

How Can Evolutionary Psychology Successfully Explain Personality and Individual Differences?

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ABSTRACT—*Although evolutionary psychology has been successful in explaining some species-typical and sex-differentiated adaptations, a large question that has largely eluded the field is this: How can the field successfully explain personality and individual differences? This article highlights some promising theoretical directions for tackling this question. These include life-history theory, costly signaling theory, environmental variability in fitness optima, frequency-dependent selection, mutation load, and flexibly contingent shifts in strategy according to environmental conditions. Tackling the explanatory question also requires progress on three fronts: (a) reframing some personality traits as forms of strategic individual differences; (b) providing a nonarbitrary, evolutionary-based formulation of environments as distributions and salience profiles of adaptive problems; and (c) identifying which strategies thrive and which falter in these differing problem-defined environments.*

With the growing acceptance of evolution as a metatheory for psychology, more and more personality psychologists are trying to conceptualize personality within an evolutionary framework.

—Penke, Denissen, & Miller, 2007, p. 553.

Evolutionary psychology is a relatively new metatheoretical paradigm that synthesizes the modern principles of psychology with the core principles of evolutionary biology. It is anchored on an idea captured eloquently by George Williams, one of the leading biologists of the 20th century: “Is it not reasonable to

anticipate that our understanding of the human mind would be aided greatly by knowing the purpose for which it was designed?” (Williams, 1966, p. 16). Although some of the roots of evolutionary psychology can be traced to Charles Darwin (Buss, 2009b), it is only recently that new theoretical syntheses have allowed the field to blossom empirically.

The scientific successes of evolutionary psychology have been most prominent in domains such as survival (e.g., evolved habitat preferences), sexuality (e.g., multiple functional motivations for intercourse), mating strategies (e.g., universal sex differences in mate preferences), sexual conflict (e.g., predictable patterns of sexual deception), parenting (e.g., adaptations in males to scale back on investment when faced with cues to paternity uncertainty), kinship (e.g., altruism preferentially channeled to kin as a function of degree of genetic relatedness), cooperation (e.g., discovery of cheater-detection and anti-free-rider adaptations), and aggression (e.g., predictable circumstances in which men adopt risky social strategies; Buss, 2008). These theoretical and empirical advances, however, have been achieved primarily at the levels of species-typical and sex-differentiated adaptations. Personality traits and other individual differences—profound and integral to human psychology—have been relatively neglected, with some notable exceptions (e.g., Buss, 1991; Buss & Greiling, 1999; Figueredo et al., 2005; Hawley, 1999, 2006; MacDonald, 1995; Nettle, 2006; Wilson, 1994; Wilson, Near, & Miller, 1996). Indeed, it is only recently that cogent evolutionary analyses have been devoted to explaining individual differences within nonhuman species (e.g., Gosling, 2001; Wilson, 1998; Wolf, van Doorn, Leimer, & Weissing, 2007).

The key question is this: How can evolutionary psychology successfully explain personality and individual differences? To begin answering this question, one might find it useful to first examine why individual differences have been

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neglected and why they are so important that they cannot be neglected.

WHY HAVE PERSONALITY AND INDIVIDUAL DIFFERENCES BEEN NEGLECTED?

There are important reasons for this neglect, starting with a paucity of powerful theories. Cogent evolutionary theories exist for predicting and explaining sex differences—the most notable being the theory of sexual selection (Buss, 1995; Geary, 1998). Evolutionary theories of species-typical adaptations, such as kin-selection theory and the theory of reciprocal altruism, also provide powerful tools. Evolutionary psychologists have synthesized these theories with principles of modern psychology to create unique theories such as social-contract theory (Cosmides & Tooby, 2005), sexual-strategies theory (Buss & Schmitt, 1993), and error-management theory (Haselton & Buss, 2000), which, in turn, have led to important empirical discoveries such as adaptive cognitive biases (Haselton, Nettle, & Andrews, 2005). In sharp contrast, comparably powerful theories that can predict and explain personality and individual differences have largely eluded both evolutionary psychologists as well as psychologists who fail to take advantage of its conceptual toolkit.

Another reason for the neglect of individual differences can be traced to the foundational assumption in evolutionary biology that natural selection has reduced or eliminated heritable individual differences because traits that are advantageous tend to spread over time to fixation and become species-typical. Consequently, some of the key founders of evolutionary psychology have argued that heritable individual differences are best viewed as “noise” and are thus irrelevant to the basic functioning of the psychological machinery, much like differences in the colors of the wires of a car engine do not affect its basic functioning (Tooby & Cosmides, 1990). This assumption seemed reasonable 20 years ago, but it has been seriously challenged by key theoretical developments in evolutionary biology and advances in evolutionary foundations of psychology (Keller, 2007; Nettle, 2006).

WHY INDIVIDUAL DIFFERENCES ARE EVOLUTIONARILY IMPORTANT

Individual differences acquire importance for several reasons—some empirical and some theoretical. First, profound and consequential individual differences have been well documented—individual differences in personality characteristics (e.g., dominance vs. submissiveness; agreeableness vs. aggressiveness), general intelligence and more specific abilities (e.g., spatial location vs. spatial rotation abilities), mating strategies (e.g., short term vs. long term), political attitudes (e.g., liberal vs. conservative), religiosity (high vs. low), body type (e.g., mesomorph, endomorph), mate value, and many others. Second, researchers have shown that most of these individual differences have a heritable component and show

stability over time. Virtually all personality characteristics, for example, show heritabilities in the range of 50% and substantial cross-time stability, even over spans of decades (Plomin, DeFries, McClearn, & Rutter, 2008). Third, these stable individual differences have been shown to have important consequences for evolutionarily relevant outcomes, such as survival, mating success, offspring production, and parenting (Buss & Greiling, 1999; Nettle, 2006; Ozer & Benet-Martinez, 2006).

Fourth, individuals often differ substantially within their own sex on characteristics that exhibit well-documented sex differences. In the domain of mating, individuals differ profoundly in the mating strategies they pursue (Thornhill & Gangestad, 2008). Some pursue a long-term mating strategy marked by lifelong monogamy. Others pursue a short-term mating strategy marked by frequent partner switching. And still others pursue a mixed mating strategy, with one long-term mate combined with some short-term sex on the side. Even in domains of well-documented species-typical characteristics, individuals still show variability. Although many individuals prefer to be higher rather than lower in status hierarchies, people differ profoundly in the strategies they use to attain status, in the actual relative rank they attain, and even in the preferred rank to which they aspire (e.g., Hawley, 1999; Lund, Tamnes, Moestue, Buss, & Vollrath, 2007). “Cheater-detection” adaptations, to take another example, prevent one from being exploited in social exchanges. Yet individuals differ profoundly in their ability to detect cheaters (Ekman, O’Sullivan, & Frank, 1999). And some individuals are more exploitable than others, enabling adaptations for exploitation to flourish (Buss & Duntley, 2008). All of these empirical observations tell us that individual differences cannot and should not be ignored.

Theoretically, individual differences are also profoundly important. Individual differences are pivotal to the vast majority of social adaptive problems. Consider selecting a mate. Constants simply do not count. No woman ever thought “Wow, this guy is really attractive—he has an opposable thumb, walks bipedally, and speaks a language.” Species-typical characteristics become invisible when solving the adaptive problem of mate selection. Only differences between individuals count—in attractiveness, intelligence, dependability, health, agreeableness, ambition, empathy, and so forth. As a consequence, humans have evolved specialized adaptations for tracking and acting on these individual differences: *difference-detecting adaptations* (Buss, 1996). These adaptations reveal the specific differences that are crucial to monitor because they have been vital to human survival and reproduction over a long period of evolutionary time.

WHAT CAN PSYCHOLOGISTS DO TO ADVANCE THE EVOLUTIONARY UNDERSTANDING OF PERSONALITY AND INDIVIDUAL DIFFERENCES?

Important theoretical advances within evolutionary biology have produced novel insights into the evolution of individual differ-

ences. In this section, I describe what I see as some of the most promising theoretical directions—a road map for future work designed to tackle the question of explaining personality and individual differences.

Life-History Theory

Each individual has finite time and energy budgets. Effort allocated to solving one adaptive problem precludes effort allocated to other adaptive problems. Life-history theory is a broad formulation of the major tradeoffs in an individual's life with respect to capturing and allocating energy (Gadgil & Bossert, 1970; Kaplan & Gangestad, 2005). Energy can be allocated to bodily growth and maintenance, which ultimately increases the ability to capture energy at a high rate in the future. Energy can be allocated toward reproduction, which subsumes all of the effort required to successfully select, attract, and retain a mate, at least long enough for successful conception. Or energy can be allocated toward parenting and other forms of kin investment, which ultimately increase the reproductive success of genetic relatives.

Because energy is finite, there are trade-offs in the adaptive problems to which it is allocated. Energy an individual allocates to bodily maintenance, for example, cannot be used to invest in children. This broad scheme, of course, represents an oversimplification because some forms of energy expenditure can contribute to two or more adaptive problems. The effort a hunter-gatherer male puts into hunting, for example, can provide meat for his own bodily maintenance and growth; increase his social status, rendering him more sexually attractive to potential mates; and provide sustenance for his children and extended kin.

The optimal trade-off between different allocations will undoubtedly differ depending on variables such as one's own qualities, life expectancy, and the total energy an individual has to expend. Those with exceptional fathering talents, for example, might scale back on mating effort. Individuals with bleak mating prospects might ratchet up investment in kin. And there is some evidence that those with a short expected life span engage in steeper future discounting, shifting to a strategy of immediate resource expenditure, risk taking, and intense competition (Daly & Wilson, 2005). What is often disparaged as a maladjusted personality marked by impulsivity and lack of self-control instead can be conceptualized within life-history theory as an adaptive stable strategy deployed in response to a realistic appraisal of a shorter time horizon (Daly & Wilson, 2005).

Some individual differences represent the different trade-offs that different individuals make with respect to the broad classes of energy allocation as they go through life. Men who happen to be highly sexually attractive to women, for example, sometimes allocate a lion's share of their effort to securing a succession of mates and forgo allocating effort to parenting—a phenomenon also seen in some avian species. Other men devote enough effort

to attract a single mate and then apportion a heavy share of their effort to provisioning and parenting.

Testosterone is one hormone that facilitates success in intra-sexual competition, status striving, and mating effort. It is interesting to note that there is evidence that men's testosterone levels drop following entry into a committed mateship and drop further after they have children (Burnham et al., 2003). So individual differences in testosterone may be predictably linked to stable individual differences in the effort allocated to mating versus that allocated to parenting, as well as to predictable life-history shifts in the adaptive problems to which individuals allocate effort. In short, life-history theory provides one evolutionary framework for understanding individual differences, and it is increasingly being used by evolutionary personality psychologists (Figueredo et al., 2005; Kaplan & Gangestad, 2005; Wolf et al., 2007).

Costly Signaling Theory

Individuals compete with one another in sending signals to others about their quality as a mate, friend, and coalition member. Those perceived as having the highest quality have an advantage in being chosen by the highest quality mates, friends, and coalitions. These social competitions provide incentives for deception. If individuals exaggerate their value, they might succeed in obtaining mates or friends who would be otherwise out of their league.

Any form of deception, however, creates selection for adaptations in signal receivers to detect deception and to discount dishonest signals. Costly signaling theory provides an evolutionary framework for understanding some forms of individual differences (McAndrew, 2002; Miller, 2000, 2007; Zahavi, 2006). Costly signals tend to be honest signals (Zahavi, 1975, 2006). Only those in the best condition, be it physical, economic, or energetic, can "afford" to send the signal. In many traditional cultures, for example, men engage in physical contests of various sorts, ranging from wrestling to chest-pounding to ax fighting. These contests can be costly for individuals, who risk injury, loss of social reputation, and sometimes death. Success cannot be faked. Winning these contests, and even the willingness to engage in them, sends a signal to others in the group about the man's physical and psychological quality—his health, strength, athletic prowess, and courage.

Some major individual differences can, in principle, be explained by costly signaling theory (Miller, 2007). Generosity and altruism that involve large expenditures, for example, can only be displayed by those who have sufficient resources to display them. Those lacking resources generally cannot afford to throw lavish parties, pick up the restaurant tab for the group, or give expensive gifts to friends and potential mates. Individual differences in generosity, courage, fidelity, magnanimity, and even possibly traits such as agreeableness and conscientiousness,

may be partially explained by a costly signaling theory analysis (Miller, 2007).

Costly signaling theory can be linked to life-history theory. A male who cannot afford to produce high-quality signals as a short-term mate, for example, might shift to a life-history strategy of heavy investment in one long-term committed mateship. Even the decision of how much energy to expend on costly signals is a life-history decision, suggesting that costly signaling theory and life-history theory can be linked in explaining individual differences.

Balancing Selection

Balancing selection occurs when genetic variation is maintained by selection, such that different levels on a trait dimension are favored, or are adaptive, in different environmental conditions to the same degree. Although all heritable variation ultimately originates from mutations, the different fitness optima of heritable variants over time and space can maintain the heritable variation. Although there are several forms of balancing selection, the two most relevant forms for personality are environmental heterogeneity in fitness optima and frequency-dependent selection (Penke et al., 2007).

Environmental Heterogeneity in Fitness Optima

If selection pressures vary over time or space, as some of them do, then selection can favor different levels of a personality trait in these different environments. Some environments, for example, may favor a risk-taking personality, whereas others favor a more cautious risk-averse personality. A plausible empirical example comes from a study that assessed the personality traits of people living in mainland Italy and on a number of small islands off the coast of Italy (Camperio Ciani, Capiluppi, Veronese, & Sartori, 2007). People inhabiting the small islands for 20 generations or more scored lower on both extraversion and openness to experience than did the recent immigrants and mainlanders with similar historical and cultural backgrounds. This particular pattern provides indirect evidence for different environments favoring different levels of heritable personality traits.

More direct evidence comes from molecular genetic studies, which find that the 7R allele of the DRD4 gene, associated with novelty seeking and extraversion (Ebstein, 2006), occurs at dramatically different rates in different geographical regions. It occurs at higher rates in America than in Asia and has been hypothesized to be favored by selection when people migrate to new environments or inhabit resource-rich environments (Chen, Burton, Greenberger, & Dmitrieva, 1999; Penke et al., 2007). Empirical evidence for this hypothesis came from a study of the migration patterns of 2,320 individuals from 39 groups (Chen et al., 1999). Migratory populations showed a far higher proportion of long-allele DRD4 genes than did sedentary populations, which could be caused by selective migration of individuals

carrying those genes, selective favoring of those genes in the new environments, or both. Recent evidence on sedentary and nomadic populations favors the hypothesis that the 7R allele of the DRD4 gene is more advantageous to nomadic populations, supporting notion of environmental heterogeneity of fitness consequences for different levels of personality traits (Eisenberg, Campbell, Gray, & Sorenson, 2008).

Frequency-Dependent Selection

A second type of balancing selection is *frequency-dependent selection*, which occurs when two or more strategies are maintained within a population at a particular frequency relative to each other, such that the fitness of each strategy decreases as it becomes increasingly common. Biological sex is the most obvious example of frequency-dependent selection. As the ratio of males-to-females in a population increases, the average fitness of males decreases, and vice versa. Frequency-dependent selection has been hypothesized to explain the personality constellation that characterizes psychopathy—a cheating strategy that involves exploiting the majority strategy of cooperation and is favored especially in males (present in roughly 4% of men versus 1% of women), since it is spread through the success at short-term seduction and abandonment of women (Mealey, 1995). Psychopaths, as part of their strategy, undoubtedly have difference-detecting adaptations that assess and evaluate the exploitability of potential victims (Buss & Duntley, 2008).

More generally, competition is typically keenest in resource-rich areas. Selection sometimes favors strategies for accruing resources, be they food, territory, or mates, in domains where competition is less keen and less costly. Penke et al. (2007) note that personality differences appear most pronounced in social species, suggesting that it may be the social environment that provides an array of different adaptive niches in which different personality strategies can succeed.

The hard work for balancing selection explanations of personality, identifying the specific costs and benefits of different levels of trait dimensions in different environments, remains for the future (Denissen & Penke, 2008a; Nettle, 2006). Nettle (2006) has broken ground on this important task by offering an analysis of the costs and benefits of the personality dimensions captured by the five-factor personality model. Extraversion, for example, appears to confer benefits on some components of fitness, such as success in short-term mating and mate poaching. But extraversion may also carry fitness costs in the currency of survival (e.g., physical risks due to violence from jealous husbands as a consequence of mate poaching). Neuroticism, to take another example, could benefit a person by leading to greater vigilance of dangers at a cost to long-term health due to prolonged psychological stress (Nettle, 2006).

Conceptualizing environments in terms of the salience and distribution of different adaptive problems offers an extremely promising direction (Buss, 2009a). Indeed, defining situations in terms of adaptive problems may provide a cogent solution to a

problem that has long plagued personality psychologists—that of identifying a nonarbitrary way in which to conceptualize situations in the search for personality coherence (Mischel, 1994). Different environments undoubtedly afford different fitness optima on these cost–benefit tradeoffs. The threat of social exclusion, for example, may be higher in some social environments than in others. The neurotic vigilance to this threat may pay higher dividends in environments with high threat, whereas lower neuroticism may be favored in environments in which this adaptive problem is less salient (Denissen & Penke, 2008a, 2008b). Progress on the big question of understanding individual differences, in short, will require a crisp conceptualization of situations as defined by adaptive problems and the identification of environments in which different cost–benefit trade-offs are favored.

Mutation Load

Each human carries mutations, which can occur on any of the approximately 25,000 genes that characterize the human genome. Some mutations are selectively neutral and can be maintained because they do not disrupt the functioning of the brain or other organs. A few provide adaptive advantage and are favored by selection. Other mutations are disruptive. Conservative estimates suggest that, on average, humans carry at least 500 brain-disruptive mutations (Keller & Miller, 2006). Although selection eventually weeds out harmful mutations, those that are only mildly harmful may not be purged by selection for many generations. Although a few new mutations are introduced within each individual, most genetic variation caused by mutation-selection balance reflects older mutations, inherited from ancestors, that have yet to be purged (Keller & Miller, 2006). Individuals differ in their mutation load. Evidence suggests that the heritability of some traits originates from individual differences in mutation load, which can plausibly explain some harmful mental disorders such as schizophrenia and autism (Keller & Miller, 2006).

It is also possible that individual differences in mutation load can explain some personality variation within the normal range. Although a mutation load explanation of individual differences may seem less interesting in that mutations merely add random noise to functional systems, the maladaptive noise they create at the phenotypic level may provide individual differences input into adaptations designed to make critical social selections such as choosing a mate, friend, coalition partner, or even a kin member for investment (Buss, 2006). Traits universally and highly valued in a mate, such as emotional stability, kindness, conscientiousness, and intelligence, which are known to be polygenic, may be disrupted by a high quantity of random mutations. Consequently, adaptations that track individual differences in mate value—one type of difference-detecting mechanism—may actually be tracking individual differences in mutation load. Because individuals at the undesirable end of

these personality dimensions, such as those who are emotional unstable, disagreeable, or cognitively challenged, create conflict in relationships, they can disrupt the adaptive functioning of individuals unfortunate enough to have chosen them. Mutation load thus can create *relationship load* (Buss, 2006). In these ways, the mutation load explanation becomes more interesting theoretically in the broader context of explaining individual differences within an evolutionary psychological framework.

Contingent Shifts According to Environmental and Phenotypic Conditions

Another key mode of explaining individual differences comes from hypotheses that invoke environmentally contingent or culturally contingent shifts (e.g., Belsky, 1999; Gangestad, Haselton, & Buss, 2006). This mode of explaining individual differences is distinct from the process described above as environmental heterogeneity in fitness optima. Environmental heterogeneity in fitness optima refers to the process by which natural selection produces heritable individual differences—different alleles are differentially selected within different environments. In contrast, the concept of contingent shifts refers to selection for species-typical psychological mechanisms that are flexibly responsive to changes in environmental conditions.

Some of these may be subsumed under life-history theory, as when a man shifts to a more cautious, risk-averse strategy after becoming a father. Others may be subsumed by costly signaling theory, as when an environmentally contingent increase in mate value affords a greater ability to emit costly signals. Still others come from situation-specific shifts, such as becoming more risk-taking during times of famine when food resources are scarce and require dangerous action to obtain. Another example is the environmentally contingent personality change from submissiveness to dominance, or vice versa, as an individual's social status shifts markedly upward or downward.

Contingent shifts also can occur in response to one's heritable phenotypic characteristics, which has been characterized as “reactive heritability” (Tooby & Cosmides, 1990). Males with larger body size at age 3, both in height and bulk, tend to be less agreeable and more aggressive at age 11 (Ishikawa, Raine, Lencz, Bihle, & LaCasse, 2001). Perhaps those with larger physical size can more effectively pursue an aggressive strategy, whereas their more diminutive peers opt for a more pacific strategy of agreeableness and conciliation. The key point is that contingent shifts can occur in response to individual phenotypic qualities as well as to external environmental conditions.

Life-history theory, costly signaling theory, environmental heterogeneity, frequency-dependent selection, mutation load, and environment-contingent and phenotypic-contingent shifts in strategy all provide theoretical options for explaining personality and individual differences. The big question of understanding individual differences ultimately will require the use of multiple conceptual tools within the evolutionary toolkit.

Reframing Personality as Strategic Individual Differences and the Environment as Distributions of Adaptive Problems

One key toward a deeper understanding of personality and individual differences will come from changing the ways in which psychologists conceptualize them. Specifically, at least some personality differences can be conceptualized as alternative strategies for solving recurrent adaptive problems (Buss, 1996; Denissen & Penke, 2008a, 2008b; Hawley, 1999; Nettle, 2006). All human groups, for example, pose adaptive problems that involve negotiating status hierarchies, forming social alliances, extracting resources from others, and resolving conflicts with kin. Some individual differences may reflect differences in the strategies individuals use to solve these adaptive problems.

Consider an adaptive problem all humans confront—that of negotiating status hierarchies. Hawley (1999) discovered individual differences in strategies used to achieve position in dominance hierarchies, focusing on the key distinction between prosocial and coercive strategies. In a related vein, Lund et al. (2007) found three fundamental strategies of hierarchy negotiation: deception/manipulation, emission of positive externalities, and industriousness. Extraverts tended to emit positive externalities to get ahead. Those low on agreeableness tended to use deception and manipulation to get ahead. And those high on conscientiousness tended to use sheer hard work to advance in hierarchies. Stable individual differences, in short, reflect the deployment of particular strategies used to solve the adaptive problem of negotiating social hierarchies.

Another adaptive problem involves extracting resources from other people who inhabit one's social environment. Buss (1992) discovered that individual differences in personality captured by the five factor model are reliably linked to 12 different influence strategies people use for securing resources from others. Those low on agreeableness, for example, are especially likely to use coercive strategies (e.g., demanding, criticizing, and yelling) to get what they want. People low on emotional stability are especially likely to use regression strategies (e.g., sulking, pouting, and whining) to get what they want. And those scoring low on extraversion are especially likely to use monetary rewards (e.g., gifts or money) and self-abasement (e.g., degrading themselves) to extract resources from others. Some personality traits, in short, reflect individual differences in strategies used to solve social adaptive problems such as attaining dominance and extracting resources.

A related development along these lines is conceptualizing personality dispositions as “motivational individual reaction norms” to specific classes of environmental circumstances or adaptive problems (Denissen & Penke, 2008a, 2008b). Denissen and Penke propose an explanatory theory of the five-factor personality model that makes it less of a purely descriptive model. Agreeableness, for example, is conceptualized as a motivational individual difference to cooperate or act selfishly. Denissen and Penke also propose that conscientiousness

reflects a strategy of tenacity versus frame shifting under distracting circumstances.

Another conceptual tact involves breaking away from or adding to traditional conceptions of personality, such as those anchored in the five-factor model. Individual differences in sociosexuality provide one example of an evolutionarily framed stable individual difference (Gangestad & Simpson, 1990). Another example from the sexual domain involves other stable sexual strategies that are beyond the five-factor model or only weakly correlated with it (Schmitt & Buss, 2000). Reaching further, individuals differ stably on evolutionarily defined dimensions such as mate value, friend value, coalition value, and even kin value (Sugiyama, 2005), which in turn can influence the strategies individuals pursue.

An evolutionary psychological formulation of environments as the distribution and salience of adaptive problems each individual confronts (Buss, 2009a) will provide a much-needed advance on a conceptual problem that has plagued the field of personality since its inception—how to provide a nonarbitrary formulation of situations in the search for personality coherence. Because personality differences appear to be most profound within social species, identifying social adaptive problems will form the core of this formulation. Social adaptive problems include threats from within the group (e.g., dealing with an intrasexual competitor who is damaging one's social reputation) as well as threats from outside the group (e.g., attack from a competing coalition). They will range from the adaptive problem of mate selection to the adaptive problems faced in the aftermath of a breakup (Perilloux & Buss, 2008). And they will vary developmentally along with life-history shifts in energy allocation from growth to mating to parenting to extended kin investment.

In summary, scientifically satisfactory answers to the big question of explaining personality and individual differences may entail conceptualizing some personality differences as strategic differences; conceptualizing different environments in terms of the distribution and salience of adaptive problems, many of which will be social in nature; and identifying the costs, benefits, and trade-offs of strategic individual differences in these different problem-defined environments. Although we are a long distance from answering the question of how to explain personality and individual differences, modern evolutionary psychology provides some powerful conceptual tools for doing so.

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REFERENCES

- Belsky, J. (1999). Modern evolutionary theory and patterns of attachment. In J. Cassidy & P.R. Shaver (Eds.), *Handbook of attachment: Theory, research, and clinical applications* (pp. 141–161). New York: Guilford.

- Burnham, T.C., Chapman, J.F., Gray, P.B., McIntyre, M.H., Lipson, S.F., & Ellison, P.T. (2003). Men in committed, romantic relationships have lower testosterone. *Hormones and Behavior*, *44*, 119–122.
- Buss, D.M. (1991). Evolutionary personality psychology. *Annual Review of Psychology*, *42*, 459–491.
- Buss, D.M. (1992). Manipulation in close relationships: The five factor model of personality in interactional context. *Journal of Personality*, *60*, 477–499.
- Buss, D.M. (1995). Psychological sex differences: Origins through sexual selection. *American Psychologist*, *50*, 164–168.
- Buss, D.M. (1996). Social adaptation and five major factors of personality. In J.S. Wiggins (Ed.), *The Five-Factor Model of Personality: Theoretical perspectives* (pp. 180–207). New York: Guilford.
- Buss, D.M. (2006). The evolutionary genetics of personality: Does mutation load signal relationship load? *Behavioral and Brain Sciences*, *29*, 409.
- Buss, D.M. (2008). *Evolutionary psychology: The new science of the mind* (3rd ed.). Boston: Allyn & Bacon.
- Buss, D.M. (2009a). Adaptive problems define situations: An evolutionary formulation of person-situation interactions. *Journal of Research in Personality*, *43*, 241–242.
- Buss, D.M. (2009b). The great struggles of life: Darwin and the emergence of evolutionary psychology. *American Psychologist*, *64*, 140–148.
- Buss, D.M., & Duntley, J.D. (2008). Adaptations for exploitation. *Group Dynamics*, *12*, 53–62.
- Buss, D.M., & Greiling, H. (1999). Adaptive individual differences. *Journal of Personality*, *67*, 209–243.
- Buss, D.M., & Schmitt, D.P. (1993). Sexual strategies theory: An evolutionary perspective on human mating. *Psychological Review*, *100*, 204–232.
- Camperio Ciani, A.S., Capiluppi, C., Veronese, A., & Sartori, G. (2007). The adaptive value of personality differences revealed by small island population dynamics. *European Journal of Personality*, *21*, 3–22.
- Chen, C., Burton, M., Greenberger, E., & Dmitrieva, J. (1999). Population migration and the variation of dopamine D4 receptor (DRD4) allele frequencies around the globe. *Evolution and Human Behavior*, *20*, 309–324.
- Cosmides, L., & Tooby, J. (2005). Neurocognitive adaptations designed for social exchange. In D.M. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 584–627). New York: Wiley.
- Daly, M., & Wilson, M. (2005). Carpe diem: Adaptation and devaluing the future. *Quarterly Review of Biology*, *80*, 55–61.
- Denissen, J.J.A., & Penke, L. (2008a). Motivational individual reaction norms underlying the Five-Factor model of personality: First steps towards a theory-based conceptual framework. *Journal of Research in Personality*, *42*, 1285–1302.
- Denissen, J.J.A., & Penke, L. (2008b). Neuroticism predicts reactions to cues of social inclusion. *European Journal of Personality*, *22*, 497–517.
- Ebstein, R. (2006). The molecular genetic architecture of human personality: Beyond self-report questionnaires. *Molecular Psychiatry*, *11*, 427–445.
- Eisenberg, D.T.A., Campbell, B., Gray, P.B., & Sorenson, M.D. (2008). Dopamine receptor genetic polymorphisms and body composition in undernourished pastoralists: An exploration of nutrition indices among nomadic and recently settled Ariaal men of northern Kenya. *BioMed Central Evolutionary Biology*, *8*, 173.
- Ekman, P., O'Sullivan, M., & Frank, M.G. (1999). A few can catch a liar. *Psychological Science*, *10*, 363–366.
- Figueredo, A.J., Sefcek, J.A., Vasquez, G., Brumbach, B.H., King, J.E., & Jacobs, W.J. (2005). Evolutionary personality psychology. In D.M. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 851–877). New York: Wiley.
- Gadgil, M., & Bossert, W.H. (1970). Life historical consequences of natural selection. *American Naturalist*, *104*, 1–24.
- Gangestad, S.W., Haselton, M.G., & Buss, D.M. (2006). Evolutionary foundations of cultural variation: Evoked culture and mate preferences. *Psychological Inquiry*, *17*, 75–95.
- Gangestad, S.W., & Simpson, J.A. (1990). Toward an evolutionary history of female sociosexual variation. *Journal of Personality*, *58*, 69–96.
- Geary, D.C. (1998). *Male, female: The evolution of human sex differences*. Washington, DC: APA Press.
- Gosling, S.D. (2001). From mice to men: What can we learn about personality from animal research? *Psychological Bulletin*, *127*, 45–86.
- Haselton, M.G., & Buss, D.M. (2000). Error management theory: A new perspective on biases in cross-sex mind reading. *Journal of Personality and Social Psychology*, *78*, 81–91.
- Haselton, M.G., Nettle, D., & Andrews, P.W. (2005). The evolution of cognitive bias. In D.M. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 724–746). New York: Wiley.
- Hawley, P.H. (1999). The ontogenesis of social dominance: A strategy-based evolutionary perspective. *Developmental Review*, *19*, 97–132.
- Hawley, P.H. (2006). Evolution and personality: A new look at Machiavellianism. In D. Mroczek & T. Little (Eds.), *Handbook of personality development* (pp. 147–161). Mahwah, NJ: Erlbaum.
- Ishikawa, S.S., Raine, A., Lencz, T., Bihrl, S., & LaCasse, L. (2001). Increased height and bulk in antisocial personality disorder and its subtypes. *Psychiatry Research*, *105*, 211–219.
- Kaplan, H.S., & Gangestad, S.W. (2005). Life history theory and evolutionary psychology. In D.M. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 68–96). New York: Wiley.
- Keller, M.C. (2007). The role of mutations in human mating. In G. Geher & G. Miller (Eds.), *Mating intelligence: Theoretical, experimental, and differential perspectives* (pp. 173–192). Mahwah, NJ: Erlbaum.
- Keller, M.C., & Miller, G. (2006). Resolving the paradox of common, harmful, heritable mental disorders: Which evolutionary genetic models work best? *Behavioral and Brain Sciences*, *29*, 385–452.
- Lund, O.C.H., Tammes, C.K., Moestue, C., Buss, D.M., & Vollrath, M. (2007). Tactics of hierarchy negotiation. *Journal of Research in Personality*, *41*, 25–44.
- MacDonald, K. (1995). Evolution, the five factor model, and levels of personality. *Journal of Personality*, *63*, 525–568.
- McAndrew, F.T. (2002). New evolutionary perspectives on altruism: Multilevel selection and costly signaling theories. *Current Directions in Psychological Science*, *11*, 79–82.
- Mealey, L. (1995). The sociobiology of sociopathy: An integrated evolutionary model. *Behavioral and Brain Sciences*, *18*, 523–599.
- Miller, G. (2000). *The mating mind*. New York: Penguin.
- Miller, G. (2007). Sexual selection for moral virtues. *Quarterly Review of Biology*, *82*, 97–125.
- Mischel, W. (1994). Toward an integrative science of the person. *Annual Review of Psychology*, *55*, 1–22.

- Nettle, D. (2006). The evolution of personality variation in humans and other animals. *American Psychologist*, *20*, 622–631.
- Ozer, D., & Benet-Martinez, V. (2006). Personality and the prediction of consequential outcomes. *Annual Review of Psychology*, *57*, 401–421.
- Penke, L., Denissen, J.J.A., & Miller, G.F. (2007). The evolutionary genetics of personality. *European Journal of Personality*, *21*, 549–587.
- Perilloux, C., & Buss, D.M. (2008). Breaking up romantic relationships: Costs experienced and coping strategies deployed. *Evolutionary Psychology*, *6*, 164–181.
- Plomin, R., DeFries, J.C., McClearn, G.E., & Rutter, M. (2008). *Behavioral genetics* (4th ed.). New York: Freeman.
- Schmitt, D.P., & Buss, D.M. (2000). Sexual dimensions of person description: Beyond or subsumed by the Big Five? *Journal of Research in Personality*, *34*, 141–177.
- Sugiyama, L. (2005). Physical attractiveness in adaptationist perspective. In D.M. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 292–342). New York: Wiley.
- Thornhill, R., & Gangestad, S.W. (2008). *The evolutionary biology of human female sexuality*. New York: Oxford University Press.
- Tooby, J., & Cosmides, L. (1990). On the universality of human nature and the uniqueness of the individual: The role of genetics and adaptation. *Journal of Personality*, *58*, 17–68.
- Williams, G.C. (1966). *Adaptation and natural selection*. Princeton, NJ: Princeton University Press.
- Wilson, D.S. (1994). Adaptive genetic variation and human evolutionary psychology. *Ethology and Sociobiology*, *15*, 219–235.
- Wilson, D.S. (1998). Adaptive individual differences within single populations. *Philosophical Transactions of the Royal Society of London, Series B*, *353*, 199–205.
- Wilson, D.S., Near, D., & Miller, R.R. (1996). Machiavellianism: A synthesis of the evolutionary and psychological literatures. *Psychological Bulletin*, *119*, 285–299.
- Wolf, M., van Doorn, G.S., Leimer, O., & Weissing, F.J. (2007). Life-history trade-offs favour the evolution of animal personalities. *Nature*, *447*, 581–584.
- Zahavi, A. (1975). Mate selection: A selection for a handicap. *Journal of Theoretical Biology*, *53*, 205–214.
- Zahavi, A. (2006). Sexual selection, signal selection and the handicap principle. In B.G.M. Jamieson (Ed.), *Reproductive biology and phylogeny of birds* (pp. 143–159). Enfield, NH: Science Publishers.