13 Varieties of Evolutionary Psychology

INTRODUCTION

What is evolutionary psychology? The answer to this question is complicated by the fact that the term "evolutionary psychology" is commonly used in two distinct senses. In one sense, evolutionary psychology is simply the study of human behavior and psychology from an evolutionary perspective. In this sense, evolutionary psychology is a *field of inquiry*, a loose confederation of research programs that differ significantly in theoretical and methodological commitments. These diverse research programs attempt to explain a wide variety of phenomena, ranging from foraging and birth spacing in traditional hunter-gatherer societies to encephalization (the progressive increase in brain size relative to body size in the human lineage) and the evolution of altruism and language. What unites these research programs is not a shared commitment to specific theories regarding the evolution of human behavior and psychology, but only a commitment to articulating questions about human behavior and psychology, and articulating answers to those questions, with conceptual and theoretical tools drawn from evolutionary theory.

In this broad sense, evolutionary psychology dates back to Darwin's *The Descent of Man* (published in 1871) and *The Expression of the Emotions in Man and Animals* (published in 1872). But, despite Darwin's early efforts, there was relatively little concerted study of human behavior and psychology from an evolutionary perspective until the latter half of the twentieth century, when several research programs emerged and attracted significant numbers of researchers (Laland and Brown 2002). The earliest of these

255

research programs was *human ethology*, exemplified by Konrad Lorenz's 1963 book *On Aggression*. The field really took off, however, with the emergence of *human sociobiology* in the 1970s, and in the ensuing decade additional research programs known as *evolutionary anthropology* and *human behavioral ecology* emerged. These research programs differ in the methods by which they apply evolutionary theory to the study of human behavior and psychology, and they differ in their theoretical accounts of how evolution has affected the human mind. Nonetheless, in the broad sense of the term, "evolutionary psychology" encompasses all of these research programs.

In a narrower sense, the term "evolutionary psychology" often designates just a *specific research program* within the field of evolutionary psychology, the foremost theoreticians of which are the anthropologists John Tooby and Donald Symons and the psychologists Leda Cosmides and David Buss. This group of researchers is united in the belief that adoption of an evolutionary perspective on human psychology immediately entails a number of very specific theoretical and methodological doctrines, and often the term "evolutionary psychology" specifically refers to this set of doctrines. So as to clearly distinguish the field of inquiry from the specific research program, I will refer to the field of inquiry as "evolutionary psychology" (in lowercase) and the research program as "Evolutionary Psychology" (capitalized).

Since its emergence in the late 1980s, Evolutionary Psychology has become the single most dominant research program in the field of evolutionary psychology, having garnered the lion's share of attention both within academia and throughout the popular media. But there is more to evolutionary psychology than Evolutionary Psychology. In particular, while Evolutionary Psychology has occupied the limelight, human behavioral ecology has quietly become a vibrant research program with impressive credentials. Indeed, it is the strongest rival to Evolutionary Psychology within the field of evolutionary psychology. In this chapter, I strive to give some sense of the diversity of research in evolutionary psychology by comparing and contrasting the theoretical and methodological principles of Evolutionary Psychology and human behavioral ecology. Both of these research programs, however, grew out of human sociobiology, so that is where we will begin.

HUMAN SOCIOBIOLOGY

Although many researchers have contributed to the program of human sociobiology, without doubt its leading theoretician has been Edward O. Wilson. In the mid-1970s, Wilson published several works that showcased numerous applications of evolutionary theory to the explanation of animal behavior and that articulated a theoretical framework within which to view them. Wilson called this framework *sociobiology*, which he defined simply as ''the extension of population biology and evolutionary theory to social organization'' (1978, x). Wilson further argued that the very principles that successfully explain the social organization of bee hives and dominance hierarchies in spider monkeys could be extended to human social behavior as well. This extension of sociobiology to human behavior became known as *human sociobiology*, and Wilson conceived it as the study of the biological basis of human social behavior.

The core idea of Wilson's sociobiology was that behavior has evolved under natural and sexual selection just as aspects of organic form have. Evolution by natural or sexual selection occurs when organisms in a population exhibit phenotypic variation, that variation is heritable, and organisms with one of the phenotypic variants are, on average, better adapted to their environment than organisms with the alternative phenotypes. When these conditions are met, selection causes the better-adapted phenotype to increase in frequency in the population, and the population as a whole becomes better adapted to its environment. Over very long stretches of time, selection has this effect on many different phenotypes, and populations thereby become well adapted to the environments they inhabit. The simple idea at the foundation of Wilson's program was that these explanatory principles are applicable to *behavioral*, not just morphological and physiological, phenotypes. For example, females of many species choose a mate on the basis of the quality of male courtship displays. If males' courtship displays vary in quality, and that variation is heritable, then sexual selection will cause the superior display to increase in frequency, and males will become behaviorally adapted to female preference. In this way, selection can shape the way that organisms behave just as it shapes their bodies.

This simple idea has two important corollaries. First, it entails that behaviors that have been shaped by selection are *adaptations*.

Thus, just as organisms in a population possess anatomical adaptations, they possess behavioral adaptations as well. Accordingly, part of Wilson's program was an effort to provide adaptationist explanations of how certain forms of behavior evolved. Second, since selection has shaped behavior to the environment in which it occurs, and since an organism's total environment includes its social environment, Wilson's simple idea entails that some behaviors are *adaptations to social life*. Accordingly, Wilson's program was principally concerned with explaining how individuals in a population are behaviorally adapted to social life with one another – explaining behavioral adaptations for dominance hierarchies, for manifesting and dealing with aggression, and for mating. Indeed, Wilson took the central theoretical problem of his program to be explaining the evolution of *altruism* – explaining why so many organisms have evolved to perform acts that benefit other organisms at a cost to themselves.

To illustrate these aspects of Wilson's program of human sociobiology, consider sex differences in human mating behavior. Both sexes need to reproduce in order to be successful in the evolutionary long haul, but reproduction entails very different costs for the two sexes. In order to produce a single child, a woman must invest one of her very limited number of eggs, physiological resources for a nine-month gestation, and the metabolic costs of lactation (often lasting two or three years). Moreover, during pregnancy and lactation, a woman is unable to reproduce with males other than – and possibly *better than* – the father of her child. In contrast, in order to produce a single child, a male need only invest the energy expended in copulation and the contents of a single ejaculate. After a fruitful copulation, a man can reproduce with other women, whereas a woman is committed to the costly act of childbearing. This is a radical asymmetry in the *minimum obligatory parental investment* required of the sexes in order to produce a single offspring: Women are obligated to a far higher investment in offspring than are men. Given this asymmetry, selection should have made women very choosy when selecting a mate, since they have to invest a great deal in a single offspring and, hence, have a great deal to lose by choosing a poor sire. In contrast, since men incur such a minimal obligation in order to produce an offspring, and since they can (theoretically) impregnate innumerable women during the time it takes a woman

to bear one man's child, selection should have made men indiscriminately promiscuous. As Wilson says, selection should have created ''males to be aggressive, hasty, fickle, and undiscriminating,'' and ''females to be coy'' (1978, 125). In other words, in humans, male promiscuity and female coyness are behavioral adaptations.

EVOLUTIONARY PSYCHOLOGY

The starting point of Evolutionary Psychology is a corrective to the core idea of Wilson's sociobiology. Evolutionary Psychologists argue that treating behavioral phenotypes as just like morphological and physiological phenotypes obscures a fundamental difference between them, for behaviors are *events*, which are the output of an information-processing brain reacting to informational input about the current conditions in both the environment and the brain itself. The only way that selection can affect behavior, then, is by altering the information-processing structure of the brain (Tooby and Cosmides 1992). So, when a behavior has evolved under selection, there is an important sense in which it is not the behavior itself that has been selected for, but rather the *psychological mechanism* (cognitive or motivational) that is causally responsible for producing that behavior under appropriate conditions. Since behavioral evolution involves selection for the psychological mechanisms that cause behavior, the adaptations that emerge in the process of behavioral evolution are the psychological mechanisms that cause behavior. Consequently, Evolutionary Psychologists conclude, sociobiology was mistaken in seeking adaptation at the level of behavior; adaptation must be sought at the level of the psychological mechanism (Tooby and Cosmides 1992). The goal of Evolutionary Psychology is thus to discover and describe the information-processing structure of our psychological adaptations (Buss 1995).

From this starting point, Evolutionary Psychologists derive a number of theoretical and methodological doctrines. First, they argue, our psychological adaptations are undoubtedly complex, and the construction of complex adaptations typically requires hundreds of thousands of years of cumulative selection. Our ancestors spent the Pleistocene – the epoch spanning 1.8 million to 10,000 years ago – living in small hunter-gatherer groups, but only the past 10,000 years living as agriculturists and the past few hundred years living in

industrial societies. Consequently, it is highly improbable that humans have evolved adaptations to post-Pleistocene environments. Rather, Evolutionary Psychologists argue, our psychological adaptations must have been designed during the Pleistocene to solve the adaptive problems faced by our hunter-gatherer ancestors (Symons 1992). As Cosmides and Tooby colorfully put it, "Our modern skulls house a Stone Age mind" (1997, 85).

Adaptive problems are commonly characterized as problems whose solutions enhance the ability to survive or reproduce. And the adaptive problems faced by our Pleistocene ancestors ranged from acquiring mates and forming social alliances to avoiding predators and inedible flora. These problems are very diverse in character, and each requires a unique behavioral solution; a successful behavioral solution to one problem would not have transferred to another. Thus, Evolutionary Psychologists argue, each adaptive problem would have selected for its own dedicated problem-solving psychological mechanism (Symons 1992). Moreover, since our Pleistocene ancestors faced such an enormous variety of adaptive problems, Cosmides and Tooby conclude that "the brain must be composed of a large collection of circuits, with different circuits specialized for solving different problems. One can think of each specialized circuit as a minicomputer that is dedicated to solving one problem. Such dedicated minicomputers are sometimes called *modules*" (1997, 81). Indeed, Cosmides and Tooby estimate that the human mind contains hundreds or thousands of such modules, and this view has accordingly been dubbed the *massive modularity thesis*.

According to Evolutionary Psychologists, evolved modules have the following properties (Cosmides and Tooby 1997, Tooby and Cosmides 1992). First, they are *domain specific*, specialized to deal only with a restricted task domain. As such, their information-processing procedures are activated by, and sensitive to, only information about a particular aspect of the world, in much the way the ear is responsive only to specific vibratory frequencies. Second, they are equipped with substantial innate knowledge about their proprietary problem domains and with a set of innate procedures specialized in employing that knowledge to solve problems in their domains. And, third, they develop reliably, and without formal instruction in their problem domains, in every "normal" member of our species.

Since evolved modules are complex adaptations, and since "selection usually tends to make complex adaptations universal or nearly universal in a species," Evolutionary Psychologists argue that "humans must share a complex, species-typical and species-specific architecture of adaptations" (Tooby and Cosmides 1992, 38). Indeed, Evolutionary Psychologists believe that evolved psychological modules constitute a "universal and uniform human nature" (Tooby and Cosmides 1992, 79). Accordingly, Evolutionary Psychologists interpret differences between individuals within the same culture, and differences between individuals in different cultures, as "the product of a common, underlying evolved psychology operating under different environmental circumstances" (Tooby and Cosmides 1992, 45).

However, because our network of modules – our universal human nature – evolved to solve the adaptive problems faced by our Pleistocene ancestors, and because the environments we now inhabit differ enormously from those inhabited by our Pleistocene ancestors, Evolutionary Psychologists argue that our evolved modules often fail to produce adaptive behavior among modern humans. For example, fear evolved as an emotional alarm that signals a threat to survival. But, since human fears evolved during the Pleistocene, humans tend to fear snakes but not cars and guns, despite the fact that more people are killed by cars and guns than by snakes. In addition, people in modern industrialized societies could maximize their reproductive success by donating their sperm or eggs to cryo-banks, but very few people pursue this reproductive option. The reason is that this option was not available in the Pleistocene, and we have minds designed to maximize reproductive success only under Pleistocene-like conditions, in which such success was achieved only through the pursuit of copulation. Because of this mismatch between human nature and contemporary human environments, Symons argues that the study of whether contemporary human behavior is adaptive will "rarely shed light on human nature or the selective forces that shaped that nature" (1992, 146). Thus, Evolutionary Psychologists claim, in order to discover the evolved design of the mind, we must "reverse engineer" the mind from the vantage of our evolutionary past.

The method by which Evolutionary Psychologists propose to reverse engineer the evolved structure of the mind is *evolutionary*

functional analysis (Tooby and Cosmides 1992, Buss 1995). Evolutionary functional analysis begins with the specification of an adaptive problem that Pleistocene humans presumably faced. That adaptive problem is then analyzed into a number of subproblems whose solutions collectively constitute a solution to the adaptive problem. (For example, Pleistocene era males faced the problem of intrasexual competition for reproductive access to females, and solving this problem presumably required solving the subproblems of acquiring the resources desired by females, successfully courting females, and retaining mates, among other things.) The next step is to determine what forms of behavior would have constituted adaptive solutions under Pleistocene conditions to these subproblems. A module is then postulated, which is assumed to have evolved to generate solutions to all of these subproblems. The final step is to determine the information-processing procedures by which the module generates its behavioral solution(s) from its inputs. Evolutionary Psychologists then conduct standard psychological experiments in order to determine whether people behave in ways predicted by the modular hypothesis generated in these last two steps.

Evolutionary Psychologists claim to have made many discoveries regarding the evolved nature of the mind by employing this method. Consider just one example by way of illustration. Throughout our evolution as Pleistocene hunter-gatherers, men invested resources (food, protection, and paternal care) in the offspring of their mates. But because ovulation is concealed and fertilization occurs internally in our species, a Pleistocene human male could never be 100 percent certain when he was likely to impregnate his mate or, if his mate was pregnant, whether it was he who had impregnated her. This posed the following problem for an ancestral male: If his mate was surreptitiously unfaithful, a man could waste his resources on a child that was not his own. Pleistocene human women, in contrast, were always 100 percent certain that offspring born to them were their own. An ancestral woman's problem was that infidelity by her mate could lead to his falling in love with another woman, abandoning her, and withdrawing the resources on which she depended to rear her children successfully. Evolutionary Psychologists argue that jealousy evolved as an emotional alarm to protect against these respective potential losses due to a mate's infidelity. However, since the threats posed by infidelity were different for the sexes,

Evolutionary Psychologists argue, males and females must have evolved different psychological mechanisms: ''The inputs that activate jealousy for men will focus heavily on the sex act per se, whereas for women they will focus on cues to the loss of the men's commitment and investment'' (Buss 1995, 14). Evolutionary Psychologists have conducted numerous studies to test this prediction, and they claim that it is confirmed by the evidence (Buss 1995, 14–15). Thus, they conclude, men and women have evolved distinct psychological adaptations for monitoring, and emotionally responding to, cues of potential infidelity.

HUMAN BEHAVIORAL ECOLOGY

Whereas Evolutionary Psychology is an attempt to blend evolutionary theory with cognitive psychology, human behavioral ecology derives from the branch of biology known as *behavioral ecology*. Behavioral ecology is the study of how animal behavior is adaptively responsive to conditions in animals' physical and social environments. The fundamental premise of behavioral ecology is that ''animals are maximizers of one sort or another – efficient predators or foragers, or elusive prey. The usual ground for believing this is the presumption that natural selection has made them so'' (Grafen 1991, 5). Behavioral ecologists view animals as behaving so as to maximize their shares of a variety of ''currencies'' that are correlated with survival and reproductive success. These evolutionarily significant ''currencies'' include caloric intake, offspring survivability, clutch size, territory, number of copulations, quality of mate, number of sperm in an inseminate, number of inseminates ''harvested'' per fertile period, and number of mates per fertile period. Behavioral ecologists presuppose that animals tend to adopt behavioral strategies that enable them to maximize these ''currencies'' in the particular environmental conditions in which they find themselves. And this presupposition, in turn, entails that animals are capable of behaving adaptively across a very wide range of ecological conditions, flexibly altering their behavior in response to current conditions in order to maximize their chances of survival and reproductive success.

Behavioral ecologists study animal behavior with optimality models and evolutionary game theoretic models. Such models begin

with the specification of some *currency* whose maximization is to be studied. For example, a model may study "clutch size" (that is, number of offspring born and cared for at the same time) in some species of bird. The models then identify a number of alternative *strategies* that animals may pursue by way of attempting to maximize that currency. If the currency is clutch size, the alternative strategies would be various clutch sizes: one strategy would be to have two chicks, another would be to have three, and so on. The models then identify the *costs and benefits* associated with each of the available strategies. In the case of clutch size, the benefits of the alternative strategies are easily measured in terms of number of offspring reared to reproductive viability. Accordingly, benefits appear to increase with increasing clutch sizes. However, offspring need to be fed and cared for, and those activities exact a high cost in parental energy; indeed, the greater the number of fledglings, the more food that needs to be captured and returned to the nest. Moreover, if clutch size becomes too large, parents cannot adequately provide for all the chicks in the brood, and fledgling mortality increases. So there are also costs associated with each strategy (each clutch size). Behavioral ecologists calculate the costs and benefits of each strategy in order to determine which of the available strategies maximizes the average ratio of benefits to costs – that is, in order to determine which is the optimal strategy. For example, behavioral ecologists may predict that, for a particular species of bird, five fledglings is the optimal clutch size. They then predict that the studied animals will pursue that optimal strategy, and they test their prediction against the actual behavior in a population of the studied species.

There are two points to note about modeling in behavioral ecology. First, the particular costs and benefits associated with a particular behavioral strategy depend heavily on the specific features of the environment in which that strategy is pursued. In an environment in which food is scarce and difficult to obtain the optimal clutch size will be smaller than in an environment in which food is abundant and easily obtainable. Thus, predictions regarding the optimal strategy in a population are always relative to the particular environment inhabited by the population. Second, although sometimes an animal's optimal strategy is independent of the strategies of other population members, at other times it is not. For example, for

many animals there is an optimal amount of time spent foraging for food, which maximizes the energy intake per unit of foraging time, and this optimum is independent of the amount of time other population members spend foraging. However, when population members directly compete with one another for resources (including members of the opposite sex, who are reproductive resources), the optimal strategy for any particular population member will depend on the strategies of other population members. If most males competing for territory only engage in threatening displays and retreat when attacked, a tactic of extreme aggression may be greatly beneficial. But, if most males are extremely aggressive, then aggression could entail the costs of injury or death. So the costs and benefits of a behavioral strategy in a competition depend on the strategies adopted by other population members. In such cases, a population may be characterized by an *evolutionarily stable ratio* of alternative behavioral strategies.

When behavioral ecologists find that animals are, in fact, pursuing the strategy predicted by an optimality or evolutionary game theoretic model, they are confident that their model has correctly identified the selective forces in the environment to which animal behavior is responsive and the cost-benefit structures of the available alternative strategies in that environment. However, if animal behavior fails to conform to the predicted optimal strategy, behavioral ecologists assume that the model needs to be revised. Models can be revised by altering the set of strategies assumed to be available to the population or by changing the costs and benefits associated with the strategies in the set. But when a model does not accurately predict behavioral strategies, behavioral ecologists typically assume that the model has failed to include some variables to which animals are responding in ''choosing'' a behavioral strategy. In particular, behavioral ecologists typically assume that the studied animals are not pursuing the predicted strategy because of a *trade-off* among competing life demands. The assumption is that the need to maximize another currency places constraints on the ways in which population members can pursue maximization of the currency in the model.

In fact, for the typical animal, life is little more than a series of trade-offs (Laland and Brown 2002, 117–18). In very general terms, animals face a trade-off between somatic effort (effort expended

toward bodily growth and maintenance) and reproductive effort. Within the category of reproductive effort, there is a trade-off between mating effort (effort expended to increase the number of offspring) and parenting effort (effort expended to care for already produced offspring). And, within the category of parenting effort, parents of two or more offspring face a trade-off between caring for one offspring and caring for another. Accordingly, when animal behavior fails to conform to the predictions of a model, behavioral ecologists typically assume that the animals are trying to simultaneously maximize several currencies and that efforts to maximize one currency place constraints on efforts to maximize another. ''Unlike a robot designed to excel at sweeping or stamping,'' behavioral ecologists believe, ''natural selection is unlikely to design organisms to maximize outputs of any particular task; rather, selection should favor organisms that optimize these abilities (trade off amounts and efficiencies in each), thus maximizing their chances of surviving and reproducing'' (Smith, Borgerhoff Mulder, and Hill 2001, 130). Thus, the presupposition underlying modeling in behavioral ecology is that selection has designed animals to achieve an *optimal allocation of effort* among competing life demands. In the ideal limit, then, behavioral ecology aims to provide a set of interconnected models showing how animal behavior strikes the optimal compromise in pursuing all evolutionarily significant currencies.

Human behavioral ecology is simply the application of these ideas to humans, and it thereby involves several theoretical commitments regarding human behavior. First, human behavioral ecology assumes that human decision making is flexibly responsive to current environmental conditions, resulting in the choice of behavioral strategies that will optimize the allocation of effort among competing life demands and maximize lifetime reproductive output relative to the constraints imposed by the environment (Borgerhoff Mulder 1991, 70). As a result, second, human behavioral ecology sees behavioral differences between individuals as adaptive responses to differing environmental conditions. Human behavioral ecology thus seeks ''to determine how ecological and social factors affect behavioural variability within and between populations'' (Borgerhoff Mulder 1991, 69). Accordingly, human behavioral ecologists often interpret human behavior as the result of *conditional strategies*, behavioral strategies of the form ''In environmental

conditions A, do x; in conditions B, do y; in conditions C, do z''
(Smith et al. 2001, 128). Third, human behavioral ecologists assume
that human behavior is adaptive across a very wide range of envir-
onmental conditions, including many environmental conditions to
which our species was never exposed during its evolutionary history.
Thus, whereas Evolutionary Psychology expects human behavior to
be frequently maladaptive in contemporary environments (because
evolution in our psychological adaptations is lagging behind the
rapid changes in post-Pleistocene human environments), human
behavioral ecology expects human behavior ''to be well-adapted
to most features of contemporary environments, and to exhibit
relatively little adaptive lag'' (Smith 2000, 30).

   In addition, human behavioral ecologists believe that adaptive
behavioral responses can be produced and reproduced by a variety of
different mechanisms. The same adaptive behavior could be
achieved by one individual through the output of an innate module,
but by another individual as the result of domain-general learning.
Moreover, the same adaptive behavior could be genetically trans-
mitted across generations through genes for modules or learning
biases, through direct teaching by others, or through indirect cul-
tural transfer of learnable information. Since adaptive behavior can
be achieved through a variety of different mechanisms, human
behavioral ecologists adopt a methodological strategy known as
the *phenotypic gambit*: They ignore details about underlying
mechanisms (which are typically not known anyway) in the belief
that these details will not matter with respect to understanding
human behavior. That is, human behavioral ecologists believe that
a focus on evolutionarily significant ecological conditions, and the
adaptive demands these place on humans, will enable them
to understand why humans behave as they do even in the absence
of knowledge of the mechanisms responsible for producing that
behavior (which, in any case, may vary from one individual to
another). Thus, human behavioral ecologists are ''generally agnostic
about mechanisms (including the question of cognitive modularity)''
(Smith 2000, 30).

   To illustrate these principles of human behavioral ecology,
consider the phenomenon of *polyandry*, a marital system in which
one woman has more than one husband. Nearly all systems of
marriage in ethnographically recorded human societies are either

monogamous or polygynous (in which one man has more than one wife). But, of 849 recorded societies, polyandry is practiced in four, all of which are located in the Himalayan highlands (Borgerhoff Mulder 1991, 82). At first glance, polyandry appears to defy evolutionary logic, for a woman's lifetime reproductive output is limited by the number of pregnancies she can carry to term, whereas a man's lifetime reproductive output is limited only by the number of women he can impregnate. At the theoretical limit, a woman can achieve her maximal reproductive output with a single mate, whereas a man can achieve his maximal reproductive output only with multiple mates. Thus, polyandry appears to entail no reproductive benefits for women, while involving a vastly suboptimal reproductive arrangement for men. From an evolutionary cost-benefit standpoint, polygyny would appear to provide the greatest benefits for men, while nonetheless allowing women to achieve their maximal lifetime reproductive output. So why would men ever agree to enter a polyandrous marriage?

Human behavioral ecologists study polyandrous populations with an eye to understanding the ecological factors that may make polyandry an adaptive choice, and they have identified several ecological factors that may affect the cost-benefit calculations in the decision making of those who enter polyandrous marriages. Human behavioral ecologists have discovered that polyandrous marriages are typically fraternal – that is, marriages in which one woman is married to two or more brothers. This helps, in part, to offset the costs of polyandry to the cohusbands, since their resources are pooled to rear only offspring to which they are all genetically related. Moreover, human behavioral ecologists have also discovered that polyandry typically occurs among brothers who have inherited farmland that is too small to be divided into parcels that could each sustain a family. In addition, farming the inherited land is highly labor intensive, so that no one of the brothers could successfully cultivate it in order to support a family. Finally, where polyandrous marriages occur, there are not alternative sources of income available to the brothers; cultivating the family farm is the only available means of subsistence. Thus, human behavioral ecologists have concluded, polyandry pays brothers under such circumstances, since they do better by maintaining joint possession of the farm, working it together, marrying one woman, and rearing their joint offspring

than they would do by trying to go their own ways (Borgerhoff Mulder 1991, 84). As further confirmation of this hypothesis, human behavioral ecologists have discovered that when alternative sources of income sufficient to raise a family became available, younger brothers typically leave their polyandrous marriages in order to start a family of their own (Laland and Brown 2002, 123–24). Human behavioral ecologists therefore believe that polyandry is an adaptive marriage system in the ecological conditions of those who choose it.

COMPLEMENTARY RESEARCH PROGRAMS OR COMPETING PARADIGMS?

There are several apparent differences between Evolutionary Psychology and human behavioral ecology (summarized in Table 13.1). First, whereas Evolutionary Psychology strives to discover psychological adaptations to Pleistocene environments, human behavioral ecology studies human behavior and how it is adaptively responsive to ecological conditions. Second, Evolutionary Psychology expects human behavior to be frequently maladaptive in contemporary environments, because of adaptive lag in psychological evolution,

Table 13.1. *Comparison of Evolutionary Psychology and Human Behavioral Ecology*

	Evolutionary psychology	Human behavioral ecology
What is evolutionary theory employed to explain?	Psychological adaptations	Adaptive behavioral strategies
Is contemporary human behavior generally adaptive?	No	Yes
From what vantage point are evolutionary principles applied?	Our Pleistocene past	The present
Committed to massive modularity?	Yes	No
Committed to a universal human nature?	Yes	No

while human behavioral ecology expects human behavior to be fairly well adapted to contemporary environments. Accordingly, third, Evolutionary Psychology believes that the evolved nature of the human mind must be "reverse engineered" from the vantage of our species's Pleistocene past, whereas human behavioral ecology believes that evolutionary principles can be applied in studying human behavior in contemporary environments. Fourth, whereas Evolutionary Psychology postulates that human behavior is caused by hundreds or thousands of modules, which are special-purpose minicomputers adapted to specific adaptive problems faced by our Pleistocene ancestors, human behavioral ecology is agnostic about the nature and number of psychological mechanisms that are causally responsible for adaptive human behavior. Finally, Evolutionary Psychology strives to discover a universal human nature underlying behavioral differences between cultures and between individuals in the same culture, whereas human behavioral ecology studies how environmental differences between individuals affect behavioral differences between them.

Some have argued that these differences between Evolutionary Psychology and human behavioral ecology are more a matter of explanatory emphasis than substantive scientific disagreement (Smith 2000, 33–36; Laland and Brown 2002, chap. 8). According to this ecumenical view, Evolutionary Psychology is simply the investigation of the psychological mechanisms about which human behavioral ecology remains agnostic in its focus on behavior. Whereas human behavioral ecology studies the behavioral "outside" of the human organism, Evolutionary Psychology studies the behaviorally generative psychological "inside." So, while human behavioral ecology aspires to explain how our behavior is adaptively responsive to our ecological conditions, Evolutionary Psychology aspires to explain how our psychological adaptations cause that behavior. Similarly, the argument goes, human behavioral ecology seeks to explain how variation in ecological conditions affects behavioral variation both within and between populations, whereas Evolutionary Psychology seeks to explain how this behavioral variation is caused by a universal human nature responding differentially to differing environmental conditions. Thus, it is possible to see Evolutionary Psychology and human behavioral ecology as offering complementary, rather than competing, explanations.

But the ecumenical position greatly exaggerates the extent to which the two research programs are compatible. For, while human behavioral ecology is compatible with *some* evolutionary account of the mechanisms underlying the behavior it studies, it is not compatible with Evolutionary Psychology's account of those mechanisms.

To see why, reconsider Evolutionary Psychology's massive modularity hypothesis. According to this hypothesis, each adaptive problem our lineage faced in its Pleistocene past was solved by a dedicated module; adaptive behavior was achieved in each problem domain by an "expert system," which was designed to achieve adaptive performance in its problem domain, but was ineffective outside its area of expertise. Indeed, Evolutionary Psychologists claim, humans often fail to behave adaptively in contemporary environments because modules, with their "tunnel cognition," are incapable of functioning effectively when not encountering precisely the conditions for which they were designed.

This contrasts sharply with human behavioral ecology's presupposition that humans can flexibly alter their behavioral strategies so as to strike optimal trade-offs among numerous adaptive problems. According to human behavioral ecologists, "effective adaptive design requires integrative mechanisms for measuring tradeoffs (which themselves vary in complex and contingent ways), and adjusting behavior according to the weighted effect of different activities" on reproductive success (Smith et al. 2001, 130–31). But, since the problem of striking the optimal trade-off *across* adaptive problem domains is not a problem *in* any of those domains, no domain-specific module could weigh the costs and benefits of alternative trade-off strategies and adjust behavior accordingly. Such strategic trade-offs could be struck only by some *domain-general* psychological mechanism. Moreover, that domain-general mechanism could not simply be a mechanism that turned on and off the various modules that are relevant to one's circumstances, leaving the modules to solve their own problems in their own ways. It would have to be a domain-general mechanism that could adjust behavior *within* each adaptive problem domain in a way that allowed for the optimal allocation of effort and efficiencies among competing demands. But any psychological mechanism capable of adjusting behavior within problem domains so as to strike optimal trade-offs would not need to be supplemented with mechanisms that are

specialized for functions within each problem domain. Thus, although human behavioral ecology's presupposition that humans can flexibly alter behavior so as to optimize trade-offs is compatible with *some* account of the psychological mechanisms that make such adaptive trade-offs possible, it is not compatible with Evolutionary Psychology's massive modularity hypothesis. If human behavioral ecology is right about the flexible adaptiveness of human behavior, Evolutionary Psychology is wrong about the psychological mechanisms underlying that behavior.

This substantive difference between the two research programs is related to another difference, which Evolutionary Psychologists have taken to be substantive, but is only partly so. Because human behavioral ecology seeks to explain adaptive human behavior, while remaining agnostic about the psychological adaptations underlying that behavior, Evolutionary Psychologists have often claimed that it is not a genuinely evolutionary theory of human behavior. According to Evolutionary Psychologists, the theory of evolution by natural selection is a theory of *adaptation*, so "nothing in the theory of evolution by natural selection justifies an adaptation-agnostic science of adaptiveness" (Symons 1992, 150). Since Evolutionary Psychology's goal is to discover human psychological adaptations, it claims to be the only truly evolutionary theory of human behavior and psychology.

But human behavioral ecology is not agnostic as to *whether* adaptations underlie the adaptive behavior it studies. Indeed, human behavioral ecologists assume that "human decisions are guided by complex processes of observation, evaluation, recalled experience, experimentation and strategizing which ... have themselves been shaped by past selection pressures" (Borgerhoff Mulder 1991, 70). In this respect, human behavioral ecologists are no more agnostic about adaptations than Evolutionary Psychologists. Human behavioral ecology merely refuses to commit itself to hypotheses regarding the precise causal mechanisms comprising the adaptations that underlie adaptive human behavior. There are two reasons for this restraint, and these reasons substantively differentiate human behavioral ecology from Evolutionary Psychology.

First, human behavioral ecologists believe that the best way to discover human psychological adaptations is to study the ways in

which humans respond adaptively to their ecological conditions rather than to attempt to ''reverse engineer'' them from the vantage of our Pleistocene past (Smith et al. 2001, 131–32). Thus, we will achieve knowledge of the adaptations underlying human behavior only after we understand the actual decisions humans make regarding survival and reproduction. Second, the belief that humans can flexibly alter their behavior, so as to behave adaptively even in evolutionarily novel environments, presupposes that human psychological adaptations are mechanisms of *adaptive plasticity* (in which a single genotype produces more than one phenotype by responding appropriately to environmental conditions). Since mechanisms of adaptive plasticity are not yet well understood, human behavioral ecologists currently treat them as ''black boxes'' in their studies of human behavior. But whatever the details about the causal workings inside such black boxes, mechanisms of adaptive plasticity contrast sharply with Evolutionary Psychology's modules, which are functionally specialized to produce particular forms of behavior and which develop reliably across a broad range of environmental conditions. Consequently, while human behavioral ecology does not presuppose hypotheses about specific psychological adaptations, it differs from Evolutionary Psychology regarding the *kinds* of adaptation that underlie human behavior.

Thus, although human behavioral ecology can be fruitfully supplemented with explanations of the nature and evolution of the psychological mechanisms underlying adaptive human behavior, its theoretical commitments preclude being conjoined with the particular explanations that Evolutionary Psychology offers. Despite some superficial complementarities, human behavioral ecology and Evolutionary Psychology are actually competing paradigms rather than complementary research programs. As the theoretical and empirical fortunes of one program wane, those of the other will wax.

CONCLUSION

The widely popularized research program of Evolutionary Psychology is not the only game on the field of evolutionary psychology. Indeed, human behavioral ecology is a vibrant alternative paradigm for

understanding human behavior from an evolutionary perspective. And, since much recent research has detailed numerous problems with the theory and methodology of Evolutionary Psychology (see, for example, Buller 2005), human behavioral ecology is the paradigm that holds the greatest promise for the future of evolutionary psychology.