



Review

Evolutionary personality psychology: Reconciling human nature and individual differences

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ABSTRACT

Personality, from an evolutionary perspective, represents a meta-category of the output of a suite of species-typical, relatively domain-specific, evolved psychological mechanisms designed in response to the social adaptive problems recurrently faced by our ancestors. This conceptualization of human personality provides for novel and valuable reinterpretations of several areas of personality psychology including personality consistency, individual differences in personality, sex differences and similarities, and contextual determinants of personality. Explaining human personality from an evolutionary perspective has led to discoveries about the function of social information conveyed through standings on the Big-Five personality dimensions and discoveries in topics such as social anxiety, jealousy, altruism, aggression, psychopathology, mate preferences, and desire for sexual variety. We argue that limitations of the application of evolutionary theory to personality science are surmountable and that, despite these limitations, large strides have been and will continue to be made through a union of personality science and evolutionary science.

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1. Introduction

The ontogeny, structure, and processes of human personality and of human nature, more generally, have been crafted over hundreds of thousands of generations by natural and sexual selection. There is no scientifically viable alternative for understanding the historical origins of human personality. The meta-theory of evolution by natural and sexual selection (Darwin, 1859/1958; Darwin, 1871) has been supported, at various theoretical levels, by thousands of investigations spanning the disciplines of, for example, biology, ecology, medicine, anthropology, psychology, and ethology (see, e.g., Barkow, Cosmides, & Tooby, 1992; Daly & Wilson, 1983; Krebs & Davies, 1987; Smith & Winterhalder, 1992; Strickberger, 1990; Trivers, 1985). The application of evolutionary theory to these disciplines has yielded new insights, generated new lines of research, and in some cases, added a much needed theoretical foundation. Personality psychology could be strengthened similarly by integrating principles borrowed from evolutionary biology.

Human personality is often framed without consideration of its evolutionary origins and consideration of the functionality of psychological mechanisms generating individual differences in the development, structure, and processes of personality. Throughout the history of personality psychology, we have examined the

existence of personal constructs (Kelly, 1955), needs (Freud, 1930/1949; Maslow, 1970; Murray, 1937; Murray, 1938), traits (Allport, 1931; Allport, 1960), factors (Eysenck, 1981; John, 1990), drives (Freud, 1930/1949; Murray, 1938), motives (McClelland, 1961; Winter, 1973), and life tasks (Cantor, 1990) with little or no recourse to questions central to an evolutionary perspective. Importantly, however, evolutionary processes are as relevant to humans as they are to other species. There is no reason to expect that human nature or personality is exempt from natural or sexual selective pressures.

Human personality is thus best conceptualized within the framework of *evolutionary psychology* (see, Barkow et al., 1992; Buss, 1991; Buss, 1990; Crawford, Krebs, & Smith, 1987; Daly & Wilson, 1983). Evolutionary psychology suggests that the way we think, feel, and behave today can be understood by considering which thoughts, feelings, and behaviors increased the relative survival and reproduction of our ancestors. Manifesting certain thoughts, feelings, and behaviors in certain contexts increased ancestral humans' abilities to out-survive and out-reproduce less successful conspecifics. The offspring of these ancestors had some probability of inheriting the genetic structure coding for the development of the psychological mechanisms that in response to certain cues produce that same pattern of thoughts, feelings, and behaviors. This process continued for the span of human evolutionary history such that patterns of thoughts, feelings, and behaviors guided by the evolved psychological mechanisms are species-typical and encompass what we call human nature.

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Any comprehensive theory of personality should provide answers to the following questions: What is human nature? What underlies individual differences in personality? Is personality age-graded? Of the numerous variables on which humans differ from one another, which criteria do we use to establish what constitutes a personality trait? What supportive empirical evidence is there for the theory? Does the theory generate specific testable predictions, or is it based upon *post hoc* explanation of findings? In what ways are the sexes predicted to be different? In what ways are the sexes predicted to be similar? What causes these similarities and differences? What follows is a presentation of a theoretical framework of personality which aspires to answer each of these questions.

2. Darwinian concepts and evolutionary products

The observation that species change over time was known long before Darwin. Archaeological evidence had revealed changes in morphology and had revealed structures of organisms that appeared well-suited to the ecological niche occupied by members of that species. What was lacking before Darwin was a causal mechanism to explain *how* species change over time. The theory of natural selection filled a gap in the explanatory framework which allowed researchers to explain changes in species over time. Darwin proposed natural selection as a solution to explain how variation in morphological (including psychological) characteristics better enabled organisms to survive and reproduce. The process of natural selection requires three key components. Darwin proposed that selection operates when (a) the characteristics of individuals of a population vary, (b) this variation is heritable, and (c) individuals reproduce differentially (Darwin, 1859; Mayr, 1982). Variation, selection, and differential reproduction are the bases of natural selection. Among humans, for example, we vary along a wide variety of dimensions. We vary in morphological characteristics such as height and weight and we vary along psychological dimensions such as sexual orientation, sexual desire, and personality dimensions such as Dominance, Extraversion, and Emotional Stability. There are also a variety of characteristics along which humans do not vary. We do not currently vary, genetic mutations excluded, along characteristics such as number of fingers, the presence of belly buttons, and number of eyes. From Darwin's perspective, it is only along those characteristics on which we vary that natural selection can operate. Once variation on a particular trait or feature exists, natural selection operates on those features best suited for survival and reproduction in the organism's current environment (whether physical, developmental, ecological, social, etc.). The operation of natural selection requires that those characteristics be heritable. Individuals lacking traits that increased direct survival or reproduction or the survival or reproduction of kin would have been out-reproduced by those individuals in ancestral environments who did have such traits. Through this process, successful variants would have become more frequently represented among organisms of a species.

Darwin was puzzled, however, by the characteristics of organisms that thwart survival and that are developmentally costly to produce. Reconciliation of characteristics that impeded survival through increased predation, for example, was accomplished by Darwin with a second evolutionary theory—sexual selection theory (Darwin, 1871).

Darwin's (1871) theory of sexual selection was constructed to explain traits that seemingly reduced an organism's chances of survival. A human male's greater aggression compared to human females comes at the cost of developing bodies capable of engaging in such conflicts (e.g., larger size, greater caloric intake necessary to grow and maintain such a body, maintaining higher

levels of testosterone which acts as an immunosuppressant). Darwin's theory suggests that those features of organisms that increase (a) the chances of being selected by the other sex as a mate or (b) success in competition among members of the same sex for sexual access to the other will be selected. These facts of sexual selection are called intersexual selection and intrasexual selection, respectively. For nearly a century after the publication of sexual selection theory, focus was placed on biological sex as the driving force behind sexual selection. Publication of Trivers's (1972) parental investment theory forced evolutionary scientists to reformulate the impact of biological sex on sexual selection. Trivers proposed that it is not biological sex that drives sexual selection, but differences in the *minimum* obligatory parental investment. Parental investment is defined by Trivers as any investment that a parent makes in its offspring that increases that offspring's chances of survival at the expense of the parent's ability to invest in current or future offspring. This definition captures the metabolic costs of investing in offspring and all other forms of investment that benefit offspring.

Among humans, females make the larger obligatory investment in their offspring (Clutton-Brock, 1991). Female sex cells are larger and metabolically more costly to produce than are male sex cells. Additionally, fertilization occurs internally within females. As a result, females incur the costs of gestation, parturition, and lactation. A male's minimum obligatory investment can end with the placement of his sex cells in the reproductive tract of a female. Because the costs associated with parental investment are not isomorphic between the sexes, a suite of psychological characteristics are proposed to exist in human females that are not expected to exist in males. Following impregnation, a female's reproductive opportunities are constrained by the investment that must be made during pregnancy. A male's reproductive opportunities are not constrained in similar fashion. A feature of this theory reveals that there are trade-offs between mating effort and parenting effort that are magnified in comparative research between species with sexually-asymmetric parental investment. Among humans, for example, a host of sex differences are expected to exist (Symons, 1979) that reflect investment differences that parents recurrently made in their offspring. These sex differences are expected to have arisen by processes of sexual selection that operated as a consequence of the difference between the sexes in parental investment in ancestral environments. Parental investment theory predicts that human females will be the more discriminating sex. Research has found consistently that females are less willing to engage in sex, desire fewer sexual partners, require greater time to pass prior to consenting to sex, have higher standards for sex partners, and report being more upset over emotional aspects of a partner's infidelity compared to sexual aspects of his infidelity (for a review see Buss & Schmitt, 1993).

Cross-culturally, men invest substantially less than do women in their offspring (Geary, 2000). Even in cultures with relatively high paternal investment, maternal investment dwarfs paternal investment. Parental investment theory generates expectations of many sex-differentiated psychological mechanisms. The investment asymmetry between the sexes sets the stage for the evolution of mechanisms to solve social dilemmas posed by other family members. Offspring, for example, would have been selected to not allow the expression of genes that signaled dissimilarity to a putative father. Fertilization, being internal to women, results in paternity uncertainty for men. If men have psychological mechanisms designed to detect dissimilarities (or similarities) between themselves and their putative offspring, then selection would operate on offspring to produce phenotypic anonymity.

Future research is necessary to understand the developmental trajectories of specific psychological mechanisms designed in response to the selection pressures hypothesized by parental invest-

ment theory. One avenue of sex-differentiated psychology awaiting further empirical scrutiny is the impact of early family experiences on later mating strategies. Research on attachment styles and mating strategies reveals that female mating strategies may be calibrated to anticipate certain mating environments later in life based on the availability of parents and expectations that others will invest earlier in life. This relationship does not hold as strongly for males. Future research is necessary to examine why some features of sexual psychology and behavior related to early childhood experiences are present for females (Belsky, Steinberg, & Draper, 1991) and others emerge only for males (Michalski & Shackelford, 2002). Michalski and Shackelford, for example, found that men's desired sexual strategies later in life are related to their birth order. Similar relationships do not hold for women. Why might men's mating strategy be calibrated by their birth order and women's mating strategy be calibrated by the attachment they develop with their parents? To answer these questions it is necessary to understand the products of evolutionary processes.

The filtering processes of natural and sexual selection result in three products: adaptations, by-products of adaptations, and random variation or noise. Adaptations are the primary products of natural and sexual selection and can be defined as a "reliably developing structure in the organism, which, because it meshes with the recurrent structure of the world, causes the solution to an adaptive problem" (Tooby & Cosmides, 1992, p. 104). Adaptive problems refer to recurrent features of ancestral environments that impeded successful survival or reproduction. Buss (2007) presents the example of a preference for sweet, calorically dense foods. In ancestral environments, when access to food was less reliable than it is today, selection favored adaptations in humans that functioned to increase immediate caloric content. The criteria utilized to identify adaptations are stringent (Williams, 1966); adaptations must show features of special design, including efficiency, precision, and reliability.

Some products of evolution, however, were not directly selected. By-products of adaptations include features or effects that are not considered to be adaptations but that tag along with an adaptation. In this sense, and as has been debated among evolutionary psychologists, rape may be an example of one such by-product (Thornhill & Palmer, 2000). Men, more often than women, are perpetrators of rape. Men, more than women, report a greater desire for sexual variety and for short-term sexual intercourse and a greater propensity to use physical violence to secure many different types of resources. Rape therefore might represent a phenomenon that is a by-product of adaptations that performed other functions for ancestral men (e.g., increased reproductive success from pursuit of a short-term mating strategy and greater resource acquisition and reputational advantages through the use of physical aggression).

Random variation or noise refers to those characteristics that are selectively neutral or "overlooked" by natural and sexual selection but that are produced through random mutation or developmental anomalies. In the design of certain physical characteristics, for example, the shape of one's belly-button serves no adaptive function but is a characteristic along which people do vary.

3. Applications of evolutionary psychology to personality psychology

The marriage between concepts developed within evolutionary psychology and within personality psychology has a brief history. The historical divide between these two areas lies in the historical focus of each area. Evolutionary psychological accounts of human nature have focused largely on species-typical and sex-typical characteristics that have evolved in response to the problems of survival

and reproduction faced by our ancestors. Personality psychology, in contrast, has been concerned largely with the ways in which humans differ. The divide between these two fields is obvious and raises questions that evolutionary psychologists need to address. If natural and sexual selection operates to filter less successful variants, why are stable, heritable individual differences maintained? The first theoretical link between these two literatures and attempt to reconcile this issue was provided by Buss (1984), who outlined four criteria according to which important sources of evolutionarily informed individual differences can be identified. These include heritability, inclusive fitness, sexual selection, and assortative mating. Each of these four criteria can be used to bridge the theoretical gap between evolutionary psychology and personality psychology.

Buss (1991) and Buss and Greiling (1999) propose that personality may not reflect evolutionary noise or represent by-products of other adaptations but may instead reflect the social landscape of adaptive strategies. Buss highlights that there are at least four explanations for personality and individual differences in humans

- 1) Differences in personality are heritable alternative strategies.
- 2) Differences in personality are calibrations to fluctuating strategies throughout development.
- 3) Differences in personality are due to contextual differences and personality reflects those contexts.
- 4) Personality differences emerge through calibration to various thresholds in development.

Appreciating that personality differences between individuals may reflect social landscapes, it is reasonable to question whether personality has an impact on shaping sexual desire, motivation, and attraction. Personality can be used as a source of information that answers some of the most important social dilemmas that humans have evolved to solve. Evolutionary psychologists have argued, for example, that the Big-Five personality characteristics summarize the most important facets of social landscapes. Perceiving, attending to, and acting upon differences in others likely would have yielded important benefits in ancestral environments. For example, Conscientiousness may be evaluated to assess whom to trust to complete important tasks. Agreeableness may be evaluated as an index of an individual's willingness to cooperate and to conform to group norms by suspending their individual concerns. Openness/Intellect of others can be used as a criterion for seeking out advice. Neuroticism may signify the inability to negotiate tasks effectively. Extraversion or surgency may be assessed as an index of who is likely to rise in the local status hierarchy.

From an evolutionary psychological perspective, human personality structure is comprised of a finite though numerous collection of species-typical, relatively domain-specific psychological mechanisms that have evolved over human evolutionary history because they solved the adaptive problems ancestral humans confronted. Personality is the output of *psychological mechanisms*. Every theory of human personality—even the most environmentalistic—assumes that personality is at some basic level constructed of psychological mechanisms (Symons, 1987). If two members of a given species, or if two members of two different species are exposed to identical stimuli and respond in non-identical ways, we must infer the existence and operation of mechanisms internal to the organisms. These mechanisms can best be described as information-processing devices. These mechanisms take in certain classes of information, process that information according to a set of decision rules, and then generate output correlated with survival or reproductive success in ancestral environments. The information accepted for processing into the mechanism may come from other psychological mechanisms internal to the organism, or it may originate in the external environment—more often than not the particularly social

environment comprised of other humans operating according to like mechanisms. The output generated by a psychological mechanism may be in the form of information which is channeled to and accepted by other psychological mechanisms internal to the organism. The output alternatively may be in the form of behavior, affect, or cognition enacted by the organism (Buss, 1991).

The psychological mechanisms underlying personality have evolved over human evolutionary history because they solved the adaptive problems ancestral humans confronted. Certain problems have been recurrently faced by ancestral humans. Consider the problem of which foods to ingest. To survive, certain nutrients had to be ingested and, conversely, various toxins had to be avoided. This is a complicated problem when considered at the level of basic decision processes. Ancestral humans had to distinguish nutritive from non-nutritive goods, poisonous from non-poisonous fruits, vegetables, and organisms, calorically dense foods from less calorically dense foods, and so on. Those proto-humans who could not distinguish nutritive from non-nutritive foods are not our evolutionary ancestors, for they were out-reproduced by their more discriminating conspecifics.

Personality is comprised of a finite though numerous collection of evolved psychological mechanisms. The adaptive problems our ancestors faced were many and varied in nature: from mate selection, to food ingestion, to forming successful reciprocal dyadic alliances (friendships). The solution to each of these problems has evolved as a circumscribed set of decision rules that guide human behavior, thought, and affect (in concert with relevant cues). The fact that one might be successful in selecting a reproductively valuable mate has little or no bearing on whether one can successfully select and ingest the most nutritive foods available. Mate selection and food selection are qualitatively different adaptive problems that will have selected for qualitatively different sets of psychological mechanisms over human evolutionary history. Thus, the psychological mechanisms that comprise human personality structure will be as numerous as the adaptive problems that selected for those mechanisms. Relatedly, because the number of adaptive problems that ancestral humans confronted was finite though numerous, we expect that the number of mechanisms comprising the structure of personality are finite though numerous. Moreover, it follows that these finite though numerous mechanisms are *domain-specific*—that is, they serve as evolved solutions to *specific* adaptive problems. Because ancestral humans did not confront a single “survive and reproduce” adaptive problem, we have no reason to expect that personality is comprised of a single “survive and reproduce successfully” psychological mechanism that evolved as a relatively domain-general adaptive solution (Buss, 1991; Symons, 1987; Tooby & Cosmides, 1990; Tooby & Cosmides, 1992). Over the history of research on evolutionary theories of psychological phenomena, confusion has surrounded and continues to surround whether invoking concepts such as domain-specific evolved psychological mechanisms implies reflexive triggering of that particular mechanism (Barrett & Kurzban, 2006).

Finally, the basic structure of human personality is comprised of a *species-typical* collection of evolved psychological mechanisms. That is, the mechanisms that evolved as solutions to the adaptive problems confronting all ancestral humans over evolutionary history are presently characteristic of all representatives of the human species (with the exception of mutations and genetic drift). This is expected because all modern humans are, by definition, the evolutionary descendants of those ancestral humans who successfully solved the various adaptive problems they confronted. If it is the case, then, that personality is comprised of a finite though numerous species-typical and domain-specific psychological mechanisms, does this mean that personality is stable or consistent throughout the lifespan? Or might it be somehow dependent on the context or environment?

Evolutionary psychological theories do not imply the existence of adaptations that are incapable of change or are forever bound by our genome (Bjorklund & Pellegrini, 2002; Buss, 2003; Tooby & Cosmides, 1992). The environment is integral in shaping the expression of evolved modules of the mind. Examinations of the arguments surrounding the claims that evolutionary psychology is a theory of genetic determinism must start with an examination of what evolutionary psychologists *actually* propose. Tooby and Cosmides (1992) argue that developmental programs responsible for assembling an adaptation are also adaptations whose primary function is to reconstruct in offspring the design that enhanced reproduction in the preceding generation. They specifically note that it is useful to consider genes *together with* developmental programs as an integrated suite of adaptations. The reliable development of an organism's phenotypic features (including personality) does not imply that these features are not modifiable. Developmental programs do not assemble an organism of fixed design but rather a set of expressed adaptations according to variables such as age, sex, and circumstance-dependent design specifications. Adaptive problems are often specific to particular life stages. Organisms benefit from the necessary adaptations for their particular age regardless of whether they appear before they are necessary or continue after they are necessary. Tooby and Cosmides argue that every feature of every phenotype is *equally determined* by the interaction of that organism's genes and its ontogenetic environment. Biology, therefore, cannot be applicable to some but not all traits. In stressing the role of the environment, Tooby and Cosmides note that the “developmentally relevant environment” refers to those features of the world that are rendered developmentally relevant by the evolved design of an organism's developmental adaptations. The assumption that genes are, therefore, the *only* target of natural selection is a misconception. Genes and developmentally relevant environments (species-typical environments) are both products of the evolutionary process. By sifting between alternative developmental programs, for example, the evolutionary process also is selecting the triggers that the mechanisms will use to build an adaptation. Regarding the expected age-graded structure of human personality, different adaptive problems confronted ancestral humans at different ages or developmental stages, as is true of modern humans. Thus, for example, an adaptive problem of late infancy or early childhood, but presumably not of older individuals selected for mechanisms that come online at or around the time in which these adaptive problems were likely to have been confronted in ancestral environments.

Evolution by natural and sexual selection is recognized as the origin of the many special-purpose and domain-specific cognitive decision rules (psychological mechanisms) according to which humans function. However, and crucial to this perspective, evolutionary psychology holds as a central goal to determine the historical, developmental, and situational forms of contextual input processed by the psychological mechanisms that guide human behavior. *Evolutionary psychologists are not genetic determinists*. Rather, a key message of evolutionary psychology is that the complex architecture of species-typical, domain-specific psychological mechanisms allows for the impressive *context-dependent* flexibility of human behavior, cognition, and affect (Buss, 1991; DeKay & Buss, 1992). Modern evolutionary approaches aspire to understand—in addition to our species-typical, culturally differentiated, and sex-specific human nature—the ways that individuals differ within species, within cultures, and within sex.

4. Understanding individual differences

There is not just one evolutionary approach to understanding a particular domain of human thought, behavior, and emotion. There

are several competing or perhaps complementary evolutionary perspectives that are proposed to explain a given behavioral, cognitive, or affective phenomenon. This also is the case regarding attempts to explain the manifestations of individual differences (see Buss, 2009). There are numerous evolutionary approaches to the study of individual differences (Buss, 1991; DeKay & Buss, 1992). Some of these approaches include life-history theory (Kaplan & Gangestad, 2005), costly signaling theory (Miller, 2007), fitness optima (Penke, Denissen, & Miller, 2007), frequency-dependent selection (Penke et al., 2007), mutation load (Keller & Miller, 2006), and flexibly contingent shifts dependent upon environmental conditions (Belsky, 1999). In this section, we will introduce readers to four of these approaches.

One approach is that of contingent shifts dependent upon environments. The key argument here is that individual differences are contingent upon or are expressed depending on the environment to which the organism is exposed. Belsky et al. (1991), for example, argue that individual differences in mating strategies are in part explicable in terms of whether the father was present or absent during the offspring's childhood years. The general argument of this developmental approach is that mechanisms will be activated and operative only under certain developmental conditions or stages. Without input providing the appropriate developmental information, the mechanism presumably remains at or returns to an inactive or latent state.

A second evolutionary approach investigates the environment that is currently inhabited for an explanation of manifest individual differences. Thus, for example, Flinn (1988) finds that mate guarding of Trinidadian females by males varies as a function of the reproductive status of the female; she is guarded against other males significantly more when she is fecund (impregnable) than when she is not fecund. The implication behind this approach is that human nature is embedded with a suite of psychological mechanisms that feed input into other psychological mechanisms. In this case, mechanisms generating the behavioral output of mate guarding are triggered within the context of a relationship and that information concerning the probability of defection of the partner or the poaching of a partner based on assessments of fecundity is relayed to these mate guarding mechanisms.

A third evolutionary approach to individual differences examines reactive individual differences. The general approach is that there are evolved mechanisms which take as input a circumscribed class of anatomical data. Based on the processing of such information, the mechanisms guide the organism to adopt one strategy over an alternative in a given domain of behavior. For example, individuals who are small in stature and without physical size and strength will likely be most successful pursuing a strategy of diplomacy (rather than, say, aggressivity) in interacting with conspecifics. A person with a large, muscular build, on the other hand, may be anatomically and physiologically prepared to pursue an aggressive strategy in interactions with others (DeKay & Buss, 1992; Tooby & Cosmides, 1990). Hiraishi, Yamagata, Shikishima, and Ando (2008) present the results of a twin study designed to examine reactive individual differences in trust. Hiraishi et al. document that trust is adjusted based on internal factors like the personality traits of Extraversion and Agreeableness and on nonshared environmental factors that may possibly include assessments of the trustworthiness of individuals with whom they have interacted.

A fourth evolutionary approach to explaining individual variation is exemplified by the work of Gangestad and Simpson (1990), who conceptualize the adoption of one of two general sexual strategies in terms of genetic differences arising through frequency-dependent selection. Gangestad and Simpson argue that individuals differ on the dimension of sociosexuality. Sociosexuality refers to an individual's willingness to engage in sexual intercourse with little or no emotional investment in or commitment

to the relationship. Gangestad and Simpson present evidence supporting the proposal that two alternative sexual strategies (high and low sociosexuality) have been selected for depending on the frequency of alternative strategies within the population—as one strategy increases in frequency within the population, selection favors the expression of the alternative strategy. This frequency-dependent selection results in a bimodal distribution of these strategies in the current population.

Another approach examines the trade-offs of personality traits (Nettle, 2005, 2006). Nettle argues that a comprehensive theory of personality must incorporate a deeper understanding of the trade-offs between the costs and benefits of personality traits. In Nettle's analyses, he presents theoretical and empirical support for the reproductive and survival advantages that may have accrued to ancestors based on individual differences in personality. Extraversion, for example, is associated with mating success, exploration of the local environment, the development of social alliances but these reproductively relevant outcomes come at the cost of being exposed to higher levels of risk. Extraverts have increased probabilities of being arrested and suffering injury resulting in hospitalization and females who score higher on Extraversion have an increased probability of exposing their children to stepparents via more frequent termination of their relationships (Nettle, 2005). Nettle's argument is that there is not going to be an "optimum" position along the array of individual differences in Extraversion or other personality dimensions. Instead, we have to appreciate how individual differences in local environments are processed by evolved psychological mechanisms to produce output that may have been correlated with reproductive or survival advantages in ancestral environments. It is important to recognize that each of these approaches to understanding individual differences can be complementary, rather than competing explanations of individual differences in personality. Each perspective offers a different window through which to glimpse the structure of human personality. One area of research that has benefitted from an understanding of adaptive individual differences is human sexual psychology.

5. Personality and sexual psychology

Examinations of the relationships between personality and sexuality began in earnest with Eysenck (1976). Following from the guidance offered from an evolutionary perspective, we can attempt to couch our understanding of the relationships between personality and sexual psychology as a function of sexual selection. Parental investment theory (Trivers, 1972) predicts that human males will devote more resources to mating effort and that human females will devote more resources to parental investment by virtue of asymmetries in assurances of parentage. It is, therefore, not surprising that we observe differences in pursuit of social status, sensation seeking, extraversion, and risk-taking favoring men and that we observe differences in love/nurturance favoring women (MacDonald, 1998).

An extensive body of research has documented that the sexes differentially emphasize certain characteristics when evaluating possible long-term and short-term partners. Surbey and Conohan (2000) found that female undergraduate students desired personality characteristics such as brightness, generosity, and having a sense of humor in a hypothetical partner with whom they would consider having sexual intercourse. Jensen-Campbell, Graziano, and West (1995) reported that females prefer as mates males high on altruism and Agreeableness, with the highest ratings of attraction provided for males who were agreeable and dominant. Buss and Barnes (1986) report that women rank characteristics such as considerate, honest, dependable, kind, and understanding higher in a prospec-

tive mate than do men. Given that the obligatory parental investment costs are greater for women than for men, ancestral women with preferences that guided them towards prospective mates who were more likely to provision them and their offspring would have been at a selective advantage relative to those women in ancestral environments who were indifferent to the personality characteristics linked with status and resources in men (Buss, 2003).

Research has revealed that personality plays an integral role in human sexual psychology. Personality is a critical component of understanding mate choices (Buss, 2003) and is associated with the dissolution of relationships (Betzig, 1989). Figueredo, Sefcek, and Jones (2006), for example, report that men and women rate ideal romantic partners higher than themselves on the personality dimensions of Extraversion, Agreeableness, and Conscientiousness and lower than themselves on Neuroticism. A significant difference between self Openness ratings and ideal partner Openness ratings did not emerge in this study. Using a sample of undergraduate women, Toney and Michalski (2008) replicated the results of Figueredo et al. and found that women rated ideal romantic partners significantly higher on Openness/Intellect than their own Openness/Intellect scores.

Sex differences are expected only in those domains of behavior, cognition, and affect for which males and females have historically had to solve qualitatively different adaptive problems. Conversely, for those domains in which ancestral males and females confronted similar problems, there is no reason to expect that the related behavioral, cognitive, or affective output of the psychological mechanisms that evolved will be sex-differentiated. We relate an example of the sort of sex differences and similarities that are expected, from research conducted on perceptions of relationship betrayal (see Shackelford & Buss, 1996).

Feelings of betrayal are expected when a relationship partner fails to provide, accept, or exchange benefits or resources expected in that relationship context. Extra-relationship sexual involvement will incite intense feelings of betrayal in the context of a committed, romantic, sexual relationship. This is expected to be true for both males and females: Exclusive sexual access is a resource expected of and by both partners in a mateship (Buss, Larsen, Westen, & Semmelroth, 1992; Buss & Schmitt, 1993; Wiederman & Allgeier, 1993; Wilson & Daly, 1992). Importantly, however, human reproduction is characterized by fertilization and gestation internal to the female. Consequently, males—but not females—over evolutionary history confronted the adaptive problem of paternity uncertainty. A mate's sexual infidelity placed that male at risk of investing in offspring to whom he is genetically unrelated. Those males who were indifferent to the sexual fidelity of their mates are not our ancestors because they would have been out-reproduced by males who invested effort in and were sensitive to retaining exclusive sexual access to their mates. Feelings of betrayal incited in a male in response to the real or imagined sexual infidelity of his mate can thus be understood as the output of psychological mechanisms that functioned to alert the male to the threat of cuckoldry.

Although females have not faced the adaptive problem of uncertain parentage, the sexual infidelity of their mate likely served as a cue to the potential or current loss of other reproductively valuable and mateship-specific resources. That is, a woman may fear that the resources her mate contributes to their relationship (e.g., protection of her and their offspring from predation and hostile conspecifics; social and political support of her and their offspring; and basic provisionment of food, shelter, and related resources to her and their offspring) will be diverted to another woman and that woman's offspring (Buss & Schmitt, 1993; Daly & Wilson, 1988). Feelings of betrayal incited in a woman in response to the real or imagined sexual infidelity of her mate can thus be understood as a response to the threatened loss of reproductively valuable resources (Buss & Schmitt, 1993; Buss et al., 1992).

Similarly, extra-relationship romantic emotional involvement will incite intense feelings of betrayal in the context of a mateship. This is true for both males and females (Buss & Schmitt, 1993; Buss et al., 1992; Wiederman & Allgeier, 1993; Wilson & Daly, 1992). A woman may fear that the resources her mate contributes to their relationship will be diverted to another woman and the other woman's offspring (Buss & Schmitt, 1993; Daly & Wilson, 1988). A man, on the other hand, may fear that the romantic, emotional involvement of his mate with another male will escalate to sexual involvement, potentially rendering him a cuckold (see Buss, 2000, for a review of research).

Both sexes are predicted to feel betrayed by the sexual or romantic emotional infidelity of their long-term mate. Indeed, research that does not disassociate sexual and emotional infidelity (reviewed in Wiederman & Allgeier, 1993) find no significant quantitative sex differences in what are effectively global measures of incited betrayal or jealousy. Consistent with the logic of evolutionary psychology, however, when the disassociation of sexual from romantic infidelity is made, men display greater psychological, physiological, and behavioral distress to a mate's sexual infidelity, whereas women display greater distress to a mate's romantic emotional infidelity (Buss & Haselton, 2005; Buss et al., 1992; Buunk, Angleitner, Oubaid, & Buss, 1996; DeSteno & Salovey, 1996; Edlund, Heider, Scherer, Farc, & Sagarin, 2006; Edlund & Sagarin, 2009; Geary, Rumsey, Bow-Thomas, & Hoard, 1995; Harris, 2000; Harris & Christenfeld, 1996; Shackelford, Buss, & Bennett, 2002; Wiederman & Allgeier, 1993; Wiederman & Kendall, 1999; but see Harris, 2000, and Grice & Seely, 2000, for partial failures to replicate the sex difference using physiological measures). To reiterate, the pressing adaptive problem for mated men is the threat of cuckoldry—associated directly with a mate's sexual infidelity. The pressing adaptive problem for mated females is the threatened loss of reproductively valuable time and resources contributed by her mate—associated with her mate's emotional involvement (and concomitant resource investment) in another woman and the other woman's offspring. That is, for the mated woman, the adaptive problem is not the sexual infidelity of her mate per se; rather, it is the threatened diversion of his time and resources to another woman in a bartering effort to gain (and perhaps retain) sexual access to her. Thus, assuming the two types of infidelity are disassociated, men experience more intense feelings of betrayal in response to the sexual infidelities of their mates. Women, on the other hand, experience more intense feelings of betrayal in response to the emotional infidelities of their mates.

Evolution by natural and sexual selection is recognized as the origin of the many special-purpose and relatively domain-specific psychological mechanisms that comprise the structure of human personality. As noted earlier, however, these mechanisms are dependent for their activation on the appropriate contextual or environmental input. Only certain classes of information will be accepted and processed by a given psychological mechanism. Consider again the case of extra-pair sexual involvement (see Shackelford & Buss, 1996).

Evolutionary logic suggests that the betrayal felt by a mate's extra-pair sexual involvement will be most intense when it occurs with an enemy/rival of the mate's partner: Not only is exclusive sexual access (and perhaps various other forms of reproductively valuable resources) lost; in addition, it is lost to one's competitor. Similarly devastating would be the case where one's mate engages in sexual relations with one's close same-sex friend. Again, exclusive sexual access (and perhaps other forms of reproductively valuable resources) is lost; in addition, a close reciprocal alliance is disrupted in the process.

In the context of the typical close same-sex friendship or same-sex coalition, sexual involvement outside of the friendship or coalitional relationship will not generate feelings of betrayal, assuming otherwise appropriate relationship participation. Exclusive sexual

access is not the (or even a) resource garnered from these relationships. If sexual involvement does occur, the relationship between the parties by definition is no longer only a friendship or coalitional relationship. The friendship or alliance may remain, but a new twist has been added, necessitating a reconsideration of the relational boundaries (Buss, 1990). However, if the sexual involvement is between a close friend or ally and one's mate, feelings of betrayal are likely to arise. Feelings of betrayal are likely to arise if the extra-pair sexual involvement is with a personal enemy of the other relationship member (in the friendship context), or with someone associated with an enemy/rival coalition (in the coalitional context)—another form of the “double whammy”. In both relationship contexts, these feelings of betrayal will be greater when the sexual involvement is with the mate of the other relationship member, relative to when such involvement is with an enemy of the other relationship member. This is expected because loss of exclusive sexual access to a mate is likely to be far more (negatively) reproductively consequential than is the loss associated with losing an alliance to a personal or coalitional enemy. Moreover, loss of exclusive sexual access and perhaps other forms of reproductively valuable resources to a mate is *direct* and *certain*. The benefit gained by a personal or coalitional enemy, however, is *indirect* and *uncertain*. That is, if the close friendship or coalitional relationship is lost, this does not guarantee that a new alliance will be formed between the previous friend or coalition member and the personal or coalitional enemy.

These examples have highlighted how an evolutionary perspective on human sexual psychology and personality—and human nature, more generally—recognizes the relevance of context in attempting to understand the manifest behavioral, cognitive, and emotive output of the evolved psychological mechanisms that comprise the structure of human nature.

6. Concluding comments

An evolutionary reconceptualization of the development, structure, and processes of human personality provides for a novel and valuable reinterpretation of several areas of personality psychology. These areas include the issue of personality consistency/variability, individual differences as well as a ubiquitous human nature, sex differences and similarities, age-graded and developmentally contingent personality phenomena, and the contextual determinants of personality. The scientific value of evolutionary theory offers guidance to areas that have largely operated outside of the evolutionary sciences. One such area is an understanding of psychopathology. An appreciation of the adaptive output of evolved psychological and physiological mechanisms can result in a richer and more strongly theoretically grounded understanding of psychopathology and personality disorders than currently exists (Nesse, 2005; Nesse & Williams, 1994). Applications of evolutionary theory to understanding human personality will improve the scope and viability of personality psychology. Inroads already have been made into developing a richer theoretical understanding of human personality and a more complete merging of evolutionary psychology and personality psychology, we believe, lies ahead.

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