Psychological Inquiry
2000, Vol. 11, No. 1, 1–21

TARGET ARTICLE

Are Evolutionary Explanations Unfalsifiable? Evolutionary Psychology and the Lakatosian Philosophy of Science

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Are the methods and strategies that evolutionary psychologists use to generate and test hypotheses scientifically defensible? This target article addresses this question by reviewing principles of philosophy of science that are used to construct and evaluate metatheoretical research programs and applying these principles to evaluate evolutionary psychology. Examples of evolutionary models of family violence, sexual jealousy, and male parental investment are utilized to evaluate whether the procedures for developing and testing evolutionary psychological models are consistent with contemporary philosophy of science. Special attention is paid to the generation of competing theories and hypotheses within a single evolutionary framework. It is argued that this competition is a function of the multiple levels of scientific explanation employed by evolutionary psychologists, and that this explanatory system adheres to the Lakatosian philosophy of science. The charge that evolutionary theories and hypotheses are unfalsifiable is unwarranted and has its roots in a commonly accepted, but mistaken, Popperian view of how science operates. Modern evolutionary theory meets the Lakatosian criterion of "progressivity," based on its ability to digest apparent anomalies and generate novel predictions and explanations. Evolutionary psychology has the hallmarks of a currently progressive research program capable of providing us with new knowledge of how the mind works.

> Although psychologists assume that the mind is a whole and integrated unity, no metatheory subsumes, integrates, unites, or connects the disparate pieces that psychologists gauge with their different calipers.… An important new theoretical paradigm called "evolutionary psychology" is emerging that offers to provide this metatheory. (Buss, 1995, p. 1)

Evolutionary psychology is the application of the principles and knowledge of evolutionary biology to psychological theory and research. Its central assumption is that the human brain is comprised of a large number of specialized mechanisms that were shaped by natural selection over vast periods of time to solve the recurrent information-processing problems faced by our ancestors (Symons, 1995). These problems include such things as choosing which foods to eat, negotiating social hierarchies, partitioning investment among offspring, and selecting mates. The field of evolutionary psychology focuses on explicating the nature of the specific information-processing problems encountered during human evolutionary history, and on developing and testing models of the psychological adaptations (mechanisms and behavioral strategies) that may have evolved as solutions to these problems (Buss, 1999; Cosmides, Tooby, & Barkow, 1992).

Despite the recent emergence of evolutionary psychology as a promising new perspective in the behavioral sciences (see Barkow, Cosmides, & Tooby, 1992; Buss, 1995, 1999; Pinker, 1997; Simpson & Kenrick, 1997; Wright, 1994), this approach has been subject to frequent criticism (e.g., Berwick, 1998; Horgan, 1995; Lewontin, 1990; Piatelli-Palmarini, 1994). A major concern is the apparent willingness of evolutionary psychologists to generate a plethora of seemingly untestable and post hoc explanations for any given psychological phenomenon. According to this view, evolutionary explanations are infinitely flexible "stories" that can be constructed to fit any set of empirical observations and can neither be confirmed nor disconfirmed by data. This criticism was forcefully articulated by Gould and Lewontin (1979):

> We would not object so strenuously to the adaptationist program if its invocation, in any particular case, could lead in principle to its rejection for want of evidence. But if it could be dismissed as failing some explicit test, then alternatives could get their chance. Unfortunately, a common procedure among evolutionists does not allow such definable rejection for two reasons. First, the rejection of one adaptive story usually leads to its replacement by another, rather than to a suspicion that a different kind of explanation might be required.… Secondly, the criteria of acceptance of a story are so loose that they may pass without proper confirmation. Often, evolutionists use consistency with the data as the sole criterion and consider their work done when they concoct a plausible story. (pp. 587–588)

The charge that evolutionary explanations are unfalsifiable centers on two related claims: (1) The basic assumptions of modern evolutionary theory are said to be untestable, and (2) specific evolutionary models and hypotheses that are drawn from these basic assumptions are said to be untestable. This second charge has taken at least two forms. Either: (2a) Specific evolutionary models and hypotheses are said to be—in principle—not rejectable on the basis of evidence; or (2b) even if specific evolutionary models and hypotheses can in principle be rejected, it is said that the standards of evidence employed by evolutionary psychologists to evaluate these models and hypotheses do not adhere to established principles of philosophy of science; or both of these forms can apply.

To address these criticisms, we review principles of contemporary philosophy of science that are used to construct and evaluate metatheoretical research programs and employ these principles to evaluate evolutionary psychology. In the first half of this article, we evaluate the criticism that specific evolutionary models and hypotheses are untestable. We consider the first part of this criticism (2a) to be a nonissue: Scientists using an evolutionary perspective have clearly generated many testable models and hypotheses that can be—and have been—either supported or rejected on the basis of data (see Betzig, 1997, for a collection of empirical works in the field). Thus, we focus on the second part of the criticism (2b): the concern that evolutionary psychologists do not employ scientifically defensible criteria for evaluating theoretical models in relation to the performance of their derivative hypotheses and predictions. Our treatment of this criticism centers on evolutionary models of family violence, sexual jealousy, and male parental investment. Drawing on these topics, we evaluate whether the procedures for developing and testing evolutionary models are consistent with contemporary philosophy of science. Special attention is paid to the generation of alternative or competing explanatory models within a single evolutionary framework (i.e., when different evolutionary models generate opposing predictions). We argue that this competition is a function of the multiple levels of scientific explanation employed by evolutionary psychologists, and that this explanatory system adheres to the well-established Lakatosian philosophy of science (Lakatos, 1970, 1978). The Lakatosian model can accommodate the development and testing of alternative (evolutionary) explanations within the unifying framework of a single (evolutionary) metatheory.

In the second half of this target article, we examine how the basic assumptions of modern evolutionary theory have been evaluated. Using the problem of altruism as a case study, we argue that the criticism that the core assumptions of modern evolutionary theory are untestable is not justified. Modern evolutionary theory meets the Lakatosian criterion of progressivity, based on its ability to "digest" (successfully account for) apparent anomalies and generate novel predictions and explanations. Evolutionary psychology has the hallmarks of a currently progressive research program capable of providing us with new knowledge of how the mind works.

The Lakatosian Philosophy of Science in Psychology: A Necessary Addendum to Popper's Method of Falsification

To provide a set of criteria for demarcating science from pseudoscience, the philosopher Karl Popper introduced the strategy of *falsificationism*[1] (see Popper, 1959, esp. pp. 27–48). According to Popper, scientific explanations are comprised of statements that can be empirically tested to determine whether they are verified (supported by the data) or falsified (inconsistent with the data). Popper (1959) applied this method of falsification to deductive theory testing:

> We seek a decision as regards these (and other) derived statements by comparing them with the results of practical applications and experiments. If this decision is positive, that is, if the singular conclusions turn out to be acceptable, or verified, then the theory has, for the time being, passed its test: we have found no reason to discard it. But if the decision is negative, or in other words, if the conclusions have been falsified, then their

[1] Popper, of course, introduced the strategy of falsificationism for several reasons, including his claim that falsification could provide a solution to the problem of induction (see Lakatos, 1974; Popper, 1959). For the purpose of clarity, we focus on Popper's discussion of the role of falsificationism in deductive theory testing.

> falsification also falsifies the theory from which they were logically deduced. (p. 33)

The cognitive scientist Alan Newell (1973, 1990) argued that from a Popperian perspective, psychology is viewed as a discriminating science that promises to deliver truths about the mind by revealing the falsehoods and leaving us to piece together the remaining "not-yet-falsified" explanations to achieve great insight. In Newell's (1973) eyes, psychology's reliance on a strictly Popperian philosophy of science resulted in too many empirical findings being cast in terms of their support or refutation of binary oppositions, such as nature versus nurture, central versus peripheral, serial versus parallel. This strategy had the appearance of a game of 20 questions in which the essential structure of the mind would be revealed by (a) accumulating negative knowledge about what the mind did not do and then (b) inferring positive knowledge about how the mind operated by considering the explanations that were left unrefuted. Newell (1973) argued that a discriminating approach to research, such as Popper's, only created negative knowledge about the mind and therefore, by itself, could not be an efficient strategy for advancing positive knowledge about how complex mental processes actually operated.[2]

Newell (1973) called for psychology to replace the *discriminating approach* of a strictly Popperian perspective with the more *approximating approach* proposed by Popper's contemporary, Imre Lakatos (1970, 1978). Borrowing from Lakatos's philosophy of science, Newell (1990) argued that the goal of psychological science is more accurately described as the process of increasing our knowledge base by constructing better and better approximations of phenomena based on current theory. Newell referred to Lakatos's philosophy of science as an "approximating" approach because the day-to-day workings of scientists are viewed as competing attempts to create the best approximations of phenomena, based on certain agreed-on metatheoretical assumptions. A scientist using an approximating approach begins with a set of first principles on which everyone in the field can agree (such as Newton's four principles in physics) and then structures scientific progress around the task of using these principles to construct theoretical models—approximations—of particular phenomena. Newell (1990) wrote:

> Theories are approximate. Of course, we all know that technically they are approximate; the world can't be known with absolute certainty. But I mean more than that. Theories are deliberately approximate.… They are refined and reformulated, corrected and expanded. Thus, we are not living in the world of Popper (Popper, 1959), as far as I'm concerned, we are living in the world of Lakatos (Lakatos, 1970). Working with theories is not like skeet shooting—where theories are lofted up and bang, they are shot down with a falsification bullet, and that's the end of the story. Theories are more like graduate students—once admitted you try hard to avoid flunking them out.… Theories are things to be nurtured and changed and built up. One is happy to change them to make them more useful. (p. 14)

Although Newell's (1990) argument sounds like a forceful renunciation of the Popperian perspective, it can be treated as the recognition of a necessary caveat to Popper: Although the method of falsification is useful for evaluating the scientific status of specific statements, it is an inappropriate strategy for directly evaluating the theories that generate such statements. Theories are evaluated relative to each other. From a Lakatosian perspective, a theory may be retained as the best available explanation of a given domain, even if the theory has experienced predictive failures. Newell (1990) called for psychology to recognize the utility of the Lakatosian philosophy of science as an addendum to Popper, as did Meehl (1978, 1990), because he saw Lakatos's approximating model as better suited to the task of constructing a unifying metatheory for psychology. (The strict use of Popper's method of falsification has been challenged by many philosophers of science as an inaccurate depiction of theory testing in science; see Kuhn, 1977; Lakatos, 1970, 1974; Maxwell, 1972; Meehl, 1978, 1990; Putnam, 1974.)

Understanding the basic logic of the Lakatosian philosophy of science can allow a fuller appreciation of the powerful conceptual tool that a shared set of basic assumptions can provide. There are two major aspects of Lakatos's philosophy of science that provide a basis for constructing and evaluating metatheories in a given scientific domain. The first aspect is that metatheoretical research programs are centered on a "hard core" of basic assumptions surrounded by a "protective belt" of auxiliary hypotheses. The second is that competing metatheories are judged as progressive or degenerative based on the performance of their protective belt, rather than as false or not yet falsified (as a strict Popperian might contend). The remainder of this target article explicates these concepts and applies them to an evaluation of the structure, performance, and testability of the core assumptions and theoretical models employed by evolutionary psychologists.

The Role of Metatheory in Science

Scientists typically rely on basic (although usually implicit) metatheoretical assumptions when they con-

[2]We thank Geoffrey Miller for first alerting us to Newell's depiction of Popperian falsificationism as a strategy of null hypothesis testing. See also Gigerenzer and Murray (1987, esp. pp. 8–15) for an excellent discussion of the problems with a strictly null hypothesis testing strategy in science.

struct and evaluate theories. Evolutionary psychologists have often called on behavioral scientists to make explicit their basic assumptions about the origins and structure of the mind (see Gigerenzer, 1998). In this article, we refer to a metatheory[3] as a set of consensually held basic assumptions that shape how scientists generate, develop, and test middle-level theories and hypotheses. These basic assumptions, once they have been empirically established, are often not directly tested thereafter. Instead they are used as a starting point for further research; that is, they provide the a priori assumptions that one uses to build more specific theoretical models. Lakatos (1970) referred to these basic a priori assumptions as the hard core of a metatheoretical research program. Newton's laws of motion form the metatheory for classical mechanics, the principles of gradualism and plate tectonics provide a metatheory for geology, and the principles of adaptation through natural selection provide a metatheory for biology. Several scholars (e.g., Bjorklund, 1997; Lykken, 1991; Richters, 1997) have argued that the greatest impediment to psychology's development as a science is the absence of a coherent, agreed-on metatheory. Many evolutionary psychologists believe that this impediment could be removed through the adoption of evolutionary metatheory.

A metatheory operates like a map of a challenging conceptual terrain. It specifies both the landmarks and the boundaries of that terrain, suggesting which features are consistent and which are inconsistent with the core logic of the metatheory. In this way a metatheory provides a set of powerful methodological heuristics: "Some tell us what paths to avoid (negative heuristic), and others what paths to pursue (positive heuristic)" (Lakatos, 1970, p. 47). In the hands of a skilled researcher, a metatheory "provides a guide and prevents certain kinds of errors, raises suspicions of certain explanations or observations, suggests lines of research to be followed, and provides a sound criterion for recognizing significant observations on natural phenomena" (Lloyd, 1979, p. 18). The ultimate contribution of a metatheory is that it synthesizes middle-level theories—those theories that lie at an intermediate level between the basic metatheoretical assumptions and derivative hypotheses and predictions. This synthesis allows the empirical results of a variety of different theory-driven research programs to be explicated within a broader metatheoretical framework, leading to systematic cumulation of knowledge and progression toward a coherent "big picture" of the subject matter.

The Metatheory Level of Analysis in Evolutionary Psychology

In the case of evolutionary psychology, the metatheoretical level consists of the general principles of genetical evolution drawn from modern evolutionary theory, as outlined by W. D. Hamilton (1964) and instantiated in more contemporary "selfish gene" theories of genetical evolution via natural and sexual selection. (See Cronin, 1991; Dawkins, 1976, 1982, 1986; Dennett, 1995; Mayr, 1983; Tooby & Cosmides, 1992; and Williams, 1966, 1992, for good overviews of the basic assumptions of modern evolutionary theory.) Evolutionary psychologists assume that the basic assumptions of modern evolutionary theory are correct, and then work forward from these assumptions to examine how they can be applied to our understanding of the origins and nature of the mind (e.g., Buss, 1995, 1999; Cosmides et al., 1992; Symons, 1987).

At the metatheoretical level, evolutionary psychology affords a broad outline for the study of psychology. Specifically, the modern theory of evolution provides a set of core assumptions that enables one to distinguish between plausible and implausible a priori psychological hypotheses. To illustrate, consider a Venn diagram of three embedded circles (see Figure 1). Each of the three circles contains a class of psychological mechanisms.[4] The largest circle refers to the exhaustive and virtually infinite set of all the psychological mechanisms that one could imagine.

Psychological scientists, of course, do not give equal consideration to all of these hypothetical mechanisms. Rather, they operate primarily within the next set of possibilities, focusing on a smaller set of putative mechanisms that meet some a priori agreed-on criteria of plausibility (see Holcomb, 1993, for a discussion of the concept of plausibilism). This is represented by the second largest circle (depicted as the nonshaded region in Figure 1) in the Venn diagram, which is embedded within the larger set of all possible psychological

[3]Lakatos (1970, 1978) did not actually use the term *metatheoretical research program.* Rather, Lakatos (a) used the term *hard core* to refer to what we are calling the *metatheoretical assumptions* level of analysis and (b) used the term *research programme* to refer to what we are calling *the entire hierarchy of scientific explanation* shown in Figure 2. Other terms have been used to describe metatheoretical assumptions, including *paradigms* (Kuhn, 1962) and *pretheoretical ideas* (Lachman, Lachman, & Butterfield, 1979, pp. 88–129).

[4]Buss (1995) defined an evolved psychological mechanism as a "set of processes inside the organism that (1) exists in the form it does because it (or other mechanisms that reliably produce it) solved a specific problem of individual survival or reproduction recurrently over evolutionary history; (2) takes only certain classes of information as input, where input: a) can be either external or internal, b) can be actively extracted from the environment or passively received from the environment, and c) specifies to the organism the particular adaptive problem it is facing; (3) transforms that information into an output through a procedure (e.g., decision rule) where output a) regulates physiological activity, provides information to other psychological mechanisms, or produces manifest action, and b) solves a particular adaptive problem." (p. 5–6)

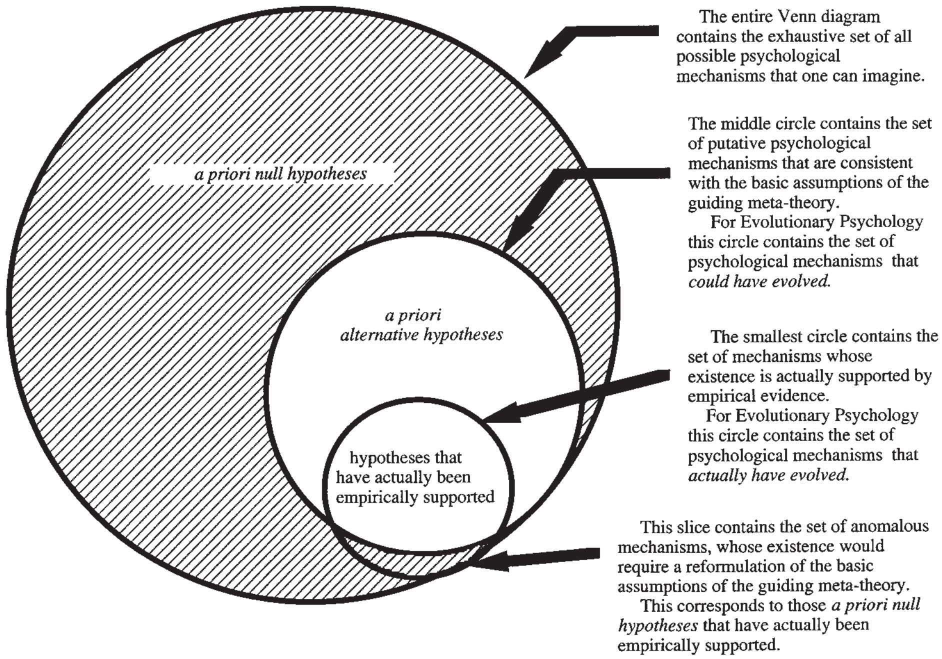

Figure 1. Venn diagram representing how a metatheory narrows the scope of research to a delimited set of plausible a priori hypotheses.

mechanisms that one could imagine. The boundaries of this smaller second circle are determined by the particular metatheoretical assumptions that one adopts. In the case of the metatheory employed by evolutionary psychologists, this second set is restricted to the set of psychological mechanisms that could have—in principle—evolved through natural and sexual selection. Evolutionary psychologists focus their attention on testing hypotheses about these kinds of mechanisms, ignoring the larger set of hypotheses about psychological mechanisms that one could imagine but that could not have evolved (and are thus unlikely to receive empirical support).

For example, most evolutionary psychologists would be quite skeptical of the hypothesis that risk of interpersonal violence is largely determined by frequency of contact between individuals (i.e., the *mutual access hypothesis*). This hypothesis has been suggested by criminologists to explain why the family is the single most common locus of all types of interpersonal violence: “It cannot be surprising that more violence is directed against those with whom we are in more intimate contact. We are all within easy striking distance of our friends and spouses, for a goodly part of the time” (Goode, 1969, p. 941). The mutual access hypothesis suggests that children who are most often within easy striking distance of their parents are at the greatest risk for physical abuse, regardless of whether those children are steprelations or biological offspring. The mutual access hypothesis specifies a general set of psychological mechanisms underlying aggression (direct violence toward others who are around you most often and affect you most frequently and directly) that cuts across different types of social relationships.

From an evolutionary perspective, however, the existence of such general mechanisms would constitute an *a priori null hypothesis* (located in the shaded region of the Venn diagram shown in Figure 1). This is because natural selection favors psychological mechanisms that function to promote the survival and reproduction of one’s direct descendants and close relatives. Accordingly, a basic metatheoretical assumption of evolutionary theory is that natural selection favors *nepotism,* the inclination to discriminate in favor of genetic relatives. Given identical levels of physical proximity and social interaction, parents should be much more inhibited against harming or killing their own biological children than against harming or killing stepchildren (Daly & Wilson, 1988). If this supposition was shown to be false (i.e., if the psychological mechanisms underlying family violence were not nepotistically biased but instead followed a general “easy striking distance” rule that applied equally across different genetic relations), then it would call into question a basic metatheoretical assumption of modern evolutionary theory. This type of anomalous mechanism would be located in the thin slice at the bottom of the Venn diagram (Figure 1).

Because it is often the case that the criteria for specifying the range of plausible mechanisms vastly underdetermines the range of actual mechanisms observed, a third circle is needed that is embedded within the first two. For evolutionary psychologists, this third circle corresponds to the set of psychological mechanisms that have, in fact, evolved (or, more conservatively, mechanisms whose existence is supported by empirical evidence). In sum, the use of a metatheory places boundaries on the inner two circles of psychological mechanisms represented in the Venn diagram. By eliminating a priori null hypotheses from consideration, the use of a metatheory plays the important role of narrowing the scope of research to a delimited set of plausible a priori alternative hypotheses (see Figure 1).

The Protective Belt of the Metatheory

According to the Lakatosian model of science, the hard core of the metatheory is surrounded by a protective belt of auxiliary hypotheses. A primary function of the protective belt is to provide an empirically verifiable means of linking metatheoretical assumptions to observable data. In essence, the protective belt serves as the problem-solving machinery of the metatheoretical research program because it is used to provide indirect evidence in support of the metatheory's basic assumptions (Lakatos, 1970). The protective belt does more, however, than just protect the metatheoretical assumptions: It uses these assumptions to extend our knowledge of particular domains. For example, a group of physicists who adopt a Newtonian metatheory may construct several competing middle-level theories concerning a particular physical system, but none of these theories would violate Newton's laws of mechanics. Each physicist designs his or her middle-level theory to be consistent with the basic assumptions of the metatheory, even if the middle-level theories are inconsistent with each other. Competing middle-level theories attempt to achieve the best operationalization of the core logic of the metatheory as it applies to a particular domain. The competing wave and particle theories of light (generated from quantum physics metatheory) are excellent contemporary exemplars of this process (see Gribbin, 1984).

Once a core set of metatheoretical assumptions becomes established among a community of scientists, the day-to-day workings of these scientists are generally characterized by the use of, not the testing of, these assumptions.[5] Metatheoretical assumptions are used to construct plausible alternative middle-level theories. After empirical evidence has been gathered, one of the alternatives may emerge as the best available explanation of phenomena in that domain. Lakatos (1970) argued that the activity of constructing and evaluating middle-level theories characterizes the typical activities of scientists attempting to use a metatheory to integrate, unify, and connect their disparate lines of research.

In a metatheoretical research program, the protective belt provides a powerful means of defending the hard core from refutation. It is this secondary function that gives the concept of a protective belt its name. The protective belt insulates the hard core from refutation by providing an indirect link between observable data and hard core assumptions. Thus, falsifying a single hypothesis or rejecting an intermediary theoretical model does not lead one to reject the entire metatheoretical research program. In this case the metatheory can prove its mettle by generating an alternative hypothesis (or theory) to replace the previously falsified one. When a horrific and tragic explosion destroyed the space shuttle *Challenger* in 1986, scientists did not question the basic laws and assumptions of physics. Rather, they questioned how they had applied those laws and assumptions to the construction of the O-rings, which sealed the shuttle's booster rockets (Feynman & Leighton, 1988). Lakatos (1978) pointed out that the protective belt bears the burden of empirical tests and is "adjusted and re-adjusted, or even replaced, to defend the thus hardened-core" (p. 48) of the research program. It follows that anomalies that arise typically lead to changes in the protective belt, not the hard core. In this way, the protective belt is used as a tool in the service of a larger program of research centering around the metatheory.

The Protective Belt in Evolutionary Psychology

Whereas the Lakatosian model of science describes two levels of analysis (the hard core of assumptions and its protective belt of auxiliary hypotheses), the evolutionary psychology model breaks down the protective belt into three levels of analysis (middle-level theories, hypotheses, and predictions). In total, the evolutionary psychology research program constitutes four levels of scientific explanation. These levels are described in Buss (1995, 1999) and are shown in Figure 2. The generation of alternative hypotheses within an evolutionary framework is a function of this hierarchy of explanation. In this section, we use the related topics of sexual jealousy and male parental investment as case studies to demonstrate (a) the hierarchical structure of evolutionary psychology's protective belt, (b) how each tier in this hierarchy differentially informs the study of sexual jealousy and male parental investment, and (c) how competing models and hypotheses about sexual jealousy and male parental investment can be developed and tested within the unifying framework of modern evolutionary theory.

[5]Lakatosian scientists, like most scientists, do not focus their efforts on attempting to falsify the hard core of their metatheoretical research program. This hard core consists of assumptions so basic that to question their validity would be tantamount to abandoning the metatheory they use to construct all of their middle-level theories and hypotheses. This does not imply that the hard core of a metatheory is untestable (as discussed later; see Evaluating the Hard Core of a Metatheory). Rather, the Lakatosian model points out that it is often much more difficult than one might think to accumulate overwhelming evidence against a metatheory (see also Kuhn, 1962, 1977, for a discussion of these issues).

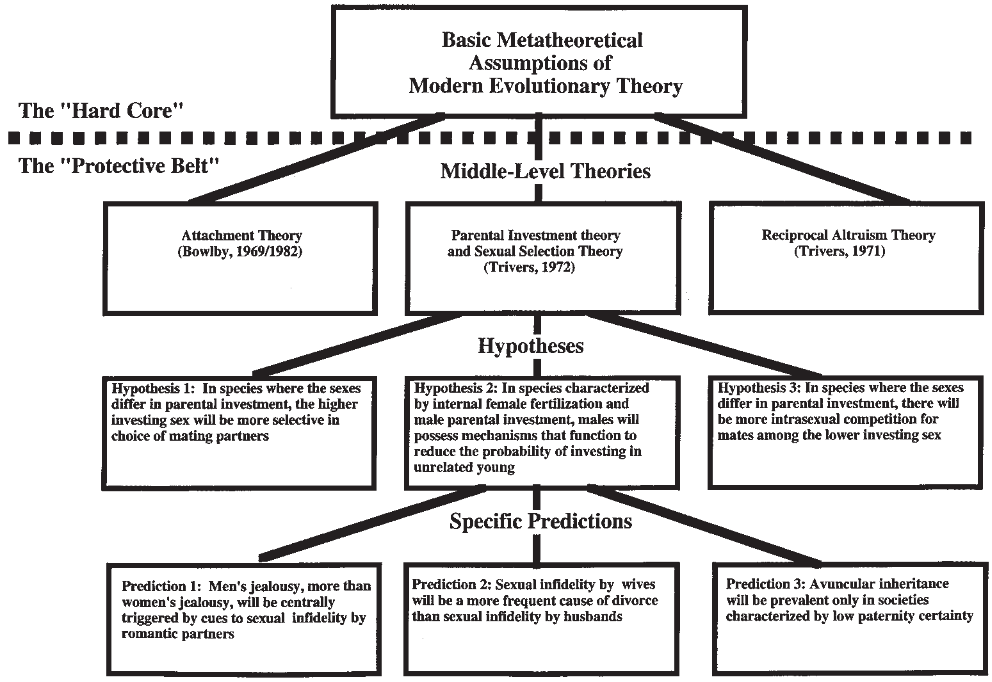

Figure 2. The hierarchical structure of evolutionary psychological explanations (based on Buss, 1995).

The Middle-Level Theory Level of Analysis

At the highest level of the protective belt, just below metatheory, are middle-level evolutionary theories: the specific theoretical models that provide a link between the metatheoretical assumptions and specific hypotheses and predictions (see Figure 2). Middle-level evolutionary theories are consistent with and subsumed by evolutionary metatheory but in most cases cannot be directly deduced from it (Buss, 1995). Middle-level theories elaborate the basic assumptions of the metatheory into a particular psychological domain. Because the coverage area of a single middle-level theory is sometimes quite broad (e.g., mating, cooperation), a given middle-level theory may subsume several more narrowly focused conceptual models. For example, Trivers's (1972) theory of parental investment and sexual selection (which is a grand middle-level theory that guides most evolutionary research on mating and parenting) provides the foundation for a more specific evolutionary model of sexual jealousy (see Daly, Wilson, & Weghorst, 1982).

In some cases, different middle-level theories compete to provide the best explanation of the same phenomenon. For example, both the theory of parental investment and sexual selection (Trivers, 1972) and the theory of reciprocal altruism (Axelrod & Hamilton, 1981; Trivers, 1971; Williams, 1966) have been applied to the question: Why do adult males interact with infants? This section elaborates the different answers to this question that have been derived from these two middle-level theories. The goal of this section is to demonstrate how competing middle-level theories can be developed and evaluated within the larger framework of evolutionary metatheory.

Parental investment and sexual selection theory. The theory of parental investment and sexual selection provides a strong framework for the study of mating and parental behaviors. As articulated by Trivers (1972), the key force driving the evolution of male and female reproductive strategies is relative parental investment in offspring. In mammals, females tend to invest more heavily in offspring than males do, including gestation, parturition, lactation, and the majority of offspring care. Whereas females must invest a great amount of time and energy to reproduce at all, males must only invest their sperm. This difference in minimal (as opposed to typical) parental investment sets very different reproductive constraints on males and females.

For males more than females, reproductive success is limited by number of matings with fertile partners. Males should thus be selected to be more risk-taking and aggressive than females in pursuing sexual contacts, and to allocate more competitive effort toward monopolizing sexual access. Further, in species with internal fertilization, males cannot identify their offspring with certainty. In such species, males who invest paternally run the risk of devoting time and energy to offspring who are not their own. Thus, male parental investment should only evolve as a reproductive strategy when fathers have reasonably high confidence of paternity. That is, males should be selected to be high-investing fathers only to offspring who share their genes. When male parental investment does evolve, selection should concomitantly favor the evolution of male strategies designed to reduce the chance of diverting parental effort toward unrelated young (Daly et al., 1982; Symons, 1979). Daly et al. suggested that, in human males, these strategies include "the emotion of sexual jealousy, the dogged inclination of men to possess and control women, and the use or threat of violence to achieve sexual exclusivity and control" (p. 11). Evolutionary psychologists have proposed that men's jealousy is centrally triggered by cues to sexual infidelity (Buss, Larsen, & Westen, 1996; Buss, Larsen, Weston, & Semmelroth, 1992).

Reciprocal altruism theory. Whereas parental investment and sexual selection theory focuses on mating and parental behaviors, reciprocal altruism theory focuses on the conditions under which genetically unrelated individuals cooperate. The two theories overlap insofar as biparental care of young involves cooperation between males and females who are not genetically related via common descent. Reciprocal altruism theory posits that natural selection can favor the evolution of mechanisms designed to deliver benefits to other individuals who are not genetic relatives, provided that during the selective history of those mechanisms the costs to Party A of delivering the benefits were, on average, outweighed by the return of reciprocal benefits by Party B. As long as each side does better by cooperating than by failing to cooperate, cooperation can evolve. The exchange of altruistic favors does not have to be simultaneous. In most cases, Party A performs a good deed at one point in time, to increase the probability that Party B will reciprocate the good deed at some future point in time.

Drawing on reciprocal altruism theory, Smuts (1985) suggested that: "Male primates care for and protect infants (and their mothers) in order to derive reciprocal benefits from females and infants" (p. 255). These benefits might include preferred sexual access to the mothers as well as female coalitional support during competition with other males. Smuts's (1985; Smuts & Gubernick, 1992) reciprocity model suggested that male care of infants is most common when (a) females are able to discriminantly provide substantial benefits to some males at the expense of others and (b) when infants derive substantial benefits from male care. In essence, the reciprocity model posits that male care of infants functions to increase male mating success by facilitating relationships with particular females. From this perspective, the male does not have to be the father of the infant to benefit from its care. This stands in contrast to the perspective on male parental investment articulated by Trivers (1972), which suggested that the evolution of male parental care is predicated on a reasonable degree of paternity certainty, and that this care functions to enhance the survival and reproduction of genetic offspring.

Comparison of competing theories. In sum, both the theory of parental investment and sexual selection and the theory of reciprocal altruism provide frameworks for the analysis of biparental care of young. Working within these different frameworks, evolutionary scientists have generated competing models about the evolution of male parental behavior. These models produce competing hypotheses about the social contexts in which male parental care is most likely to occur (see following, The Hypothesis Level of Analysis). Despite this competition, both models are firmly grounded in the metatheoretical assumptions of modern evolutionary theory. At a general level, both models share the assumption that the evolution of male parental care is predicated on a selective history of fitness benefits to the fathers who engaged in it. Thus, neither model would expect a general paternal instinct to evolve, but rather a tendency to affiliate with and invest in infants in particular contexts that historically promoted male reproductive success. At a more specific level, both models posit that female choice of mating partners on the basis of either care, protection, or provisioning of young, or all three, played a significant causal role in the evolution of male parental behavior.

Following the Lakatosian philosophy of science, competing evolutionary theories at the middle level of analysis are evaluated in terms of their relative success in applying the core assumptions of the metatheory to a given domain. One theory may be judged as more useful than another because it possesses greater *explanatory power;* that is, it solves more of the existing puzzles and accounts for a wider range of known facts (including apparently anomalous findings). In addition to this ability to account (post hoc) for what is known, one theory may be judged as more useful than another because it possesses greater *predictive power;* that is, it better anticipates the data by specifying (a priori) previously unobserved phenomena (Lakatos, 1970, 1978). The explanatory and predictive power of competing middle-level theories can be evaluated both in terms of confirmational and disconfirmational success (see Holcomb, 1993, for an excellent discussion of the role of confirmation and disconfirmation in theory evaluation). *Confirmational success* refers to the extent to which empirical data support the pertinent statements of the theory and its auxiliary models and hypotheses. *Disconfirmational success* refers to the extent to which the theory specifies observable situations that would count as reasons for thinking it false, has undergone such attempts at falsification, and yet has not been found false. For example, parental investment and sexual selection theory specifies an observable situation—if in any given species the sex that invests more in offspring (usually females) was, in general, less discriminating in mate selection than the sex that invests less (usually males)—that would count as a reason for thinking it false; this situation has been searched for in numerous species and has not been found. Ultimately, competing middle-level evolutionary theories are evaluated indirectly through the performance of their derivative hypotheses and predictions.

The Hypothesis Level of Analysis

At the next level down are the actual hypotheses drawn from middle-level evolutionary theories and their subsidiary models (see Figure 2). A *hypothesis* is a general statement about the state of the world that one would expect to observe if the theory from which it was generated was in fact true. Competing evolutionary hypotheses can be generated either within the context of a single middle-level theory or across different middle-level theories. In addition, competing hypotheses can be generated from nonevolutionary sources. At the current stage in the development of evolutionary psychology, tests of competing evolutionary and nonevolutionary hypotheses are still common (and are often designed to legitimate the use of evolutionary approaches). As the field of evolutionary psychology matures, however, empirical tests should increasingly shift toward more refined variants of competing evolutionary hypotheses (Holcomb, 1998).

Competing hypotheses from within a single middle-level evolutionary theory. An array of hypotheses can often be derived from a single middle-level theory. These hypotheses can be considered to vary along a continuum of confidence (Ellis & Symons, 1990). At the top of the continuum are *firm hypotheses* (such as the relation between relative parental investment and mate selection) that are clear and unambiguous derivations from an established middle-level evolutionary theory. As one moves down the continuum, however, firm hypotheses give way to more typical formulations—hypotheses that are inferred from a middle-level theory but not directly derived from it. This distinction can be illustrated by considering the issue of paternity uncertainty. The supposition that in species characterized by both internal female fertilization and substantial male parental investment,[6] selection will favor the evolution of male mechanisms for reducing the probability of expending that investment on unrelated young is a firm hypothesis that can be directly derived from the theory. What form these mechanisms will take, however, cannot be directly derived from the theory because natural and sexual selection underdetermine specific phylogeny. Selection could favor the evolution of sexual jealousy, or it could favor the evolution of sperm plugs to block the cervix of female sexual partners following copulation. Given the universal occurrence of jealousy in humans (Daly et al., 1982), evolutionary psychologists have hypothesized that men's jealousy should be centrally triggered by cues to sexual infidelity whereas women's jealousy should be centrally triggered by cues to loss of commitment and investment. This hypothesis is reasonably inferred from the theory but cannot be directly deduced from it. We refer to this type of hypothesis as an *expectation.* This hypothesis was originally proposed by Daly et al. (1982) and has since received considerable empirical support (Buss et al., 1992; Buss et al., 1999; Buunk, Angleitner, Oubaid, & Buss, 1996; DeSteno & Salovey, 1996; Wiederman & Allgeier, 1993).

As one moves farther down the continuum of confidence, into the area where inferences from middle-level theories are drawn farther from their core, expectations grade inevitably into interesting questions or hunches. At this level, different interpretations of the theory can and do generate different hypotheses. For example, Buss and Shackelford (1997) proposed two competing evolutionary hypotheses concerning the effects of unequal attractiveness between romantic partners on women's mate retention behavior. The first hypothesis suggested that individuals (women and men) married to others who are perceived as more attractive than the self will devote more effort to mate retention than individuals married to others who are perceived as equal to or less attractive than the self. The logic behind this hypothesis is that individuals who are married to relatively attractive partners are at greater risk of losing them. The second hypothesis suggests the opposite, but only for women: Women married to men who are perceived as more attractive than the self will relax their mate retention efforts. The logic behind this hypothesis focuses on the greater ability of men to fractionate their reproductive investment among multiple partners. For example, a man can simultaneously beget and raise children with three different women (a phenomenon that is quite common in polygynous societies), whereas it would take a woman several years to bear and raise children with three different men. As a consequence of men's ability to partition investment, women may face the trade-off of obtaining a fraction of the attention and resources of a highly attractive man or the full attention and resources of a less attractive man. Buss and Shackelford suggested that women in unevenly matched marriages might devote less effort to mate retention, an implicit

[6] By definition, parental investment involves activities that have a positive effect on the survival and future reproduction of offspring at a reproductive cost to the parent. Some forms of paternal care clearly meet the definition of parental investment. For example, in several small New World monkeys, males often carry heavy infants (weighing 7%–27% of adult body weight) with them during foraging, and this burden markedly reduces foraging efficiency (Whitten, 1987). Other forms of paternal care may not meet the definition of parental investment, even though this care may be beneficial to infants. For example, maintenance of spatial proximity, huddling, and even baby sitting probably require little energetic expenditure by adult males (Whitten, 1987).

acknowledgment of the potential costs involved in trying to prevent the more attractive partner from devoting some of his resources to outside relationships.

Although this type of theorizing is admittedly speculative, it is inevitable at the lower end of the continuum of confidence, in domains where there is not strong middle-level theoretical development and about which relatively little is known. Studies designed to test these hypotheses often have an exploratory quality. The data obtained from testing such hypotheses, however, can work their way back up the explanatory hierarchy to enable the development of more rigorous theoretical models.

Competing hypotheses from different middle-level evolutionary theories. Competing evolutionary hypotheses can also be generated from different middle-level theories. For example, the paternity certainty and reciprocity models generate competing hypotheses about variations in levels and specificity of paternal investment. The paternity certainty model predicts that male parental investment—paternal behaviors that benefit young at some cost to the man—will be overwhelmingly directed toward a man's own offspring rather than the offspring of unrelated men (Trivers, 1972); thus, the degree of male parental investment should vary as a function of paternity certainty, both across and within species (e.g., Alexander & Noonan, 1979). The reciprocity model, by contrast, suggests that male care of young is likely to arise in the context of a "mutually advantageous, reciprocal exchange of benefits between males and females" (Smuts, 1985, p. 257); it predicts that the quality of the relationship between the male and the infant's mother, rather than the degree of genetic relatedness between the male and the infant, will be the most important determinant of paternal investment. In contrast to the paternity certainty model, the reciprocity model posits that substantial male parental investment will sometimes evolve in species in which paternity certainty is low.

Evaluation of opposing hypotheses. In total, competing evolutionary hypotheses can be generated both within and across middle-level theories. This generation of opposing hypotheses exemplifies what evolutionary psychology has been most criticized for: its apparent ability to explain anything and its opposite. Several points must be made about this criticism. First, strictly speaking, the criticism is untrue. As the body of established theory and data in evolutionary psychology increases, it places internal constraints on hypothesis generation. Specifically, at the top of the continuum of confidence, established middle-level evolutionary theories generate firm hypotheses with which all Darwinians are likely to concur. For example, Trivers's (1972) theory of parental investment and sexual selection clearly and unambiguously implies that in species in which the sexes differ in parental investment, the sex that invests less (usually males) will engage in more intersexual competition for sexual access to the sex that invests more (usually females). The opposite proposition would be an a priori null hypothesis (located in the outer circle of the Venn diagram; see Figure 1). Second, this criticism conflates the distinction between the process of scientific inquiry (the process of hypothesis generation and evaluation) and the products of scientific inquiry (the nearly consensual facts about why and how the world works the way it does). The process of scientific inquiry often begins with a host of initially viable, alternative hypotheses generated by competing theoretical models. The generation of alternative (competing) hypotheses within a single evolutionary framework is in principle no different (see Daly & Wilson, 1988; Mayr, 1983). Third, the generation of competing evolutionary models is defensible to the extent that they are rigorously formulated so that they produce clear, testable hypotheses. Vague models that do not have testable consequences represent poor science no matter what theoretical perspective they come from. Finally, when competing models generate competing hypotheses, the ultimate arbiter is empirical data. Competing evolutionary models wax and wane in prominence (with better models driving out their rivals through normal scientific channels) as our empirical and theoretical knowledge base increases.

The Predictions Level of Analysis

Because hypotheses are often too general to be tested directly, it is at the next level of explanation—the level of specific predictions—where the battles between competing theoretical models are often played out. Predictions correspond to specific statements about the state of the world that one would expect to observe if the hypothesis was in fact true. They represent explicit, testable instantiations of hypotheses. One might argue that predictions form the substance of any theory, for it is here where most of the action takes place as specific predictions are either supported or refuted.

The performance of evolution-based predictions provides the basis for evaluating the more general hypotheses from which they are drawn. For example, a number of specific predictions have been derived from the evolutionary hypothesis that men (more so than women) will be intensely concerned about the sexual fidelity of reproductive age partners. Some of these predictions include: (a) Sexual infidelity by wives will be a more frequent cause of divorce than sexual infidelity by husbands (Betzig, 1989); (b) the use or threat of violence by husbands to achieve sexual exclusivity and control of wives will vary as a function of wives' reproductive value, which peaks in the late teens and declines monotonically thereafter (Wilson & Daly, 1996); and (c) in the context of competing for romantic partners, the tactic of spreading rumors that a same-sex rival is sexually promiscuous will be more effective when performed by women than by men (because it raises the specter of cuckoldry; see Buss & Dedden, 1990). The fact that the first two predictions have been supported by extensive cross-cultural data whereas the third prediction has not been supported factors into one's evaluation of the more general hypothesis from which these predictions were generated. That two of the three predictions garnered strong support provides indirect support for the hypothesis. That the third prediction was rejected raises questions about the hypothesis. Ultimately, the value of the more general hypothesis and theoretical model is judged by the cumulative weight of the evidence.

Revision of evolutionary psychological models and hypotheses after a prediction has been rejected. In evolutionary psychology, as in the rest of science, specific theoretical models and hypotheses are proposed, developed, revised, and replaced on evidential grounds. When the data fail to support a prediction, it is back to the drawing board, either to attempt a better translation of the hypothesis (into a specific prediction) or to actually modify or reject the hypothesis altogether. In the preceding case of spreading rumors about same-sex rivals, the predictive failure led to a rethinking of the problem of paternity uncertainty and to the recognition of an error in the original conceptualization: the failure to distinguish between long-term and short-term mating contexts (see Schmitt & Buss, 1996). Although men want sexual exclusivity in long-term mates, they may consider sexual promiscuity desirable in potential short-term mates because it signals sexual availability and less chance of entanglement. Schmitt and Buss thus predicted and subsequently found a moderating effect of temporal context: In the context of competing with other women for long-term mates, spreading rumors that a same-sex rival was sexually promiscuous was judged to be an effective means of reducing that rival's attractiveness; but in the context of competing with other women for short-term mates, spreading rumors that a same-sex rival was sexually unavailable was judged to be an effective means of reducing that rival's attractiveness.

At a more general level, Buss and Schmitt (1993) recognized that a limitation of Trivers's (1972) theory of parental investment and sexual selection was its failure to explicitly distinguish between short-term and long-term mating contexts. Buss and Schmitt proposed an extension of parental investment and sexual selection theory—sexual strategies theory—that specifically incorporated this temporal dimension. Sexual strategies theory generated a multitude of new predictions about between- and within-sex variation in mating strategies. It enabled the parent theory (parental investment and sexual selection) to digest a series of anomalous findings and turn them into positive evidence. The process began with a set of predictive failures at the lowest level of the hierarchy, which in turn led to reevaluation of more general hypotheses and ultimately to an adjustment of the middle-level theory. This adjustment spawned a host of new research (e.g., Cramer, Schaefer, & Reid, 1996; Landolt, Lalumiere, & Quinsey, 1995; Schmitt & Buss, 1996) that has significantly advanced our understanding of human mating strategies. Consistent with Lakatos's (1970) description of scientific progress, the feedback process between theory and data was critical to the acquisition of knowledge.

This example demonstrates why, in most cases, falsifying a specific evolutionary prediction does not directly falsify evolutionary metatheory (unless that prediction directly tests a hard core metatheoretical assumption, such as nepotism; see earlier discussion of family violence). This is because the generation of predictions depends on the specification of appropriate auxiliary assumptions. These auxiliary assumptions are part of the middle-level theory, which applies the basic assumptions of the metatheory to a particular content domain. If a middle-level theory fails to specify some important auxiliary assumption (e.g., the distinction between short-term and long-term mating contexts), then the falsification of a lower level hypothesis or prediction does not directly call into question the higher level (metatheoretical) assumptions from which the middle-level theory was drawn (see Figure 2). Instead, the middle-level theory itself is questioned. This logic is consistent with (among others) the Lakatosian philosophy of science and illustrates how middle-level theories, hypotheses, and predictions provide a protective belt that insulates the basic assumptions at the hard core of a metatheory from direct refutation (Lakatos, 1970, 1978).

Summary and Conclusion

To summarize, an evolutionary psychological approach to the related topics of sexual jealousy and male parental investment involves multiple levels of analysis. At the metatheoretical level, modern evolutionary theory provides a set of basic assumptions for guiding psychological research. Drawing on these assumptions, the theory of parental investment and sexual selection presents a useful framework for the study of sexual jealousy and male parental investment. In addition, reciprocal altruism theory provides a competing framework for the study of male parental investment. Competing hypotheses can be developed both within and across middle-level theories. These hypotheses vary on a continuum of confidence, ranging from firm to speculative. At the speculative end of the continuum, different interpretations of a single middle-level theory can and do generate competing hypotheses. This plurality is defensible to the extent that competing theories and their derivative hypotheses are formulated so that they generate specific, testable predictions. When a prediction fails, it calls into question the more general hypothesis from which it was drawn, and this may in turn lead to revision or abandonment of the middle-level theory that generated it. At each level of analysis, evaluation is based on the cumulative weight of the evidence. These standards and procedures for evaluating evolutionary explanations are consistent with "normal paradigm science" (Kuhn, 1962).

In conclusion, the structure of evolutionary psychological explanations clearly adheres to the Lakatosian model of science. This adherence occurs both in terms of the structure of scientific explanations (i.e., the multiple levels of analysis) and the consequences for one level of analysis of falsifying an explanation at another level of analysis. The middle-level theories, hypotheses, and predictions described in the evolutionary psychological model clearly constitute the problem-solving machinery that enables one to indirectly test the basic metatheoretical assumptions of modern evolutionary theory. It is within this protective belt that competing middle-level evolutionary theories vie to achieve the best operationalization of the metatheory as it applies to a given domain (such as male parental investment). Paralleling the logic of Lakatos, these competing theories and their derivative hypotheses and predictions are largely characterized by the use of, not the testing of, the basic assumptions of modern evolutionary theory. Finally, the evolutionary psychological framework and the Lakatosian model of science ascribe similar consequences to the act of falsifying an explanation at a given level of analysis. That is, the two approaches provide consistent descriptions of how these different levels of explanation affect one another. Central to both the Lakatosian model and the evolutionary psychology research program is the idea that it is the protective belt, not the basic assumptions of the metatheory, that is replaced or modified in the face of recalcitrant facts. From the Lakatosian perspective, metatheories are kings and hypotheses are their humble servants, to be sacrificed, if need be, to protect the hard core of the metatheory from refutation. "Of interest in the Lakatosian model is, once again, the *primacy* of theory: theoretical assumptions lie in the hard core and survive all but the most sustained attack against the program as a whole" (Galison, 1988, pp. 204–205).

Evaluating the Hard Core of a Metatheory

What if the metatheoretical assumptions are wrong, and the researcher proceeds as if they are correct? How can these assumptions be evaluated, given their relative protection from recalcitrant facts?

Rather than using the method of falsificationism to evaluate metatheories as false or not yet falsified (as a strict Popperian perspective might imply), Lakatos (1970) argued that metatheories are more properly evaluated as progressive or degenerative based on the performance of their protective belt. A metatheory that uses its protective belt to (a) digest apparent anomalies and (b) generate novel predictions and explanations is viewed as a progressive metatheory. By contrast, a metatheory that utilizes its protective belt primarily to deal with anomalies and contributes relatively little new knowledge is viewed as a degenerating metatheory. Prior to the Newtonian revolution, for example, astronomers had to make so many ad hoc adjustments to prevailing theoretical models of the solar system—the Copernican system, and prior to that, the Ptolemaic system—that the complexity of these models eventually far outweighed their accuracy (Kuhn, 1962; see also Meehl, 1978, for a discussion of degenerative theories in psychology).

Lakatos's (1970) description of scientists working within the Newtonian metatheory provides a powerful example of how a progressive metatheory both removes anomalies and creates new knowledge:

> The classical example of a successful research programme is Newton's gravitational theory: possibly the most successful research programme ever. When it was first produced, it was submerged in a sea of "anomalies" (or, if you wish, "counter examples"), and opposed by the observational theories supporting these anomalies. But Newtonians turned, with brilliant tenacity and ingenuity, one counter-instance after another into corroborating instances, primarily by overthrowing the original observational theories in the light of which this "contrary evidence" was established. (p. 48)

Lakatos (1970) suggested that metatheories often continue to thrive despite early recognition of counterexamples. In fact, he argued that any revolutionary metatheory, by definition, begins within a sea of such anomalies and counterexamples. Scientists using a particular metatheory then proceed to accommodate these anomalies by reevaluating old "facts" and creating new middle-level theories and auxiliary hypotheses. The ability of a metatheory to accommodate such anomalies is one of the key criteria used to identify a metatheory as progressive or degenerative. In the case of early counterexamples to Newtonian metatheory, previous measures of the earth's circumference were called into question by Newton's model. After new measurements of the circumference of the earth had been made, Newton saw that the figures on which he had based his initial test of this theory were false and that the corrected figures agreed with his description of planetary motion (Reichenbach, 1951; cf. Lakatos, 1970). Recalculating the circumference of the earth is an instance of reevaluating an old "fact," digesting it, and in this case turning it into positive evidence. Calculating the position, mass, and velocity of a previously unknown planet to explain an anomaly in the motion of a known planet would be an example of a generative auxiliary hypothesis used to protect the hard core of a metatheory (see Churchland, 1986, pp. 261–262, for further discussion of this point).

> As long as the adding of auxiliary assumptions led to fruitful new discoveries and explanations, the program was progressive; when the auxiliary assumptions needed to protect the core began contributing only marginally to the advancement of learning, the program "degenerated" and was discarded. (Galison, 1988, p. 204)

According to the Lakatosian philosophy of science, then, the key scientific criteria for evaluating evolutionary psychology's guiding metatheory is not whether its core assumptions are false or not yet falsified, but rather how well the metatheory accommodates anomalies and whether it leads to fruitful new discoveries, explanations, and avenues of research.

Is Evolutionary Metatheory Progressive?

To address this key question, we examined (a) whether modern evolutionary theory has been successful in digesting major anomalies and (b) whether the evolutionary psychology research program has been successful in generating novel predictions and explanations of human behavior. (See also Holcomb, 1993, and Ruse, 1989, for applications of Lakatosian ideas to evolutionary theory.)

Has Evolutionary Metatheory Been Successful in Digesting Major Anomalies?

According to the Lakatosian view of science, a progressive metatheory can thrive despite early recognition of counterexamples, given that it can accommodate such anomalies by either challenging the existing facts on which the anomalies are based or by creating new facts (consistent with the metatheory) to account for the anomalous data. We already discussed one counterexample to evolutionary principles: the "fact" that the family is the most frequent single locus of homicide (Gelles, 1979; Straus & Gelles, 1990). This fact appears anomalous, given that individuals should be strongly inhibited against terminating their own fitness vehicles. Evolutionary psychologists (Daly & Wilson, 1988) challenged this fact by reevaluating the definition of family. The old fact was based on a sociological definition of family (that included both genetically related and unrelated cohabitants). Daly and Wilson created new facts based on a biological definition of family. In an analysis of Detroit homicide data, Daly and Wilson found that cohabitants who were not genetic relatives of the killer were more than 11 times as likely to be murdered as cohabitants who were genetic relatives of the killer, and that only 6.3% of all homicides occurred between genetic relatives. These new facts digested the apparent anomaly and turned it into positive evidence.

A major early anomaly for evolutionists—one that nearly spelled the death of Darwinism—was the so-called altruism problem, which was first identified by Darwin (1859) himself. The solution to this problem came more than a century later (Hamilton, 1964) and is one of the great triumphs of modern evolutionary theory. This triumph is perhaps the best exemplar in modern science of a progressive metatheory digesting an apparent anomaly and turning it into positive evidence.

There existed in Darwin's time (and still exist today) species in which every generation produce castes of sterile "workers" (individuals who do not reproduce but instead spend their entire lives in the apparently altruistic service of the reproduction of other members of their colony). It appears that *eusociality* (as the phenomenon has been called) has evolved several times over, appearing in different species of ants, termites, wasps, and bees (see Alexander, Noonan, & Crespi, 1991, and Cronin, 1991, for good reviews). The well-known existence of sterile castes of worker insects had the makings of a falsification bullet for Darwin's theory of adaptation through natural selection. Indeed, Darwin (1859) wrote that the existence of sterile castes "at first appeared insuperable, and actually fatal to my whole theory" (p. 236; see Sherman, Jarvis, & Alexander, 1991). Eusociality seemed to violate a basic assumption of evolutionary theory, which stated that only changes in organismic design that enhance individual reproduction can evolve through natural selection.

The solution to the altruism puzzle was presaged by Darwin (1859), who suggested that eusociality might be a trait that one can possess without necessarily expressing it: So long as those individuals who express it contribute enough to the reproduction of others who carry the same trait, but who do not express it, then the trait itself could evolve. Almost a century later, after the discovery of genetic coding, one evolutionary biologist expressed this idea somewhat differently:

> We should expect individuals in species like our own to have evolved to give their lives only for more than two brothers or more than eight cousins, since brothers have a one in two chance of carrying alleles for such bravery and cousins a one in eight chance. (Haldane, cited in Sherman et al., 1991, p. 5)

This conjecture bears striking similarity to the logic behind what came to be the solution to the altruism problem: Hamilton's (1964) kin selection theory. The theory posits that if individuals can discriminantly allocate investment to particular relatives who are likely to possess the genetic basis for a given trait, then that trait can thrive in that genetic population, even if the investment in relatives caused the individual to forgo his or her own reproduction.

The elegance of kin selection theory came from the simple recognition that evolution works by increasing copies of genes, not copies of the individuals carrying the genes. Thus, the genetic code for a trait that reduces personal reproductive success, such as eusociality, could be selected for if the trait, on average, led to more copies of that genetic code in the population. The genetic code for eusociality could spread through a population as long as (a) it causes an organism to help close relatives to reproduce and (b) the cost to the organism's own reproduction is offset by the reproductive benefit to those relatives (discounted by the probability that the relatives who receive the benefit have inherited the same genetic code from a common ancestor). Drawing on kin selection theory, evolutionary biologists were able to formulate an elaborate set of hypotheses about how eusocial insects should distribute their reproductive effort toward sisters, half-sisters, brothers, and offspring. These hypotheses were tested and confirmed (e.g., Frumhoff & Baker, 1988; Trivers & Hare, 1976). Hamilton's (1964) theory of kin selection has been found to provide a strong account of numerous—previously anomalous—cases of apparent altruism, such as the alarm calls given in prey species that appear to benefit kin by alerting them of danger, but put the caller at greater risk for predation (see Cronin, 1991, for an excellent review of the history of research and thought on kin selection).

In sum, evolutionary metatheory used its problem-solving machinery to digest an apparent anomaly: the problem of altruism. The development of kin selection theory not only defended evolutionary theory from refutation, but also enabled the metatheory to turn a series of counterexamples (e.g., eusociality, predator alarm calls) into positive evidence. Although modern evolutionary theory still faces some vexing counterexamples (e.g., homosexuality, schizophrenia), the basic assumptions of the theory have been so strongly empirically supported that they are now widely accepted as fact in the biological community.

Does Evolutionary Metatheory Generate Novel Predictions and Explanations?

The second criterion in determining whether a metatheory is progressive is its generativity. Perhaps the issue of greatest interest to psychologists is whether an evolutionary framework can be used to generate new, testable hypotheses about aspects of mind and behavior that are as yet unobserved (rather than simply account—in post hoc manner—for existing data), and whether these novel predictions can withstand empirical scrutiny. To demonstrate how the use of modern evolutionary theory has led to the acquisition of new knowledge, we consider one dramatic animal example (the naked mole rat) and a series of human examples.

About a decade after the publication of Hamilton's (1964) classic article on kin selection, a zoologist—Richard Alexander—gave a lecture on the evolution of eusociality during which he attempted to explain why this strategy had apparently not evolved in vertebrates. In doing so:

> He hypothesized a fictitious mammal that, if it existed, would be eusocial. This hypothetical creature had certain features that patterned its eusocial evolution after that of termites (e.g. , the potential for heroic acts that assisted collateral relatives, the existence of an ultrasafe but expansive nest, and an ample supply of food requiring minimal risk to obtain it). Alexander hypothesized that this mythical beast would probably be a completely subterranean rodent that fed on large tubers and lived in burrows inaccessible to most but not all predators, in a xeric tropical region with heavy clay soil. (Sherman et al., 1991, p. viii)

After his lecture, a member of the audience told Alexander of a researcher at the University of Cape Town who was studying the species *H. glaber*, the naked mole rat. It turned out that the naked mole rat provided almost an exact fit to the description of the fictitious eusocial mammal that Alexander had described! Many letters, phone calls, and field trips to Africa later, it became strikingly clear that *H. glaber*, the naked mole rat, had all of the ecological and behavior features (e.g., altruistic acts that assisted collateral relatives, existence of an ultrasafe expansive nest, an ample supply of food requiring minimal risk to obtain it) predicted by this evolutionary model of eusociality in a hypothetical mammalian species. The initial results of this discovery of the first eusocial vertebrate were published in *Science* (Jarvis, 1981). Since then dozens of articles and one book (see Sherman et al., 1991) have been written on the ecology and behavior of this fascinating eusocial species.

Does Evolutionary Psychology Generate Novel Predictions and Explanations of Human Behavior?

Examples such as the confirmation of evolutionary hypotheses about a eusocial mammal suggest that the basic assumptions of modern evolutionary theory, which evolutionary psychologists employ to construct middle-level theories, do in fact constitute a progressive metatheory capable of producing new knowledge and forming specific predictions. There are many generative research programs in evolutionary psychology. Here we present four samples for illustrative purposes.

Reasoning about social contracts. The issue of how humans reason assumes a central place in cognitive science. Based on reciprocal altruism theory, Cosmides and Tooby (1992; Cosmides, 1989) generated a rich set of hypotheses about the design features of the cognitive programs that regulate reasoning about social contracts. This work has provided a bold new explanation for the once elusive content effects in conditional reasoning tasks (e.g., the Wason selection task). The Wason selection task (Wason, 1966) is one of the most widely used experimental paradigms for examining people's ability to detect violations of conditional rules. Versions of the Wason selection task have been used in hundreds of experiments, and performance on the task has been found to vary widely depending on propositional content. For years it was not clear why novice and expert reasoners invariably had great difficulty with certain versions of the Wason selection task but found other logically equivalent versions to be quite easy. What was it about the hard cases that made them hard and the easy cases that made them easy? Prior accounts that stressed domain-general explanations of conditional reasoning could not answer this question. Cosmides and Tooby (Cosmides, 1989) demonstrated that the easy cases consistently involved patrolling social contracts (i.e., looking for cheaters in social exchanges). Cosmides and Tooby presented extensive data showing that humans do not have a general-purpose ability to detect violations of conditional rules, but rather that human reasoning appears well-designed for detecting violations of conditional rules that correspond to instances of cheating in social contracts. These results support the evolutionary hypothesis that we possess dedicated mental software for detecting cheaters in cooperative social exchanges.

The cheater-detection model has survived the first round of critical alternative models (see Cheng & Holyoak, 1989) by introducing novel data that could not be predicted by existing alternatives and, more important, has contributed new knowledge to our understanding of how the mind works (Gigerenzer & Hug, 1992; see also Pinker, 1997, for a review). This research has provoked a new approach to the study of human reasoning, one that focuses less on errors of inference and more on identifying the design features of the cognitive mechanisms that regulate reasoning in specific domains as well as the information contents that activate the decision rules of these mechanisms (see Oaksford & Chater, 1994; Sperber, Cara, & Girotto, 1995).

Father involvement and timing of daughters' pubertal development. Draper and Harpending (1982, 1988) proposed a middle-level evolutionary theory of the role of father involvement in the development of female reproductive strategies. This theory posits that individuals have evolved to be sensitive to specific features of their early childhood environments, and that exposure to different early environments biases individuals toward acquisition of different reproductive strategies. Specifically, Draper and Harpending (1982, 1988) posited that an important function of early experience (approximately the first 5 years of life) is to induce in girls an understanding of the quality of male–female relationships and male parental investment that they are likely to encounter later in life. According to the theory, this understanding has the effect of canalizing a developmental track, which has predictable outcomes for girl's reproductive behavior at maturity. Girls whose experiences in and around their family of origin are characterized by discordant male–female relationships and relatively low paternal investment (e.g., father absence) perceive that male parental investment is not crucial to reproduction; these girls are hypothesized to develop in a manner that accelerates onset of sexual activity and reproduction, reduces reticence in forming sexual relationships, and orients the individual toward relatively unstable pairbonds (Draper & Harpending, 1982, 1988). Belsky, Steinberg, and Draper (1991; see also Surbey, 1990) added to this theory the hypothesis that girls from paternally deprived homes should also experience earlier pubertal maturation. From an evolutionary perspective, early pubertal maturation, precocious sexuality, and unstable pairbonds are integrated components of an accelerated reproductive strategy. During human evolution, this accelerated strategy may have promoted female reproductive success in ecological contexts in which male parental investment was not crucial to reproduction.

Although variation in the timing of pubertal maturation in girls is a socially relevant topic (i.e., early-maturing girls experience relatively high rates of breast cancer, teenage pregnancy, depression, and alcohol consumption [e.g., Caspi & Moffitt, 1991; Graber, Lewinsohn, Seeley, & Brooks-Gunn, 1997; Udry & Cliquet, 1982; Vihko & Apter, 1986]), there was almost no research on the psychosocial antecedents of this variation prior to publication of the evolutionary model. This gulf occurred because no other theory of socialization and child development provided a framework for studying timing of puberty. Indeed, researchers operating outside of the evolutionary umbrella had never thought to look at the relation between fathers' role in the family and daughters' maturational tempo. With the introduction of the evolutionary model of pubertal timing (see esp. Belsky et al., 1991), this topic developed into a fruitful new area of research. Most studies suggest that girls reared in father-absent homes reach menarche several months earlier than their peers reared in father-present homes (Moffitt, Caspi, Belsky, & Silva, 1992; Surbey, 1990; Wierson, Long, & Forehand, 1993). Moreover, some of these studies have found that the longer the period of father absence, the earlier the onset of daughters' menstruation (Moffitt et al., 1992; Surbey, 1990).[7] Finally, Ellis, McFadyen-Ketchum, Dodge, Pettit, and Bates (1999) presented longitudinal data showing that father effects on daughters' pubertal timing involve more than just father-absent effects: Within father-present families, girls who had more distant relationships with their fathers during the first 5 years of life experienced earlier pubertal timing in adolescence. Consistent with the original theorizing of Draper and Harpending (1982), the quality of fathers' investment in the family emerged as the most important feature of the proximal family environment in relation to daughters' reproductive development (Ellis et al., 1999).

Sex differences in spatial ability. Sex differences in cognitive abilities has remained a prominent topic in psychology for several decades (Halpern, 1986). One of the most reliable and robust findings in this area has been the male advantage in tests of spatial abilities (Halpern, 1986; Linn & Petersen, 1985). The idea, however, that men have an across-the-board advantage over women in spatial skills was called into question by an adaptationist analysis. This analysis emphasized that the design features of the cognitive programs that generate spatial abilities are adaptations to the recurring visual–spatial problems encountered by women and men in ancestral environments. Although there was surely much similarity between the sexes in the kinds of visual–spatial problems they faced during human evolution, there were also likely to have been important differences (Silverman & Eals, 1992). Foraging for edible plants, which was engaged in predominantly by females during human evolution (Tooby & DeVore, 1987), entails the solution of different kinds of visual–spatial problems than does tracking and killing animals, which was engaged in predominantly by males during human evolution (Tooby & DeVore, 1987). Silverman and Eals (1992) suggested that successful gathering involves the ability to encode the location of stationary food sources that are embedded within complex arrays of vegetation and to remember the location of those food sources at some later time. Successful hunting, by contrast, involves the ability to orient oneself in relation to objects or places, whether in immediate view or conceptualized across distances (to enable the pursuit of prey animals across unfamiliar territory), and to perform the mental transformations necessary to maintain accurate orientation during movements (to enable accurate placement of projectiles). According to this model, the male advantage on traditional spatial tasks (e.g., mental rotations, space relations) is a consequence of those tasks assessing types of cognition that were historically related to hunting. Silverman and Eals proposed the radical hypothesis that (contrary to all published studies) women should outperform men on spatial tasks that involve recognition and recall of spatial configurations of objects.

To test this "gathering hypothesis," evolutionary psychologists used spatial tasks that model the cognitive demands of foraging. For example, McBurney, Gaulin, Devineni, and Adams (1997) used the commercial game Memory™ as a gathering task analog. This game involved searching for matched pairs of objects that are depicted on cards arrayed face down on a table. The game of Memory™ places a premium on spatial location memory. It involves searching for stationary "resources" in a complex array, wherein players "slowly discover the nature and location of 'resources' by exploring their table-top 'habitat' and have subsequent opportunities to harvest their 'resources' only if they can remember their locations" (McBurney et al., 1997, p. 172). McBurney et al. had female and male participants both play Memory™ and complete a 20-item mental rotation task. As in previous research, men outperformed women in the mental rotation task (d = .67). By contrast, women outperformed men at Memory™ by a wide margin (d = –.89). In total, there have now been more than 20 empirical tests of the gathering hypothesis using a variety of research designs. The data from these studies indicate that women tend to outperform men in memory for both frequencies and locations of objects (Eals & Silverman, 1994; James & Kimura, 1997; McBurney et al., 1997; Silverman & Eals, 1992). These data provided a needed corrective to the notion of across-the-board male superiority in spatial abilities. As predicted only by the evolutionary psychological model (Silverman & Eals, 1992), women outperform

[7]Not all studies (see Campbell & Udry, 1995) have found an accelerating effect for years of father absence on menarcheal age. Ellis and Garber (in press) found that years of stepfather presence, rather than years of biological father absence, best accounted for girls' pubertal timing (suggesting a possible pheromonal effect).

men in some spatial domains whereas men outperform women in other spatial domains, corresponding to the different kinds of spatial processing problems that may have been important to women and men in ancestral environments.

Fluctuating asymmetry and behavior in sexual and romantic relationships. Females in sexually reproducing species can be expected to prefer mates who have good genes and (in paternally investing species) are likely to provide external benefits to the female and her offspring (Trivers, 1992). If males vary in genetic quality, then selection should favor female preferences for male features advertising the presence of good genes (i.e., genes that enhance the health and well-being of offspring). Good-genes models of sexual selection propose that these kinds of female preferences could evolve and lead to sexual selection for male features indicative of good genes (Gangestad & Thornhill, 1997). One possible marker of variation in genetic quality is a phenomenon known as *fluctuating asymmetry* (FA)—the extent to which an organism's bilateral physical traits deviate from symmetry. Individual differences in FA are thought to result from heritable variation in the ability to withstand various disruptions during development, including both environmental stressors (such as parasitic infections) and genetic disturbances (such as deleterious recessive genes; Gangestad & Thornhill, 1997; Shackelford & Larsen, 1997). Across a variety of species, FA is inversely related to survival rates, growth rates, fecundity, and male mating success (Gangestad & Thornhill, 1997; Watson & Thornhill, 1994).

The good-genes model of sexual selection posits that females possess psychological mechanisms designed to detect and prefer male features indicative of good genes (e.g., low FA). Accordingly, men who have low FA should be more desirable to women than their less symmetrical counterparts, and they should be able to use this advantaged position to obtain more sexual opportunities at lower costs per relationship. This hypothesis has been tested in an initial series of studies on American undergraduates conducted by Gangestad and Thornhill (reviewed in Gangestad & Thornhill, 1997; see also Thornhill & Gangestad, 1994). FA was assessed by totaling right–left disparities in seven bilateral traits (e.g., ankle girth, wrist girth). Consistent with the hypothesis, men who were low in FA were found to have more lifetime sexual partners (even after controlling for age and physical attractiveness), to have more extrapair sexual encounters during ongoing dating relationships (even after controlling for relationship length, partners' extrapair sex, and both partners' physical attractiveness), and to devote less investment to their dating partners (even after controlling for relationship length).

One of the most intriguing hypotheses from the good-genes model of sexual selection is that females should possess mechanisms that discriminantly promote conception with males who evidence phenotypic markers of genetic benefits. Initial tests of this hypothesis have also been conducted. Thornhill, Gangestad, and Comer (1995) found that the female partners of men who were low in FA not only had more orgasms during sexual intercourse (even after controlling for men's physical attractiveness) but also were more likely to time those orgasms in a way that enhanced sperm retention (e.g., simultaneous orgasm with male partner). Further, in a set of experiments using a "stinky T-shirt" design, women in the fertile stages of their menstrual cycle (especially days 6–14) were found to prefer the scent of low FA men over the scent of high FA men (Gangestad & Thornhill, 1998; Thornhill & Gangestad, 1999). No such preference was found among women who were not in the fertile stages of their cycle. In sum, this research suggests that women may be responding to low FA men in ways that increase the chance of being impregnated by them. It is difficult to imagine how these observations could have been made in the absence of an evolutionary perspective to make them theoretically relevant.

In sum, the evidence that evolutionary psychology introduces new ideas and opens up valuable lines of inquiry grows each year (see Barkow et al., 1992; Betzig, 1997; Buss, 1999; Crawford & Krebs, 1998; Pinker, 1997; Simpson & Kenrick, 1997, for reviews of empirical findings). In all four of the sample research programs, evolutionary models generated sophisticated predictions that had not—and in many cases could not—be derived from other theoretical perspectives. The point is not that evolutionary accounts are better or worse than alternative accounts, but rather that evolutionary models have introduced a proliferation of new data to the field of psychology, changing the very nature of the content covered in our introductory psychology textbooks (Buss, 1995, 1999).[8] Evolutionary

[8] It is important to note that, although the four middle-level evolutionary theories presented in this section have demonstrated predictive power (by generating uncanny predictions that successfully anticipated the data), this does not mean that there is sufficient reason to regard these middle-level theories as true. There may be plausible post hoc explanations for the data that can be generated by other theories. For example, the association between low investment by fathers and early pubertal timing in daughters may be the result of a third variable: genetic transmission of early pubertal timing from mothers to daughters (early-maturing mothers not only tend to have early-maturing daughters but also might tend to form unstable marriages with low-investing fathers). In retrospect, both the evolutionary psychological model and the alternative behavior genetic model have explanatory power in this domain; that is, each model can account for the (now) known relation between paternal investment and daughters' pubertal timing. However, only the evolutionary psychological model anticipated the data (thus aiding in the acquisition of knowledge). Consistent with the Lakatosian approach to science, future research employing genetically informative designs is needed to determine which of the two models provides the best account of the data.

psychology has the hallmarks of a currently progressive research program capable of providing us with new knowledge of how the mind works.

Conclusion

Evolutionary approaches to the study of human social behavior, which first gained wide currency in the 1970s (Wilson, 1975), have been remarkable for their explanatory power. Various middle-level evolutionary theories have been used to explain fears and phobias, depression, aggression, competition, sexual coercion, parental love, observational learning, child abuse, marital dissolution, sexual jealousy, mate preferences, sexual fantasy, sperm volume, sequestering of women, incest taboos, morning sickness, color vision, conditional reasoning, judgment under uncertainty, aesthetics, self-deception, social illusions, maturational tempo, language acquisition, and so on (e.g., Alexander, 1979; Barkow et al., 1992; Crawford & Krebs, 1998; Pinker, 1997; Simpson & Kenrick, 1997; Symons, 1979; Wilson, 1975). Evolutionary theory has been used to generate explanations of social behavior in nearly all known species, and it appears applicable to the full range of topics in psychology. Yet this breadth has also been its weakness. Evolutionary psychology has been accused of being promiscuous, not just because of its emphasis on sex, but because it seems to account for an endless variety of phenomena. Critics charge that when our understanding of the phenomena change, so do the evolutionary explanations. Evolutionary models of social behavior are dismissed as being too elastic (i.e., unfalsifiable), too post hoc, and lacking strong empirical anchors.

A generation ago these criticisms carried some weight. The field of evolutionary psychology was quite young and had too high a ratio of theory to data. Its post hoc explanatory power exceeded its ability to make surprising new predictions that could be clearly confirmed by data. There was no shortage of speculating about human psychology and behavior, but these speculations lacked grounding in a well-developed body of theory and data. Many evolutionary explanations had the ring of untestable "just-so stories."

As the field of evolutionary psychology has matured, however, speculations have become more rigorous and tethered to data, often resulting in formal hypotheses that are articulated with sufficient precision to render them testable (Buss, 1997). The central thesis of this target article is that the procedures for testing evolutionary hypotheses, and more generally for testing the theoretical models and core assumptions these hypotheses are drawn from, adhere to well-established principles of contemporary philosophy of science (e.g., Lakatos, 1970, 1978). We have argued that evolutionary psychology is a currently progressive research program. Not only has evolutionary metatheory been largely successful in digesting apparent anomalies (such as the problem of altruism), but the most important advance in evolutionary psychology has been the development of a rich network of theoretical models that have yielded an array of surprising new hypotheses about human psychology and behavior. The empirical tests of these hypotheses have contributed important new data to the field of psychology and, most important, have enhanced our understanding of how the mind works (see Barkow et al., 1992; Crawford & Krebs, 1998; Pinker, 1997; Simpson & Kenrick, 1997).

Drawing on the Lakatosian philosophy of science, we have argued that one can subscribe to a particular set of metatheoretical assumptions and still accept that science is the process of sorting through *multiple alternative* (competing) models of phenomena. This enables a community of scientists to consider alternative middle-level theories and hypotheses within the context of a delimited set of a priori starting assumptions. The existence of alternative models merely reflects the fact that scientists can disagree about how to apply the shared "higher level" assumptions to particular phenomena at "lower levels" of analysis, whether those phenomena concern O-rings on space shuttle booster rockets or conditions that facilitate male parental investment. In evolutionary psychology, this lower level (middle-level theories and their derivative hypotheses and predictions) is generally characterized by the use of, not the testing of, the basic assumptions of modern evolutionary theory. It is concepts in this lower level—the protective belt—that are replaced or modified in the face of recalcitrant facts. At each level in the metatheoretical research program, evaluation is based on the cumulative weight of the evidence.

Within the protective belt of the metatheory, the development of competing middle-level theories is defensible to the extent that they are rigorously formulated so that they generate clear, testable hypotheses and predictions. In evolutionary psychology, as in the rest of science, rival theories are evaluated on the basis of their explanatory and predictive power: their relative ability to provide coherent accounts of known phenomena (including apparently anomalous findings) and to generate novel predictions that lead to the acquisition of knowledge. Loosely formulated models without clear, testable consequences represent poor science (whatever their theoretical origins). Well-formulated evolutionary models, anchored by data and grounded in the larger metatheoretical research program, rest at the heart of the new science of evolutionary psychology.

Notes

Timothy Ketelaar was supported by NIMH Grant T32 MH18931 to the Postdoctoral Training Program in Emotion Research (Paul Ekman, Director) and by a

Postdoctoral Fellowship at the Center for Adaptive Behavior and Cognition, Max Planck Institute for Psychological Research, Munich, Germany (Gerd Gigerenzer, Director).

Bruce Ellis was supported by NIMH Grant T32 MH18921 to the Postdoctoral Training Program in Developmental Psychopathology (Ken Dodge, Director).

We thank Constantine Sedikides, Mark Schaller, and two anonymous reviewers for helpful comments on this article. Nancy Alvarado, David Buss, Brian Haig, Ralph Hertwig, Neil Malamuth, Geoffrey Miller, Jeff Simpson, and the participants of the Developmental Psychopathology Proseminar at Vanderbilt University provided helpful comments on earlier drafts of this article. Portions of this article were presented at the annual meeting of the Human Behavior and Evolution Society, Davis, CA, July 1998.

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