
Evolutionary Psychology

Controversies, Questions, Prospects, and Limitations

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Evolutionary psychology has emerged over the past 15 years as a major theoretical perspective, generating an increasing volume of empirical studies and assuming a larger presence within psychological science. At the same time, it has generated critiques and remains controversial among some psychologists. Some of the controversy stems from hypotheses that go against traditional psychological theories; some from empirical findings that may have disturbing implications; some from misunderstandings about the logic of evolutionary psychology; and some from reasonable scientific concerns about its underlying framework. This article identifies some of the most common concerns and attempts to elucidate evolutionary psychology's stance pertaining to them. These include issues of testability and falsifiability; the domain specificity versus domain generality of psychological mechanisms; the role of novel environments as they interact with evolved psychological circuits; the role of genes in the conceptual structure of evolutionary psychology; the roles of learning, socialization, and culture in evolutionary psychology; and the practical value of applied evolutionary psychology. The article concludes with a discussion of the limitations of current evolutionary psychology.

Keywords: evolutionary psychology, misconceptions, adaptation, psychological mechanisms, natural selection

The goal of evolutionary psychology is to study human behavior as the product of evolved psychological mechanisms that depend on internal and environmental input for their development, activation, and expression in manifest behavior. Although empirical research within evolutionary psychology has grown steadily over the past 15 years (Cornwell, Palmer, Guinther, & Davis, 2005), some within mainstream psychology remain unfamiliar with its theoretical framework and application, and misconceptions about it are common (e.g., Cornwell et al., 2005; Park, 2007). The purpose of this article is to clarify some of the tenets of evolutionary psychology and to dispel several common misconceptions about it. By doing so, we hope to provide some conceptual tools to facilitate a greater integration of evolutionary psychology with mainstream psychological theory and research.

Theoretical Background

The fundamental basis of evolutionary psychology dates back to Darwin's (1859) theory of natural selection. Darwin postulated that if variant traits could be inherited by offspring from parents, then those variants that aided an organism's survival and reproduction would be transmitted to future generations at greater frequencies than alternatives. Variants with less beneficial effects—such as those that hinder an organism's ability to survive or reproduce—would not replicate because the organisms possessing them would transmit them at lower rates. This causal process results in three products: (a) **adaptations**,¹ inherited characteristics that reliably solved problems related to survival and reproduction better than competing alternatives during the time period in which they evolved (example: fear of dangerous snakes); (b) **by-products**, artifacts without functional value that persist because they are inherently coupled with adaptations (example: fear of harmless snakes); and (c) **noise**, variations in a given characteristic that are due to random environmental events or genetic mutations (example: random low base-rate fears, such as fear of sunlight, that occur because of stochastic genetic or developmental factors) (Tooby & Cosmides, 1992).

Although these principles historically have been applied to anatomy and physiology, there is now widespread recognition that they also provide powerful tools for explaining the origins of psychological, strategic, and behavioral adaptations in nonhuman animals as well as in humans (Alcock, 2005; Buss, 2005). Just as physiological adaptations solve specific problems associated with survival and reproduction (e.g., the immune system has evolved as a defense against disease), psychological adaptations too have evolved because they solved problems related to survival and reproduction (e.g., preferences for

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¹ Key terms defined in the Appendix are printed in boldface the first time they appear.



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statistically reliable cues of fertility in potential mates). *Psychological adaptations* are information-processing circuits that take in delimited units of information and transform that information into functional output designed to solve a particular adaptive problem.

Evolved fear adaptations provide relatively uncontroversial examples that are well supported empirically (Mineka & Öhman, 2002; Öhman & Mineka, 2003). Snakes and spiders, for example, signal potentially dangerous threats to survival. A programmatic series of studies has shown that an intense fear of snakes exists in humans and other primates; snakes and spiders embedded in complex visual arrays automatically capture attention far more than do harmless objects—they “pop out” of the visual array; humans rapidly condition to fear snakes more than most other stimuli; and the snake fear adaptation is selectively and automatically activated, it is difficult to extinguish, and it can be traced to specialized neural circuitry (Mineka & Öhman, 2002; see Rakison & Derringer, 2008, on the evolution of specialized spider detection adaptations). Evolutionarily ancient dangers such as snakes, spiders, heights, and strangers consistently appear on lists of common fears and phobias far more often than do evolutionarily modern dangers such as cars and guns, even though cars and guns are more dangerous to survival in the modern environment. The functional outputs of evolved fear adaptations, such as freezing, fighting, and fleeing, are specifically designed to solve the adaptive problems posed by these evolutionarily recurrent threats to survival (Bracha, 2004).

Adaptive problems are many in number. Solutions to one problem often fail to successfully solve other problems. Solutions to the adaptive problems of *food selection* (e.g., avoiding substances containing toxins) generally can-

not be used as solutions to the adaptive problems of *mate selection* (e.g., avoiding those who inflict costs) or *habitat selection* (e.g., choosing a site containing resources and refuge). Consequently, evolutionary psychologists suggest that the human mind is a complex integrated assembly of many functionally specialized psychological adaptations that evolved as solutions to numerous and qualitatively distinct adaptive problems—a premise about adaptations shared widely by evolutionary biologists in understanding nonhuman animals (Alcock, 2005). Psychological adaptations often interact with each other to produce adaptive behavior, as when a person is faced simultaneously with the adaptive problems of hunger and a threatening lion; fear of the lion will temporarily suspend hunger pangs until the threat of imminent death has passed (Buss, 2008).

The list of adaptive problems extends far beyond avoiding snakes, selecting nutritious food, and favoring fertile mates. It includes problems of parental investment (e.g., socializing sons and daughters), kinship (e.g., channeling altruism toward close rather than distant genetic relatives), friendship (e.g., detecting cheaters), coalitional cooperation (e.g., punishing free riders), selective aggression (e.g., diffusing a violent confrontation), negotiating status hierarchies (e.g., besting close rivals; dealing with subordinate status), and many others (Buss, 2008). Psychological adaptations are not separate “modules” in the Fodorian (Fodor, 1983) sense of informational encapsulation; rather, they often share components and interact with each other to produce adaptive behavior (see Barrett & Kurzban, 2006, for a cogent discussion of this issue).

Evolutionary psychologists are not monolithic in their theoretical stances. There exist legitimate scientific differences on key issues such as the importance and meaning of individual differences (Buss, 2009; Nettle, 2006; Tooby & Cosmides, 1990), the existence and functions of more domain-general psychological mechanisms such as fluid intelligence (Geary, 2009), and the importance of **group selection** (Williams, 1966; D. S. Wilson & Wilson, 2007). Nonetheless, evolutionary psychologists all share the view that understanding the evolved functions of psychological adaptations—the problems they were “designed” by a prior history of selection to solve (no forward-looking intent implied)—is an indispensable, not an optional, ingredient for a mature psychological science. Understanding the evolved function of a psychological mechanism, or *why* it exists (often referred to as an **ultimate explanation**) provides a complementary level of analysis to that of understanding the details of *how* the mechanism works (often referred to as a **proximate explanation**). Both types of explanation are required for a complete understanding, and indeed they mutually inform one another. Knowledge of the human liver, for example, would be incomplete without understanding its evolved functions (e.g., to neutralize toxins) as well as the specific processes by which those functions are achieved (e.g., the lobules that produce bile and emulsify lipids). Similarly, knowledge of psychological adaptations such as stranger anxiety in infants would be incomplete without understanding their functions (to avoid potentially dangerous humans) as well as the specific pro-



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cesses by which they operate—a predictable developmental emergence at 6 to 8 months, a special sensitivity to strange males more than strange females, emotional systems activated internally, external behavioral signaling to caregivers through crying, the activation of specific neural circuitry, and so on. Knowledge of ultimate functions is invaluable in guiding the search for the proximate causes, just as understanding proximate implementation informs the search for ultimate function.

Evolutionary psychology uses all of the standard methods of investigation available to psychologists to test hypotheses, including laboratory experiments, observational techniques, questionnaires, physiological techniques, mechanical recording devices, genetic methods, and brain imaging techniques. In addition, evolutionary psychologists sometimes use methods not typically used by psychologists, such as comparative analyses across species, ethnographic records, archeological records, paleontological data, and life-history data (Schmitt & Pilcher, 2004).

Common Queries About Evolutionary Psychology

We now turn to some common queries about evolutionary psychology and endeavor to provide answers to them.

1. Can evolutionary psychological hypotheses be empirically tested or falsified?

The logic of hypothesis testing in evolutionary psychology is the same as hypothesis testing in all sciences (see Keteleer & Ellis, 2000, for an extended discussion of falsifiability). The researcher first formulates a hypothesis about an evolved psychological mechanism and then generates testable predictions about the attributes or **design features** of that mechanism that have not previously been discov-

ered or documented (the phrase **design features** is standard shorthand in evolutionary biology for attributes or component parts of an adaptation that have been forged or “designed” by a past history of natural selection; no forward-looking or intentional process is implied by this phrase; see, e.g., Hauser, 1999).

A recent example comes from a research program on “adaptive memory.” Nairne and his colleagues hypothesized that evolved memory systems should be at least somewhat domain specific, sensitive to certain kinds of content or information (Nairne & Pandeirada, 2008; Nairne, Pandeirada, Gregory, & Van Arsdall, 2009; Nairne, Pandeirada, & Thompson, 2008). They hypothesized that human memory should be especially sensitive to content relevant to evolutionary fitness, such as survival (e.g., food, predators, and shelter) and reproduction (e.g., mating). Using a standard memory paradigm involving a scenario priming task and a surprise recall task, they found that words previously rated for survival relevance in scenarios were subsequently remembered at significantly higher rates than words rated for relevance in a variety of control scenario conditions. Furthermore, Nairne and his colleagues conducted additional experiments that pitted survival processing against well-documented powerful encoding techniques, such as ease of generating a visual image, ease of generating an autobiographical memory, and intentional learning in which subjects were instructed to remember the words for a later test. Interestingly, rating the item’s relevance in the survival scenario produced better recall performance than did *any* of the other well-known memory-enhancing techniques. The researchers concluded that “survival processing is one of the best encoding procedures yet identified in human memory research” (Nairne & Pandeirada, 2008, p. 242). Had the results failed to confirm the predictions about specialized sensitivity to survival-relevant content, Nairne’s adaptive memory hypothesis would have been falsified.

A second example of a collection of hypotheses that have been tested and subjected to the risk of falsification derives from *error management theory* (Haselton & Buss, 2000, 2003, in press; Haselton & Nettle, 2006). In an uncertain world in which observable cues are only probabilistically related to the true state of reality, there are two possible ways to err. One way to err is to infer that a state exists when it does not, as when a rustle in the leaves does not signal a snake but rather was caused by a gust of wind. The other way to err is to infer that a state does not exist when it actually does, as in a failure to infer that a snake exists on the basis of a rustling of leaves when a snake truly does exist. According to error management theory, the costs of making these two types of errors (false positive vs. false negative) under conditions of uncertainty were often recurrently asymmetric in the currencies of survival and reproduction. The cost of failing to detect a snake in the leaves, in this example, could result in death; the cost of erroneously inferring a snake that does not exist results in a trivial expenditure of energy in avoiding something harmless. If these and other asymmetric costs of errors recur over generations, selection is hypothesized to favor the



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evolution of cognitive biases that are designed to err in the least costly direction.

Error management theory logic has been used to test hypotheses about adaptive biases in domains ranging from visual and acoustic perception to inferences about sexual and homicidal motivation in other people. In the domain of visual perception, for example, the *descent illusion hypothesis* (Jackson & Cormack, 2007) was used to predict that people would make asymmetric distance estimations when judging from the top versus the bottom of a tall structure, owing to the dangers associated with falling from heights. Tests of the descent illusion hypothesis show that people perceive distances viewed from the top of tall structures to be 32% greater than precisely the same objective distances when viewed from the bottom, confirming the prediction (Jackson & Cormack, 2007). On the basis of error management theory logic, Neuhoff (2001) confirmed empirically that humans have an *auditory looming bias*—they overestimate the closeness of approaching sounds compared with receding sounds, because of the historically greater dangers associated with approaching rather than receding objects and predators. In the social realm, Haselton and Buss (2000) confirmed the existence of a *commitment skepticism bias* in women, such that they underinfer levels of romantic commitment (compared with men) that are based on cues such as declarations of love. The important point is that had any of the empirical tests failed, they would have falsified the descent illusion hypothesis, the auditory looming hypothesis, or the commitment skepticism hypothesis.

The science of confirming and falsifying hypotheses, of course, is typically more complex than these examples indicate. Often a hypothesis is embedded within a larger theoretical network. For example, one evolutionary *predic-*

tion is that women will prefer men as potential mates who express a willingness to invest in them and their offspring (Buss, 1995). This is derived from the *hypothesis* that in paternally investing species, females will use cues to a man's willingness to invest as a criterion for mate selection. In turn, this hypothesis is derived from *parental investment theory*, which posits that the sex that invests more in its offspring will be the choosier sex when selecting mates (Trivers, 1972). Finally, the logic behind parental investment theory is derived from *inclusive fitness theory* (Hamilton, 1964a, 1964b), the modern formulation of evolution by natural selection. As in all realms of psychological science, the evaluation of each evolutionary psychological hypothesis, as well as the broader theories within which they are embedded, rests with the cumulative weight of the empirical evidence.

Although evolutionary psychology is a relatively young field, hundreds of empirical studies have been conducted to test a variety of evolutionary psychological hypotheses. Some have been confirmed; others have been falsified; and others have not yet been subjected to enough empirical tests to render a firm scientific conclusion. Among those that have been confirmed by multiple methods in multiple samples by multiple investigators are anti-free-rider adaptations in cooperative groups (e.g., Price, Cosmides, & Tooby, 2002); cheater-detection adaptations in social exchange (e.g., Cosmides & Tooby, 2005); female superiority in spatial location memory as part of a gathering adaptation (e.g., Silverman & Choi, 2005); functional attributes of male and female short-term mating strategies (e.g., Greiling & Buss, 2000; Schmitt, 2005; Schmitt & International Sexuality Description Project, 2003); sex-differentiated deception tactics in human mating (e.g., Haselton, Buss, Oubaid, & Angleitner, 2005; Tooke & Camire, 1991); antipredator adaptations in children (e.g., Barrett, 2005); and dozens more (see Buss, 2008, for a recent review).

Among those that either have been falsified or have failed thus far in empirical tests are the kin altruism theory of male homosexuality (Bobrow & Bailey, 2001); the hypothesis that males have an evolved preference for virginity in selecting long-term mates (Buss, 1989); and at least one version of the “competitively disadvantaged male” hypothesis about rape (Lalumière, Chalmers, Quinsey, & Seto, 1996). The kin altruism hypothesis of male homosexuality, for example, contends that homosexuality is an adaptation that involves a shift among those whose heterosexual mating prospects are not promising from direct mating effort to investing in kin, such as the children of one's brothers and sisters (E. O. Wilson, 1978). In a direct test of this hypothesis, Bobrow and Bailey (2001) used samples of heterosexual and homosexual men matched for age, education, and ethnicity. They assayed generosity toward family members; financial and emotional investment; avuncular tendencies, such as willingness to give gifts or cash to support nieces or nephews; and general feelings of closeness toward genetic relatives. The results proved conclusive—they found no evidence for any of the key predictions made by the kin altruism hypothesis of male



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homosexuality. Subsequent empirical tests have also failed to support the kin altruism hypothesis, finding no significant differences between homosexuals and heterosexuals in generosity toward kin, general feelings of familiarity, or willingness to invest in nieces or nephews (Rahman & Hull, 2005). On the basis of the current empirical evidence, we can conclude that the kin altruism theory of male homosexuality has been refuted.

The key point is that precisely formulated evolutionary psychological hypotheses that yield specific predictions about design features that are not known to exist prior to empirical testing are fully amenable to empirical confirmation and falsification. Evolutionary psychological hypotheses, like those from other theoretical perspectives within psychology, vary in their quality, their precision, and the degree to which they are anchored in well-established theoretical foundations. Sloppy and imprecise evolutionary hypotheses that fail to generate precise predictions deserve scientific criticism. The sometimes reflexive charge that evolutionary psychological hypotheses as a rule are mere “just-so stories,” however, is simply erroneous, as the examples above demonstrate.

2. Don't people just solve problems using rationality? Wouldn't one domain-general rationality mechanism be more parsimonious than postulating many domain-specific mechanisms?

Some psychologists react to hypotheses about evolved psychological mechanisms by invoking concepts such as domain-general rationality as alternative explanations, suggesting that “people just figure it out.” Some propose that it is more parsimonious to postulate one or a few domain-general mechanisms such as “rationality” rather than nu-

merous domain-specific adaptations. Although these claims may have intuitive appeal, we suggest that they are of dubious validity as cogent scientific explanations.

The emotion of romantic jealousy provides a concrete example. Although dozens of studies had been conducted on romantic jealousy, it was not until evolutionary psychologists hypothesized sex differences in evolved design features that such differences were discovered (Buss, Larsen, & Westen, 1992; Daly, Wilson, & Weghorst, 1982; Symons, 1979). Because **paternity uncertainty** has been a recurrent adaptive problem for men, evolutionary psychologists hypothesized that men's jealousy would be especially triggered by cues to sexual infidelity, whereas women's jealousy would center on emotional infidelity (i.e., cues that signal the long-term diversion of commitment and resources, such as a mate falling in love with another woman).

Although both sexes experience jealousy over a partner's sexual *and* emotional infidelity, abundant empirical evidence from studies employing more than half a dozen different experimental methods supports the existence of sex differences in the relative weighting given to cues to infidelity (for recent reviews, see Buss, 2008; Buss & Haselton, 2005; and Sagarin, 2005). Independent replication is the hallmark of the scientific method, however, and a meta-analysis of 72 studies found a strong effect size ($d = 0.64$) in support of the hypothesized sex differences (Hofhansl, Voracek, & Vitouch, 2004), although an occasional study will fail to find full support for them (e.g., Penke & Asendorpf, 2008). The fact that the sex differences have been documented using highly diverse empirical methods, ranging from spontaneous memorial recall of cues of sexual versus emotional infidelity (Schützwohl & Koch, 2004) to sex-differentiated patterns of neural activation using fMRI technology (Takahashi et al., 2006) suggests that the burden of proof must now shift to those who doubt the existence of evolved sex differences in the emotion of jealousy (Buss & Haselton, 2005).

After these previously unknown sex differences were discovered as a consequence of evolutionary psychological hypotheses, others have offered post hoc explanations for their existence that invoke domain-general rationality. C. R. Harris and Christenfeld (1996), for example, suggested that the sex differences are due to “rationality combined with the general desire people have to keep what is theirs” (p. 378). They concluded by proposing that “the domain-general mechanism of rational thought” (p. 379) can explain the findings. Although we do not deny that humans are capable of rational thought, there are several problems with “the domain-general mechanism of rational thought” as an alternative explanation for most hypotheses that invoke specialized evolved psychological mechanisms: failure to predict, combinatorial explosion, poverty of the stimulus, and context-specificity. We address these problems in turn.

The failure-to-predict problem. Domain-general rational thought, as it has been used as an explanation, is typically invoked post hoc to account for new empirical findings discovered as a consequence of novel evolutionary psychological hypotheses. Domain-general



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rational thought has not, to our knowledge, been used to predict or discover new empirical findings. Consequently, it appears to lack both heuristic and predictive power. Hypotheses about motivational priorities are required to explain empirically discovered phenomena, yet they are not contained within domain-general rationality theories. A mechanism of domain-general rationality, in the case of jealousy, cannot explain why it should be “rational” for men to care about cues to paternity certainty or for women to care about emotional cues to resource diversion. Even assuming that men “rationally” figured out that other men having sex with their mates would lead to paternity uncertainty, why should men care about **cuckoldry** to begin with? In order to explain sex differences in motivational concerns, the “rationality” mechanism must be coupled with auxiliary hypotheses that specify the origins of the sex differences in motivational priorities. Because it requires the postulation of additional post hoc explanatory clauses for each new empirical phenomenon, “rationality” itself acquires the “lack of parsimony” problem sometimes erroneously leveled against specific evolutionary hypotheses.

The problem of combinatorial explosion.

Domain-general theories of rationality imply a deliberate calculation of ends and a sample space of means to achieve those ends. Performing the computations needed to sift through that sample space requires more time than is available for solving many adaptive problems, which must be solved in real time. Consider a man coming home from work early and discovering his wife in bed with another man. This circumstance typically leads to immediate jealousy, rage, violence, and sometimes murder (Buss, 2000; Daly & Wilson, 1988). Are men pausing to rationally deliberate over whether this act jeopardizes their paternity in future offspring and ultimate reproductive fitness, and then becoming enraged as a conse-

quence of this rational deliberation? The predictability and rapidity of men’s jealousy in response to cues of threats to paternity points to a specialized psychological circuit rather than a response caused by deliberative domain-general rational thought. Dedicated psychological adaptations, because they are activated in response to cues to their corresponding adaptive problems, operate more efficiently and effectively for many adaptive problems. A domain-general mechanism “must evaluate all alternatives it can define. Permutations being what they are, alternatives increase exponentially as the problem complexity increases” (Cosmides & Tooby, 1994, p. 94). Consequently, combinatorial explosion paralyzes a truly domain-general mechanism (Frankenhuis & Ploeger, 2007).

The poverty of the stimulus problem.

The sexual infidelity of a man’s mate has been statistically associated with increased paternity uncertainty over deep evolutionary time. It is highly improbable, however, that men could learn this statistical regularity during development. To do so, men would have to observe a large sample of instances of sexual infidelity (which tend to be cloaked in secrecy) and then associate them with potentially detectable cues to lack of paternity that would be displayed nine months, or even several years, later (e.g., lack of phenotypic resemblance to the putative father). In contrast, selection can favor specialized adaptations that exploit statistical regularities that are not detectable ontogenetically.

The context-specific rationality problem.

From an evolutionary perspective, there exists no domain-general criterion of “rationality.” It is often reproductively rational for a mateless man on a path toward reproductive oblivion to take life-shortening risks to change course—to engage in steep future discounting (M. Wilson & Daly, 2004). In contrast, such risk taking would be reproductively irrational from the perspective of a man who has a wife and three young children to protect. What would have been rational from the perspective of an attractive high-status man in our ancestral past (e.g., securing multiple mates through polygyny, affairs, or short-term mating) would be evolutionarily irrational from the perspective of an attractive high-status woman, who would be better off securing a long-term mate of high genetic quality who is both willing and able to invest in her and her children (Buss & Shackelford, 2008). Because what is “rational” differs across adaptive problems, sexes, ages, and life circumstances, there exists no single domain-general criterion of rationality.

In sum, domain-general mechanisms such as “rationality” fail to provide plausible alternative explanations for psychological phenomena discovered by evolutionary psychologists. They are invoked post hoc, fail to generate novel empirical predictions, fail to specify underlying motivational priorities, suffer from paralyzing combinatorial explosion, and imply the detection of statistical regularities that cannot be, or are unlikely to be, learned or deduced ontogenetically. It is important to note that there is no single criterion for rationality that is independent of adaptive domain.



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3. Aren't human behaviors the result of learning and socialization, not evolution?

The framework of evolutionary psychology dissolves dichotomies such as “nature versus nurture,” “innate versus learned,” and “biological versus cultural.” Instead it offers a truly interactionist framework: Environmental selection pressures shape evolved mechanisms at the phylogenetic level (Fraley, Brumbaugh, & Marks, 2005). Environmental input influences their development at the ontogenetic level (e.g., Belsky, 2007; Bjorklund & Pelligrini, 2000; Ellis & Bjorklund, 2005). And the environment provides cues that activate psychological adaptations at the immediate proximal level (e.g., Buss, 1995; Cosmides & Tooby, 2000). Thus, it does not make sense to ask whether calluses or mating decisions are “evolved” or “learned” or due to “nature” or “nurture.” All evolved mechanisms require some environmental input for their activation, be it repeated friction to the skin in the case of calluses or observable cues to mate value in the case of mating decisions.

The term *learning* is sometimes used as an explanation for an observed effect and is the simple claim that something in the organism changes as a consequence of environmental input. Invoking “learning” in this sense, without further specification, provides no additional explanatory value for the observed phenomenon but only regresses its cause back a level. Learning requires evolved psychological adaptations, housed in the brain, that enable learning to occur: “After all, 3-pound cauliflowers do not learn, but 3-pound brains do” (Tooby & Cosmides, 2005, p. 31). The key explanatory challenge is to identify the nature of the underlying learning adaptations that enable humans to change their behavior in functional ways as a consequence of particular forms of environmental input.

Although the field of psychology lacks a complete understanding of the nature of these learning adaptations, enough evidence exists to draw a few reasonable conclusions. Consider three concrete examples: (a) People learn to avoid having sex with their close genetic relatives (*learned incest avoidance*); (b) people learn to avoid eating foods that may contain toxins (*learned food aversions*); (c) people learn from their local peer group which actions lead to increases in status and prestige (*learned prestige criteria*). There are compelling theoretical arguments and empirical evidence that each of these forms of learning is best explained by evolved learning adaptations that have at least some specialized design features, rather than by a single all-purpose general learning adaptation (Johnston, 1996). Stated differently, evolved learning adaptations must have at least some content-specialized attributes, even if they share some components.

Solving the adaptive problem of incest avoidance requires learning to avoid sexual contact with close genetic relatives who are, from a reproductive standpoint, inappropriate sexual partners due to **inbreeding depression**. Empirically, there is good evidence for an evolved incest avoidance learning mechanism that is highly sensitive to reliable cues of close genetic relatedness, such as coresidence during development (Lieberman, Tooby, & Cosmides, 2003, 2007). Coresidence in the ancestral environment was a reliable cue of genetic relatedness, although this does not always hold true in the modern environment, as in experiments with Israeli kibbutzim. Duration of coresidence with a member of the opposite sex during childhood powerfully predicts lack of sexual attraction as well as the degree of emotional repulsion at the idea of having sex with him or her (Lieberman et al., 2003, 2007; see Tyber, Lieberman, & Griskevicius, 2009, for empirical evidence for three evolved functions of emotional repulsion—sexual disgust, pathogen disgust, and moral disgust).

Food aversions, on the other hand, require a different set of learning mechanisms and therefore result in a different set of learned behaviors. Humans, and most omnivores, learn food aversions through a mechanism that efficiently associates the nausea with the ingestion of toxins or pathogens in food recently consumed, thereby producing disgust and avoidance reactions to future encounters with the associated food (Domjan, 2004). Food aversion learning helps organisms to avoid ingesting substances that previously caused nauseous reactions to substances containing toxins or infectious microorganisms.

Another set of learning mechanisms is responsible for incorporating information about status and prestige in the psychology of hierarchy negotiation (Henrich & Gil-White, 2001). Among hunter-gatherer societies, good hunting skills lead to prestige (Hill & Hurtado, 1996). In academia, individuals attain high prestige by publishing prominent papers that are cited by other scholars (Pennebaker, 2009). People learn prestige criteria, in part, by scrutinizing the attention structure: Those high in prestige are typically those to whom the most people pay the most attention (Chance, 1967). By attending to and imitating the qualities, clothing styles, and behaviors of those to whom others pay



David M. Buss

the most attention, humans learn the prestige criteria of their local culture (one form of social learning) (Henrich & Gil-White, 2001).

These three forms of learning—incest avoidance, food aversion, and prestige criteria—require at least some content-specific specializations to function properly. Each operates on the basis of inputs from different sets of cues: coresidence during development, nausea paired with food ingestion, and group attention structure. Each has different functional output: avoidance of relatives as sexual partners, disgust at the sight and smell of specific foods, and emulation of those high in prestige. It is important to note that each form of learning solves a different adaptive problem.

There are four critical conclusions to draw from this admittedly brief and incomplete analysis. First, labeling something as “learned” does not, by itself, provide a satisfactory scientific explanation any more than labeling something as “evolved” does; it is simply the claim that environmental input is one component of the causal process by which change occurs in the organism in some way. Second, “learned” and “evolved” are not competing explanations; rather, learning requires evolved psychological mechanisms, without which learning could not occur. Third, evolved learning mechanisms are likely to be more numerous than traditional conceptions have held in psychology, which typically have been limited to a few highly general learning mechanisms such as classical and operant conditioning. Operant and classical conditioning are important, of course, but they contain many specialized adaptive design features rather than being domain general (Öhman & Mineka, 2003). And fourth, evolved learning mechanisms are at least somewhat specific in nature, containing particular design features that correspond to evolved solutions to qualitatively distinct adaptive problems.

Socialization is another explanation that is sometimes proposed as an alternative to evolutionary psychological explanations. Indeed, for much of 20th-century psychology, socialization was thought to be a powerful influence on human development, personality, and sex differences. This view was based on an old but extremely influential idea that “individual natures are merely indeterminate material that the social factor molds and transforms” (Durkheim, 1895/1962, p. 106). Although psychologists are increasingly recognizing that evolved tendencies play some role in psychological development, historically many theories of socialization implicitly assumed that the mind was more or less a blank slate upon which parents, teachers, and other agents of socialization wrote scripts (Pinker, 2002). Empirical work over the past few decades has gradually changed this assumption. Plomin and Daniels (1987), using behavioral genetic methodologies, showed that shared environmental influences within the family (those typically assumed by traditional socialization theories) account for a trivial percentage of variance in personality and other psychological variables. Furthermore, a meta-analysis of 172 studies of differential parental socialization practices of boys and girls discovered that “most effects were found to be non-significant and small” (Lytton & Romney, 1991, p. 267).

The sole exception to this conclusion, from among the 19 key domains examined in the meta-analysis, centered on sex-typed activities. Parents apparently encourage girls to play with dolls and houses and boys to play with balls, bats, and toy trucks. Even within this delimited domain, however, the assumption of a unidimensional parent-to-child direction of effects has been undermined by other studies. Male vervet monkeys, like boys, prefer playing with “masculine” toys such as trucks; female vervet monkeys, like most girls, prefer “feminine” toys such as Barbie dolls (Hines, 2004). Levels of prenatal exposure to androgens influence within-sex differences, with females exposed to higher levels of androgens displaying more masculine appearance and behavior (Hines & Green, 1991). The relative dearth of evidence for the potency of parental socialization on subsequent psychological development has caused some theorists to shift their emphasis away from parental socialization practices shared by children within families and instead to focus on peers (J. R. Harris, 2007) and within-family birth order (Sulloway, in press) to explain the non-shared environmental influences that behavioral genetic methods have shown must exist.

Given the large amount of effort that parents in all cultures expend on socializing their children, it would defy evolutionary logic if there were no adaptations in parents associated with socialization practices. Consequently, evolutionary psychologists fully accept the potential importance of environmental influences, whether coming from parents, siblings within families, or peers, but they suggest that socialization theories will become more powerful if informed by evolutionary psychological analyses (Buss, 2008; Ellis, Jackson, & Boyce, 2006).

The *daughter guarding hypothesis*—the idea that parents have evolved adaptations designed to socialize their

daughters and sons differently in the sexual realm—exemplifies one approach to evolution-based theorizing about socialization (Perilloux, Fleischman, & Buss, 2008). According to the daughter guarding hypothesis, greater parental constraint on the sexuality of daughters would have provided three functional benefits: (a) protecting their daughter's sexual reputation, (b) preserving their daughter's mate value, and (c) preventing their daughter from being sexually exploited (Perilloux et al., 2008). Using two separate data sources, young adults and their parents, Perilloux and her colleagues found that parents were more likely to control their daughter's than their son's mating decisions (e.g., by imposing an earlier curfew); reported more emotional upset over their daughter's than their son's sexual activity; and exerted more control over their daughter's than their son's mate choice decisions. In a massive cross-cultural study, Low (1989) found support for the evolution-based daughter guarding hypothesis in a study of 93 cultures—girls across cultures are taught to be more sexually restrained than boys.

These studies illustrate just one evolutionary approach to socialization practices (see Geary & Flinn, 2001, for an evolutionary analysis of parenting, and Ellis et al., 2006, for an evolutionary theory of adaptive phenotypic plasticity). Much theoretical and empirical work remains to be done, but we can already see that evolutionary and socialization explanations are not necessarily mutually exclusive; in some cases, they can be usefully integrated to provide novel predictions.

4. How does evolutionary psychology take culture into account?

Culture is sometimes advanced as competing with explanations that invoke evolved psychology, most frequently when cross-cultural variability is observed. Cultural explanations sometimes invoke the notion that differences between groups are *prima facie* evidence that “culture” is an autonomous causal agent that creates the content of the human mind (see Buss, 2001, for an extended discussion of the myth of culture as a causal explanation). Although the ambiguous referent “culture” is generally presumed to have a single, coherent meaning, it can actually refer to at least two distinct concepts: (a) **evoked culture**—differential output elicited by variable between-group circumstances operating as input to a universal human cognitive architecture; and (b) **transmitted culture**—the subset of ideas, values, and representations that initially exist in at least one mind that come into existence in other minds through observation or interaction (Tooby & Cosmides, 1992). Neither of these distinct senses of culture, however, can be divorced from the content-structuring, evolved organization of the human mind.

Evoked culture arises from human cognitive architecture and expresses itself differentially according to local conditions. Mate preferences for physical appearance, for example, have been hypothesized to vary across cultures according to local levels of pathogen prevalence. Parasites are known to degrade physical appearance. In geographic regions with higher parasite loads, both men and women

place greater value on a potential mate's physical attractiveness (Gangestad & Buss, 1993; Gangestad, Haselton, & Buss, 2006). In fact, ecological variation in parasite prevalence accounts for 52% of the cultural variation in the importance placed on physical appearance in a mate. The key point is that evolutionary hypotheses about evoked culture can explain some forms of cultural variation, although obviously the extent to which it can do so remains to be determined.

Transmitted (or adopted) culture describes a second form of cultural phenomena (e.g., Norenzayan, 2006). Examples of transmitted culture include beliefs about the afterlife, local moral repugnance at the thought of ingesting certain foods such as beef or pork, the content of certain stereotypes about outgroup members, and information transmitted through gossip. In a series of studies testing hypotheses about adaptations for information transmission, McAndrew, Bell, and Garcia (2007) found predictable patterns of content and persons to whom gossip is spread. Individuals spread damaging gossip rapidly and widely about rivals but tend to conceal it about friends or lovers. Sexual rivals tend to target potential mates as recipients of derogatory rumors about their competitors. And men and women differ in the content of gossip they spread about their rivals, with men focusing more on deficiencies in athletic and professional prowess and women focusing more on appearance and sexual conduct (Buss & Dedden, 1990; Campbell, 2004). No one claims to have articulated a comprehensive explanation of any particular instance of transmitted culture. Nonetheless, satisfying explanations of transmitted culture will involve at least the following elements: (a) psychological adaptations in individuals designed to selectively transmit ideas, beliefs, or representations to others; (b) psychological adaptations in receivers designed to selectively accept some ideas from among the available welter of ideas (Flinn, 1997); and (c) psychological adaptations designed to discount or reject other ideas from the available cultural pool on the basis of qualities such as source credibility and conflicts of fitness interests (Cosmides & Tooby, 2000). As Allport and Postman (1947, p. 314) astutely observed long ago, “Rumor is set into motion and continues to travel based on its appeal to the strong personal interests of the individuals involved in the transmission.”

Transmitted culture, if it is passed down over many generations, can in turn create new selection pressures for novel human adaptations (Cochran & Harpending, 2009). An adaptation for the digestion of dairy products, a product of the cultural invention of agriculture, provides one well-documented physiological example. A possible psychological example is the modern rise of sociopathic traits as a consequence of living in large cities, which lowers the reputational costs of pursuing a strategy of deception, cheating, and defection (Buss & Duntley, 2008; Mealey, 1995). Just as transmitted culture rests on a foundation of evolved psychological adaptations, novel adaptations can evolve as a consequence of transmitted culture. Whether humans have evolved psychological adaptations over the past 10,000 years for other culturally transmitted inven-

tions, such as cash economies, remains an open question. Although ground has barely been broken on adaptation–culture coevolutionary processes (sometimes called gene–culture coevolution), theoretical work suggests that this is a promising avenue of research (Cochran & Harpending, 2009; Richardson & Boyd, 2005).

The stance of evolutionary psychology toward culture can be summarized by several key points: (a) Cultural phenomena are real and require explanation; (b) labeling something as “culture” is simply a description, not a causal explanation; (c) it is useful to distinguish between different forms of cultural phenomena, such as evoked culture and transmitted culture; (d) explaining evoked cultural phenomena requires an understanding of the evolved psychological mechanisms and the relevant environmental input involved in their elicitation; (e) explaining transmitted culture requires the invocation of evolved psychological mechanisms in both transmitters and receivers; and (f) transmitted culture, if recurrent over generations, can influence the evolution of novel adaptations, which in turn can affect transmitted culture, theoretically producing adaptation–culture coevolutionary processes.

5. How do recent novel environmental phenomena affect human evolutionary psychology?

Extremely novel recent environments, of course, have not had enough time to influence the evolution of psychological adaptations. Humans live in modern environments that differ in some important ways from the ancestral environments to which our hominid ancestors adapted. Rather than collecting food via hunting or gathering, people eat at restaurants and buy prepackaged food at the grocery store. Modern computers have partially replaced face-to-face communication, whereas increased geographic mobility has brought together previously isolated peoples. Through contraceptive technology, modern humans can sever the link between sexual intercourse and reproduction. How do these recent environmental novelties affect human evolved psychology?

There are at least two approaches to answering this question. First, mismatches between modern and ancestral environments may negate the adaptive utility of some evolved psychological mechanisms. Mechanisms that once influenced reproductive success may no longer have the same effect. Our evolved taste for foods containing fat and sugar, adaptive in the past, now leads to obesity and Type 2 diabetes in modern environment replete with highly processed foods available cheaply and in great abundance. Second, novel environmental stimuli, such as media images or pornography, may trigger, hijack, or exploit our evolved psychological mechanisms.

Male sexual jealousy provides a specific example of a mismatch between ancestral and modern environments. Male sexual jealousy almost certainly evolved, in part, to serve a paternity certainty function—motivating men to ward off mate poachers, deterring a mate from sexually straying, and avoiding investing in a rival’s offspring

(Buss, 2000). In the modern world, however, if a man’s wife is taking birth control, male sexual jealousy adaptations could be considered superfluous in the prevention of investing in unrelated offspring.

If the relevant adaptation were a general motivation to maximize reproductive success (which cannot evolve in principle—see Tooby & Cosmides, 1990), then the wife’s contraception should short-circuit or dispel her partner’s sexual jealousy. If the relevant adaptation is a powerful emotion triggered by modern instances of ancestral cues, such as witnessing one’s mate kissing a rival, then knowledge of the wife’s contraception would not prevent the activation of her partner’s sexual jealousy. Psychological adaptations will be activated by the cues, or close approximations of those cues, that those adaptations were designed to detect, regardless of whether the adaptations currently serve the functions for which they originally evolved.

In order for contraception to affect male sexual jealousy, the selection pressures introduced by its invention would have to fashion new, or modify existing, psychological mechanisms. For such complex adaptations to evolve, the selection pressures responsible for their design must be reliably and recurrently faced for multiple generations. Effective contraception is a very recent invention on the timescale of human history. Consequently, there has not been enough time for natural selection to forge or modify complex psychological adaptations to effectively utilize the evolutionarily novel inputs associated with birth control. In some ways, there exist mismatches between the social world in which humans evolved and the modern worlds they now inhabit.

The other way in which novel environmental influences can affect evolved psychology is when they hijack our evolved psychological mechanisms by closely mimicking ancestral cues that the psychological adaptation was designed to detect. Pornography, for example, can activate a man’s sexual arousal adaptations, despite his inability to copulate and impregnate a two-dimensional image of a woman on a page or computer screen (Symons, 1979). This activated adaptation was designed to elicit arousal at the sight of an attractive, unclothed, sexually receptive woman. In ancestral environments, such a sight would only have occurred in a woman’s actual presence, reliably indicating a sexual opportunity. Consequently, there would have been no selection pressure to design a mechanism capable of distinguishing between a situation in which a nude woman was seen and a sexual opportunity existed, and a similar situation lacking such sexual opportunity (e.g., a photograph of a nude woman). In short, modern cues that mimic ancestral cues can artificially hijack evolved psychological adaptations in ways that may not be currently adaptive. In some ways, of course, modern environments do resemble ancestral environments, and adaptations functional in the past may continue to be functional in the present, so the continuity of functionality must be determined on a case-by-case basis.

6. What role do genes play in the framework of evolutionary psychology?

This is a complicated question that can be analyzed at a minimum of three levels—genetic determinism versus interactionism, genes underlying adaptations, and inferences about adaptations in the absence of knowledge of molecular-genetic substrate.

Genetic determinism versus interactionism. Genetic determinism is the view that genes determine phenotypes, such as morphology, psychology, or behavior, with little or no environmental influence. Evolutionary psychology forcefully rejects a genetic determinism stance and instead is organized around a crisply formulated interactionist framework that invokes the role of the environment at every step of the causal process. Environmental input includes (a) the selection pressures that give rise to psychological adaptations; (b) the environments needed for the proper development of these mechanisms in individual humans; and (c) immediate proximate inputs necessary for their activation. Indeed, adaptations exist in their current form precisely because they historically solved adaptive problems posed by various environmental contingencies.

To illustrate the inaccuracy of the notion that evolutionary psychology holds to a genetic determinist stance, consider one example of an environmental variable activating a plausible evolved psychological mechanism—the decrease in testosterone that occurs when men enter a long-term relationship such as marriage (Burnham et al., 2003) and the further decrease in testosterone after the birth of their first offspring (Gray, Yang, & Pope, 2006). This candidate adaptation is hypothesized to function to redirect the effort that a man allocates away from mating and toward the adaptive problem of parenting. The evolved mechanisms involved in the regulation of androgens in males obviously have a genetic basis, but in this context they are designed to use specific social cues in adjusting their levels (Gray, Parkin, & Samms-Vaughan, 2007). The key point of this example, whether or not further research confirms its nature and hypothesized function, is that evolutionary psychology furnishes an interactionist perspective. Psychological adaptations are designed to respond to social conditions such as being mated or unmated, being a parent or being childless, being high or low in the status hierarchy, and more generally, confronting one suite of adaptive problems rather than another. Although evolutionary psychology clearly rejects a blank slate view of the human mind, it just as clearly rejects genetic determinism and instead provides a detailed interactionist framework (Pinker, 2002).

Is there a gene for each behavioral adaptation? Evolutionary psychologists sometimes receive questions such as “Is there a jealousy gene?” or “Is there a gene for male aggression?” Genes do not code directly for particular physiological or behavioral characteristics; rather, they code for specific proteins. When geneticists say there is a gene for a particular trait, this is a shorthand way of indicating that the gene is involved in some way in the

expression of that trait. Most characteristics are polygenic, that is, they are regulated by complex interactions of many genes in conjunction with specific forms of environmental input. Single genes rarely code for any complex mechanism, be it physiological or psychological. Although the discovery of the sickle cell gene led some scientists to be optimistic about finding other single-gene adaptations, decades of subsequent research have revealed few others. All adaptations, by definition, must have a genetic basis. If they did not, they could not have evolved by the process of natural selection. This applies as much to brain-based psychological adaptations such as snake fear and cheater detection as it does to body-based physiological adaptations such as the kidneys and lungs.

Can you provide evidence for a psychological adaptation without documenting its genetic basis? Evolutionary psychologists often formulate hypotheses about adaptations, although some test hypotheses about by-products of adaptations (e.g., Kurzban, Tooby, & Cosmides, 2001) or noise generated by mutations (e.g., Keller & Miller, 2006). Adaptations are typically defined by the complexity, economy, and efficiency of their design and their precision in effecting specific functional outcomes, not by the ability of scientists to identify their complex genetic bases (Williams, 1966). For example, the human eye is indisputably an adaptation designed for vision, based on the design features for solving the particular adaptive problems such as detecting motion, edges, colors, and contrasts. The reliably developing, universal, and complex design features of the eyes provide abundant evidence that they are adaptations for specific functions, even though scientists currently lack knowledge of the specific genes and gene interactions involved in the visual system.

The same logic applies to psychological adaptations. Just as empirical research has documented snake fears, the auditory looming bias, and the descent illusion as adaptations without identifying their genetic basis, so too can research confirm the existence of adaptations for kin altruism, differential parental investment, and cheater detection in social exchange without identifying their genetic basis. The demonstration of specialized functional design provides some of the most compelling forms of evidence for adaptation. Identifying the genetic basis of a trait is neither necessary nor sufficient for demonstrating that the trait is an adaptation.

Nonetheless, we expect that developments in molecular genetics will be increasingly useful in both testing and informing evolutionary psychological hypotheses. Individual variations in the alleles of the DRD4 gene provide one example. The 7R allele has been linked with novelty seeking and extraversion (Ebstein, 2006), and it occurs at dramatically different rates in different geographical regions (e.g., higher in North America than in Asia). This 7R allele of the DRD4 gene has been hypothesized to be advantageous in exploiting resources in novel environments (Chen, Burton, Greenberger, & Dmitrieva, 1999; Penke, Denissen, & Miller, 2007). The finding that the 7R allele is substantially more common in nomadic than in sedentary popula-

tions supports this evolutionary psychological hypothesis (Eisenberg, Campbell, Gray, & Sorenson, 2008). In short, although molecular genetic analysis is not necessary for carrying out the research program of evolutionary psychology, we anticipate that it will become increasingly useful to test and to inform some evolutionary psychological hypotheses.

7. What is the practical value of evolutionary psychology?

Evolutionary psychology is a basic science, and as such it seeks a fundamental understanding of human nature—our evolved mechanisms of mind. Its conceptual framework was developed as a metatheory for aiding psychological science, not specifically as an aid for practical applications. Nonetheless, insights provided by evolutionary psychology have increasingly been applied to practical societal problems.

One practical application is in the field of clinical psychology. The evolutionary clinical psychologist Steve Ilardi has developed effective treatment for depression based on what he has hypothesized to be plausible mismatches between ancestral and modern environments. In ancestral times, people spent much of their day outdoors in sunshine, engaging in high-activity tasks such as hunting, gathering, building shelters, making tools, and tending to children. They lived in small tightly knit groups rather than isolated nuclear families. And their diets differed from most modern diets. His six-step treatment for depression includes increasing omega-3 fatty acid consumption, getting at least 30 minutes of daily exposure to sunlight, ramping up exercise, socializing daily with friends and family, engaging in antiruminative activity, and adopting patterns of good sleep hygiene—all procedures designed to mimic ancestral living conditions. This evolution-based therapy has produced a 14-week success rate of 75.3%, defined as a greater than 50% reduction in depressive symptoms, compared with a 22% success rate for a wait-list control group (Ilardi et al., 2007).

These results do not imply that depression was absent in ancestral times. Indeed, there is evidence that some forms of depression (or low mood) may serve different adaptive functions, such as disengaging from strategies that are not working, aiding people to be more objective in reassessing their goals, signaling to loved ones that they are in need of help, or conserving energy (e.g., Andrews & Thompson, 2009; Keller & Nesse, 2006; Nesse & Williams, 1994; Stevens & Price, 1996; Watson & Andrews, 2002). Nonetheless, rates of depression appear to have increased dramatically in the modern environment (Kessler & Üstün, 2008). A deeper evolutionary understanding of the common modern problem of depression, including its possible functions as well as the ways in which mismatches between ancestral and modern environments exacerbate it, can lead to better prevention and treatment. Although clinical applications are just beginning, evolutionary psychology is starting to yield practical benefits from clinical treatment and lifestyle recommendations.

Another practical application is in the area of law. Legal scholars are increasingly using knowledge of evolved psychological adaptations to understand how to better regulate human behavior and guide policy decisions. Evolutionary psychology helped to inspire the formation of the Society for Evolutionary Analysis in Law (SEAL: see www.sealsite.org), which now has over 400 members spanning more than 30 countries. The practical legal applications include uncovering conflicts among simultaneously pursued legal policies; sharpening the cost–benefit analyses that often influence legal policymaking; increasing our understanding about human decision making; disentangling the multiple causes of various law-relevant behaviors; exposing a variety of unwarranted assumptions underlying legal approaches for inspiring behavioral changes; assessing the comparative effectiveness of legal strategies used to change specific behaviors; and identifying undernoticed and unintended selection pressures that legal systems can themselves create (Jones & Goldsmith, 2005).

Evolutionary analysis sheds light on the complex factors behind sexual harassment, sexual assault, and infanticide, helping guide legal initiatives to aid in deterring future assaults (Jones, 1997, 1999; Jones & Goldsmith, 2005). To take one concrete example, sexual harassment and stalking laws typically invoke what is called a “reasonable person standard,” which means that a person can be liable for behavior if a reasonable person would have found the behavior to be sexually harassing or fear inducing. Evolution-guided research, however, has shown that women consistently judge a variety of acts to be more sexually harassing than do men, and women experience greater levels of fear than do men in response to specific acts of being stalked (Buss, 2003; Duntley & Buss, in press). But if reasonable women and reasonable men have different reactions, how exactly can a jury apply an ungendered “reasonable person standard”? Although no firm solutions have been attained, legal scholars are beginning to evaluate evolution-based findings such as these for constructing laws that are more effective for their intended purpose, such as the reduction of illegal sexual harassment and stalking (Jones & Goldsmith, 2005).

Although evolutionary psychology is a scientific discipline with no social agenda, greater knowledge of evolved psychological mechanisms and the environmental cues that activate them can, in principle, aid the effectiveness of preexisting widely desired social policies. Reducing the rate of child abuse, for example, could be facilitated by knowledge of the evolutionary forces that affect its occurrence. The fact that an evolutionary hypothesis led to the discovery of the single largest predictor of child abuse to date—the presence of a step-parent in the home—provides a “lever” for social policies designed to reduce the incidence of child abuse (Daly & Wilson, 2005; Herring, 2009; Jones & Goldsmith, 2005).

8. What are the limitations of evolutionary psychology?

Although we have articulated what we see as some of the valuable properties of evolutionary psychology and clari-

fied some common misconceptions, it is also important to highlight its limitations—both empirical phenomena that are genuinely perplexing and current conceptual constraints. One class of limitations pertains to phenomena that are truly puzzling from an evolutionary perspective, such as those that appear to reduce an individual's reproductive success, and cannot be explained by mismatches with, or hijacking of, our psychological mechanisms by modern-day novel environmental inputs. The most obvious example is homosexual orientation, which has been called "the Darwinian paradox." Exclusive homosexual orientation seems to defy evolutionary logic since it presumably fails to increase an individual's reproductive success. Although evolutionary hypotheses have been proposed for homosexuality, as discussed earlier, none have received empirical support thus far (e.g., Bobrow & Bailey, 2001).

Another puzzling phenomenon is suicide. In the United States, more than 30,000 individuals intentionally take their own lives each year (Gibbons, Hur, Bhaumik, & Mann, 2005). It is more common among males than females and shows age spikes in adolescence and old age. De Catanzaro (1995) and others (Brown, Dahlen, Mills, Rick, & Biblarz, 1999) argued that suicide is most likely to occur in those who have a dramatically reduced ability to contribute to their own reproductive fitness. In several studies, they found that ill health, burdensomeness to kin, and failure in heterosexual mating were strong predictors of suicidal ideation. Although burdensomeness to kin provides a plausible explanation for some suicides among the elderly, it strains credulity to argue that it would be beneficial to a healthy adolescent's reproductive success to end his or her life permanently, regardless of the current mating prospects. Such suicides are likely to be nonadaptive by-products of evolved mechanisms that malfunction (Wakefield, 2005). In brief, there are puzzling phenomena such as homosexuality and suicide that remain at least somewhat inexplicable on the basis of current evolutionary psychological accounts.²

Another limitation is that we lack detailed knowledge of many selection pressures that humans faced over the millions of years of their evolution. We do not possess a videotape of deep time that would reveal in precise detail all of the selective events over millions of years that have led to the current design of the human body and mind. Nonetheless, this limitation is not total. There is a surprisingly abundant amount of information about the human ancestral environment that we do know to a reasonable degree of certainty. For example, ancestral humans "had two sexes; chose mates; had color vision calibrated to the spectral properties of sunlight; lived in a biotic environment with predators; were predated on; bled when wounded; were incapacitated from injuries; were vulnerable to a large variety of parasites and pathogens; and had deleterious recessives rendering them subject to inbreeding depression if they mated with siblings" (Tooby & Cosmides, 2005, pp. 23–24).

Scientists also know that fertilization occurred internally within females, not within males; that females, not males, bore the metabolic costs of breastfeeding; that our

ancestors engaged in hunting for at least the past one million years (Leakey & Lewin, 1992; Milton, 1999); that our ancestors lived in small groups, ranging in size from a few dozen to 150 (Dunbar, 1993); and that our ancestors made and used tools for hunting, gathering, cooking, and warfare (Ambrose, 2001; Bingham, 2000; Klein, 2000). We also know that bipedal locomotion (Tattersall, 1995), extended childhood (Harvey & Clutton-Brock, 1985), long-term pair bonds, biparental investment (Hawkes, 2004), and relatively concealed ovulation (Sillén-Tullberg & Møller, 1993) distinguish our ancestors from their closest primate relative, the chimpanzee.

Evolutionary psychologists also use evidence from anthropology, archaeology, primatology, comparative biology, and ethology to elucidate some aspects of an otherwise scientifically uncertain ancestral past. For example, the paleontological evidence is rife with ancient caches of skulls and skeletons showing patterned lethal injuries, corresponding in size and shape to ancient weapons discovered in the vicinity. When combined with cave art depictions of fighting and many other sources of evidence, the cumulative findings yield reasonable inferences that human warfare was a potent hostile force of nature for human ancestors, that males were far more often perpetrators and victims of homicide than females, and that the majority of ancestral attackers were right handed (Duntley & Buss, 2008).

Evolutionary psychologists also use a task analysis of existing mechanisms to provide a window into the past. Just as astronomers use phenomena such as three degree black body radiation and an expanding universe to develop cogent and testable theories about events in the universe's past, evolutionary psychologists can use the functional design of the human psychological architecture to make cogent inferences about the past. The universal and reliably developing fear of snakes, even in modern environments containing few snakes, reveals that snakes were a hostile force of nature in our evolutionary past (Nesse, 1990). Similar scientific inferences can be drawn from universal human taste preferences (e.g., the substances humans find bitter often contain toxins), landscape preferences (e.g., desire for habitats containing prospect and refuge), and mate preferences (e.g., attraction to observable cues statistically correlated with fertility). Humans are living fossils. They are walking archives that provide a wealth of knowledge of the past. In sum, although convergent evidence from independent data sources yields especially reasonable inferences about *some* past selection pressures, evolutionary psychology, and indeed the entire field of psychology, will always be limited by incomplete knowledge of past selection pressures.

A final limitation of evolutionary psychology centers on a current relative deficiency in explaining cultural and individual differences. Evolutionary psychology has been

² Modern-day adoption of genetically unrelated children may represent another empirical puzzle; for detailed discussion of adoption in evolutionary perspective, see Silk (1990).

far more successful in predicting and explaining species-typical and sex-differentiated psychological adaptations than explaining variation within species or within the sexes (Buss, 2009). Although evolutionary psychologists have discovered a female superiority in spatial location memory (Silverman & Choi, 2005), a likely adaptation to gathering, they have not yet explained the considerable variation within women, nor why some men are better than women at this ability. Although progress is starting to occur in explaining individual differences (e.g., Buss, 2009; Keller & Miller, 2006; Nettle, 2006; Penke et al., 2007) and cultural differences (e.g., Gangestad et al., 2006; Schaller & Murray, 2008; Schmitt, 2005), the field has barely scratched the surface of the formidable task of explaining this variability.

Conclusions

Over the past 15 years, evolutionary psychology has grown from being viewed as a fringe theoretical perspective to occupying a central place within psychological science. Courses in evolutionary psychology are being offered at many colleges and universities throughout the United States and, indeed, in countries throughout the world. Evolutionary psychology is now covered in all introductory psychology textbooks, albeit with varying degrees of accuracy. One quantitative study of the coverage of evolutionary psychology in these texts came to three conclusions: (a) Coverage of evolutionary psychology has increased dramatically; (b) the “tone” of coverage has changed over the years from initially hostile to at least neutral (and in some instances balanced); and (c) there remain misunderstandings and mischaracterizations in each of the texts (Cornwell et al., 2005; Park, 2007).

The purpose of this article has been to answer frequently raised questions, to clarify evolutionary psychology’s stance on controversial issues, to correct some of the more common misunderstandings, and to highlight some of its current limitations. We hope that these clarifications will increase the accuracy of coverage in psychology journals and textbooks, aid communication between psychologists who do and do not adopt the theoretical perspective of evolutionary psychology, and ultimately help to advance knowledge in psychological science, which is the shared goal of all psychologists regardless of theoretical perspective.

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Appendix

Definitions of Key Terms

Adaptation. “Mechanisms or systems of properties crafted by natural selection to solve the specific problems posed by the regularities of the physical, chemical, developmental, ecological, demographic, social, and informational environments encountered by ancestral populations during the course of a species’ or population’s evolution” (Tooby & Cosmides, 1992, p. 62).

By-products. “Characteristics that do not solve adaptive problems and do not have functional design; they are “carried along” with characteristics that do have functional design because they happen to be coupled with those adaptations” (Buss, 2008, p. 39).

Cuckoldry. When a “mate poacher” has sex with an already married woman. Genetic cuckoldry occurs when a child results from this act. Evolutionarily, a cuckolded man risks investing unknowingly in another man’s offspring.

Design features. Attributes or component parts of an adaptation that have been forged or “designed” by a past history of natural selection (no forward-looking or intentional process is implied by this phrase).

Evoked culture. “Cultural differences [that] are explained simply by invoking a universal shared evolved mechanism combined with local between-group differences in input into that mechanism” (Buss, 2008, p. 417).

Group selection. “Selection operating between groups of individuals rather than between individuals. It would produce attributes beneficial to a group in competition with other groups, rather than attributes beneficial to individuals” (Ridley, 2004, p. 685).

Inbreeding depression. Occurs when genetic relatives together reproduce offspring that have decreased fitness due to the compounding of recessive alleles.

Mutations. Changes in the nucleotide sequence of a gene as a result of a copying error during cell division, ultraviolet radiation, viruses, or other mutagens.

Naturalistic fallacy. The misconception that ethical principles can be derived from what happens in the natural world. Also called the “is–ought fallacy,” that because something does exist it should exist.

Noise. Random phenomena produced by forces such as chance mutations, sudden and unprecedented changes in the environment, or chance effects during development.

Polygenic. An effect of two or more gene loci on a single phenotypic character.

Paternity uncertainty. See also *cuckoldry*; As a consequence of internal female fertilization, females can be 100% sure they are the mother of their offspring. For this same reason, males can never be 100% certain they are their offspring’s father.

Proximate explanation. Explaining *how* a mechanism works and is implemented, which can include identifying how a mechanism develops, the stimuli that activate it once it has developed, the procedures by which it operates, and the behavioral output it produces.

Transmitted culture. The subset of ideas, values, and representations that initially exist in at least one mind that come into existence in other minds through observation or interaction (Tooby & Cosmides, 1992).

Ultimate explanation. Explaining the attributes of a mechanism by identifying its evolved function, or the adaptive problem it was “designed” by selection to solve.