladaptive behaviors or the extent to which culture itself affects genetic selection.

Proponents of other perspectives have critiqued gene-culture coevolutionary approaches as well. Cultural inheritance does not proceed along distinct lineages, as genetic evolution does; that is, ideas are not replicated in the same way that genes are; rather, they are repeatedly reconstructed in the mind of each individual (Sperber, 1996). The units of cultural inheritance, therefore, are not easy to define. Variants of new ideas do not arise through a random process, such as mutation; rather, they may emerge through systematic processes (e.g., creative innovation); therefore, cultural evolution does not obey the same principles that genetic evolution does. To their credit, Boyd and Richerson (1985) have emphasized many differences between genetic and cultural evolution in their coevolutionary model. The critical issue is not whether differences between cultural and genetic evolution exist; they do (see Laland & Brown, 2002). The critical issue is what implications these differences have for understanding how each "evolutionary process" impacts human perceptions and behavior.

Critiques of Evolutionary Psychology within Psychology

As evolutionary psychology has gained prominence within psychology, some psychologists and psychologically minded philosophers have questioned some of its foundations and core assumptions. One set of criticisms has come from neurobiologists, developmental neuropsychologists, and philosophers, who argue that the assumption of "massive modularity" is untenable. According to this critique, evolutionary psychologists should expect brain maturation to be precisely programmed by genetic information needed to yield the many postulated Darwinian modules. In addition, many "modules" should be established early in life. Advances in developmental neurobiology, however, indicate that precise genetic programming does not characterize brain development. Instead, interactions with the physical and social world shape development of neural areas, and these effects persist for prolonged periods of time, often through adolescence. Higher cortical areas-those that integrate and organize information to create complex representations of the world and then dictate basic information processing-are characterized by prolonged, environmentally contingent development. The general picture emerging from developmental neurobiology, therefore, is one in which how humans process information is constructed through prolonged interactions with the physical and social world, not precise "prewired" programming (see Quartz & Sejnowski, 2002). In fact, Buller (2005) recently concluded that the basic neural adaptation of higher cortical regions is "plasticity"—the ability to adapt to the specific world in which one develops.

A related set of criticisms has come from developmental systems theorists (e.g., Oyama, Griffiths, & Gray, 2001), who claim that evolutionary psychology is grounded on naive and misleading views of how development actually occurs. Development transpires through interactions between elements that comprise a "developmental system," some of which emerge as development proceeds (maternal environments, intracellular entities, environmental interactions with the world that influence gene expression, etc.). The outcomes of a system depend on all of its elements, whose effects are not only additive but may also be interactive. Importantly, no single set of developmental elements is privileged. Thus, according to this view, it is incorrect to conceive of genes as "blueprints" that act as master plans for development and then orchestrate it. It is also incorrect to believe that orchestration of development by genetic "blueprints" leads to specific developmental outcomes that are "prespecified" by genes. Developmental processes are much more dynamic and highly epigenetic; the introduction of new environmental influences can sometimes generate unexpected outcomes that cannot be anticipated from the selective history of an organism.

Selective history, therefore, cannot serve as a complete explanation of evolved outcomes. Selection does not generate variants; it selects between existing variants. Variation is introduced through alterations in developmental processes. As a result, a complete understanding of how a given outcome evolved requires more sophisticated developmental science, which many evolutionary psychologists seem to ignore (see Lickliter & Honeycutt, 2003).

Evolutionary psychologists have, of course, addressed these criticisms. They have argued that an adaptation does not imply that development is programmed directly by genes. Much reliable information in the world guides development down adaptive trajectories. Genes may in fact affect developmental outcomes by leading people to be sensitive to particular information in the world, thereby exerting their effects through epigenetic developmental processes. The adaptive design that results from selection for these outcomes and associated developmental processes still fits with biologists' notion of what an adaptation is. Accordingly, the facts that neural development is not precisely programmed, and that it occurs over extended periods of time do not necessarily invalidate many evolutionary psychologists' claims about adaptations. Though maladaptive developmental outcomes can be produced by novel environments, selection usually shapes developmental processes toward adaptive outcomes in the developmental environments most commonly experienced by the population under selection. Indeed, the fact that many human psychological universals exist suggests that development typically does lead to specific robust outcomes, regardless of the processes through which those developmental outcomes are achieved.

THE HISTORY AND STRUCTURE OF THIS BOOK

Human evolutionary behavioral science is still undergoing a formative process. Several metatheories and methodologies have been put forward. Many paradigmatic exemplars of how these metatheories and methodologies can and should be applied to investigate and explain myriad human preferences and behaviors now exist. During the growth of a science, these paradigmatic exemplars—success stories—begin to anchor new approaches (Kuhn, 1962). Over time, however, critical self-evaluation, debate, and discussion start to shape or revise explicit assumptions that are necessary to, and still coherent with, the metatheories developed to explain certain phenomena. This process of critical evaluation does not reflect that a field is undergoing a "crisis" (Kuhn, 1962) or "degeneration" (Lakatos, 1970). Rather, it is part of normal, progressive science.

This book is intended to foster this process and, we hope, nudge human evolutionary science in fruitful directions. As is evident from our brief history of the field, several pressing issues involving the nature and study of human behavior remain matters of heated debate. Some of these fundamental issues arise from the fact that different theoretical and methodological approaches for studying evolution and human behavior exist—human behavioral ecology, evolutionary psychology, and gene–culture coevolutionary approaches. Although these approaches might be integrated, they have not been well-synthesized to this point. Other fundamental debates have centered on critiques from the developmental sciences. Still others involve specific proposals about certain core facets of human evolution (e.g., the nature of culture, the role of group selection, the evolution of human intelligence, the features of mating systems that distinguish humans from other species).

When planning this book, we identified 12 fundamental controversies. We then formulated each controversial issue in the form of a general question. We asked three to six major theoretical and empirical contributors to the study of evolution and human behavior to address each question in a short essay (approximately 2,000 words). Thus, authors had to focus on only a few aspects of the pertinent issues, which were of their choosing and defining, and were told that they did not need to answer each question fully.

When choosing contributors, we attempted to represent multiple perspectives, identifying authors who had expressed their views on a given topic or issue in earlier writings. Thus, we explicitly tried to solicit a diverse set of viewpoints, each one offered by a highly regarded expert in his or her specific field. Authors were also asked to limit their references, choosing exemplars of important points or principles. In most cases, individual authors were asked to address a single question. In cases in which certain authors were particularly well-known for holding views on multiple issues, we requested more than one chapter.

The 12 fundamental issues that we identified fall into three broad categories:

Methodological Issues

Four major issues center on the utility of using particular methodologies to study human behavior from an evolutionary perspective:

- 1. What methodologies can or should be used to reconstruct the evolution of the human mind?
- 2. What is the utility of tracking current fitness outcomes?
- 3. How is it useful to understand our closest ancestors (other primates) to comprehend human evolutionary outcomes?
- 4. What is the proper role of examining costs and benefits of behaviors or using quantitative modeling with respect to evolutionary outcomes?

Although all of these issues address the utility of applying different methodologies, different answers are likely to reflect different theoretical or metatheoretical assumptions. Indeed, as the reader will see, specific theoretical assumptions tend to be closely aligned with views about the utility of certain methodological approaches.

Metatheoretical Issues

Three issues involve metatheoretical themes:

- 5. Should the mind or psychological functions be thought of as modular and, if so, in what specific ways?
- 6. What are the implications of the developmental systems perspective—the idea that entire developmental systems, not simply genes, are targets of selection—for advancing our understanding of psychological adaptations?
- 7. What role, if any, did group selection assume in human evolution?

Issues Pertaining to Important Evolutionary Outcomes

Five issues reflect current debates over key evolutionary outcomes:

- 8. What major changes in selection pressures drove human evolution and led humans to be distinct from our closest ancestors?
- 9. What evolutionary processes contributed to the evolution of large brains in humans?
- 10. What is the significance of general abstractive abilities in understanding the evolution of humans?
- 11. How should culture be understood from an evolutionary perspective?
- 12. What are the most important features of hominid mating systems that have shaped how women and men relate to each other?

Admittedly, our division of questions and issues into these three categories is somewhat arbitrary. As mentioned earlier, many methodological issues are closely related to specific metatheoretical positions or assumptions. Answers to one question or issue (e.g., the role of understanding close ancestors) may be informed by views on other, key evolutionary outcomes in the hominid line. Similarly, whereas views of group selection might be more theoretical than metatheoretical, views on the role of culture might be more metatheoretical than theoretical. The organization of this book, therefore, is partly pragmatic.

We solicited and assembled this collection of essays to facilitate critical self-evaluation and to promote greater synthesis across the human evolutionary behavioral sciences. To date, debates have often resulted in greater polarization of viewpoints rather than integration or synthesis. We did not dictate how authors expressed their views on particular questions or issues. Close comparison of individual essays may reveal some polarization or entrenched views. We reasoned, however, that greater self-evaluation and synthesis might be fostered in two ways. First, by being able to compare and contrast specific positions directly, readers can discern for themselves where lingering questions and issues remain in major debates and perhaps new ways in which they might be resolved. Second, we (the editors) provide an integrative capstone chapter at the conclusion of the volume. Admittedly, this final chapter reflects some of our own views on where consensus may or may not be emerging with regard to certain questions and issues, points where important debate remains, and possible ways of clarifying or resolving certain debates. Though we tried not to express our personal views on various issues, we acknowledge that our own theoretical and empirical perspectives influenced how we addressed different responses each question/issue.

WHO SHOULD READ THIS BOOK

Several audiences should find this book particularly interesting. First, anyone who is interested in understanding the broad field of human evolutionary behavioral science—whether professionals, graduate students, or interested laypersons—will learn a great deal from this volume. Our primary intention was not to create a book that introduces major issues, perspectives, and assumptions in the human evolutionary behavioral sciences; several textbooks and primers already serve that function. This book attempts to be dialectical, describing, comparing, and contrasting different theoretical and metatheoretical views on important issues presented by respected scholars from different disciplines. Readers will learn much about how proponents of different perspectives think, and the different viewpoints can be directly compared and contrasted.

Second, we hope that this volume will also be read by persons who are invested in the future of human evolutionary behavioral science, those on whom the future of the field rests. Although we hope that it will be read and discussed by major scholars in the field, we also hope that it will reach graduate students and advanced undergraduates who are interested in evolutionary behavioral science, particularly those in the disciplines of psychology, biology, and anthropology. If this book succeeds at its primary task, it will lead scholars and students to gain a deeper appreciation of other views and perspectives, to understand the core assumptions and foundations of their own disciplines better, and to develop a clearer and more detailed "road map" outlining where the field needs to head in the future. In summary, the function of this book is to *provoke* critical analysis and *stimulate* new and creative thinking. Enjoy the intellectual ride.

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Cultural Adaptation and Maladaptation: Of Kayaks and Commissars

Robert Boyd Peter J. Richerson

Humans are an oddly contradictory species. On the one hand, we are spectacularly adaptable. Our species occupies a wider range of habitats, utilizes a much greater range of resources, and lives in a more diverse range of social systems than any other animal species. We constitute a veritable adaptive radiation, albeit one without any speciation. For better or worse, our ability to convert matter and energy into people in almost every terrestrial habitat has made us the earth's dominant species. At the same time, humans engage in spectacularly maladaptive behaviors. We take dangerous drugs, risk life and limb to reach mountain summits, restrict our fertility to attain economic and professional success, and march off to war to defend God or liberty or nation. How can it be that we are both so clever and so stupid?

In evolutionary psychology, the usual answer to the first part of the question is that we are talented adaptors, because we are so smart. Our brains are powered by an array of content-rich mental modules that enable us to respond adaptively to a much wider range of contingencies than any other species. The answer to the second part of the question is that we

behave maladaptively because these modules are tuned to Pleistocene foodforaging environments and sometimes misfire in the very different environments of the present.

It is likely that people are smarter than the average bear (or primate), and that formerly adaptive predispositions sometimes cause us to do peculiar things. However, we do not think that these factors are the whole, or even the most important explanations, of either our success or our peculiarities. Instead, we think that culture is the key to our cleverness and our stupidities. Humans are much better at learning from others than any other animal. This ability is a powerful adaptive mechanism, because it allows populations of humans to gradually accumulate massive amounts of information about technology, ecology, and institutions over generations—much more than any individual human could invent on his or her own. However, it comes with a built-in trade-off: Culture provides a rich source of adaptive information, but to use it efficiently, individuals have to be "credulous," mainly adopting the beliefs of those around them. This credulity allows maladaptive beliefs to spread.

To convince yourself that human intelligence alone doesn't account for our ability to adapt, imagine that you and some friends are marooned on an arctic beach with a small cache of food. Help is *not* on the way; you're going to have to make it on your own. The Inuit survived here, so you might be able to survive too. There seem to be lots of seals in the sea, so maybe the first task is to build a kayak. You already know a lot-what a kayak looks like, roughly how big it is, and something about its construction. Nonetheless, you would likely fail. Suppose you make a passable kayak. To survive in the Arctic, you would still have to invent dozens of other tools-warm clothing, toggle harpoons, oil lamps, shelters built of skin and snow, goggles to prevent snow blindness, dog sleds, the tools to make these tools, and so on. And then you have to figure out how to use all of this stuff, where and when to hunt, where and when to gather, what is tasty, how to process food that you do manage to collect, and more. Then you must decide how to organize your society: how to regulate exchange of resources, organize marriage, resolve conflicts, and establish relationships with members of neighboring groups.

Individuals cannot learn to make complex, habitat-specific adaptations such as kayaks, oil lamps, and all the rest because, as Tooby and Cosmides (1992) have emphasized, widely applicable learning mechanisms are more imperfect and error prone than highly constrained, domainspecific ones. A kayak is a highly complex object with many different attributes. Designing a good one means finding one of the extremely rare combination of attributes that produces a useful boat. The number of combinations of attributes grows geometrically as the number of dimensions increases, rapidly exploding into an immense number. The problem would be much easier if we had a kayak module that constrained the problem, so we would have fewer choices to evaluate. However, evolution cannot adopt this solution, because environments change much too quickly and are far too variable spatially for selection to shape the psychologies of arctic populations in this way. The same learning psychology that provides people with all the other knowledge, institutions, and technologies necessary to survive in the Arctic also has to do for birch bark canoes, reed rafts, dugout canoes, rabbit drives, blow-guns, *hxaro* exchange, and the myriad marvelous, specialized, environment-specific technology, knowledge, and social institutions that human foragers have culturally evolved. Our general-purpose learning and inference mechanisms simply aren't up to the task.

The Inuit could make kayaks, and do all the other things that they needed to do to stay alive in the Arctic, because they could make use of a vast pool of useful information available in the behavior and teachings of other people in their population. The information contained in this pool is adaptive, because even limited, imperfect learning mechanisms combined with cultural transmission can lead to relatively rapid, cumulative adaptation. Even if most individuals imitate most of the time, some people will attempt to improve on what they learned. Many of these attempts will be unsuccessful, but occasionally innovators will succeed. Relatively small improvements are easier to come by than large ones, so most successful innovations lead to small changes. These modest attempts at improvement give behaviors a nudge in an adaptive direction on average. Cultural transmission preserves the advantageous nudges and exposes the modified traditions to another round of nudging. By the standards of ordinary evolution by natural selection, many small nudges generate new adaptations very rapidly.

Cumulative cultural change is adaptive, because it generates complex, habitat-specific adaptations using relatively domain-general cognitive mechanisms. The mind cannot be a blank slate: Cumulative cultural evolution *requires* an evolved "guidance system." People must be able to evaluate alternatives, to know that boats that don't sink and are easy to paddle are better than leaky, awkward designs. They have to be able to judge whose boats are best, and when and how to combine information from different sources. The elaborate psychological machinery that allows children to bootstrap general knowledge of the world is also clearly crucial. This guidance system is not "domain-general" in the sense that it allows people to learn *anything*. It is highly specific to life on earth, in a regime of middlesized objects, relatively moderate temperatures, living creatures, and small social groups. However, it *is* domain-general in the sense that nothing in our evolved psychology provides the crucial details about making kayaks. These crucial details were stored, preserved, and improved by the action of a population of evolved psychologies, using mechanisms that are equally useful for improving and preserving a vast range of knowledge.

This fact means that cultural adaptation comes with a built-in tradeoff. The ability to learn from others gives humans access to extremely valuable information about how to adapt to the local environment on the cheap. But, like opening your nostrils to draw breath in a microbe-laden world, imitating others exposes the mind to maladaptive ideas. Selection cannot shape our psychology to protect us from this, because it cannot build a powerful, general-purpose learning device. A young Inuit cannot readily compute the optimal kayak design. He can try one or two modifications and see how they work, and he can compare the performance of the different designs he sees. But small samples, multiple dimensions of variability, and noisy data will severely limit his ability to choose the best design. If most of the people around him use an inferior design, so will he. And kayaks are an easy problem. Is witchcraft effective? What causes malaria? Are natural events affected by human pleas to their governing spirits? What sort of person should one marry? How many husbands are best? What mixture of devotion to work and family will result in the most happiness or the highest fitness? For hard questions such as these, it can be best mainly to imitate (for formal analyses, see Boyd & Richerson, 1985, 1995). When we imitate, we are vulnerable to adopting maladaptive ideas from the people around us.

Moreover, the fact that much culture is acquired from people other than parents means that, for some traits, there are lots of maladaptive behaviors to imitate. It is good that cultural variants are acquired from all kinds of people, not just parents, because sampling a wider range of models increases the chance of acquiring useful information. For most traits, this causes no problem—the fastest kayak is the fastest kayak, whether or not it belongs to Dad or to somebody else. But when parents are not the only source of information, maladaptive ideas in some domains are more likely to spread. For example, in the modern world, beliefs that increase the chance of becoming an educated professional can spread even if they limit reproductive success, because educated professionals have higher status and are more likely to be emulated. Professionals who are childless can succeed culturally as long as they have an important influence on the beliefs and goals of their students, employees, or subordinates. The spread of such maladaptive ideas is a *predictable* by-product of cultural transmission.

Group selection acting on culture also leads to the spread of genetically maladaptive beliefs and values. Different human groups have different norms and values, and the cultural transmission of these traits can cause such differences to persist for long periods of time. The norms and values that predominate in a group may affect the probability that the group survives, whether it is economically successful, whether it expands, and whether it is imitated by its neighbors. For example, suppose that groups with norms that promote patriotism are more likely to survive than groups lacking this sentiment. This creates a selective process that leads to the spread of patriotism. Of course, this process may be opposed by an evolved, innate psychology that makes us more prone to imitate, remember, and invent nepotistic beliefs than patriotic ones. The long-run evolutionary outcome would then depend on the balance of these two processes.

Much of an individual's behavior is a product of beliefs, skills, ethical norms, and social attitudes that are acquired from others with little modification. This does not mean that the evolved predispositions that underlie individual learning become unimportant. Without an evolved guidance system, cultural evolution would be uncoupled from genetic evolution. However, once cultural variation becomes heritable, it can respond to selection for behaviors that conflict with genetic fitness. Selection on genes that regulate the cultural system will balance the advantages of imitation against the risk of catching pathological superstitions. Our vulnerability to adopting dangerous beliefs may be the price we pay for the marvelous power of cumulative cultural adaptation. As the saying goes, "You get what you pay for."

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