
AUTHORS' RESPONSE

On the Natural Selection of Alternative Models: Evaluation of Explanations in Evolutionary Psychology

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A central goal of our target article was to evaluate the soundness of evolutionary psychology's epistemology in relation to the critical claim that evolutionary explanations are unfalsifiable. None of the 16 commentators challenge our central assertion—that the methods and strategies employed by evolutionary psychologists to generate and test hypotheses are scientifically defensible—and thus we consider our basic goal to have been achieved. However, the commentators raise a number of thoughtful and thought-provoking points. In our response to these commentaries we focus on a subset of philosophical and metatheoretical issues that we believe are most deserving of further discussion. The first part of this rejoinder addresses issues concerning evolutionary psychology and the philosophy of science; the second part addresses issues concerning the core assumptions of evolutionary psychology.

Issues in Evolutionary Epistemology

Epistemology is that branch of philosophy concerned with understanding the nature of knowledge, including the criteria for evaluating claims to knowledge (see Dancy & Sosa, 1992; Flew, 1979). The commentators raise several issues concerning our presentation of evolutionary psychology's epistemology, including our choice of the Lakatosian framework, the distinction between verification and falsification, the relative importance of prediction versus explanation, and whether evolutionary psychology meets the criteria of scientific progressivity.

Why Lakatos?

Several commentators suggest that our argument would have been stronger if we had established the superiority of Lakatos over other approaches in philoso-

phy of science. Holcomb, for example, questions why we applied such a "fine-grained" analysis to Lakatos (e.g., elaborating the Lakatosian "protective belt" into three levels of explanation) but not to other philosophers such as Kuhn, Popper, Laudan, or Quine. Caporael and Brewer claim that our choice of Lakatos was out of date and that we ignored more recent trends in philosophy of science such as Cartwright's (1983) putatively "antireductionist" bent. Still other commentators (Fletcher; Haig & Durrant) wonder why we did not attempt to fully integrate the Lakatosian framework with other approaches such as Thagard's (1992) conception of "explanatory coherence."

We do not believe that the success of our argument hinges on establishing the superiority of Lakatos over alternative approaches in philosophy of science. Our goal was simply to demonstrate that the Lakatosian framework provides an adequate description of how psychological scientists actually go about their day-to-day epistemological business of constructing and evaluating explanations. Using the Lakatosian framework we illustrated how the generation of competing explanations from a single metatheory is simply a function of the multiple levels of explanation in science rather than evidence of unfalsifiability or faulty epistemology. We maintain that the success of this line of argumentation is predicated on the descriptive adequacy of the Lakatosian framework, and not on its superiority over alternative philosophical approaches. Nonetheless, there are specific reasons why the Lakatosian philosophy of science is particularly well-suited to the task of evaluating evolutionary psychology's epistemology.

First, and foremost, the Lakatosian framework is especially relevant to addressing the Popperian unfalsifiability criticism that has been repeatedly leveled against evolutionary psychological explanations.

In particular, much of Lakatos's (1970) philosophy of science emerged as a direct response to Popper's (1959) problematic description of science and its emphasis on falsification (Newell, 1990). Popper portrayed science as fundamentally a competition between a protagonist (a theory that champions an idea) and an antagonist (the facts about the world that can prove the idea wrong). To Popper, the only interesting outcome of this competition—and indeed the only genuine scientific discovery—was defeat of the protagonist (i.e., falsification of the theory by contrary facts). Popper viewed science as proceeding by bold speculations (that can never be proven true), followed by powerful refutations that eliminate them, followed by newer speculations that are, at least at the beginning, still unrefuted. Lakatos (1970), by contrast, portrayed science as fundamentally a competition between rival protagonists (theories). Whereas Popper viewed facts as executioners of theory, Lakatos viewed facts as arbitrators that determined the outcome of disputes between theories. From a Lakatosian perspective, if a theory generates novel predictions that lead to new knowledge, then it gains in the competition. Conversely, if a theory tinkers with its assumptions to accommodate chance discoveries or facts that were anticipated by a rival theory, then it loses in the competition. Thus, some of the most interesting results of the competition between theories involve corroboration rather than refutation, and theories are judged by the cumulative weight of the evidence rather than by a single crucial experiment. We have argued that the Lakatosian philosophy of science provides a better description of actual theoretical development in scientific psychology than does the Popperian philosophy of science (see Meehl, 1978, 1990; Newell, 1990).

Further, our target article was written by psychological scientists for psychological scientists. Thus, we tried to focus on those issues and concepts that were both relevant to the unfalsifiability criticism and familiar to most psychologists. Popper, Kuhn, and Lakatos are all fairly well entrenched in modern psychology (see Meehl, 1978, 1990; Newell, 1990) and have substantially influenced how psychologists think about and conduct their science. Laudan, Thagard, and Quine, for better or worse, have at best been esoteric influences in scientific psychology. Even Kuhn's (1962) influential writings on scientific progress are much more relevant to discussions of scientific objectivity than to the issue of falsifiability–unfalsifiability per se. In this light, Lakatos and Popper (more so than Laudan, Thagard, Quine, or even Kuhn) provide appropriate frameworks for evaluating evolutionary explanations in psychology. By adopting this tack, we avoided discussing many of the conceptual and definitional nuances that so dominate the day-to-day workings of philosophers of science and theoreticians in evolutionary biology (see Dennett, 1995; Holcomb,

1993; and Ruse, 1998, for overviews of current debates in evolutionary epistemology).

Verification Versus Falsification

Several commentators (Caporeal & Brewer; Holcomb; Richardson; Schaller & Conway) state that evolutionary psychological explanations are unverifiable because evolutionary accounts make inferences about historical processes that cannot be directly observed. This point is important because charges of unverifiability are often invoked by creationists and other critics (e.g., Watchtower Bible and Tract Society of New York, 1985) who argue that natural selection is only a theory and that scientists cannot prove it to be true. Although it is, of course, true that explanations of phenomena that cannot be directly observed are unverifiable, there are two important qualifications to this criticism that must be appreciated when evaluating evolutionary explanations.

First, as discussed by Schaller and Conway, unverifiability is conceptually distinct from unfalsifiability. Perhaps Popper's greatest legacy to scientific psychology is that he forcefully articulated a fundamental asymmetry between verification and falsification. Popper (1959) argued that although particular statements (hypotheses) cannot be unequivocally verified, they can be refuted or falsified.¹ For this reason Popper placed corroboration (establishing that an explanation is consistent with the data), rather than verification, in opposition to falsification. Popper argued that although it is possible to gather corroborating data to support a particular explanation, no amount of empirical evidence would allow, for example, Sherlock Holmes to unequivocally verify (i.e., prove) a particular explanation for the discovery of a cadaver (such as "the butler committed the murder with a pistol in the pantry"). This is because it is possible to identify an infinity of alternative inductive inferences that are consistent with the existing corpus of data (a conundrum known as the problem of induction; see Popper, 1959; Salmon, 1967, 1990). Nonetheless, a single piece of evidence (e.g., the fact that the maid had been dead for 3 years) could be used to unequivocally reject an alternative explanation (such as "the murder was committed by the maid"). In science, then, just as in the judicial system, certain accounts are accepted over alternative accounts, not because they have been absolutely verified (shown to be true), but rather because they alone are the best

¹Of course, many qualifications to Popper's original claims have now been identified, including the counterclaim that the standards for falsification are as difficult to obtain as the standards for verification (see Kuhn, 1977; Lakatos, 1970, 1974; Maxwell, 1972; Meehl, 1978, 1990; Putnam, 1974).

available explanation that emerges from the set of corroborated alternative accounts.

Hence, even though accounts of evolutionary origins cannot be directly verified, they can be empirically corroborated or empirically falsified. More specifically, well-formulated evolutionary models generate testable hypotheses and predictions that have important empirical consequences. Indeed, contrary to the assertions in Holcomb's commentary, evolutionary explanations are falsifiable at all levels of explanation, including the metatheoretical level of analysis. For example, mechanisms in one species designed exclusively to promote the welfare of another species, or mechanisms in an individual designed specifically to promote the welfare of a conspecific reproductive competitor, cannot arise through natural selection (Symons, 1987); the existence of such mechanisms would constitute a falsification of a core assumption of the evolutionary metatheory. Likewise, as discussed in the target article, if the species-typical psychological mechanisms that underpinned family violence were not nepotistically biased but instead followed an "easy striking distance" rule that applied equally across different degrees of genetic relatedness, then this would constitute a falsification of a basic assumption of inclusive fitness theory. Similarly, if in any species the sex that invests more in offspring (usually females) was in general less discriminating in choice of mates than the sex that invests less (usually males), then this would constitute a falsification of a key assumption within Trivers's (1972) theory of parental investment and sexual selection.²

²Of course, none of these theories are likely to be shot down by a single falsification bullet. As emphasized by Lakatos (1970, 1978), theories are evaluated by the cumulative weight of the evidence in relation to alternative theories. Even in the face of predictive failures or falsifications, a theory may be retained as the best available explanation in a given domain. A good example of this was the apparent falsification of natural selection theory in the latter part of the 19th century, when calculations made by Lord Kelvin (based on laws of thermodynamics) placed numerical strictures on the length of geologic time available for evolutionary forces to operate (Burchfield, 1975; see discussion by Fletcher, 1996, this issue). These strictures ostensibly demonstrated that the age of the earth was too young to have enabled evolution by natural selection to occur. Darwin, however, did not regard Lord Kelvin's calculations as adequate grounds for rejecting natural selection theory. Rather he regarded these observations as an anomaly, which he (correctly) expected would be resolved by future research. Although the anomaly caused turmoil for evolutionary theory, one reason that Darwinism survived was because there was no plausible alternative theory to take its place. That is, there was no alternative theory that could (a) account for the large range of diverse facts that were so parsimoniously explained by natural selection theory and (b) successfully predict so many new facts. Darwinism emerged from the turmoil in the early 20th century when the discovery of radiation (an internal source of heat) dramatically increased estimates of the age of the earth. The new estimates enabled natural selection theory to digest the apparent anomaly and turn it into positive evidence.

Second, in modern philosophy of science, verification is generally considered too high a standard to be of practical use in evaluating scientific explanations (e.g., Feigl, 1956; Haig & Durrant, this issue; Hooker, 1987; Meehl, 1990; Salmon, 1967, 1990). As Popper (1959) first explained, verification is untenable as a criterion for evaluating specific statements (hypotheses and predictions) because no amount of empirical evidence actually proves (verifies) that a particular explanation is true. Indeed, strict adherence to verifiability as an evaluative criterion would all but eliminate (among others) archeology, cosmology, evolutionary biology, forensic medicine, paleontology, tectonic geology, quantum physics, and all of the behavioral sciences as legitimate scientific enterprises. Instead, a more common approach to science (e.g., Cronbach & Meehl, 1955; Hooker, 1987; Meehl, 1990) emphasizes the process of establishing acceptable claims to knowledge (rather than "truth" per se) through methods analogous to construct validation. To establish construct validity, it is necessary for a middle-level evolutionary theory to specify the meaning of a construct (i.e., to specify the functional design of a proposed adaptation), distinguish it from other constructs, and generate precise, testable predictions about how measures of the proposed construct should and should not relate to other variables (see the American Psychological Association's [1985] discussion of construct validation). In this manner, well-validated evolutionary explanations can count as acceptable knowledge claims; that is, these explanations can be corroborated (or falsified), even though they cannot be directly verified (see Salmon, 1967, 1990, 1992, for detailed discussion of verification and inductive reasoning in science).

Prediction Versus Explanation

Several commentators (Fletcher; Haig & Durrant) ask why we emphasized predictive success over other evaluative criteria. A common concern was that the Lakatosian perspective unnecessarily "devalues" post hoc explanatory power in favor of a priori predictive success. Ironically, as discussed in the target article, early critics of evolutionary psychology argued exactly the opposite, claiming that "evolutionists use consistency with the data as the *sole criterion* [italics added] and consider their work done when they construct a plausible story" (Gould & Lewontin, 1979, p. 4). We countered this claim by describing how evolutionary scientists test divergent predictions generated by different evolutionary accounts. Rather than simply searching for confirmatory data, we argued that testing evolutionary explanations involves sorting through a set of plausible alternative accounts. Better evolutionary explanations then drive out weaker ones through

normal scientific channels (as discussed in the target article).

We concur with the Haig and Durrant commentary as well as with Fletcher that the history of science reveals many cases in which the ability to provide a coherent and parsimonious account of known facts has proven to be at least as important in the evaluation and acceptance of a theory as has the ability to successfully predict new facts. Explanatory power is an especially important criterion for theory evaluation during periods of "normal paradigm science" (in which there are coherent, agreed-upon metatheoretical assumptions; in which there is a well-established base of knowledge; in which scientific questions are carefully anchored in this base and are designed to extend it; and in which discrepancies between theory and observation can be clearly identified and analyzed [see Kuhn, 1962; Richters, 1997]). It follows that in normal paradigm science there are constraints not only on the scope and nature of theories but on the ad hoc amendments that can be made to theories. In this context, successful explanation of previously known facts, in and of itself, is an important component of theory evaluation: The more that a theory can explain, the better the theory.

By contrast, explanatory power, in and of itself, provides a less compelling basis for theory evaluation during periods of "preparadigm science" (in which disagreement over fundamental starting assumptions occurs in the mainstream of scientific activity rather than on the frontiers; in which there is a minimum of cumulative theoretical progress; in which there is a diversity of fact-gathering activities but little integration of knowledge; and in which there is relatively little ability to discriminate between real and illusory phenomena [see Kuhn, 1962; Nagel, 1961; Richters, 1997]). It follows that in preparadigm science there are relatively few constraints on the scope and nature of theories and on the number and type of ad hoc amendments that can be made to those theories. This makes it relatively easy to stretch theories to accommodate known facts. Consequently, post hoc explanatory power, in and of itself, provides a weaker basis for theory evaluation in preparadigm science than it does in normal paradigm science.

Although scientists working within the evolutionary psychology research program appear to be operating in a state of normal paradigm science (see our discussion following), evolutionary psychology is still a minority perspective within mainstream psychology. As noted by many observers (e.g., Bevan & Kessel, 1994; Koch & Leary, 1992; Richters, 1997), the broader field of psychology remains in a preparadigm state. A compelling demonstration of this is found in Monte's (1999) introductory textbook on theories of personality (see also Meehl, 1978). This book reviews 19 different theories of human nature, ranging from Freud's psychoanalytic theory to Klein's object relations theory, from Erikson's

psychosocial life-span theory to Kelly's personal construct theory, from Maslow's self-actualization theory to Skinner's radical behaviorism, from Bandura's social learning theory to Eysenck's biological trait theory. These grand theories of personality form a central junction for psychology and have fundamentally influenced the allied areas of social, developmental, and clinical psychology. In the final chapter of his book, however, Monte (1999) concluded:

So many aspects of the theories presented in this book, or major aspects of them, are not refutable that we are prompted to ask two questions: 1. Is there any reasonable way to decide which theory is right? 2. If psychology is a science, why does it tolerate so many "unscientific" theories? ... With a minority of exceptions, such as the social cognitive theory of Bandura and the biological typology of Eysenck, most of the theories we have reviewed [a] make no precise or testable predictions, [b] generate few, if any, laboratory studies, and [c] frequently lead to disputes of opinion rather than fact. (p. 933)

Like the grand theories of personality reviewed by Monte, many grand theories in psychology are so loosely formulated that they can account for almost any data (and are falsified by none; see Meehl, 1978). Consequently, post hoc explanation carries relatively little weight in psychology (especially post hoc accommodation of a theory to explain unanticipated findings). We surmise that there are very few empirical findings in psychology that, after the fact, could not be claimed by multiple theories as falling within their explanatory purview. Moreover, still other theories could claim the finding after making a few ad hoc adjustments to their auxiliary assumptions.

It is worth noting that the Lakatosian view of science anticipates this post hoc scramble to amend one's theories. In particular, the Lakatosian scientist wishes to discover which of a series of alternative theories is best able to generate new knowledge and accommodate known anomalies without having to specify ad hoc assumptions. Successful prediction is critical because it leads to the acquisition of knowledge. Although post hoc accommodation of anomalies is to be expected, Lakatos argued that when an explanatory model begins to contribute only marginally to the advancement of knowledge because it is employed primarily in dealing with anomalies, this explanatory system is viewed as degenerative rather than progressive. Due to the problem of accommodation, a solid track record of predictive success by one explanatory account is more informative about the progressivity of a theory (relative to other theories) than are claims of post hoc explanatory power. This is why forward-looking predictive success is a more compelling basis for theory evaluation in psychology than is backward-looking explanatory power.

Is the Evolutionary Psychological Research Program Progressive?

Several commentators (Caporael & Brewer; Forster & Shapiro; Holcomb) question whether the evolutionary psychological research program meets the criteria of progressivity. Forster and Shapiro treat this issue in the most detail. They propose that, because the hard-core assumptions of evolutionary theory are now well-confirmed, the general evolutionary research program is in a period of “normal science” (Kuhn, 1962). Accordingly, evolutionary scientists focus on applying the hard-core assumptions to investigate puzzles and questions that have aroused their interest (rather than on testing the hard-core assumptions *per se*). Such applications, Forster and Shapiro suggest, occur within the protective belt of a metatheoretical research program. It follows, therefore, that evolutionary psychology—the application of the hard-core assumptions of general evolutionary theory to questions concerning the origins, design, and function of human psychological mechanisms—is part of the protective belt of general evolutionary theory and should be evaluated as such. This line of reasoning takes the methodological spotlight off general evolutionary theory and shifts it to evolutionary psychology *per se*. The question then becomes: Does evolutionary psychology (which represents only one of the many possible applications of the hard-core assumptions) meet the criteria of scientific progressivity?

Although we believe that the hard-core assumptions are an indispensable part of evolutionary psychological explanations (any building is only as strong as its foundation), it is nonetheless reasonable to ask whether the evolutionary psychological research program (below the level of general evolutionary theory) is currently progressive. Lakatos (1976) provided clear criteria for answering this question:

A research programme is said to be *progressing* as long as its theoretical growth anticipates its empirical growth, that is, as long as it keeps predicting novel facts with some success (“*progressive problemshift*”); it is “*stagnating*” if its theoretical growth lags behind its empirical growth, that is, as long as it gives only *post hoc* explanations either of chance discoveries or of facts anticipated by, and discovered in, a rival programme (“*degenerative problemshift*”). (p. 11)

The evidence that evolutionary psychology is a currently progressive research program is overwhelming. As discussed in the target article, evolutionary studies have played a crucial role in the growth of knowledge in psychology. Buss, Haselton, Shackelford, Bleske, and Wakefield (1998; Table 1) listed 30 recent empirical discoveries about human psychology that are clearly tied to theoretical growth in evolutionary psy-

chology, including: evolved landscape preferences; sexually dimorphic mating strategies; waist-to-hip ratio as a determinant of attractiveness judgments; women’s desires for mates with resources found in 37 cultures; men’s preferences for younger mates documented in 37 cultures; the use of cheater detection procedures in social exchange reasoning; stepchild abuse at 40 times the rate of nonstepchild abuse; relationship-specific sensitivity to betrayal; sex-linked shifts in mate preferences across the lifespan; predictable patterns of spousal and same-sex homicide; pregnancy sickness as an adaptation to teratogens; maternal–fetal conflict during human pregnancy; predictably patterned occurrence of allergies; different human sperm morphs; superior female spatial location memory; design of male sexual jealousy; sex differences in sexual fantasy; deception in mating tactics; profiles of sexual harassers and their victims; sex differences in the desire for sexual variety; facial asymmetry as an indicator of poor psychological and physical health; frequentist reasoning in human cognition; predictable courses of conjugal dissolution in 89 cultures; socialization practices across cultures differing by sex and mating system; patterns of risk taking in intrasexual competition for mates; shifts in grandparental investment according to sex of grandparent and sex of parent; perceptual adaptations for entraining, tracking, and predicting animate motion; universal perceptual adaptations to terrestrial living; and mate guarding as a function of female reproductive value. In sum, the theoretical growth of evolutionary psychology has not only anticipated an array of novel facts but has also yielded a substantial empirical harvest across a range of topics in psychology.

Holcomb argues that, according to Lakatosian criteria, we did not demonstrate the progressivity of the evolutionary psychological research program because we did not compare it to a rival research program. We believe that this criticism is invalid for at least two reasons. First, it is important to distinguish between attempts to evaluate a research program and attempts to reject it. As indicated in the preceding quotation by Lakatos, the progressivity of a research program can be evaluated in absolute (noncomparative) terms based on the extent to which its theoretical growth anticipates its empirical growth. It is only rejection of a research program that must be comparative. Thus, comparison of rival research programs is not necessary to demonstrate progressivity or degenerativity (see also Kuhn, 1962).

Second, there is no rival research program to evolutionary psychology; that is, there is no alternative scientific explanation for the origins and complex functional design of the human brain–mind (Buss, 1995; Symons, 1987; Tooby & Cosmides, 1992; Williams, 1966). Consequently, comparisons with a rival research program are not currently relevant. Moreover, because the

hard-core assumptions of general evolutionary theory and its derivative middle-level theories can be applied to virtually all aspects of human psychology, the evolutionary psychological research program offers a unifying framework for psychological science. This framework enables cumulation of knowledge across diverse areas of psychology and progression toward a "big picture" of the human brain–mind. Although nonevolutionary theories of the origins of particular psychological phenomena can often be developed in competition with middle-level evolutionary theories of these phenomena, nonevolutionary theories are not unified by a coherent, agreed-upon metatheory. Consequently, different nonevolutionary explanations are often largely independent and (taken together) yield a mountain of empirical generalizations rather than an integrated body of knowledge. Because of this lack of conceptual integration, there is no single overarching nonevolutionary research program that can be tested against the content domain of evolutionary psychology.

Comparisons can be made, however, at the level of middle-level theories. We fully agree with Wood and Eagly (and Forster & Shapiro) that specific middle-level evolutionary theories should be tested against other middle-level theories, both from outside of the evolutionary psychological research program and from within it. Normal criteria of theory evaluation apply. An excellent exemplar of this process is the current rivalry between Buss's (1989) explanation of sex differences in human mate preferences based on parental investment and sexual selection theory and Eagly and Wood's (1999) explanation of sex differences in human mate preferences based on social structural theory.

Do Evolutionary Psychologists Employ the Right Set of Metatheoretical Assumptions?

Several commentators voice concerns over our choice of metatheoretical assumptions and suggest various caveats. Caporael and Brewer challenge our use of inclusive fitness theory as the metatheory for evolutionary psychology and advocate instead the use of multilevel selection theory. Richardson questions our focus on adaptation through natural selection and echoes Gould and Lewontin's (1979) concerns regarding the potential "overapplication" of the adaptationist program to human psychology. Miller, although concurring with our gene-centered adaptationist approach, voices concerns over the common emphasis in evolutionary psychology on the modularity, efficiency, and universality of psychological mechanisms (e.g., Tooby & Cosmides, 1990a, 1992) and suggests that sexually selected fitness indicators violate these claims. To address these points, we briefly discuss the metatheoretical underpinnings of evolutionary psy-

chology (i.e., the adaptationist program in evolutionary biology) and then apply a Lakatosian analysis to the question of why the commentators' proposed metatheoretical revisions have or have not (yet) been incorporated into the evolutionary psychological research program.

Evolutionary Psychology and the Adaptationist Program

Evolutionary psychology is the application of the adaptationist program in evolutionary biology to the study of human psychology. The core logic of the adaptationist program can be stated quite simply: Random variation (i.e., mutation) exists in the genetic material of individuals. This variation (together with environmental inputs during ontogeny) produces differences between individuals in their manifest attributes (i.e., in their phenotypes). In each generation, natural selection acts like a sieve on this variation (Dawkins, 1996). Whereas most genetic variants are either selectively neutral or produce phenotypic effects that detract from the organism's ability to survive and reproduce (and thus are eventually filtered out), other genetic variants produce phenotypic effects that contribute to the organism's survival and reproduction and thus pass through the sieve (becoming more prevalent in future generations). Through this filtering process, natural selection (a) produces small incremental modifications of preexisting phenotypes and (b) leads to accumulation of phenotypic characteristics that are organized for reproduction (specifically, gene reproduction). These characteristics are referred to as adaptations because they served specific functions (such as a change in color increasing an organism's ability to avoid detection by predators) that, during their period of evolution, recurrently promoted the survival of the genes that direct their construction. Adaptations are reliably developing characteristics of species that, over long periods of evolutionary time, interacted with the physical, social, or internal environment of individuals in ways that recurrently solved problems of survival and reproduction (Dawkins, 1976, 1982; Tooby & Cosmides, 1990a, 1992; Williams, 1966, 1992). These basic assumptions of the adaptationist program are largely accepted as "true" in the scientific community and are not disputed by any of the commentators.

Drawing on the adaptationist program, a central assumption of evolutionary psychology is that the human brain–mind is comprised of a large number of specialized cognitive adaptations that were shaped by natural selection over vast periods of time to solve the recurrent information-processing problems faced by our ancestors (Symons, 1995). Although there is ongoing debate about the level of domain specificity of cognitive mechanisms (e.g., Cosmides & Tooby, 1994;

Hirschfeld & Gelman, 1994; Miller, this issue), Daly and Wilson (1999) stated that

It does not appear that any substantive controversy remains about the validity of the proposition that human cognition comprises a multiplicity of information-processing capabilities, executed by a multiplicity of “mental organs” and/or “algorithms” with distinct adaptive functions (see, e.g., Gazzaniga, 1995). (p. 510)

In total, evolutionary psychology imported the adaptationist program from evolutionary biology, added the core assumption of domain specificity of many psychological adaptations, and then trained the theoretical and empirical spotlight on human mental processes.³

Inclusive Fitness Theory Versus Multilevel Selection Theory

Caporael and Brewer assert that evolutionary psychologists rely on an outdated form of evolutionary theory—inclusive fitness theory—and should shift their orientation to multilevel selection theory (MLST). Whereas inclusive fitness theory conceptualizes genes or individuals as the units of selection (see Dawkins, 1976; Hamilton, 1964; Williams, 1966), MLST is based on the premise that natural selection is a hierarchical process that can operate at many levels, including genes, individuals, groups within species, or even multispecies ecosystems. Thus, MLST is conceptualized as an elaboration of inclusive fitness theory (adding the concept of group-level adaptation) rather than an alternative to it (Sober & Wilson, 1998; Wilson & Sober, 1994). Proponents of MLST argue that indi-

vidual and group level adaptations can be distinguished:

If the genes for the trait spread within a population, then they evolve by individual selection, and the trait is an individual-level adaptation. If the genes for the trait are selectively neutral or disadvantageous within populations, but cause entire populations to survive and reproduce better than other populations, then they evolve by group selection and the trait is a group-level adaptation (Wilson, 1997, pp. 346–347).

For example, individual-level selection within a population tends to favor even sex ratios because each offspring has one male and one female parent; thus, whichever sex is less common tends to produce more offspring, resulting in frequency-dependent selection for greater numbers of the less common sex (Fisher, 1958). By contrast, MLST theorists have hypothesized that group-level selection between populations may favor female-biased sex ratios because it enables greater total production of offspring. According to MLST, group-level adaptations are most likely to arise when members of a group have a high degree of “shared fate,” when there is a highly subdivided population structure, when there are low levels of reproductive competition within groups, and when there is differential survival and reproduction between groups. There is currently a debate among evolutionary biologists and psychologists about whether group-level adaptations are theoretically possible and, if so, over how viable a force group selection is in nature (see Cronk, 1994; Dawkins, 1976, 1994; Sober & Wilson, 1998; Wilson & Sober, 1994). In general, MLST is not widely used or accepted by evolutionary psychologists. Nonetheless, a number of evolutionary scientists have employed multilevel selection principles to explain existing puzzles (such as female-biased sex ratios [e.g., Colwell, 1981; Smith & Hagen, 1996] and decreased parasite virulence [e.g., Lenski & May, 1994]) and to solve practical problems (such as increasing egg production in multihen cages [Muir, 1996]).

Will evolutionary psychologists heed the call of Caporael and Brewer (and of Wilson & Sober, 1994) to incorporate MLST into their metatheory? We believe that this is ultimately an empirical question. Consider, for example, the issue of female-biased sex ratios. Although natural selection generally favors a 1:1 sex ratio, there are many examples in nature of deviations from this ratio. Drawing on the metatheoretical principles of inclusive fitness theory, a series of important middle-level evolutionary theories (e.g., Fisher, 1958; Hamilton, 1967; Trivers & Willard, 1973; van Scheik & Hrdy, 1991) have been developed to explain these deviations. In addition, as stated previously, group selection principles have also been evoked to explain these deviations (Colwell, 1981). To date, only the

³As emphasized by Wood and Eagly, there is not a single, clear road from the adaptationist program to the specifics of human psychology and behavior. Daly and Wilson (1999) included both evolutionary psychology (as presently defined) and behavioral ecology (e.g., Cronk, 1991) as part of the evolutionary psychological research program because both approaches employ the adaptationist program in biology as a guiding framework for the study of human behavior. However, we view evolutionary psychology and behavioral ecology as conceptually distinct applications of the adaptationist program to humans for two major reasons. First, at a theoretical level, behavioral ecologists do not accept the core assumption of domain specificity of many psychological adaptations and instead assume that humans have a domain-general capacity for scenario building and learning of behaviors that produce positive reproductive outcomes under a wide range of conditions (even evolutionarily novel conditions). Second, at an empirical level, behavioral ecologists do not specifically study mental processes, and thus they do not share their central content area with evolutionary psychologists. (For comparisons of evolutionary psychology and behavioral ecology, see Crawford, 1993; Smith, in press; Symons, 1992.) Thus, we believe that it is legitimate to evaluate evolutionary psychology separately from behavioral ecology.

gene-centered middle-level theories have proved useful in predicting the conditions under which individuals adjust offspring sex ratios (Ridley, 1993; Trivers, 1985, chapter 11). As one proponent of the gene-centered view (Trivers, 1985) stated:

Our ability to explain the facts concerning the primary sex ratio in dozens of contexts and hundreds of species is one of the great achievements of modern evolutionary biology and one that gives strong support to a whole host of assumptions. (p. 271)

According to a Lakatosian perspective, for a multi-level selection approach to supersede the gene-centered approach as an explanation for female-biased sex ratios, it must both account for the empirical successes of the inclusive fitness-based middle-level theories and successfully predict novel facts about the occurrence of female-biased sex ratios—facts that have not been (and ideally cannot be) accounted for by a selfish gene approach. If, for example, the conditions that ostensibly facilitate group selection (see previous discussion) successfully anticipated the distribution of female-biased sex ratios, then many skeptics would be convinced.

In terms of evolutionary psychology, MLST needs to demonstrate its usefulness in increasing our understanding of how the mind works. If group selection has been an important force in human evolution, then it would have tremendous implications for personality and social psychology and group-level adaptations would be apparent in studies of the human brain–mind. Some proponents of MLST (Sober & Wilson, 1998; Wilson, 1997; Wilson & Sober, 1994) contend that such adaptations are apparent, and they have applied group selectionist analyses to a variety of known human psychological phenomena (e.g., selfless behavior in Hutterite communities, cooperative team behavior, group-level decision-making processes such as “groupthink”). These post hoc explanations of known phenomena, however, are not enough. As Lakatos (1970, 1978) showed, it is relatively easy to stretch theories to accommodate known facts (see our previous discussion of prediction vs. explanation). The key question, as in the sex ratio example, is whether group selection models can predict facts about human psychology that were not known in advance and are not easily explained by a selfish gene account. When and if MLST begins to contribute significantly to the growth of knowledge in psychology by anticipating new facts and resolving old puzzles, then it would naturally become part of evolutionary psychology’s metatheory. Until then MLST will be to human psychology what the notion of “cold fusion” is to physics: an idea whose theoretical plausibility is currently being debated, but for which little empirical evidence has been marshaled.

Critiques of the Traditional Adaptationist Approach

Some critics of evolutionary psychology actually oppose the very idea of the adaptationist approach in evolutionary biology. Richardson, for example, criticizes a particular interpretation of the adaptationist program that (we would argue) is actually not endorsed by evolutionary psychologists. Specifically, in challenging our focus on adaptation through natural selection, Richardson argues that the study of current function of putative adaptations is a central theme in evolutionary psychology. Moreover, he portrays evolutionary approaches as adopting a kind of “optimality analysis” that emphasizes “the extent to which a trait optimizes fitness” (this issue). By contrast, we view the adaptationist program as emphasizing precisely the opposite (see Buss, 1995, for a lucid discussion of the distinction between “fitness-optimizing” approaches and evolutionary psychology). Rather than describing evolved characteristics as “optimally designed” mechanisms, evolutionary psychologists more typically use words such as gerrymandered devices, Rube-Goldberg machines, or weird contraptions to describe adaptations (see Dawkins, 1982; Dennett, 1995). This is the case because evolutionists acknowledge many possible constraints on optimal design, such as the slow speed of evolution, the lack of available genetic variation, and the necessity of coordination with other mechanisms (Buss et al., 1998; Dawkins, 1982). Thus, evolutionary psychologists view the generation and testing of hypotheses about evolved mechanisms as a process of sorting through a stockpile of “evolutionarily plausible” devices rather than a process of identifying the one “evolutionarily optimal” mechanism for solving a particular adaptive problem.

Along these lines, the application of the adaptationist program to cognitive psychology has been dominated by precisely the opposite approach claimed by Richardson. Whereas the traditional approach in cognitive psychology has been to compare models of human judgment to optimal standards of reasoning such as the normative rules of inference of the logical calculus or optimal Bayesian algorithms, evolutionary inspired research places an emphasis on satisficing (rather than optimizing) when describing plausible information-processing devices (Gigerenzer & Todd & the ABC Research Group, 1999; Ketelaar & Todd, in press).⁴ In sum, there is a world of difference between the computational modeling approaches em-

⁴The modern origins of the term *satisficing* are often attributed to Simon (1956), who co-opted this archaic English term to describe decision processes that were both adequate (merely satisfactory) and successful. Satisficing approaches are thus contrasted with approaches that “optimize” or “optimize under constraints” (see Gigerenzer et al., 1999, for an excellent overview of these issues).

ployed by evolutionary psychologists and the sorts of “optimality analyses” that Richardson and other critics worry about (see Cosmides & Tooby, 1987; Gigerenzer et al., 1999; Tooby & Cosmides, 1992).

Richardson further suggests that the study of current function of putative adaptations is of primary importance to the evolutionary psychological research program. By contrast, evolutionary psychologists actually emphasize how our minds evolved to meet the selection pressures of ancestral, not current, environments (see Symons, 1992; Tooby & Cosmides, 1992). Bowlby (1967), perhaps the first modern era evolutionary psychologist, coined the term *environment of evolutionary adaptedness* (EEA) to emphasize this very point. The EEA refers to a description of the enduring properties of the environment in which a particular characteristic evolved (Tooby & Cosmides, 1990b, 1992). Rather than viewing the EEA as an actual place (like Pittsburgh) or a type of place (like a jungle or savanna), evolutionary psychologists characterize the EEA as a statistical composite of the recurring structural features of the environments that constituted the specific selection pressures that were present during the course of a particular adaptation’s evolutionary history. To avoid such long-winded descriptions, however, most evolutionary psychologists simply use the term EEA to refer to the properties of ancestral environments to which our evolved mechanisms owe their current design. Contrary to Richardson’s focus on the current function of adaptations, Bowlby (1967) emphasized that:

Not only does the new term [EEA] make even more explicit that organisms are adapted to particular environments but it draws attention to the fact that not a single feature of a species’ morphology, physiology, or behaviour can be understood or even discussed intelligently except in relation to that species’ environment of evolutionary adaptedness. (p. 64)

Along these lines, an assumption of evolutionary psychology is that mismatches between modern environments and the EEA often result in dysfunctional behavior (such as overconsumption of chocolate ice cream, television soap operas, video games, and pornography). Indeed, a central focus of the field of “Darwinian medicine” (Nesse & Williams, 1994; Williams & Nesse, 1991) is on how such mismatches compromise the effectiveness of adaptations. In sum, by characterizing the adaptationist program as the study of current function, Richardson presents a view of evolutionary psychology that many in the field would not endorse.

Further, reminiscent of Gould and Lewontin’s (1979) critique of the adaptationist program, Richardson suggests that evolutionary psychologists are sometimes too rash in applying Darwinian insights to the

study of the mind. As a result, Richardson cautions that evolutionary psychologists might invoke the term adaptation even when it is not appropriate, occasionally mistaking necessary architectural by-products (such as the red color of blood) for actual adaptations (such as the tertiary structure of hemoglobin that appears to be especially designed for binding and transporting oxygen, but also has the necessary by-product of appearing red to the human eye; see Boyd & Silk, 1997; Buss et al., 1998). We acknowledge that the majority of arbitrarily demarcated traits of organisms are not themselves adaptations but instead are byproducts of adaptations (Symons, 1995; Williams, 1966). Indeed, Williams (1966) stressed that the concept of adaptation was an onerous one, wherein special design can be recognized by the economy, efficiency, reliability, and precision with which effects are achieved (see also Buss et al., 1998; Symons, 1995; Thornhill, 1990). Richardson’s commentary highlights the debate among evolutionary scientists over the extent to which animal morphology and behavior can be understood as adaptations to the environment as opposed to by-products of adaptations or random effects of mutations (e.g., see Gould, 1991; Griffiths, 1992, for opposing views of this debate).

In addition, Richardson echoes Gould and Lewontin’s (1979) call for consideration of alternatives to natural selection (e.g., random genetic drift, developmental and structural constraints) to account for the origins of certain structures and traits of animals. These alternative approaches, although provoking an impressive volume of critical discourse (e.g., Borgia, 1994; Dawkins, 1986; Dennett, 1995; Mayr, 1983; Queller, 1995), have borne surprisingly little empirical fruit. (See Dennett, 1995; Millikan, 1993, for reviews of the theoretical and empirical status of these alternatives to natural selection.) Contrary to Richardson’s claims, the adaptationist program remains as strong as ever, both on theoretical and empirical grounds. As one evolutionary psychologist (Daly, 1991) stated:

Adaptationism, the paradigm that views organisms as complex adaptive machines whose parts have adaptive functions subsidiary to the fitness-promoting function of the whole, is today about as basic to biology as the atomic theory is to chemistry. And about as controversial. Explicitly adaptationist approaches are ascendant in the sciences of ecology, ethology, and evolution because they have proven essential to discovery; if you doubt this claim, look at the journals. Gould and Lewontin’s call for an alternative paradigm has failed to impress practicing biologists both because adaptationism is successful and well-founded, and because its critics have no alternative research program to offer. Each year sees the establishment of such new journals as *Functional Biology* and *Behavioral Ecology*. Sufficient research to fill a first issue of *Dialectical Biology* has yet to materialize. (p. 219)

What About Sexually Selected Fitness Indicators?

Miller (this issue) questions the emphasis in evolutionary psychology on efficiency, modularity, low heritability, and universality as necessary criteria for identifying psychological adaptations (see Tooby & Cosmides, 1990a, 1992). Although Miller concedes the importance of these criteria for identifying adaptations shaped by natural selection for survival purposes, he proposes that “the opposite arguments make more sense for adaptations that have been shaped by sexual selection as indicators of heritable fitness” (this issue; see also Miller, 1998, in press-a, in press-b). Miller argues that the existence of traits such as the peacock’s tail or the “stotting” behavior of gazelles⁵ (see Zahavi & Zahavi, 1997) presents a special challenge to some evolutionary psychological accounts of adaptation precisely because these characteristics appear to contradict basic assumptions regarding functional efficiency and low heritability.

Miller’s (1998, in press-a, in press-b) thesis deserves attention because it demonstrates how good genes and runaway models of sexual selection could, in principle, lead to identification of plausible alternative explanations for many important human cognitive and cultural capacities such as art, music, religion, humor, and intelligence. To date, such capacities have often been portrayed as nonadaptive by-products of other evolved mechanisms, largely because of their high heritability,⁶ high costs, large individual differences, and high correlations with other mental and physical abilities, all of which suggests that they are not good candidates for naturally selected adaptations. Yet, as Miller points out, high heritability and high costs are properties that one actually expects to observe in sexually selected fitness indicators. Miller suggests that by including the notion of sexually selected fitness indicators (and the specialized sensory apparatus for perceiving them) under the adaptationist umbrella, evolutionary psychologists may do a better job of accounting for the origins and possible

⁵Contrary to intuition, when approached by a predator not all gazelles will automatically hightail it and run, leaving only the weak and the sick to be taken by an attacking wolf. Rather, some of the more fit members of the herd will actually engage in a costly signaling display—referred to as “stotting”—that involves jumping high into the air several times prior to running off (see Zahavi & Zahavi, 1997). Only the fittest gazelles can afford to deploy the time and energy to send this costly message of “I’m so fit that I can afford to waste energy letting you know it, thus you’re better off attacking one of my weaker conspecifics, whom you’re more likely to catch.” If a gazelle that is slow or weak sends the wolf a phony signal about its fitness by engaging in stotting, it is likely to expend what little strength and energy it has just by transmitting this phony message. As Miller (1998, in press-a) pointed out, these sorts of traits (e.g., stotting in gazelles, peacocks’ tails) make valid and reliable signals of the individual’s level of fitness precisely because of this “unfakeable” linkage between the trait and the individuals’ underlying genetic fitness.

functions of currently perplexing, individually differentiated human capacities such as musical ability, artistic talent, creativity, and intelligence.

Does this constitute a radical departure for evolutionary psychology? As discussed in the target article, the evolutionary psychological research program has already incorporated the concept of sexually selected fitness indicators and applied it successfully to the study of fluctuating asymmetry and human sexual behavior. Miller, however, envisions a much broader role for sexually selected fitness indicators in the study of complex (and extravagant) mental capacities. If Miller’s theorizing about the origins of these capacities is correct, then it would require a reformulation of some current standards for identifying adaptations (e.g., low heritability, high functional efficiency).

Miller (1998) proposed that:

If a behavior is uniquely human, is selectively displayed by adult humans during courtship and sexual competition, is displayed in different forms and frequencies by males and females, and is clearly valued as a sexual display, then it is worth investigating as a sexually selected adaptation. (p. 117)

According to Miller, many aspects of human culture and cognition meet these adaptationist criteria (e.g., music, sports, and politics).

⁶Contrary to popular belief, naturally selected traits should exhibit low heritability. This is often misunderstood because some people fail to distinguish between an inherited trait and a heritable trait. The former refers to traits that are passed on from parents to offspring. In a trivial sense, any given gene-based trait (in a sexually reproducing species) is inherited from that individual’s parents; however, this does not imply that all traits necessarily entail genetic differences (variant genetic designs that differ between individuals) that can be inherited. For example, the genes underlying the number of eyes you will develop (two in humans, eight in some species of spiders) is clearly inherited from your parents (if both your parents are spiders, you will develop eight eyes; if they are humans, you will develop only two). Yet, because there is virtually no variance in the genetic basis for this trait within a given species (all humans have genes for two eyes), any differences in the phenotypic expression of this trait (how many eyes you develop) are due to differences in environments (whether or not you get an eye poked out) and cannot be due to differences in genes. By contrast, the genes underlying the color of your eyes are both inherited from your parents and heritable in the sense that different genetic variants for the trait of eye color do exist and can be inherited by different individuals. Some humans have genes for green eyes, others have genes for blue eyes. Eye color is both inherited (from parents) and heritable (differences in eye color are due, in part, to differences in genes); whereas the number of eyes you develop is clearly inherited, but not heritable. Because natural selection works by selecting the best reproducing variants from the population of genetic designs, one expects that the naturally selected traits that you inherit from your parents will show low coefficients of heritability (see Miller, in press-a; Tooby & Cosmides, 1990a, on this important distinction). In this sense, some adaptationists would argue that binocular vision (having two eyes as opposed to just one) is a potential adaptation, whereas having blue eyes (as opposed to green or brown) is not.

Although Miller's application of sexual selection theory generates consilience among many areas of empirical research (see Miller, in press-b), his explanations of already observed facts are only the first step in establishing acceptable claims to knowledge. A Lakatosian perspective places the spotlight on new empirical discoveries. An important strength of Miller's perspective is that good genes and runaway models of sexual selection can be used to generate clear, testable predictions about age differences, sex differences, and contextual variation in expression of specific cognitive and cultural capacities. When and if these sexual selection models begin to contribute significantly to the growth of knowledge in psychology by predicting new facts and resolving old puzzles (especially facts and puzzles about human cognitive and cultural capacities that are not easily explained by survival selection), then the notion of complex, sexually selected mental adaptations would naturally become incorporated into evolutionary psychology's metatheory. Finally, although the data demand this kind of wait-and-see approach, we believe that evolutionary psychology may benefit from more explicitly including sexually selected mental capacities (and corresponding assumptions concerning larger individual differences and higher heritabilities for these capacities) into its current conception of the adapted mind.

Summary

The Lakatosian philosophy of science provides criteria for comparing the usefulness of theories. Regarding the metatheoretical revisions suggested by the commentators—extension of inclusive fitness theory to incorporate group-level adaptations, consideration of alternatives to natural selection to account for the origins of certain structures and traits, consideration of certain types of mental traits (extravagant cognitive capacities) as sexually selected fitness indicators rather than naturally selected survival traits—the key question is whether any of these accounts

Has successfully “stuck its neck out” by predicting experimental results which had not been known in advance or whether it simply tinkers with its assumptions in such a way as to accommodate the already observed facts without successfully anticipating further, yet unobserved, novel facts, in the general spirit of the heuristic of the research programme. (Urbach, 1974, p. 101)

Gould and Lewontin's (1979) call for alternatives to the adaptationist approach in evolutionary biology has (thus far) failed because it has not generated an alternative research program. As emphasized by Lakatos, theories are replaced with better theories on the basis of

standards of scientific progressivity (not on the basis of clever rhetoric). The picture is somewhat more sanguine for MLST: It offers a possible extension of inclusive fitness theory that can be empirically evaluated. Specifically, the view of psychological adaptations as functionally designed to promote the survival and reproduction of groups has empirical consequences that clearly differ from the view of psychological adaptations as functionally designed solely to promote the survival and reproduction of genes. Likewise, the view of psychological adaptations as sexually selected fitness indicators has empirical consequences that clearly differ from the view of psychological adaptations as naturally selected survival devices. Both MLST theorists and sexual selection theorists have shown that they can account for known phenomena. We look forward to the proponents (and opponents) of these theories “sticking their necks out” in the future by making and testing bold predictions about phenomena that are as yet unobserved. May the best theories prevail.

Notes

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