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## Epicycles and Explanations in Evolutionary Psychology

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Evolutionary psychology incorporates the view that human cognitive and social abilities are the consequences of natural selection: Human inferential capacities, choices of mates, sexual preferences, and tendencies to aggression are adaptations no less than are analogous traits in social insects or our primate kin. There is no serious question that evolutionary explanations and selectionist explanations are testable.<sup>1</sup> Illustrations are easy to come by (cf. Endler, 1986). The sickle cell gene ranges widely through central Africa, India, and Central America. In heterozygote form, it provides some immunity to malaria and is sustained by balancing selection. The discovery of penicillin in 1928 imposed simple, extreme, directional selection. The result is antibiotic-resistant strains of bacteria. *Cepaea nemoralis* is a snail common in Europe. Thrushes are fond of the snails, and the broken shells left behind offer a record of selection that varies with habitat and season. The result is a shifting pattern of selection that results in a polymorphic population. All

these are adaptations, shaped and maintained by natural selection. It is, likewise, an easy matter to find traits that are not the result of natural selection. To use an elegant example from Darwin (1859/1964), skull sutures are certainly useful to humans, because they facilitate passage through the birth canal. They have an important, and even essential, current use. Skull sutures are nonetheless not an adaptation for parturition, because birds and reptiles also have skull sutures, although they hatch rather than being live born. Sutures are the consequence of evolution, but not of natural selection.

What Ketelaar and Ellis (this issue) think of as the Lakatosian "hard core" of evolutionary theory is thus secure, insofar as it amounts to a commitment to natural and sexual selection as central to evolution. This by no means implies that all evolutionary explanations are testable, or that it is practically feasible to evaluate the claim that some particular trait is the product of natural selection. The critical question for evolutionary psychology is the practical one: Can we, in practice, validate the explanations offered for human psychology?

The study of adaptation within a robustly evolutionary framework involves inferring historical process from contemporary products. The focus is on historical sequence and causal antecedents, emphasizing prior conditions as determinants of contemporary patterns

<sup>1</sup>In its classic formulations, due to Popper, falsifiability is used as a demarcation criterion, distinguishing science from non-science. Although at one point Popper did hold, notoriously, that evolutionary biology was on the nether side of his demarcation criterion, he was wrong (see Brandon, 1990, for discussion).

(Lauder, 1981; Lewontin, 1969). As it turns out, this is a difficult task, because information concerning ancestral environments, variability, social structure, and other relevant features is often not available. As a result, there are reasons to be skeptical about whether human psychology is a tractable case for such historical analysis (Lewontin, 1990; Richardson, 1996). Some biologists, especially evolutionary ecologists and behavioral ecologists, focus instead on questions of current form and function abstracting from the historical paths that produced them. It is here that we find the more specialized evolutionary models that most interest Ketelaar and Ellis, and that they treat as part of the "protective belt" surrounding the core evolutionary commitments to natural and sexual selection. The models developed for parental investment by Trivers (1972), for reciprocal altruism by Axelrod and Hamilton (1981), and for inclusive fitness by Hamilton (1964), are elaborations of the theory of natural selection, and are species of optimality models. In such applications, the question at the focus of investigation is not historical, but, rather, the extent to which a trait optimizes fitness among a specified set of variants and within a specific environment. The standard for adaptation is optimality of design, measured by current utility.<sup>2</sup>

Lewontin and Gould (1979) famously, or infamously, attacked what they called the "adaptationist program," the view that natural selection is "so powerful and the constraints upon it so few that direct production of adaptation through its operation becomes the primary cause of nearly all organic form, function and behavior" (p. 76). Their target was exactly the kind of optimality analysis that Ketelaar and Ellis place in the protective belt of middle-level theory. In place of a complacent commitment to adaptation as the explanation of organic form, Lewontin and Gould argued for a more pluralistic approach to evolutionary biology, in which a wider array of alternatives to natural selection need to be systematically considered. Showing that some trait is the product of natural selection requires eliminating alternative explanations, or at least showing that they are less likely. Lewontin and Gould offered a variety of alternatives to natural selection, including genetic drift, but the image of the spandrels of San Marco suggests strongly the role that developmental or structural constraints might play in evolutionary processes (cf. Alberch, 1982; Gould, 1977; Maynard Smith et al., 1985). The attraction of the idea is not difficult to see. The construction of a phenotype from a genotype is a complex affair, and the idea that the phenotype could be indefinitely molded to meet the

demands of the environment is unrealistic. Pleiotropy and epistasis entail that there are nonlinear, and nonadditive, interactions among genes. There are dependencies in ontogeny that entail that characters cannot be readily decoupled (cf. Schank & Wimsatt, 1988; Wimsatt & Schank, 1988). Suites of characters evolve in concert, in ways that are impossible to predict in the absence of specific developmental information. What has emerged in the 20 years since the spandrels article, though by no means solely as a result of that article, is, in fact, a much more eclectic, more pluralistic research program in evolutionary biology, with more sensitivity to problems involving developmental limitations; more awareness of the deep conservatism in underlying genetic mechanisms, the significance of phylogenetic analysis, and stochastic effects on evolution; and at the same time a more nuanced understanding of the action of natural selection.

Lewontin and Gould (1979) are often taken, with some cause, to be promoting a more ambitious agenda, but the reliance on optimality and reverse engineering in the analysis of adaptation is perhaps the clearest example of the sort of research they criticize. They claim that the "adaptationist program" typically involves two steps. First, an organism is "atomized" into traits that are explained as independent structures optimally designed by natural selection. This often amounts to assuming that genetic variation is both extensive and additive, and that as a consequence phenotypes are almost indefinitely malleable. Second, because assuming traits are independent is generally unrealistic, interaction effects are incorporated as trade-offs. Competing demands on organismal design are acknowledged, but without compromising the commitment to optimal design. It is tempting, and common, to treat this complaint as if it were one over the failure of falsifiability. I think this is not the most fruitful rendering.

There are a number of forms that optimality analyses can take, with varying purposes (see Amundson, 1994; Amundson & Lauder, 1994). In one form, information concerning constraints is incorporated into evolutionary models as prior constraints on the available range of biological models. This use of constraints and the resulting appeals to optimality are unobjectionable. Environmental and developmental information give structure to the problem, constraining the alternatives systematically. It is difficult to use this approach generally. Such a priori optimization requires substantive knowledge of the environmental "problem" to be solved, the range of phenotypic variation, their relative efficiency, and much more (cf. Lauder, 1996).

In many other cases, design constraints are often not specified a priori, and in many cases cannot be specified before the fact. The alternative is to develop design constraints a posteriori, using the performance of the phenotype to determine the environmental factors that shaped that design (see Beatty, 1980). The point of

<sup>2</sup>Many of the architects of evolutionary psychology resist such an ahistorical approach to the study of adaptation, but the method has left its mark, and certainly has a salient place in biological, including the work of R. A. Fisher (1930) and that of R. H. MacArthur (1957, 1960) on evolutionary ecology.

MacArthur's (1957, 1960) classic work on the abundance of species in the "broken stick" model was that the existing data on relative abundance of species fit better with a model based on nonoverlapping niches. These data, MacArthur (1960) concluded, fit better with an analysis assuming competitive exclusion than with an analysis assuming species distribution patterns are caused by, say, abiotic factors. The analysis of pattern is, for MacArthur, a vehicle for understanding evolutionary history. MacArthur found a rough qualitative fit between the observed distribution of species and a competitive model. The fit is by no means perfect, however. Common species are more abundant than the models would predict and rare species are less abundant than predicted. MacArthur (1957) pointed out that if the environment is heterogeneous, then it is possible to improve the fit between data and model. He went on to reverse the dependence: "The divergence from the ideal curve may, in fact, be regarded on this hypothesis as a measure of heterogeneity. Experimentally, for bird communities, this appears to explain most of the 'steep' curves" (MacArthur, 1957, p. 293). This is a standard strategy in handling a mismatch between model and prediction, to explain apparent lack of optimal design (see Kingsland, 1985). A deviation from initial predictions is explained by superimposing a second application of the same optimization model, taking up the slack in the fit by assuming optimal design. In a posteriori application, the degree of mismatch with the predicted optimum is used as a measure of the significance of the constraint. We no longer test for adaptation or optimality, but assume it. As Lewontin and Gould (1979) observed, this kind of retrofitting does ensure that there will be some optimal model for the behavior in question. Responses to the challenge of finding an analysis that makes a trait optimal depend primarily on the creativity of the theorist.

The methodology is directly relevant to the question of evolutionary psychology offering a progressive research program or a degenerative program constructing epicycles to save itself from anomalies. It is not enough to find new empirical applications. Retrofitting of models to observations is not a difficult matter. The epicycles of Ptolemaic astronomy allowed a very good fit to the data within a geocentric model of the universe. There was some variation in the number of minor epicycles necessary to account for planetary motions, but it is clear that the resulting system was extremely accurate and flexible (cf. Kuhn, 1957). It is likewise not enough to find some new predictions. The Ptolemaic system did often predict eclipses reasonably well, as well as the irregularities in planetary motion known as "retrograde" motion. The Ptolemaic system nonetheless collapsed. What matters is whether the predictions we have are based in empirically motivated models, with parameters and design criteria independently established. It may be true that human reasoning

can be understood in terms of the importance of social contracts and reciprocal altruism. It may be true that the development of daughters can be understood in terms of the importance of paternal involvement. It may be true that sexual selection is consistent with a sensitivity to features "indicative of good genes." Many of the suggestions Ketelaar and Ellis made from writings on evolutionary psychology may be true. What is missing, and what is needed, is knowledge of the sort that contributes to a sound, empirically motivated evolutionary model, including information concerning the sort of environmental problem cognitive mechanisms are responding to, the phenotypic and genotypic variation present, the structure of the relevant social groups, gene flow between them, and other population parameters. Without such information, we do not know whether evolutionary psychology offers us epicycles or explanations.

#### Note

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## The Illusion of Unfalsifiability and Why It Matters

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“Are evolutionary explanations unfalsifiable?” Ketelaar and Ellis (this issue) ask this question in the title of their target article, and proceed to argue that the answer is: Of course not; but so what. If the issue were merely that of falsifiability, Ketelaar and Ellis would not have had much to say. The point is abundantly clear that, when properly constructed as theories and hypotheses, evolutionary approaches to psychological phenomena offer predictions that are exactly as falsifiable as those emerging from other theoretical contexts (Kenrick & Simpson, 1997). But that is of little moment, because falsifiability is to theory as ingestibility is to food. Just as objects must be ingestible to be food, assertions must be falsifiable to be scientific theory. But so what. Not every ingestible edible is a nutritious food, and not every falsifiable conjecture is a useful theory. If we are to separate wheat from chaff in the realm of scientific inquiry, we need to aim a little higher than mere falsifiability. It is toward this end that a Lakatosian perspective on scientific theories is important. It specifies additional criteria that scientists use to discern the utility of theories and metatheoretical frameworks—to separate the chaff from the wheat, the taffy from the tofu of intellectual nourishment. Judged against these criteria, the evolutionary metatheoretical approach to psychological phenomena is generative, and the theories borne of this approach can be useful.

So, Ketelaar and Ellis make a strong case that evolutionary explanations are falsifiable and more. Will this finally put an end to the skepticism that greets evolutionary explanations of psychological phenomena? We suspect not. The problem is that the article attends

simply to the logical fact of falsifiability, rather than the psychological perception of falsifiability. Rather than raising the matter of unfalsifiability and then quickly dismissing it as a nonissue, it might be more instructive to ask, If evolutionary explanations are falsifiable, why are they perceived not to be?

There are many reasons. We discuss just one particular reason—one that has important implications for the way people think about and do evolutionary psychology. The reason is this: When people claim that evolutionary explanations are unfalsifiable, what they really mean to say is that these theories are unverifiable; and they are partly right.

### The Multiple Models Within Evolutionary Psychological Theories

To appreciate this assertion, it is necessary to attend to a point that is implicit in Ketelaar and Ellis’s Figure 2: Evolutionary psychological theories are comprised of two logically distinct conceptual models—one model that specifies the operation of psychological processes operating in contemporary contexts, and another model that specifies evolutionary processes that explain how the contemporary psychological processes emerged to begin with. Any evolutionary psychological theory identifies evolutionary processes that, operating over the course of time, could logically result in a population of individuals bearing specific features. This constitutes a model of evolutionary origins. If that were it, the theory would be evolutionary,