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〈Review〉

Optimality Modeling in Human Evolutionary Behavioral Science

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ABSTRACT: Recently, the evolutionary study of human psychology and behavior has undergone rapid growth, diversifying into a few distinct sub-disciplines. One fundamental issue over which researchers in Human Behavioral Ecology and Evolutionary Psychology (EP) have different views is the role of formal optimality modeling for making hypotheses and deriving predictions about human adaptations. The study of EP typically rests on informal inferences and rarely uses optimality modeling, a strategy which human behavioral ecologists have severely criticized. Here I argue that EP researchers have every reason to make extensive use of optimality modeling as its research method. I show that optimality modeling can play an integral role in identifying the functional organization of human psychological adaptations.

Key words: Evolutionary psychology, Human behavioral ecology, Optimality modeling, Research method

INTRODUCTION

During the last three decades, the field of evolutionary study of human psychology and behavior has shown rapid growth. As a truly interdisciplinary science, it now attracts a number of active researchers from a wide variety of disciplines: politics, art, history, literature, law, medicine, aesthetics, environmental studies, and religion, to name a few. Several handbooks for academic scholars as well as a dozen textbooks for undergraduate students have appeared within the past ten years (e.g., Gaulin and McBurney 2001, Barrett et al. 2002, Palmer and Palmer 2002, Buss 2005, Buss 2007, Dunbar and Barrett 2007, Crawford and Krebs 2008). Moreover, a number of popular books for general audiences on human behavior and evolution (e.g., Wright 1994, Dennett 1995, Pinker 1997, Ridley 1997, Pinker 2002) have been widely read among intellectuals and lay people.

At least four distinct sub-disciplines have emerged in human evolutionary behavioral sciences: Human Behavioral Ecology (HBE), Evolutionary Psychology (EP), the gene-culture coevolutionary approach, and memetics (Smith 2000, Laland and Brown 2002, Gangestad and Simpson 2007, Sears et al. 2007). This divergence became apparent when a heated controversy erupted between proponents of HBE and EP in the late 1980s. The theoretical and methodological issues raised in the controversy include the domain-specificity of psychological mechanisms, adaptive lag and evolutionarily ancestral environments, and the relevance of measuring current fitness in unraveling adaptations (Symons 1987, Symons 1989, Turke 1990). Although the need for a synthesis of human evolutionary behavioral sciences is generally acknowledged (Gangestad and Simpson 2007, Sears et al. 2007), most of the issues that sharply differentiated EP from HBE two decades ago have yet to be resolved.

Here I focus on one fundamental issue over which HBE and EP have different views: the utility of formal optimality modeling in making cost-benefit analyses of human behavior and generating testable predictions. Whereas HBE makes extensive use of formal optimality modeling, EP typically relies on verbal arguments from the reconstruction of our past as Pleistocene hunter-gatherers. Proponents of HBE have criticized EP's heavy reliance on informal inferences, arging that using verbal arguments only is equivalent to telling a 'just-so' story and making an *ad hoc* explanation of already known facts (Smith 2000, Winterhalder and Smith 2000, Smith et al. 2001). In line with Kaplan and Gangestad (2005, 2007), I suggest that HBE researchers' critique on this issue is somewhat unreasonable and that optimality modeling actually could be fruitfully utilized by EP as well as HBE. Moreover, in contrast to Kaplan and Gangestad's (2005, 2007) view that optimality modeling cannot yield novel insights into psychological processes, I argue that optimality modeling can help to characterize the functional architecture of evolved psychological mechanisms, rendering it one of the most important research tools for evolutionary psychologists as well as human behavioral ecologists.

First, I give a brief description of how adaptationism necessarily involves formulating and testing optimality models. Next, I discuss some possible reasons why EP researchers have effectively neglected optimality modeling as a research method for investigating human psychology and behavior. I then suggest that optimality modeling can play an essential role in identifying psychological as well

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as behavioral adaptations in humans.

ADAPTATIONISM AND OPTIMALITY MODELS

Living organisms fit remarkably well into the external world in which they live. The problem of how such intricate functional designs came into existence was solved by Darwin (1859), who showed that complex biological adaptations are the products of evolution by natural selection over long periods of time. Today, the adaptationist program analyzes the ways in which complex adaptations are engineered to solve specific adaptive problems that have recurred in an organism's evolutionary past (Williams 1966, Mayr 1983, Williams 1992).

Over immense lengths of time, natural selection accumulates only those design features that have aided the propagation of the underlying genes in the next generation. Natural selection can be considered as an optimizing agent, fixing the mean value of a quantitative character near the functional optimum and minimizing the variation around the mean (Williams 1992, Krebs and Davies 1997). Hence, given suitable assumptions of fitness measures, an optimality model can be constructed to specify which phenotype among a set of alternatives would be most fit or optimal for a given environment (Maynard Smith 1978). The selective accumulation of design features that confer net fitness benefits should *optimize* the parameters of the design. This is why optimization is a fundamental principle in the study of adaptation (Seger and Stubblefield 1996).

Optimality modeling has three main components. First, an optimality model identifies a *currency* in which the fitnesses of alternative phenotypes can be evaluated (e.g., the relative numbers of grandprogeny for models of sex ratios (Fisher 1930, Edwards 1998)). Second, it identifies the *control variable(s)* that quantify the states of those phenotypes (e.g., a focal parent's progeny sex ratio for the models of sex ratio). Third, it identifies a *fitness function* that describes how fitness in units of the currency depends on the control variable(s) and other parameters (e.g., the relative number of grandprogeny as a function of a focal parent's progeny sex ratio given the population sex ratio). Having defined these components, an optimality model can be constructed to predict which of the strategies for manipulating the control variables maximizes the fitness value under appropriate biological constraints (see Parker and Maynard Smith (1990) for a clear introduction to optimality modeling). If the optimum for an individual is affected by what others do, one can adopt game-theoretic (frequency-dependent) models, which aims to seek an evolutionarily stable strategy (ESS). Unlike simple optimization (frequency-independent) models, fitness is maximized here only in the sense that mutants not playing the ESS cannot invade the population (Maynard Smith and Price 1973).

Optimality modeling has played an integral role in studying the adaptive design of behavior. It is true that intuitive verbal arguments may also be conveniently used to identify adaptations, and that they have the practical merit of being easy to construct and interpret. Nonetheless, history has shown that the introduction of formal optimality modeling in 1960s was a giant step forward in the study of adaptation. Before the advent of optimality modeling techniques, classical ethology experienced a number of difficulties. One obvious problem was that ethologists' descriptions of behavior patterns were closer to being labels than causal explanations (Buss 2007). Along with inclusive fitness theory (Hamilton 1964), formal optimality models replaced *ad hoc* explanations about specific behavior patterns like foraging (MacArthur and Pianka 1966, Charnov 1976). For the first time, optimal foraging theory allowed researchers to make *a priori* predictions about how organisms are expected to behave in their natural environments. The optimality approach remains the most powerful tool for behavioral ecologists and sociobiologists, with ongoing development of more elaborate techniques such as game-theoretic models and dynamic state variable models (Maynard Smith 1982, Parker and Maynard Smith 1990, Clark and Mangel 2000).

WHY EP RESEARCHERS RARELY USE OPTIMALITY MODELING

Having observed that optimality modeling is an essential research method for the adaptationist program, I must then raise a question: why do evolutionary psychologists rarely make use of formal optimality modeling? This question is inevitable because the pioneers of EP defined the field as "the application of the adaptationist program to the study of the human brain/mind" (Symons, 1992, p. 155). The founders of EP, such as Donald Symons, John Tooby, and Leda Cosmides, charged human behavioral ecologists with confusing currently adaptive behavior with behavioral adaptations. Donating sperm to a sperm bank, for instance, would certainly qualify as an adaptive behavior: one that increases lifetime reproductive success in the current environment. It would be absurd, however, to suggest that sperm-donating behavior has been shaped by natural selection in the distant evolutionary past. Thus, the founders of EP criticized HBE's 'adaptivist' approach and claimed that a truly adaptationist approach to human psychology and behavior was needed. Below I outline a few possible reasons why students of EP have thus far effectively neglected optimality modeling techniques as a way to understand the nature of adaptations.

First of all, the strategy set in optimality models is frequently comprised of explicit behavioral options (e.g., either to forage outside or to wait inside), which may have created the impression that optimality modeling is not suitable to study the adaptive design of psychological mechanisms. During the controversy between proponents of EP and HBE, evolutionary psychologists criticized HBE on the grounds that "natural selection cannot select for behavior per se; it can only select for the mechanisms that produce behavior" (Tooby and Cosmides 1990). This has been widely interpreted as meaning that adaptive designs can be identified not at the level of external behavior but of internal psychological mechanisms. Since optimality modeling usually focuses on how alternative behavioral options bring about different fitness consequences, evolutionary psychologists may have believed that they do not need to resort to formal optimality models.

Second, optimality models are more difficult to formulate and understand than simple verbal arguments. Of course, the difficulty involved in optimality modeling presents a serious obstacle for human behavioral ecologists as well as evolutionary psychologists, yet the problem is particularly severe for evolutionary psychologists because most evolutionary psychologists' academic backgrounds are in mainstream psychology, which presents few opportunities for students to familiarize themselves with basic calculus and evolutionary genetics.

WHY EVOLUTIONARY PSYCHOLOGISTS SHOULD USE OPTIMALITY MODELING

In this section, I attempt to show that, despite widespread skepticism about the validity of optimality modeling for studying human psychological adaptations, optimality models can actually play a pivotal role in understanding evolved psychology and behavior.

More than anything else, the notion that adaptations should be sought at the level of psychological mechanisms but not behavior patterns is a gross misapprehension of what the founders of EP really meant. EP's emphasis on psychological mechanisms rather than specific behavior was an attempt to correct the conceptual error prevalent in the field of HBE that each and every human behavior was expected to be adaptive in the current environment (Symons 1992). Indeed, Tooby and Cosmides (1990) explicitly stated that "Turke (1990) argues that behavior can be an adaptation just as much as any other phenotypic property can be and, depending on exactly what is meant by the word behavior, we agree with him". If behavior is taken to be the manifest phenotypic expression of an underlying psychological trait (e.g., sweet tooth is an adaptation because craving for ripe fruits conferred higher fitness in human ancestral environments, although it may be maladaptive in current environments), Tooby and Cosmides (1990) make clear that we can call it an adaptation. By contrast, if behavior is taken to be any of the infinitely variable actions humans may show whether or not there exists an underlying psychological trait (e.g., smoking), it cannot be called an adaptation. As Symons stated, "Darwinism illuminates human behavior only insofar as it illuminates the adaptations that constitute the machinery of behavior" (Symons, 1992, p. 139). It should be noted that the founders of EP clearly specified that, as long as behavior is properly defined, both psychological mechanisms and behavior are equally appropriate levels to look for adaptations. Therefore, an optimality model of specific behavior patterns can help to demonstrate the existence of their underlying psychological adaptations.

Indeed, while practitioners of HBE often imply otherwise, theoretical evolutionary biologists stress that optimality models are an appropriate research method for investigating the psychological mechanisms underlying behavioral decisions (Krebs and Kacelnik 1991, Kacelnik and Krebs 1997). For example, optimal foraging theory is frequently applied to unravel the process of decision-making by foragers. It turns out that consideration of psychological mechanisms, such as learning and memory, has helped to reveal a much richer story than a simple focus on optimization (Krebs and Kacelnik 1991, McNamara et al. 2001). Dynamic state variable models, a variant of optimality models, are powerful enough to specify sequences of decisions made by individuals over time where each chosen action can depend on the current state and may influence the future state. The models are being extensively used to analyze a wide range of adaptive problems such as energetic gain, energy-predation trade-offs, dynamic games, state-dependent life histories, annual routines, and fluctuating environments (Houston & McNamara, 1999). Obviously, such a powerful modeling technique would be of immense help in discovering the functional organization of human psychological mechanisms.

Formal optimality modeling, as applied to study human psychology and behavior, gives a new insight into how to resolve the debate about the concept of Environment of Evolutionary Adaptedness (EEA), i.e., the past ancestral environment that has exerted selective pressures on a specific adaptation over a long time. Whereas EP researchers argue for the importance of the EEA concept, human behavioral ecologists often emphasize the great flexibility of human psychological faculties, which is assumed to allow humans to behave adaptively in a wide range of current novel environments (Smith et al. 2000). It seems that optimality modeling, which embodies the fundamental principle of optimization in the adaptationist program, supports the viewpoint of EP on this issue. According to theoretical evolutionary biologists, psychological mechanisms implementing behavioral phenotypes "will typically be simple rules of thumb that approximately maximize fitness under natural circumstances but that *may produce anomalous behavior in some circumstances*." (McNamara et al. 2001, p. 415). For instance, birds have simple rules for determining which eggs to incubate and often prefer the biggest egg. This preference rule may have adaptive value in the wild, but under artificial conditions birds may be experimentally manipulated into trying to incubate objects that are too large to be eggs. Thus evolutionary biologists recommend that, if one want to use optimality models to predict a behavior, one must observe the behavior in the natural environment in which it has evolved, which is functionally equivalent to the EEA (McNamara et al. 2001).

CONCLUDING REMARKS

In this review, I attempted to show that optimality modeling is an essential research tool for evolutionary psychologists as well as human behavioral ecologists. My argument is simple and straightforward. Given that the field of EP is oriented around the adaptationistic approach to human nature, and that optimality modeling is one of the most powerful methods of adaptationism in biology, it seems natural that evolutionary psychologists should adopt optimality modeling as one of their main research tools. Contrary to the misunderstanding common among human behavioral ecologists and evolutionary psychologists, optimality modeling offers a clear and efficient way to reveal the nature of human psychological mechanisms as well as explicit behavior patterns. I anticipate that active application of optimality modeling to the study of human psychology and behavior will contribute substantially to the reintegration of the current sub-disciplines of human evolutionary social sciences, facilitating the development of a more complete understanding of human nature.

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