Evolutionary Psychology

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Abstract
Although the name "evolutionary psychology" would appear both simple and self-explanatory, suggesting a rather straightforward application of evolutionary theory to both human and nonhuman psychology, appearances can be deceptive. The status of the discipline, and its recent history, is far from straightforward, and debates among various schools of thought have been rather fraught at times. In what follows, we lay out the origins of Evolutionary Psychology, Human Behavioral Ecology and Gene-Culture Co-Evolutionary theory, explore their central tenets, and discuss the links between them. We also identify areas of tension, and discuss some of the criticisms advanced at these different approaches, both from within and outside the discipline. We emphasize the need for a more pluralist, biosocial stance in which cultural explanations are not considered distinct from biological ones, nor as complementary, but as fully intertwined.

Main text

Introduction
Evolutionary psychology, broadly speaking, is the application of evolutionary theory to human behavior. There are several approaches that fall under this name, some less obviously psychological than others, but they share a commitment to the idea that evolutionary theory is not only useful but necessary to a full scientific understanding of human life. Typically, this involves addressing one or more of the "four questions" proposed by the ethologist, Niko Tinbergen, as central to a "biology of behavior": 1) what is the current adaptive value of a trait; 2) what are the underlying mechanisms that produce the trait; 3) how does the trait develop over the life course; and 4) what is the phylogenetic (evolutionary) history of the trait (Tinbergen 1963). As such, all evolutionary psychological approaches owe a debt to ethology (Griffiths 2010). Here, we consider three main approaches: Evolutionary Psychology; Human Behavioral Ecology; and Gene-Culture Co-evolutionary theory (sometimes known as dual inheritance theory). There is continued debate over whether these are truly distinct, or whether they should be subsumed under a more general rubric of evolutionary psychology (Laland and Brown 2011). We will not engage in this debate here, and we use the term psychology as broadly as possible to mean the investigation of human behavioral variation across both time and space. This seems reasonable given the fuzzy boundaries between anthropology, economics, evolutionary biology, psychology and sociology, although perhaps a more appropriate term would be simply the "evolutionary human sciences".

Although the different fields within evolutionary psychology ostensibly engage with all four of Tinbergen's questions, the degree to which they do so varies quite dramatically. In particular, developmental and mechanistic questions have, until very recently, received far less attention than the functional and phylogenetic perspectives. This can be traced to the manner in which the study of behavior from an evolutionary perspective has developed over time. During the 1970s, the discipline of ethology, which had a strong focus on mechanistic and developmental questions, was eclipsed by the rise of sociobiology, which asked whether particular behavioral strategies were associated with greater survival and reproductive success, and were thus a product of natural selection. The popularity of

sociobiology was made possible because of advances in both evolutionary game theory and population genetics, which enabled the generation of quantitative predictive models and highly effective experimental designs (Laland and Brown 2011; Griffiths 2010). Sociobiology, with its focus on adaptive value, became the dominant approach, and more ethologically-oriented studies of mechanism and development were sidelined (Griffiths 2010).

While sociobiology (now more commonly referred to as behavioral ecology) was embraced enthusiastically by those working on nonhuman animals, the application of sociobiology to human behavior was far more controversial, due mainly to the (notorious) last chapter of E.O. Wilson's textbook "Sociobiology: the New Synthesis" published in 1975. Here, Wilson suggested that much of human behavior could be understood in terms of evolutionary adaptation, and implied that the social sciences would eventually be subsumed by evolutionary biology. Neither of these points were well received—to say the least—by many in the social sciences (Segestråle 2000). Most objections from this quarter were ideological (Darwinian theory has been used since its conception as a justification for eugenics and racist classifications of human populations), but there were scientific objections too from those who felt that Wilson's interpretation went beyond the bounds of the available data. In particular, the minimal attention paid to non-genetic processes, and the fact that adaptive stories were more easily conjured than rigorously tested—sometimes referred to as "just-so stories"—were seen as serious limitations of a sociobiological approach (Laland and Brown 2011). One side-effect of criticism coming from outside the field was that those within it were perhaps less self-critical than they would have been otherwise. There was a perceived need to present a united front, which resulted in a less than rigorous science (Laland and Brown 2011). Such points are important to consider, not only because they help place current evolutionary approaches in historical context, but also because (as discussed below) some current approaches express similarly imperialistic ambitions with respect to the social sciences. In addition, the controversial nature of some research has again given rise to a "siege mentality", where criticism of evolutionary studies is taken to be an attack on evolutionary theory itself, rather than a call for a more critical assessment of the empirical studies produced in its name.

Evolutionary Psychology

At present, the most dominant evolutionary approach to humans is the school of thought associated with John Tooby, Leda Cosmides and David Buss (e.g., Tooby and Cosmides 1990; Barkow, Cosmides, and Tooby 1992; Buss 2014). This is due in large part to its popularization by Steven Pinker, which has resulted in a much greater prominence among the wider public, as well as within academia, compared to other evolutionary approaches. Indeed, for many, particularly those in North America, this view has come to define the term "Evolutionary Psychology" (EP).

The central theoretical premise of EP is that the human cognitive architecture consists of a large number of functionally-specialized mechanisms (often referred to as "modules"), produced by natural selection to solve recurrent problems encountered over our evolutionary past. This is known as the "massive modularity thesis". It should be clear from this that EP has obvious links to sociobiology, particularly its commitment to a strongly adaptationist paradigm. Early proponents of EP took pains, however, to distinguish their approach from Wilson's sociobiology, arguing that the latter's focus on current adaptiveness (i.e., on whether behavior is fitness-enhancing) was misguided; the rapid pace of cultural change since the rise of agriculture, it was argued, would have outstripped the capacity of genetic evolution to produce an adaptive response. Consequently, researchers working within the EP paradigm (hereafter referred to as Evolutionary Psychologists to distinguish them from the more general field of evolutionary psychology) suggests that the human mind is adapted to the period of human history spent as hunter-gatherers, which represents the "environment of evolutionary adaptedness" or EEA (e.g., Tooby and

Cosmides 1990). Evolutionary Psychologists also emphasize that their focus is on the mechanisms that underpin behavior (which they consider to be the only possible target of selection), rather than behavior itself (which therefore represents the primary contrast with human behavioral ecology: see below) (Tooby and Cosmides 1990). This, in turn, means that Evolutionary Psychologists actively reject the idea of measuring fitness-related traits in contemporary populations (a mainstay of modern day behavioral ecology). Indeed, some consider current fitness measures to be entirely irrelevant to the study of adaptation because, by definition, adaptations are the product of past selection (Tooby and Cosmides 1990). Consequently, Evolutionary Psychologists use a combination of "design thinking" and "reverse-engineering" to identify the challenges facing our ancestors (e.g., choosing mates, avoiding cheats, finding high-quality food, raising children) and use this as a guide to hypothesizing about the kinds of psychological mechanisms that could meet these challenges successfully. These mechanisms are considered to be computational algorithms that take certain inputs, and process them in ways that lead to distinctive outputs. As such, EP adheres to the computational metaphor that dominates contemporary cognitive psychology (Barrett, Pollet, and Stulp 2014). The existence of these computational mechanisms is then tested for using the tools of experimental cognitive and social psychology, including various kinds of pencil-and-paper questionnaires and vignettes, reaction time studies, and preference tests. Leda Cosmides' use of the Wason selection task as a means to test for a specialized cheat-detection mechanism remains the paradigmatic example of how evolutionary psychologists go about their business (Barkow, Cosmides, and Tooby 1992).

Evolutionary Psychologists are also committed to the idea that there is a universal cognitive architecture shared by all humans, and that any variation seen in human "cognitive adaptations" represents environmentally-induced plasticity, and not variation in genotype. This follows from the premise that the mind evolved during the period when the human species was confined to Africa, and engaged solely in a hunter-gatherer life-way, but it also enables Evolutionary Psychologists to more easily resist the accusations of genetic determinism and racism that were leveled at sociobiology (even though genetic variation in and of itself does not lead to the conclusion that different human populations will show differences in ability). This notion of a single genetically-specified but environmentally variable cognitive architecture has been justified scientifically on the grounds that complex adaptations, regulated by many genes, should not show high levels of individual genetic variation because this would make it highly unlikely that the right combination of genes would be found in any given individual to enable the trait to develop normally; instead, natural selection should lead to uniformity in the genetic architecture contributing to the trait. Empirical evidence, however, suggests that there can, in fact, be high levels of individual genetic variation in many shared human traits (e.g., the shape, color, size and acuity of our eyes), plus the developmental systems of many species are known to be robust to differences in both environments and genotypes: put simply, the same phenotype may arise from a variety of different genotypes because developmental processes contain a high level of redundancy (Griffiths 2010; Bolhuis et al. 2011).

The most distinctive features of the EP position— the massive modularity thesis, the assumption that our minds are attuned to a past that no longer exists, and the notion of the EEA —are also those that have been subject to the greatest degree of debate and criticism. Within EP, the idea that the human mind consists of a large number of specialized mechanisms is justified theoretically on the grounds that these would provide greater flexibility and functionality than a small number of general-purpose learning mechanisms, just as a Swiss Army knife with it variety of specialized tools offers more flexibility than a standard pocket knife. Moving with the times, the analogy used today is that the mind is like a smart phone containing a number of specialized applications. The most controversial aspect of this idea, however, is not modularity per se, but that each module represents a distinct evolutionary adaptation, attuned to a highly specific aspect of our ancestral past.

Buss, for example, hypothesizes the existence of 22 different evolved female mate preferences (Buss 2014). Such ideas have come in for criticism largely because the evidence presented in favor of an adaptationist explanation is often seen as weak: in many cases, the evidence presented is consistent with many other possible explanations besides an evolutionary one, and the acceptance of an adaptation on such grounds is not well justified (e.g., Gray, Heaney, and Fairhall 2003). The fact that many of these putative universal adaptations are identified on the basis of (often small) Western student samples is another weakness.

A further criticism is that reverse-engineering is not as straightforward as evolutionary psychologists argue, and this is particularly so when it comes to psychology. Specifically, EP does not reverse-engineer an actual structure to determine its function, as one would the heart or the liver, rather it generates a hypothesis about the nature of the past, and then "reverse-engineers" this hypothesized past to generate further hypotheses about how psychological processes should function. This potentially is problematic because our knowledge of the past is often too limited to formulate accurate hypotheses and, as such, too limited to accurately identify traits (or adaptive problems) that can be reverse-engineered. This, then, explains much of the controversy over the concept of the EEA: the ability to accurately characterize the nature of our evolved psychological mechanisms depends crucially on our ability to accurately characterize the EEA.

Although Evolutionary Psychologists state that the EEA does not refer to any particular time and place, but is the "statistical composite" of all the selection pressures that have acted on a given traits, it has commonly been operationalized to our Pleistocene hunter-gatherer past. This approach to developing testable hypotheses has given rise to similar criticisms to those directed at sociobiology: namely, EP simply generates just-so stories, providing intuitively appealing but highly speculative accounts of our current behavior based on an uncertain knowledge of the past (Smith, Borgerhoff Mulder, and Hill 2000). Evolutionary Psychologists have responded to this criticism by noting that the adaptive problems they identify apply regardless of particular circumstances—all humans forage, fight, flee and fornicate after all—and hence their strategy does not need the degree of specificity argued for by their critics. In addition, more recent theoretical work in EP has tended to tone down some of the early claims made by Tooby and Cosmides, suggesting that there is no clear division between domain-specific psychological processes and more general learning mechanisms (e.g., Barrett and Kurzban 2006) (thereby simultaneously addressing the critique that EP too easily dismisses domain-general processes in cognition; Bolhuis et al. 2011; Barrett, Pollet, and Stulp 2014). It also places much less emphasis on the idea that we have "stone age minds in modern bodies", instead focusing on how an evolved architecture allows for the learning of novel concepts. This in turn downplays the central importance of the EEA as a means of identifying the putative structure of the human cognitive architecture. Empirically, however, there remains a heavy emphasis on adaptationism, and a willingness to accept that current behavior is more strongly attuned to the past than the present.

Evolutionary Psychology has faced quite severe criticism from within evolutionary biology itself, as well as the social sciences and humanities, to a much greater degree than other evolutionary approaches to human behavior. On the face of it, the targeting of EP is puzzling: the idea that our evolutionary history has shaped human cognition is an idea with which few scientists would disagree—there is no reason to accept that evolution simply stopped at the neck— and it is clear that a thorough understanding of our own, and closely related species', evolutionary history is useful for placing our current psychology and behavior in context. Indeed, Evolutionary Psychologists often perceive such criticism to be unwarranted, suggesting it arises for purely ideological reasons. This is certainly true in part, as many social scientists cling to an outmoded notion of evolutionary approaches as inherently suspect due to their historical links to eugenics. We suggest, however, that a lot

of this resistance actually arises in response to the claim that EP will revolutionize the social sciences by uniting them under the banner of evolutionary theory. Like sociobiology before it, EP views the social sciences as somehow having failed, when one could argue that it is a failure on the part of Evolutionary Psychologists to recognize that other disciplines have different goals and explanatory targets. In addition, it is apparent that many evolutionary biologists also consider the theoretical framework dubious at best and are concerned by the low quality of much empirical work (Gray, Heany, and Fairhall 2003; Bolhuis et al. 2011; Laland and Brown 2011). The view that EP lacks scientific rigor parallels the early days of sociobiology, and the reasons may be similar: Evolutionary Psychologists, particularly those in the US, often feel unduly attacked by those outside academia (e.g., religious groups), resulting in a defensive stance toward all evolutionary work. Many such researchers seem to consider that criticism even from within academia (including those from fellow evolutionary scientists) arises from an objection to human evolutionary studies *per se*, rather than an objection to the weakness of particular empirical results. It is in the field's best interest, however, to fully engage with this criticism, and ensure standards of evidence are as high as possible before any conclusions or generalizations are drawn. This is particularly so because evolutionary psychologists do not shy away from "controversial" topics (such as sex differences, and the adaptive significance of rape), which attract high levels of media attention, and thus has the potential to reach and influence many individuals (Smith, Borgerhoff Mulder, and Hill 2000; Laland and Brown 2011).

Human Behavioral Ecology

Human Behavioral Ecology (HBE) is derived from an earlier incarnation known as "Darwinian Anthropology", which in turn was derived from sociobiology (Laland and Brown 2011). The central premise of a behavioral ecological approach is that animals will behave adaptively within their local ecologies, that is, they will display strategies that maximize their inclusive fitness. Behavioral ecologists use both observational and experimental methods, along with comparative analyses, to test hypotheses derived from economic optimality models that calculate the fitness pay-offs of particular strategies (Winterhalder and Smith 2000; Nettle et al. 2013). As such, behavioral ecology (of both humans and nonhumans) has, until very recently, been concerned almost exclusively with Tinbergen's adaptive value question.

Like other anthropologists, human behavioral ecologists are interested in variation in behavior within and between populations in both space and time. The central premise of HBE is that humans have evolved to be flexible enough to respond adaptively to local conditions, and that current behavior is likely to be fitness-enhancing. Human behavioral ecologists play what is known as the "phenotypic gambit": this is the idea that there are no constraints on humans' ability to respond optimally, and that natural selection will be able to produce a fitness-enhancing solution. These assumptions thus represent the primary contrast with EP, and account for a major difference in their methodological approach: human behavioral ecologists study people's actual behavior in relation to various fitness-related traits, such as reproductive success, but do not explicitly study the mechanisms that underpin their behavioral decisions. Other contrasts lie in subject matter. Whereas there has been a heavy preponderance of studies of mate choice preferences in EP, HBE has traditionally seen a heavier emphasis on studies of foraging and parental investment strategies, and the fitness consequences of adopting particular marriage systems and inheritance strategies (e.g., polygyny, matrilocal versus patrilocal residence, and the consequences of primogeniture) (Winterhalder and Smith 2000). Both fields have diversified their subject matter considerably, however, and their differences have become increasingly less pronounced over time (Nettle et al. 2013).

The earliest behavioral ecological studies focused on small-scale traditional societies, in particular hunter-gatherers, based partly on the assumption that such populations are

representative of our evolutionary history. Although such populations are likely to be more representative than agricultural or industrial ones, it should be acknowledged that extant hunter-gatherer populations are also likely to differ substantially from ancestral populations and, as such, may not offer an accurate window into our past (Barrett, Dunbar, and Lycett 2001). More generally, however, small-scale societies were studied by HBE because these were so-called "natural fertility" populations, that is, societies in which people do not engage in any parity-specific form of birth control. Given HBE's focus on "counting babies" as the key to identifying whether people follow the optimal strategy for their environmental circumstances, such populations were the obvious choice. Indeed, the only societies in which human behavioral ecologists are willing to admit to some degree of mismatch with the past are those of rich, industrialized nations, where it is sometimes assumed that modern contraception results in maladaptive behavior. The assumption that, outside of the modern industrial world, fertility has not and cannot be controlled is, however, one that could be subjected to more scrutiny: it is clear from historical sources that population sizes and birth rates shift in ways indicative of the conscious control of fertility. It is also apparent that contraceptive uptake does not necessarily result in smaller family sizes under certain conditions, and some behavioral ecologists have focused on the use contraceptive technologies as means of spacing births and thus contributing to a fitness-maximizing strategy. Another development is that industrialized societies are now being studied within an HBE framework. This is largely through the recognition that large-scale demographic databases provide a rich source of insight into people's reproductive strategies (Nettle et al. 2013). Such studies have provided novel (evolutionary) insights into modern behavior, but it is also apparent that, as suspected, individuals in such societies probably do not maximize their fitness. This has, however, spawned a great deal of interest in looking at the "demographic transition" from high fertility-high mortality regimes to low fertility-low mortality regimes in order to understand those factors that seemingly limit human fertility under conditions where evolutionary theory would predict no such limitations. In a nod to EP, such studies also seek to identify the possible mechanisms that underlie maladaptive behavior.

HBE is often considered more rigorous than EP due to its emphasis on measuring actual behavior, rather than relying on self-report measures, combined with testing predictions drawn from well-established and mathematically precise evolutionary theories. The field is also much more cross-cultural than EP, and has shown less reliance on modern Western populations for sampling purposes. Again, as with subject matter, these latter differences are becoming less pronounced as Evolutionary Psychologists have begun to incorporate work on nonWestern populations into their studies.

A weak point of HBE, which is acknowledged increasingly within the field, is that it deals almost exclusively with the question of adaptive value and, via the use of the phenotypic gambit, ignores the mechanistic and developmental aspects of behavior, which are entailed by any comprehensive evolutionary analyses. Although the phenotypic gambit was initially accepted almost without question, it has come in for criticism more recently: in particular, a number of researchers have argued that its adoption has led either to the neglect of cultural influences on behavior or to the treatment of culture simply as a proximate mechanism by which human systems respond to exogenous ecological changes (Laland and Brown 2011). The latter, in particular, is a problem because human cultural practices act as a major force on the environment, so that culture should be seen also as an ultimate source of behavioral variation. More specifically, the cultural environment created by humans itself generates and exerts novel selection pressures on human populations – a prime example of niche construction (see below). In addition, the behavioral strategies observed in a population may be constrained by cultural history in ways that are not accounted for by standard optimality models; populations may be forced to adopt locally optimal solutions, that are ultimately fitness-enhancing given the particular set of constraints that have operated, but which may appear maladaptive if the assumption is that the population will always

converge on the global optimum. Finally, understanding whether constraints represent some form of physiological limit to human capacities or whether they arise due to cultural processes makes a fundamental difference to how one should model such constraints within an optimality approach (to take a very crude example — do people have only two children in a given society because they are physiologically unable to produce more or because they are unwilling to violate cultural norms?). Incorporating a greater understanding of psychological mechanisms, which includes drawing on some aspects of EP, may therefore improve our ability to predict and explain why people behave as they do.

Gene-culture co-evolution

The call for greater attention to cultural processes within human behavioral ecology leads naturally to a consideration of a third evolutionary approach: gene-culture co-evolution (GCC) theory. GCC attempts to understand and model the interaction between cultural and genetic evolution, accepting that these represent two distinct but parallel processes, and that it is possible for cultural processes to produce very different evolutionary dynamics to those produced by a consideration of genetic evolution alone (e.g., Cavalli-Sforza and Feldman 1981). In this it differs from earlier sociobiological attempts at such modeling, which assumed that, ultimately, genes would "keep culture on a leash", i.e., cultural practices and ideas that resulted in low fitness would be selected against, and hence successful cultural practices should ultimately be fitness-promoting.

Some approaches that model cultural processes apply Darwinian principles (i.e., variation, inheritance and competition) to human cultural practices in an attempt to model and understand how and why these change over time, without further consideration for how these might influence biological evolution. Such cultural evolutionists recognize that the diffusion and spread of cultural practices do not perfectly map on to biological evolutionary processes, but their aim is not to argue for the equivalence of such processes, but to use evolutionary theory to provide a quantitative, scientific means of studying human culture over space and time (Mesoudi 2011). As with EP, this approach is sometimes presented as the means by which the social sciences will be rescued and unified. Again, this has led to the criticism that scientists are encroaching on territory that is not theirs to take.

The archetypal example of gene-culture co-evolution is that of lactose tolerance—the ability to digest milk beyond infancy (Durham 1992). Those populations that possess a history of dairying and cattle-herding are more likely to have evolved the ability to digest milk as adults, with recent genetic evidence suggesting that this has evolved independently in several areas of the world. This pattern cannot be understood without reference to both the cultural practice of herding/dairying and the presence of a mutation that enables lactose digestion. Without the mutation, the ability to digest milk as adults could not arise, but without the practice of herding/dairying, the mutation would offer no advantage and would not be selected. Co-evolutionary processes of this nature also represent an excellent example of "niche construction": human cultural practices are a means by which humans can alter the nature of their environments in ways that are likely to have consequences for subsequent natural selection. Of course, rapid innovations and drastically changing environments might result in maladaptive behavior in some cases, but humans are likely to modify their environments to suit their own (adaptive) needs. In this respect, co-evolutionary approaches and niche construction theory argue against the kind of drastic mismatch that characterizes the EP position (Laland and Brown 2006).

A lot of the early work on gene-culture co-evolution by scientists like Cavalli-Sforza, Feldman, Boyd, and Richerson, is heavily mathematical. This explains why, perhaps, this approach has taken the longest to gain traction in the human evolutionary sciences. One can, however, understand many of the principles and theories of GCC without having to

deal with formal mathematics. Indeed, Richerson and Boyd (2005) present exactly this kind of non-mathematical treatment, which may have contributed to the greater traction gene-culture co-evolutionary theory has achieved in recent years. It is also the case that there is now a younger generation of researchers, who have not only developed formal theory, but have begun empirical research programs as well.

One of the key issues with respect to studying cultural practices within an evolutionary framework is how to define culture. Within GCC, culture is typically considered to be "information that is acquired from other individuals via social transmission mechanisms such as imitation, teaching, or language" (Mesoudi 2011, 3). It is the human species' capacity for social learning and the transmission of ideas that is argued to underpin our capacity for cumulative culture (the ability to improve upon the cultural practices and artifacts of our forebears) and explain humans' global success. Treating culture, in essence, as ideas in people's heads simplifies matters by eliminating the need to identify precisely what is copied between individuals – when we inherit our grandmother's recipe for soup, do we inherit her recipe book, her pots and pans, her spoken instructions, her physical demonstrations of the actions needed, or some combination of these? — hence making the process of modeling more tractable, but it does neglect human material culture. This is seen as problematic by some researchers who argue that human cognition is "extended" via the use of such material artifacts, and that these actively constitute part of our cognitive system (Barrett, Pollet, and Stulp 2014). For example, our ability to cooperate on a large-scale with nonrelatives, which is characteristic of certain human societies, has been argued to rest on the invention of written records and accounting schemes. Similarly, our ability to engage in mathematics is argued to have come about through the use of physical symbolic artifacts that allowed us to comprehend and invent a completely new means of thinking about the world. This aside, the notion that culture can be modeled as the transmission of ideas links GCC quite closely to EP (although EP does not, in general, place much emphasis on the social transmission of ideas, referring instead to a notion of "evoked culture": the idea that our universal psychology generates different behaviors depending on the inputs received directly from the environment). That is, certain proponents of GCC argue that humans possess a number of biases and specialized learning mechanisms that are the products of natural selection (e.g., Richerson and Boyd 2005). These fall into the general categories of "content biases" (we are able to learn some things more easily than others, because they were more likely to be fitness-enhancing, such as putting salt or sugar on popcorn, rather than, say, sand), and "context biases", learning mechanisms that allow us to capitalize on the knowledge of others, and thus save the cost of individual learning. Among the most prominent of these context biases are the ideas of "conformist transmission", whereby one copies what the majority does in a given population, and "prestige bias", the idea that one selectively imitates those of high-status because, all else being equal, high-status should be positively associated with greater skill. The impact of these learning mechanisms is then modeled with respect to how they influence biological fitness, and vice versa. One outcome of such models is that a certain level of maladaptive behavior is to be expected, as this represents the inevitable consequence of relying on social information that one can obtain more cheaply and with less effort than individual learning: one may fail to recognize exactly what makes prestigious individuals more successful, for example, and copy the wrong aspect of their behavior (Richerson and Boyd 2005).

It is with respect to the issue of maladaptive behavior that one can most clearly differentiate GCC from both EP and HBE. As already noted, EP assumes that our minds are adapted to an environment that, for the most part, no longer exists. There is the implicit assumption, then, that we were once perfectly in tune with our environment, and that we are now increasingly mismatched, and unable to behave adaptively. Human behavioral ecologists lie at the other end of the spectrum, and assume that humans always have sufficient plasticity to engage in adaptive behavior, and that mismatches should be rare,

reflecting only very extreme circumstances, such as those that exist in modern industrial society. GCC, by contrast, does not assume that we are now inherently in or out of tune with our environments, instead suggesting that maladaptive behavior is likely to be present in all environments under at least some circumstances. GCC models also demonstrate formally how cultural and biological selection may sometimes be at odds, and why maladaptive behavior can arise because of the way that cultural transmission differs from genetic transmission. For example, cultural information can be transmitted both horizontally (between peers) and obliquely (from teacher to pupil) as well as vertically (from parent to offspring). Differences in rates and modes of transmission can therefore give rise to very different evolutionary dynamics than those possible with vertical transmission alone (as is typically the case for genetic information).

The various forms of gene-culture co-evolution theory, including niche construction, represent the most inclusive and integrative of the scientific approaches to human behavior by taking seriously the influence of cultural transmission systems as well as biological ones. This approach may therefore resonate most strongly with those in the social sciences, provided it is presented as complementary to, rather than as a replacement for, current practices within sociocultural anthropology and sociology. Indeed, a better understanding of how people make meaning in their lives and how social practices form part of this process is essential to developing a truly biosocial framework for the study of humans. One drawback of GCC approaches is the difficulty of acquiring the kinds of data needed to adequately test the formal models: it requires information on fitness differentials, the cultural "fitness" of particular ideas and practices, along with information on genetic variation and cultural variation over both time and space. In order to generate a comprehensive understanding of humans from a scientific evolutionary point of view, however, cultural practices and history cannot be ignored. The human adaptation is, quite simply, a cultural one, and our evolution is a process of fully intertwined biocultural change.

SEE ALSO:

Adaptation and natural selection; Anthropology, biological and evolutionary; Behavioral ecology, human; Cultural evolution; Comparative cognition; Darwin, Charles: influence on anthropology; Demographic transition; Dual inheritance theory; Niche construction; Population genetics and sociocultural behavior; Sociobiology and anthropology

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