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Evolutionary Personality Psychology

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Introduction

A remarkable dualism has characterized the history of psychology. Cronbach (1957) framed “the two disciplines of scientific psychology” as a contrast between “experimental” and “correlational” psychology, although these terms may be inapt because one refers to a method and the other to a statistical procedure. Nonetheless, the key distinction is between branches of psychology that focus on human nature or species-typical characteristics and those that focus on individual differences. When Cronbach (1975) reiterated the problem 18 years later, little progress had been made in integrating or unifying the two branches of psychology. Buss (1984) made a crude stab at integration using evolutionary psychology, but that effort was clearly inadequate given modern knowledge of evolutionary theory and evolutionary genetics (Penke, 2011).

The division remains this day. Some psychologists see individual differences as unimportant “noise” that must be controlled or eliminated in experimental procedures. Others see individual differences as the central focus of their discipline.

A historical perspective on the field of personality psychology reveals a similar division. The “grand theories” of personality such as those advanced by Freud, Jung, Adler, Kelly, Rogers, Maslow, and others were essentially theories of human nature. For Freud, all humans had the same basic instincts, notably sexual and aggressive instincts, and all humans went through a universal sequence of psychosexual stages. For Maslow,

all humans had the same hierarchy of needs, starting with physiological needs such as hunger and thirst, then moving to safety needs, then to social need such as the need to belong, and ending at the top with the need for self-actualization for those who managed to satisfy all needs lower in the hierarchy.

Individual differences could be derived from these theories of species-typical human nature. In Freud's theory, for example, one person could become fixated at the oral stage and another at the anal stage, producing individual differences in personality in adulthood. In Maslow's theory, individual differences derive from the degree to which individuals are able to satisfy their needs at each level in the hierarchy.

Modern personality psychology has largely moved away from theories of human nature, and focuses almost exclusively on individual differences (Larsen & Buss, 2010). Indeed, some define personality psychology as having this exclusive focus: "Personality is that branch of psychology which is concerned with providing a systematic account of the ways in which individuals differ from one another" (Wiggins, 1979, p. 375). In the context of the modern field of personality psychology, grand theories of human nature that once characterized the field are now largely regarded as relics of historical interest only.

In contrast, evolutionary psychology historically has focused almost entirely on human nature or species-typical characteristics. Two of the founders of modern evolutionary psychology, for example, view most heritable individual differences, with some possible exceptions such as those due to frequency-dependent selection, as "byproducts" or "genetic noise" that are largely independent of the functioning of the species-typical human nature (Tooby & Cosmides, 1990). As an analogy, they use the

colors of the wires on a car engine. One can vary the colors on these wires (individual differences) without altering the basic functioning of the engine (species-typical human nature). Consequently, most work in evolutionary psychology has focused on exploring universal species-typical mechanisms thought to characterize human nature—cheater detection adaptations in social exchange (Cosmides & Tooby, 2005), adaptations to predators and prey (Barrett, 2005), universal evolved standards of physical attractiveness (Sugiyama, 2005), adaptations for altruism as a function of genetic relatedness (Burnstein, 2005), and many others.

Recently, the field has experienced a dramatic increase in understanding personality and individual differences within an evolutionary framework (e.g., Buss & Hawley, 2011; Gangestad, 2011; Keller & Miller, 2006; Nettle & Penke, 2010; Penke, Denissen, & Miller, 2007; Reale & Dingemanse, 2011). This sea change is occurring for several key reasons.

Why Evolutionary Psychology Cannot Ignore Personality and Individual Differences

The first reason is that individual differences are omnipresent, substantial, and consequential. A tremendous amount of cross-cultural evidence suggests that individuals differ, on the broadest level, on at least five major dimensions of personality, typically captured by the five-factor model: Extraversion, Agreeableness, Conscientiousness, Emotional Stability, and Openness (Saucier, this volume; McCrae et al., 2005; John, Naumann, & Soto, 2008). Individuals also differ in general intelligence and specific cognitive abilities. And they differ in attitudes, worldviews, political orientations, mating strategies, and religiosity.

Second, all of these individual differences are moderately heritable and show stability over time. Virtually all personality characteristics, for example, show cross-time stability over spans of decades (Roberts & DelVecchio, 2000) and heritabilities in the range of 30 to 80 percent and (Johnson et al., 2008). Even though the sizes of heritability coefficients are often over-interpreted, they clearly indicate that a trait shows genetic variation and is thus potentially subject to evolutionary selection (Johnson, Penke, & Spinath, 2011).

Moreover, individuals differ on psychological adaptations that are usually conceptualized as universal, such as ability to detect cheaters in the Wason selection task paradigm (Cosmides & Tooby, 2005) or romantic interest in dating interactions (Back et al., 2011; Place et al., 2009; 2012), susceptibility to cognitive biases such as the male sexual overperception bias (Perilloux, Easton, & Buss, 2012), and degree of out-group discrimination as a coalitional psychological adaptation (Tooby, Cosmides, & Price, 2006). Even sex-differentiated adaptations in mate preferences show substantial within-sex variation (Buss, 1989; Zietsch et al., 2011).

Finally, many of the traditional personality traits, such as those captured by the five-factor model, are systematically linked with components that contribute to fitness (Buss & Greiling, 1999; Nettle, 2006; Ozer & Benet-Martinez, 2006; Roberts et al., 2007). Conscientiousness, for example, is linked with literal survival in the form of longevity (Deary, Weiss, & Batty, 2010). Extraversion is linked with sexual access to number of sex partners (Nettle, 2005; Schmitt, 2004). Agreeableness is linked with inclination to form cooperative reciprocal alliances (Graziano & Tobin, 2009). Neuroticism is linked to monitoring social acceptance and signs of social exclusion

(Denissen & Penke, 2008a). Conscientiousness is linked with negotiating status hierarchies, which in turn are linked with access to reproductively-relevant resources such as food, territory, health care, and mates. Individuals also differ in the mating strategies they pursue (i.e., sociosexual orientation), which has direct consequences for reproduction (Schmitt & Buss, 2000; Penke & Asendorpf, 2008). Indeed, various personality traits have been linked to lifetime reproductive success (Hutteman et al., in press; Jokela et al., 2009, 2010, 2011; Alvergne et al., 2010).

In short, personality and individual differences are omnipresent, stable over time, heritable, and have direct consequences for domains of functioning that historically and possibly currently have been tributary to fitness. If a trait shows additive genetic variation and affects fitness, as personality traits do, evolution by natural selection will act on it, and it can be shown that this is still the case in contemporary societies (Byars et al., 2009; Hawks et al., 2007; Stearns et al., 2010). Evolutionary psychology cannot afford to ignore them.

Why Personality Psychology Cannot Afford to Ignore Evolution

Historically, most personality psychologists have entirely ignored evolutionary processes in understanding their domains of study. Psychologists who study traits and trait taxonomies typically view the objects of their study in purely descriptive terms, with the goal of identifying the structure of personality rather than explaining it or linking it to any functional domains. Researchers who study the self, to take another example, create theories such as self-verification theory, self-enhancement theory, and social identity theory in a theoretical vacuum, uninformed by, or indifferent to, the causal processes that created the psychological mechanisms involved. Even motive approaches to personality,

which would seem to have obvious evolutionary relevance, historically have ignored evolution. McClelland's triptych of motives—achievement, power, and affiliation—are formulated and researched without evolutionary considerations.

Personality psychologists can no longer afford to ignore evolutionary psychology for several reasons. First, evolutionary psychology provides the only currently cogent meta-theory for the entire field of psychology (Buss, 1995). As noted by Boyer and Heckhausen (2000), "Evolutionary psychology is arguably one of the most important new developments in the behavioral sciences over the past 20 years" (p. 917). If another cogent meta-theory exists for the field of psychology, it needs yet to be discovered.

Second, the field of personality should aspire to *explain* personality and individual differences, not merely *describe* them. Description, of course, is often an important first step. As evolutionary biologist George Williams noted, "Many sciences develop for a time as exercises in description and empirical generalization. Only later do they acquire reasoned connections within themselves and with other branches of knowledge. Many things were scientifically known about human anatomy and the motions of the planets before they were scientifically explained" (Williams, 1966). We suggest that the time is ripe for the field of personality psychology to mature into an explanatory science.

A third reason why personality psychologists cannot ignore evolutionary theory is that it provides a set of powerful conceptual tools that can begin to transform the field into an explanatory science. These include life history theory, costly signaling theory, various forms of balancing selection, mutation load theory, as well as specific evolution-based proposals for reframing personality traits (Buss, 2009a; Denissen & Penke, 2008b). Evolutionary psychology also offers a novel solution to two problems that have long

plagued the field—how to conceptualize “situations” and how to conceptualize person-situation interactions (Buss, 2009b). The remainder of this chapter describes the value of evolution-based tools for transforming personality psychology into an explanatory science.

Ways of Conceptualizing Personality from an Evolutionary Perspective

We start by describing how an evolutionary perspective leads to a reconceptualization of fundamental building blocks in the field of personality—motives, traits, situations, and person-situation interactions. This is followed by a discussion of the major evolutionary approaches to understanding individual differences.

The Evolution of Fundamental Human Motives

Motives are usually defined as internal states that arouse and direct behavior toward specific objects or goals (Larsen & Buss, 2010). Identifying the fundamental motives of humans has been a central goal of the field of personality dating back to Freud. Murray (1938) identified 37 human motives, including the need for achievement, exhibition, recognition, acquisition, order, retention, abasement, autonomy, aggression, blame-avoidance, deference, dominance, affiliation, nurturance, play, rejection, succorance, cognizance (seeking knowledge), and exposition (teaching others). Some years ago, one of us asked Murray on what basis he identified this list of 37 needs, he did not have an answer. They were based on his own observations and internal reflections, not grounded in any foundational principles. McClelland (1985) based his life’s work researching three from Murray’s list—achievement, power, and affiliation. When one of us asked McClelland why those three and not others, he also did not have an answer.

They just seemed important to him. Again, they were not based on a non-arbitrary foundational theoretical framework.

Maslow (1970) identified five fundamental needs of humans—physiological, safety, belongingness, esteem, and self-actualization—organized in a hierarchy in which those lower on the list (e.g., physiological) had to be satisfied before a person could turn to satisfying those higher on the list, and all had to be satisfied before the final need for self-actualization could be fulfilled. Again, no theoretical basis was advanced for the selection of this set of fundamental motives and not some other set.

Recently, Kenrick and his colleagues proffered a reformulation of Maslow's theory and outlined “an updated hierarchy of fundamental human motives” (Kenrick et al., 2010, p. 293). This formulation was guided explicitly by an evolutionary perspective: Immediate physiological needs (e.g., food, water), self-protection (survival), affiliation, status/esteem, mate acquisition, mate retention, and parenting (Kenrick et al., 2010). This formulation is clearly a step in the right direction. From an evolutionary perspective, in sexually reproducing species, mate acquisition must be a central human motive, yet except for one earlier evolution-based formulation of motives (Buss, 1986), mate acquisition was omitted entirely from prior taxonomies of motives. Similarly, in species that invest in offspring, as humans do, parenting must also be a central human motive, again one absent from all but one prior taxonomy of motives and needs (Buss, 1986).

Nonetheless, we suggest that the Kenrick et al. taxonomy of fundamental human motives omits too many key motives to approach comprehensiveness and has not exploited fully an evolutionary psychological foundation. Starting from first principles, evolution by selection occurs as a consequence of differential gene replication. Genes

that have effects that increase their own replicative success better than competing genes existent at the time become more frequent in subsequent generations. For most purposes, this can be formulated at the level of the individual--a process of differential reproductive success of individuals as a consequence of heritable variants. Iterated over deep time, this process produces adaptations in individuals, along with byproducts of those adaptations and a residue of random noise. Most complex adaptations, that is those containing many design features and requiring many genes to construct, tend to be species-typical (Tooby & Cosmides, 1990).

From this perspective, motivations represent the subset of adaptations that are designed to impel and direct behavior toward specific goal states, or to solve specific evolutionarily recurrent adaptive problems. There exists no sharp dividing line between motivational adaptations and other psychological adaptations in the sense that all psychological adaptations are ultimately directly or indirectly tributary to behavior aimed at solving adaptive problems. Nonetheless, identifying the adaptive problems humans were designed to solve provides the basis for formulating a more comprehensive taxonomy of human motives.

Although we do not here offer a comprehensive taxonomy of fundamental human motives, we offer a few suggestions about what such a taxonomy must contain. Individual survival is obviously important, but "survival" is too underspecified to qualify as an evolved motivation. Rather, survival involves solving a large range of adaptive problems, including securing breast milk as an infant; eliciting protection from caregivers; avoiding dangerous snakes, spiders, and predators; avoiding the consumption of substances that contain toxins or disease-causing microbes; prioritizing food and

especially calorically-rich food when experiencing a metabolic deficit; forming hunting coalitions to secure meat from large animals; securing nuts, tubers, berries, honey and other edible objects through gathering; and importantly, avoiding getting killed by hostile humans. A comprehensive taxonomy of human motivation must include a minimum of the dozen or so psychological adaptations that direct and impel behavior to solve each of these survival problems when they come “on line.”

Moreover, some of these motivations themselves will not be singular in nature. Consider homicide-avoidance adaptations (Buss, 2005). Stranger anxiety in young children, which motivates maintaining proximity to caregivers, differs from the motivation to flee from an enraged jealous husband when one is caught *in flagrante delicto* with his wife. The motivation to preemptively kill in self-defense an intrasexual rival who is attacking with a weapon in hand differs from the motivation to form a warfare coalition to defend against incursion from a hostile neighboring tribe. The key point is that a comprehensive taxonomy of just survival motivations alone will of necessity contain a large number, each corresponding to an evolutionarily recurrent specific survival problem. And needless to say, mere survival is not enough to increase evolutionary fitness, reproduction is necessary for that as well. So a full evolutionary taxonomy of motives has to include reproductive alongside survival motives.

Situations and Person-Situation Interactions: An Evolutionary Psychological Formulation

The field of personality and social psychology still has not successfully solved the problem of how to conceptualize person-situation interactions. One of the key impediments is the nearly total lack of progress in conceptualizing situations in a non-

arbitrary manner. As Funder (2008) notes, “the situational variables examined in published research are almost completely ad hoc” (p. 571). A second limitation has been a restricted conceptualization of person variables. Evolutionary psychology provides a novel conceptualization of both, which leads to a formulation of person-situation interactions (Buss, 2009a, 2009b).

An evolutionary psychological perspective provides a novel non-arbitrary conceptualization of situations: *adaptive problems define situations*. Examples include: choosing among available partners for cooperative social alliances, dealing with cheaters in social exchange, confronting threats to status, attracting a desirable mate in a field of intrasexual competitors, fending off mate poachers, allocating limited resources to friends and genetic relatives, being socially ostracized by one’s group, fending off unwanted sexual advances, resolving coalition-weakening conflict among members of one’s group, negotiating a status hierarchy from a subordinate position, and dozens more.

These situations (adaptive problems) are non-arbitrary because humans and their ancestors have confronted situations with similar structure and fitness pay-offs and have had to solve them millions or billions of times over human evolutionary history. Consequently, humans have evolved psychological mechanisms that are specifically sensitive to cues that signal the presence of each adaptive problem, procedures for processing adaptively-relevant information about them, and decision rules for deploying behavioral strategies for solving them. These evolved psychological circuits are called adaptations.

Psychological adaptations define which aspects of the environment are rendered psychologically salient. Consider a man who suspects that his wife is having an

extramarital affair, a poignant and evolutionarily recurrent adaptive problem. The psychologically relevant aspects that define this situation include a rumor he overheard about his mate being seen with another man, eye contact between his wife and another man that lingers a split second too long, a sudden mechanical quality to their sexual interactions, or a failure to reciprocate an “I love you” (Shackelford & Buss, 1997). Other psychologically salient cues that partly define the situation include retrieved memories about events that seemed previously irrelevant, such as an unexplained absence or her inexplicable failure to answer her cell phone last Thursday.

Even the same objectively available cues are differentially psychologically salient as a consequence of adaptive individual differences. There exists strong empirical evidence, for example, that cues to emotional infidelity are more salient to women and cues to sexual infidelity are more psychologically salient to men. The sexes differ in which cues they attend to, process quickly, and remember vividly (Schützwohl, 2006). These differences occur because male and female jealousy adaptations contain sex-differentiated design features, corresponding to the sex-differentiated adaptive problems each has recurrently faced over evolutionary time—paternity uncertainty for men, and resource and commitment diversion for women (Buss & Haselton, 2005). The key point is that each psychological adaptation defines which constellation of cues among the thousands potentially available from the external world becomes psychologically relevant and which are rendered psychologically invisible.

Individuals differ in the adaptive problems they encounter. Individuals *select* some and selectively avoid others. They predictably *evoke* social reactions from other individuals. And they use strategies to *influence* or *manipulate* adaptively-relevant

aspects of situations (Buss, 1987). Selecting a narcissistic or low conscientious individual for a spouse, for example, means facing a statistically greater likelihood of confronting the adaptive problem of spousal infidelity (Buss & Shackelford, 1997). Being disagreeable and low on conscientiousness increase the odds that an individual will pursue an unfaithful short-term mating strategy (Schmitt, 2004), which in turn can evoke satellite adaptive problems such as managing damage to social reputation.

Some personality characteristics can be conceptualized as strategic individual differences—the patterned ways in which different individuals solve adaptive problems. A physically formidable (i.e., stronger) male, for example, may find it easier to approach social situations in an extraverted manner (Lukaszewski & Roney, 2011; Lukaszewski, in press) and can succeed in solving problems of social conflict through a more aggressive strategy (Sell et al., 2009) than a less formidable, weaker male. His diminutive peer performe may cultivate more conciliatory conflict resolution strategies.

An evolutionary framework, in short, provides a non-arbitrary conceptualization of situations. They are defined by adaptive problems and the relevant psychological mechanisms that render some clusters of cues psychologically salient and others irrelevant. More broadly, a person's *developmental or life history environment* is defined by the *distribution, salience, and sequencing* of adaptive problems encountered over time. *Person-situation interactions* come in two well-defined forms: (1) the ways in which person variables, through processes such as selection, evocation, and manipulation, influence non-random exposure to different suites of adaptive problems, and (2) adaptive individual differences in the strategies that people deploy toward solving the problems to which they are non-randomly exposed.

Evolutionary Genetic Origins of Personality

Evolution by selection tends to produce species-typical traits. Genetic variants that have positive effects on their own replicative success relative to competing genetic variants extant in the population at the time increase in frequency over generations until they become characteristic of most or all members of the species. Nonetheless, genetics research over the past couple of decades has revealed a surprising reservoir of genetic differences within many species, including humans, as well as indications of ongoing molecular genetic change due to natural selection (Hawks et al., 2007). In this section, we first discuss conditional adaptations, species-typical traits that can produce non-heritable individual differences. Then we will discuss adaptive sex differences, which tend to be clearly dimorphic and have a genetic component that can be ultimately linked to the sex chromosomes. Furthermore we turn to three evolutionary origins of heritable individual differences within sexes, which we will also briefly discuss in the light of recent genome-wide molecular genetic evidence. We end with a discussion of life history theory, which provides an overarching framework for integrating both species-typical adaptations and individual differences.

Conditional Adaptations

Conditional adaptations are those that produce individual differences in response to different forms of environmental input. They range from responses to immediate situational inputs at one end to stable phenotypic individual differences produced by exposure to different environments during development (Penke, 2011).

Conditional shifts due to immediate situational inputs. Jealousy provides a possible example of a conditional adaptation responsive to immediate situational inputs.

Consider a man named Cesar who enters into a romantic relationship, and after several years begins to detect cues to infidelity. He might notice cues such as unexplained absences, a sudden decrease in his partner's sexual interest in him, and his partner acting nervously when a certain man's name comes up in conversation (Shackelford & Buss, 1997). As his suspicions grow, he becomes increasingly jealous, ratcheting up vigilance and mate guarding behavior. His neighbor, while possessing the same psychological adaptation of jealousy, perceives no cues to infidelity from his partner and so displays no jealousy or mate guarding. These individual differences are relatively transient, and should disappear when the first man is no longer exposed to cues to infidelity.

Humans, as a species that shows exceptionally high behavioral plasticity, are expected to have many conditional adaptations responsive to immediate situational inputs of this sort, such as callus-producing adaptations in response to repeated friction to the skin, transient fear in response to transient exposures to snakes, spiders, or ominous strangers, shifts in mating strategy due to local changes of sex ratio in the mating market, and many others.

Conditional shifts due to recurrent occupancy of different situations. If individuals stably occupy different environments, a conditional adaptation can produce what seem to be stable individual differences. Let's consider jealousy again. Assume now that the cues to infidelity are not transient, but rather recurrent over the course of years of the romantic relationship. Perhaps Cesar's wife has a friendly disposition, likes to dress in sexually provocatively clothing, enjoys flirting with other men, or is higher in mate value than her husband. These circumstances can elicit frequent "mate poaching" attempts from other men, activating Cesar's jealousy not just once, but often over the

course of the relationship. Although observers might conclude that Cesar has the stable trait of jealousy, in fact his recurrent displays of jealousy are attributable to recurrent exposure to jealousy-inducing circumstances. Interestingly, if the tendency to seek out or end up in situations that will recurrently activate certain conditional adaptations is heritable, individual differences in the resulting behaviors might in part be heritable through this indirect route. That is, if Cesar ended up being with a provocative wife due to heritable variation in his mate preferences (Zietsch et al., 2011), his stable tendency of being jealous might in part be heritable due to genetic variation in his preferences that led to a habitual activation of his universal jealousy adaptation. In short, stable occupancy of environments can produce stable individual differences that appear trait-like, even though they are properly explained by a conditional adaptation that is species-typical.

Conditional shifts due to adjustment to one's own physical phenotype.

Individuals should adaptively adjust strategies depending on aspects of their own physical phenotype. A mesomorphic man, for example, can more successfully prosecute an aggressive strategy of resource acquisition than can an ectomorphic man (Sell et al., 2009; Price et al., 2012). A physically attractive woman will get more positive responses for behaving in an extraverted manner than a less attractive woman (Lukaszewski & Roney, 2011; Lukaszewski, in press). A physically attractive man can more successfully pursue a short-term mating strategy than a less attractive man (Gangestad & Simpson, 2000). If the individual differences in physical phenotype are partially heritable, as these are, then this form of conditional adjustment can lead to “reactive heritability” (Tooby & Cosmides, 1990), as parts of the heritability of these personality traits might be due to the phenotype's heritability it is adjusted to. In this case, all individuals presumably possess

the same adaptations to self-assess their physical phenotype, and the stable individual differences are explained by the conjunction of those adaptations with individual differences in the physical phenotype.

Conditional shifts due to environmental exposure early in development. Humans have some adaptations that are designed to produce more or less permanent individual differences due to exposure to events during critical periods of development. The most obvious example is language (Penke, 2011). Although all people possess the “language instinct,” early exposure to Chinese versus German produces stable individual differences in what language one speaks (Pinker, 1994). Another possible example is early exposure to stressful environments, such as resource scarcity, parental unpredictability, or father absence (Belsky, Draper, & Steinberg, 1991). These early stressors have been hypothesized to cause a developmentally stable shift in mating strategy pursued, namely a shift to a short-term mating strategy rather than a long-term mating strategy. Although some variants of this hypothesis have received mixed empirical support at best (e.g. effects of childhood father absence on adult female mating strategies), other versions appear more empirically plausible (e.g. effects of childhood stress on accelerated female puberty and perhaps on romantic attachment security) (Del Giudice, 2009; Ellis, 2004; Ellis et al., 2012; Mendle et al., 2009; Neberich et al., 2010; Penke, 2009).

Whatever the eventual empirical outcomes, this example illustrates that humans (and other species) can evolve species-typical conditional adaptations that shunt individuals toward different adult strategies, depending on exposure to critical events that occur during their development. Unlike conditional shifts due to immediate situational input, which induce temporary activation of adaptations to solve pressing adaptive

problems, developmental conditional adaptations produce a more permanent change in the adult phenotype, creating more stable individual differences.

Sex Differences in Psychological Adaptations

Evolutionary psychology offers a powerful and nuanced meta-theory for when to expect sex differences and when to expect psychological similarity between the sexes. Women and men are expected to differ in domains in which they have recurrently confronted different adaptive problems over evolutionary history (Buss, 1995). We expect the sexes to be psychologically similar in all domains in which they have faced similar adaptive problems over evolutionary history.

As an example, women and men, by and large, have similar (although not identical) taste preferences. Both like foods rich with sugar, fat, salt, and protein. When women get pregnant, however, they face two adaptive problems that men never face. First, they have to eat for two rather than one, so caloric needs increase. Second, they have to avoid ingesting substances that can be teratogenic—damaging to their growing fetus. Consequently, most expecting women experience predictable changes in food preferences, especially during the first trimester of pregnancy when the major organs are forming in the fetus (Profet, 1992). Toxins occur in small amounts in a variety of foods people commonly ingest, including meat, coffee, alcohol, and vegetables such as cabbage, broccoli, and Brussels sprouts. Although these toxins are not typically harmful to an adult, they can be harmful to the fetus. Indeed, pregnant women experience particular food aversions to meat, alcohol, and vegetables. If women do consume these foods, they sometimes vomit. This is sometimes referred to as “pregnancy sickness,” although that is a misnomer, since it is not really a “sickness” but rather an adaptation that prevents their

fetus from being exposed to teratogenic toxins. The key point is that when women recurrently face adaptive problems not faced by men, sex differences emerge.

The challenge is to identify the domains in which women and men have confronted different adaptive problems, hence the psychological regions in which psychologists expect to discover sex differences. Fundamental sex differences in reproductive biology provide a powerful starting point. Fertilization occurs internally within women, not within men. Consequently, men face an adaptive problem no woman has ever faced—the problem of uncertainty of paternity (“Mama’s baby, Papa’s maybe”). Because fertilization and embryo incubation occur within women, women but not men bear substantial metabolic costs, increased vulnerability to attack and exploitation (especially during the third trimester when physical mobility is hampered), and perhaps opportunity costs, such as a lesser ability to forage widely for food. Women, in short, experience greater obligatory parental investment from the moment of conception (women contribute a large nutrient-rich egg, men a small nutrient-poor sperm), which is exacerbated further by breastfeeding.

Because of these fundamental sex differences in reproductive biology, evolutionary scientists have predicted and discovered an array of psychological, strategic, and behavioral sex differences (e.g., Mealey, 2000; Taylor et al., 2000; Trivers, 1972). These include a host of sex differences in mating strategies, sex-differentiated design features of the jealousy adaptation, differences in the strength and intensity of parental love, and differences in adaptations to stress and attack (e.g., women are more inclined to “tend and befriend,” men are more likely to fight or flee).

The largest gender differences in traditional personality traits emerge for neuroticism or emotional stability. Large-scale cross-cultural studies show that women score consistently higher than men, with a magnitude of effect averaging .40 standard deviations (Schmitt et al., 2008). Nettle (2006) has proposed that there are costs and benefits associated with being high on neuroticism. The costs involve increased stress, possible damage to health, and damage to interpersonal relationships. The benefits include increased vigilance and attentiveness to dangers, including physical threats and social threats (see also Denissen & Penke, 2008a).

If correct, plausible evolutionary hypotheses can be advanced to explain why women consistently score higher on neuroticism: The costs of physical and social threats, on average, have been higher for women than for men because women have been primarily responsible for child care; consequently, physical threats from snakes, spiders, diseases, strangers, or aggressive males may have been doubly costly for women since they would have affected not only their survival but that of their children—the vehicles that contain the precious cargo of their genes. On the other hand, elevated levels of neuroticism, and the associated anxiety and wariness about dangers, would have deterred men from engaging in male-specific activities such as large game hunting and warfare that historically conferred reproductive advantages. Furthermore, it would have deterred men from risk-taking, which historically was often necessary for success in intrasexual competition. In short, several selection pressures plausibly operated to create an overall sex difference in neuroticism—hypotheses that remain to be tested by future research. In contrast, we are unaware of any hypotheses emerging from mainstream non-evolutionary personality psychology that attempt to explain these profound sex differences in traits.

In sum, evolutionary psychologists expect to discover gender differences in personality in domains in which they have recurrently faced different adaptive problems—domains linked with sex differences in reproductive biology such as internal female fertilization and greater female obligatory parental investment. These differences, in turn, created different selective payoffs for different personality traits and attendant behavioral strategies. In domains in which the sexes have faced recurrently similar adaptive problems, evolutionary psychologists predict sexual similarity in personality.

Selective neutrality

Beyond sex differences there are pronounced individual differences that cannot simply be reduced to (recurrent) conditional reactions to situations and that have a clear genetic foundation. The existence of genetic variation in within-sex personality differences have puzzled evolutionary psychologists for quite a while, since natural selection reduces genetic variation. If personality traits had shown consistent relationships to evolutionary relevant life outcomes (i.e., fitness) over human evolutionary history, genetic variation in personality should thus have disappeared. The easy solution to this was that personality traits are mostly selectively neutral--not consistently relevant for fitness (Tooby & Cosmides, 1990). However, selective neutrality is a very strong assumption. Even taking plausible parameters for large human populations into account, it has been estimated that selective neutrality would only hold if individuals with different levels of a personality trait would have the same number of offspring not only in the next, but in the next 15 generations (Penke et al., 2007; Keller & Miller, 2006). This is clearly at odds with the robust findings of predictive relationships between personality and life outcomes (Nettle, 2006; Ozer & Benet-Martinez, 2006;

Roberts et al., 2007), including number of children (Hutteman et al., in press; Jokela et al., 2009, 2010, 2011; Alvergne et al., 2010). In the following, we will discuss alternative selective mechanisms that can explain the maintenance of genetic variation in fitness-relevant personality traits.

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 appear to be *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, while 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, Veronese, Capiluppi, & Sartori, 2007). People inhabiting the small islands for 20 generations or more scored lower on both extraversion and openness to experience compared to 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, which is associated with novelty-seeking (Munafò et al., 2008), 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, et al., 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 favor the hypothesis that the 7R allele of the DRD4 gene is more advantageous among nomadic than settled populations, supporting notion of environmental heterogeneity of fitness consequences for different levels of personality traits (Eisenberg, Campbell, Gray, & Sorenson, 2008).

These results nicely exemplifies a two-way relationship that supports balancing selection on personality: Some traits seem to be more adaptive in certain environments, but these traits can also influence the choice of environments. Indeed, several personality traits relate to migration patterns that seem sensible given what would be expected as suitable for these traits (Camperio Ciani, 2011; Jokela, 2009; Jokela et al., 2008).

Humans are a species very apt to show environmental niche picking and construction, which can help them to live in the environments where their traits show the highest

adaptive benefits. This way, the maintenance of genetic variation in personality by balancing selection can be self-supportive (Penke, 2011).

Frequency-dependent selection. A second type of balancing selection is *frequency-dependent selection*, which strictly speaking is a special case of balancing selection by environmental heterogeneity that concerns a specific form of variation of the composition of the social environment over space and time. It 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. Indeed, a comparison of human genetic

diversity in Y-chromosome versus mitochondrial DNA suggests that historically sexual selection, which is necessarily social, made up 54.8% of natural selection in our species (Wade & Shuster, 2004). It can be expected that the relative importance of sexual selection only increased nowadays, given our 'ecological dominance' over many natural threats to survival (Penke, 2011). How heterogeneity in the social environment can maintain personality differences is neatly exemplified by two recent simulation studies. Del Giudice (2011) showed that sex ratios of populations will show substantial natural fluctuation over time, even in the absence of external factors influencing them. Since different sex ratios greatly alter the adaptive benefits of reproductive strategies in humans (Schmitt, 2005), fluctuating variation in sex ratios can exert balancing selection pressure on personality traits related to reproductive strategies, like sociosexuality (Schmitt, 2005) or extraversion and neuroticism (Alvergne et al., 2010).

Using evolutionary simulations of an economic game McNamara and colleagues (2009) showed that individual differences in trustworthiness (i.e., cheating) can select for and maintain individual differences in trust, even if this trait brings a fitness cost. These results might well generalize to other traits, for example costly social awareness to aggressiveness. This study is remarkable because it shows that the mere existence of socially relevant individual differences can foster the evolution of further individual differences. The hard work for balancing selection explanations of personality, of course, remains for the future—identifying the specific costs and benefits of different levels of trait dimensions in different environments (Denissen & Penke, 2008b; Nettle, 2006), and show that they balance out. 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 model of personality. 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, but 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 a promising direction. As noted earlier, 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 non-arbitrary way in which to conceptualize situations in the search for personality coherence. 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, b). Somewhat related to this is the finding that neuroticism relates to a quantity-quality reproductive trade-off in polygynously mating women in rural Senegal, with more neurotic women apparently favoring offspring quantity (more adaptive in high-risk environments) over quality (more adaptive in predictable environments) relative to more emotionally stable women (Alvergne et al., 2010). Progress on the big question of

understanding individual differences, in short, will require a crisp conceptualization of environments in which different cost-benefit tradeoffs are favored.

Mutation-Selection Balance

Each human carries mutations, which can occur on any of the approximately 25,000 genes that characterize the human genome or in any of the regulatory non-gene parts of the genome in between. The most recent molecular genetic evidence converge on an estimate of about on average 70 new mutations per individual per generation (Keightley, 2012). Some mutations are selectively neutral, and can be maintained because they do not disrupt the functioning of genes and subsequently the brain or other organs. Very rarely a mutation provides an adaptive advantage and is favored by selection. Other mutations are disruptive. Recent estimates show that humans are born with an average of 2.2 new deleterious mutations (Keightley, 2012). Few of them are so harmful that they are selected out immediately, and so some will be inherited across generations. Conservative estimates suggest that, on average, humans carry at least 500 brain-disruptive mutations (Keller & Miller, 2006). Although selection eventually weeds out harmful mutations (86% of the single nucleotide genetic variants in humans are no older than 10,000 years, Fu et al., 2012), those that are only mildly harmful can take many generations for selection to purge. Although a few new mutations are introduced within each individual, mostly stemming from the paternal germline (Kong et al., 2012), 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 individual

differences in general intelligence (Penke et al., 2007; Deary, Penke, & Johnson, 2010) and 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 (Verweij et al., 2012). Such an explanation of genetic variance in personality would either imply that one end of a personality dimension is consistently more adaptive (with the other end being marked by accumulated mutations) or that there is an optimal level of the trait and that deviations away from this optimum are marked by accumulated mutations (Gangestad, 2011). Gangestad (2010) predicted that this could be tested by looking at linear and quadratic (U-shaped) relationships between personality traits and body fluctuating asymmetry as a potential indicator of developmental stability and mutation load. However, a recent overview failed to find convincing evidence for either kind of relationship, suggesting no role of mutation-selection balance in personality (Hope et al., 2011, but see Holtzman et al., 2011).

The evolutionary genetics of personality in light of recent molecular genetic evidence

The last few years saw an explosion of molecular genetic findings relevant to an evolutionary genetic perspective on personality. The most significant change was from analyzing individual or small sets of genomic markers, often within a single gene, to genome-wide approaches, where hundreds of thousands of genetic markers are used that are representative for common variation in the genome, and recently to whole-genome sequencing of all the nucleotide letters in the DNA of studied individuals. While the

existing evidence cannot be regarded conclusive yet and a detailed review is beyond the scope of this chapter, we will here provide a short summary of the current state.

Genome-wide analyses have provided clear evidence for signatures of natural selection in the human genome that happened in the last 40,000 years (Hawks et al., 2007; Nielsen et al., 2007; Pickrell et al., 2009). Indeed, genomic differences can be shown among different human populations, even those geographically only a few hundred kilometers apart (e.g., Novembre et al., 2008), and while it is unknown to which phenotypic traits these differences relate, the evidence suggests that these differences are due to selection (esp. imposed by pathogens) rather than migration or random genetic drift (McEvoy et al., 2009; Fumagalli et al., 2011). More specifically, genome-wide data provide evidence for widespread mutation-selection balance (Keightley, 2012) and balancing selection in the human genome (Andres et al., 2009), though the latter probably rarely includes cases of long-standing balancing selection that dates back to the last common ancestor of humans and chimpanzees (Asthana et al., 2005). Similarly, strong selective sweeps that rapidly increased the frequency of beneficial mutations throughout the population have likely been rare in recent evolutionary history (Hernandez et al., 2011). Instead soft selective sweeps, where many, more or less interchangeable genetic variants underlie a trait, none of them affected strong enough by selection that they can reach fixation in the population, were probably common. Soft selection is especially likely to maintain genetic variation when selection pressures vary across time and space, as under balancing selection (Pritchard et al., 2010). Overall, natural selection has clearly affected the human genome on a very recent time scale, likely including those parts that underlie personality traits.

The last decade has greatly altered our view of the molecular genetic structure of personality. Meta-analyses of the best available candidate genes, such as the dopamine receptor gene DRD4 or the serotonin transporter gene 5HTT, have yielded negative or weak results at best (Munafo & Flint, 2011). At the same time, sufficiently powered genome-wide association studies (GWAS) have shown that there are no common (i.e., frequent in the population) genetic variants underlying broad personality traits like those of the Five Factor Model that explain more than 0.5-1% of the genetic variance (de Moor et al., 2012; Verweij et al., 2010). This means that there are either thousands or more likely tenth of thousands of common genetic variants with each very small effects underlying each personality trait or that there are many different rare, potentially family-specific mutations that account for potentially substantial proportions of genetic variation in a few individuals (Penke, 2011).

As an extended use of GWAS data, so-called genome-wide complex trait analyses have recently attempted to estimate how much of the additive heritability of traits can be explained by all the common genetic variants used in a GWAS in total, regardless of how much individual variants explain. Interestingly, while this approach is able to explain almost all of the genetic variance in traits such as height (Yang et al., 2010), only a very small percentage of the genetic variance in Cloninger's (Verweij et al., 2012) and Eysenck's (Vinkhuyzen et al., 2012) personality traits could be explained this way. Together with some evidence for inbreeding depression on some of Cloninger's scales, Verweij et al. (2012) take this as evidence for personality being under mutation-selection balance. This might indeed be a partial explanation, especially at the extreme ends of trait dimensions, where a recent genome-wide linkage analysis supports the possibility of rare

variants with substantial effects (Amin et al., 2011), but for the normal range alternative explanations are widespread gene-by-gene and gene-by-environment interactions or phenotypic measurement issues, especially unaccounted complexity of personality measures (van der Sluis et al., 2010). While the issue of which selective mechanisms maintain genetic variation in personality is still too close to call, we will very likely see more decisive results in the near future. One new, already available technology that will play a big role in this process is genome-wide re-sequencing, where instead of only half a million markers across the genome, all 3 billion nucleotide bases are read out. In large samples this technique is especially helpful to determine the role of rare mutations.

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 individuals' lives 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 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 tradeoffs 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, and also one's personality (Penke, 2011). 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 lifespan 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 tradeoffs 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 of the key hormones that facilitates success in intrasexual competition, status striving, and mating effort. Interestingly, there is evidence that men's testosterone level drops following entry into a committed mateship, and drops further after they have children (Burnham et al., 2003; Ellison & Gray, 2009; Gettler et al., 2011). So individual differences in testosterone may be predictably linked to stable individual differences in the effort allocated to mating versus 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 is increasingly being used by evolutionary personality psychologists (Kaplan & Gangestad, 2005; Penke, 2011; Wolf et al., 2007).

An Evolutionary Conceptualizations of Traits

We have discussed how domain-specific adaptations with functional design—a hallmark of evolutionary psychology—can give a more detailed and theoretically founded account of specific personality processes, such as motivations and conditional adaptations to situations. We have also discussed how evolutionary processes can explain and maintain genetic variation in broad personality dimensions such as those of the Five Factor Model or similar trait taxonomies—the hallmark of trait psychology. The biggest challenge for an evolutionary personality psychology is integrating these two levels (Penke, 2011). This challenge is very similar to the integration of personality traits and processes in that it has to deal with the fact that there is no simple one-to-one mapping of traits to processes or adaptations, with the latter greatly outnumbering the former (Cervone, 2005). Indeed, conceptualizing traits as individual differences in a specific

evolved adaptation is clearly ill-conceived, especially since adaptations are seen as universal and genetically fixated (Penke, 2011; Penke et al., 2011).

However, the conflict between these perspectives only emerges when attempting to give similar direct causal status in the determination of behavior to traits as is assumed for evolved adaptations and personality processes (e.g. McCrae et al., 2000). Such a *formative* interpretation of latent personality traits, however, is actually difficult to reconcile with the complex correlational patterns among items of established personality inventories (Cramer et al., 2012) and stands also at odds with the elusive nature of a single neuronal or genetic substrate for unitary causal personality traits.

As an alternative perspective, the robust finding of trait taxonomies like the Five Factor Model can be explained at least as well as *reflexive* latent dimensions that emerge from complex, possibly idiosyncratic interactions between lower-level affective, cognitive and behavioral personality process components. From this perspective, trait dimensions are descriptive summaries of common interaction patterns between processes (Cramer et al., 2012; Denissen, Wood, & Penke, 2012;). Various functionalist models that conceptualize personality traits this way have been proposed (Denissen, Penke, & Wood, submitted; Denissen et al., in press; Mischel & Shoda, 1995; Matthews, Deary, & Whiteman, 2009, chapter 14).

In this reflexive conceptualization of personality traits, evolved adaptations take the role of theoretically founded personality components, functional units that convert environmental (situational) input into adaptive behavioral responses. They can form trait domains when they tend to be activated in similar situations, that is when they solve somewhat interrelated adaptive problems. Indeed, various authors have equated broad

personality dimensions with important domains of life (e.g. Power, Affect, Intellect, Work, & Love, McAdams & Pals, 2006) or adaptive problems in major classes of social relationships (e.g. negotiating status hierarchies, forming social alliances, and dealing with conflicts with kin).

Denissen and Penke (2008b) propose a conceptualization of the dimensions of the Five Factor Model as “motivational individual reaction norms”, in that they capture general motivational tendencies of individuals to react to specific classes of environmental circumstances or adaptive problems. Agreeableness, for example, is conceptualized as a motivational individual difference to cooperate or act selfishly when facing resource conflict. Conscientiousness, Denissen and Penke propose, reflects differences in tenacity versus frame-shifting when facing distracting circumstances during goal pursuit.

Recently, Denissen, Penke and Wood (submitted; Denissen et al., in press) proposed a revised version of their model that sees the general reaction norms as the motivational outcome of various cybernetic self-regulation processes. For example, the Conscientiousness domain is seen as related to the emotion of guilt, which is triggered when a conflict between the desired level of goal pursuit or social norm adherence is unbalanced by encountering situational temptations to violate these goals or norms. In this case, a variety of trait-specific regulatory strategies can kick in, from situation selection, modification, and re-appraisal to emotion suppression. Individual differences in all these processes influence behaviors as well as the perception of the trait Conscientiousness in this individual.

From an evolutionary perspective, individual differences in such functionalist process models of personality can be seen as *alternative evolved strategies* for solving recurrent adaptive problems (Buss, 1996; Denissen & Penke, 2008a, b; Nettle, 2006). The adaptive problem domains solved by the sets of adaptations that underlie a trait domain are the same for all humans, but there might be different strategies that are equally adaptive, at least under different environmental circumstances (which pose different fitness pay-offs) or in the context of different overall life history strategies. These different strategies can be partly environmentally triggered in the sense of different forms of conditional adaptations (as discussed above), or they can have a genetic component, which might be under balancing selection (including frequency-dependent selection), mutation-selection balance, or soft selective sweeps.

But where do genetic differences fit in when the basic building blocks of these strategies are evolved adaptations that are supposed to be universal and genetically fixated? Even genetically fixated, conserved genetic modules often have zones where genetic variation is tolerated or even facilitated (Gerhardt & Kirschner, 2007). These might phenotypically code for parameters such as activation thresholds, reaction strength, or response sensitivities. Even assuming identical developmental histories and situational triggers, the same adaptive mechanisms, say fear of snakes or sexual jealousy, might thus show different sensitivity or reaction strengths due to genetic differences between individuals. It is important that one does not have to assume different specific genetic polymorphisms underlying each parameter for each adaptation (though that might be the case, see Cramer et al., 2012). Different parameters of different, somewhat related adaptations might just as well share the same genetic basis. As an example, the adult

romantic attachment system, the self-esteem “sociometer” that monitors social acceptance and the stress response to environmental threats can be seen as different evolved adaptations (or sets of adaptations) that solve distinct adaptive problems, yet individual differences in all these domains are correlated as part of the heritable trait dimension of Neuroticism. A partial reason for this interdependence could be that these functionally independent adaptations partly share a structural substrate, say the serotonin system, so that genetic polymorphisms related to serotonin production or receptivity relate simultaneously to activation differences in all of them.

Personality and the Adaptive Social Landscape

Stable personality traits in oneself and in inhabitants of one’s social environment are linked to the creation of adaptive problems as well as to the solution to adaptive problems. The personality-problem linkages occur for each of the major classes of social relationships—reciprocal alliances, communal friendships, coalitions, enemies, hierarchical relationships, kinships, and mateships. As a consequence of these recurrent linkages, humans have evolved difference-detecting mechanisms, or personality assessment adaptations, that function to avoid some adaptive problems and facilitate the solution to other adaptive problems. The recurrent personality-problem linkages, in short, are the *raison d’être* for the evolution of personality assessment adaptations. The personality characteristics of others in each person’s milieu, therefore, define a social adaptive landscape that difference-detecting adaptations help to navigate.

Social adaptive problems require social psychological solutions. Individuals inhabiting each person’s social world differ from each other in myriad ways. Some differences reflect temporary states. Individuals differ in transient health-status, for

example--variation in who happens to be infected by a local virus at any particular point in time. Solving the problem of avoiding infection requires identifying and selectively avoiding close contact with those who happen to be infected (Navarette & Fessler, 2006; Schaller & Park, 2011). A second example of a state difference centers on transient emotions. Humans show exceptional ability to rapidly and accurately detect an angry face from among a sea of faces (Öhman et al., 2001). This difference-detecting ability presumably alerts individuals to sources of potential danger from other humans, and enables taking action to avoid the threat or prepare to defend against the threat. Humans clearly have adaptations designed to perceive and act upon transient state-differences in other humans.

Other individual differences are more stable, and reflect relatively enduring personality traits such as those captured by the five-factor model, the HEXACO model, or individual traits of well-documented importance such as narcissism, intelligence, and some psychological disorders (Saucier, this volume; Asebdirof, this volume; Ashton et al., 2004; Buss & Chiodo, 1991; John et al., 2008; Goldberg, 1990). These traits are now known to provide at least a moderate predictive power in forecasting the future behavior of others (Fleeson & Gallagher, 2009). If that behavior has consequences for the creation of, or solution to, adaptive problems involved in interacting with those others, selection should fashion adaptations designed to detect, evaluate, and act on those stable differences (Buss, 1991a, 1996). *Personality assessment adaptations* are hypothesized to represent one class of mechanisms for solving social adaptive problems.

Assessing personality traits of others is a complicated task. It involves that behavioral samples relevant to the trait being assessed are available to the observer and

that she is able to detect this information and to utilize (combine) it correctly to form an accurate trait impression (Funder, 1995). Despite non-compensatory detrimental effects errors at each of these stages will have on the accuracy of personality assessments, people are surprisingly good at judging personality (Vazire & Solomon, this volume; Connelly & Ones, 2010), even after very short exposure and based on minimal information (Borkenau & Liebler, 1992; Gosling, 2008). This domain-specific efficiency points towards an evolved adaptation.

From this adaptive perspective, the most important theoretical and empirical issues become: (1) identifying each of the key social adaptive problems humans have recurrently confronted; (2) identifying which individual differences in others are most central to *creating* these social adaptive problems; (3) identifying which individual differences in others *interfere* with solving adaptive problems; (4) identifying which individual differences in others are most central to *solving* these social adaptive problems; and (5) identifying *difference-detecting adaptations*, including (a) the cues people use to assess the key individual differences, (b) psychological mechanisms, including motivational and emotional circuits, used to process information about key individual differences, and (c) the behavioral output directed as solving problems based on these individual differences.

Consider as an example an adaptive problem that women almost certainly have faced over deep time—the problem of sexual exploitation at the hands of some men (Buss & Duntley, 2008; Goetz et al., 2012; Lewis et al., 2012). There is good empirical evidence for stable individual differences among men in which some, but not others, pursue a sexually exploitative strategy—those roughly 4% of men who have the cluster

of traits captured by the term psychopathy (Lalumiere, et al., 2005). These men score low on the personality traits of agreeableness and conscientiousness, and lack some common human emotions such as guilt or remorse. They frequently pursue a social strategy of deception, manipulation, and conning, so avoiding becoming a victim of psychopaths is an adaptive problem that many individuals face, both men and women. For women specifically, men high on psychopathy tend to pursue short-term mating strategies marked by deception, manipulation, the threat of force, and the use of force (Lalumiere et al., 2005).

Sexually exploitative strategies usually inflict heavy fitness costs on victims. These include bypassing female choice, impregnation by a man who is unwilling to invest parentally, damage to the victim's social reputation, damage to her perceived mate value, and social stigma attached to resulting children. Given these heavy fitness costs, women who had the ability to identify which men were more prone to using a sexually exploitative strategy, even if this detection ability gave them a modest increment in predictive power, would have a selective advantage over women who were oblivious to this individual difference.

The advantage would come from adaptive action taken subsequent to detecting cues to this male strategy, such as selectively avoiding sexually exploitative men, selectively choosing mates and friends who have the physical formidability and psychological fortitude to act as "body guards," and enlisting the aid of kin and social allies to deter sexually exploitative men. In short, a social adaptive problem created by some men more than by other men can, in principle, be solved or ameliorated by difference-detecting adaptations that lead to adaptive action. Of course, difference-

detecting adaptations undoubtedly play a role in detecting all sorts of social exploiters, and there is evidence that psychopaths are not just sexually exploitative, but also tend to cheat in social exchange and other social relationships (Mealey, 1995).

This example raises an interesting issue that involves sexual conflict and sexually antagonistic co-evolutionary arms races (Arnqvist & Rowe, 2005). Men who pursue a sexually exploitative strategy also face a problem whose solution would be aided by a difference-detecting adaptation. The ability to identify more vulnerable victims—perhaps those who are more gullible, naïve, or cognitively challenged—would afford these men the ability to neutralize or circumvent whatever evolved defenses exist in potential victims and more successfully carry out their sexually exploitative strategy (Buss & Duntley, 2008). Just as cheetahs who selectively avoid gazelles who exhibit ‘stotting’ behavior (an evolved anti-predator defense that signals to the cheetah the athletic condition of the gazelle—FitzGibbon & Fanshawe, 1988) are more successful at predation, psychopaths who selectively avoid non-exploitable women will be more successful at sexual exploitation. Sexual exploitation, of course, is not limited to psychopaths, but is perpetrated, albeit at lower frequencies, by men not so characterized (Haselton et al., 2005; Lewis et al., 2012). The ability to detect and act on stable personality traits of others, in short, is important for all players in this sexually antagonistic arena for solving their respective adaptive problems.

Personality traits linked with habitual welfare tradeoff ratios. Personality traits have recently been linked to a hypothesized variable implied in a host of social adaptive problems—welfare tradeoff ratios. A welfare tradeoff ratio (WTR) refers to how much weight an individual places on his or her own interests relative to those of another person

(Tooby, Cosmides, Sell, Lieberman, & Sznycer, 2008; Sell, Tooby, & Cosmides, 2009; McCullough, Kurzban, & Tabak, in press). WTR has been hypothesized to be an internal regulatory mechanism that affects, and is affected by, variables such as genetic relatedness and physical formidability. The recalibration theory of anger, for example, proposes that anger is an adaptation designed to alter the WTR of the target of the anger in favor of the person displaying the anger (Sell et al., 2009).

Empirical studies have mostly confirmed specific predictions from this theory (Sell, et al., 2009; Price et al., 2012). Physical formidability is a stable trait linked with the ability to inflict costs on others, giving formidable individuals a better bargaining position and ability to prevail in social conflicts. Formidable men are more prone to anger and more strongly endorse attitudes toward using force to resolve interpersonal and even international conflicts (Sell et al., 2009). Women high on physical attractiveness—an attribute linked with the ability to confer benefits because of its link with fertility—are also more prone to display anger and have a greater sense of entitlement. Both findings support the notion that the stable traits of physical formidability in men and physical attractiveness in women influence WTRs and the tactics used to alter them in others, such as the display of anger.

If stable *personality* traits also influence how an individual habitually perceives WTRs, as well as the tactics used to alter WTR in his or her favor, then adaptations to assess those traits would help to solve a suite of problems associated with conflicts of interest in social interactions and relationships. A prime personality trait that should influence WTRs is that of *narcissism*. Two cardinal features of narcissism are a *strong sense of personal entitlement* and *being self-centered*. Narcissistic acts that reflect these

elements include: He asked for a large favor without offering repayment; He took the last piece of dessert without asking if anyone else wanted it; She assumed that someone else should pay for dinner when she was low on cash; He refused to share his food with others; She cut into a long line ahead of her turn (Buss & Chiodo, 1991).

Narcissists also display *a lack of empathy*, which is reflected in acts such as: He did not show much feeling when his friend was upset; She did not listen to other people's problems; and He ignored a friend who was sad. Another hallmark of narcissism is being *interpersonally exploitative*. Exploitative acts include: He insisted that his friend drop everything to see him; She did the favor only when twice as much was promised in return; She asked someone else to do her work for her (Buss & Chiodo, 1991).

In short, those high on narcissism display a wide range of acts that indicate that they *habitually* place a higher weight on their own welfare relative to the welfare of others than do individuals lower on narcissism. One explanatory possibility is that narcissists possess a selfishly-skewed WTR because they are more physically attractive, and hence affiliating with them provides benefits not provided by those who are less attractive—an effect that should be especially pronounced for women, given the centrality of attractiveness to a woman's mate value (Buss, 1989). Meta-analytically there is a weak but significant positive correlation between observer-rated physical attractiveness and narcissism (Holtzman & Strube, 2010), providing some evidence that the positive externality emitted by those high on narcissism might justify their selfishly skewed WTR.

Personality assessment adaptations that gauge the levels of narcissism in others, as well as the subcomponents of sense of entitlement, lack of empathy, selfishness, and

interpersonal exploitativeness, would aid in solutions to adaptive problems associated with conflicts of interest in social relationships. These include mate selection, friend selection, selection of coalition partners, decisions about which kin to invest in, and decisions about strategies for interacting with individuals who vary in their position within the local status hierarchy. A spouse with a selfishly skewed WTR, for example, could inflict a wide array of costs on their partner—using joint resources excessively for personal gain and withholding resources that might be allocated to the needs of their partner. Those who score high on narcissism are more likely to be sexually unfaithful in marriages than those low on this trait (Buss & Shackelford, 1997), perhaps because their selfishly skewed WTR leads them to believe that they are entitled to extramarital sex. Infidelity, however, diverts valuable reproductive resources away from their spouses.

The ability to identify individual differences in narcissism may even help to solve problems associated with kinship. The theory of parent-offspring conflict predicts differences between the fitness interests of parents and their children, as well as between siblings (Trivers, 1974). A kin member high in narcissism, by holding a selfishly skewed WTR, would have an increased likelihood of exploiting their kin, attempting to resolve conflicts of interest more in their favor than kin not high on narcissism. Consequently, knowing the level of narcissism of kin members would provide valuable information for resource allocation decisions. There should be a higher return on resources allocated toward kin low on narcissism than toward kin high on narcissism. The same logic should apply to friendships and coalition partners. A second personality trait likely to play a key role in WTRs is *agreeableness*. The qualities captured by the *agreeableness* factor

have been hypothesized to reflect a cooperative strategy (Buss, 1991a) or an altruistic proclivity (Denissen & Penke, 2008b).

Based on these proclivities, it is reasonable to advance the hypothesis that dispositionally agreeable individuals tend to set their WTRs in a way that places the welfare of their social partners at a high value relative to their own. This provides a powerful selective rationale for why agreeableness is so highly valued across a variety of social relationships and the ability of observers to assess this personality trait in others, even based on physical appearance cues (Cottrell, Neuberg, & Li, 2007; Naumann, Vazire, Rentfrow, & Gosling, 2009; Yamagishi, Tanida, Mashima, Shimoma, & Kanazawa, 2003).

Just as stable physical traits such as strength and physical attractiveness influence WTRs, stable personality traits also reflect habitual WTRs. If this hypothesis is supported by future empirical tests, it provides at least one powerful selective rationale for the evolution of personality assessment adaptations. Evolution should select for difference-detecting adaptations to the degree that they aid in the solution to adaptive problems associated with the major classes of social relationships,

such as dyadic alliances (friendships), mating, coalitions, rivals, hierarchical relationships, and kin relationships (Buss, 2011).

Conclusions

The field of psychology historically has been split between those who focus on human nature or species-typical characteristics and those who focus on the major ways in which individuals differ. This split is reflected within personality psychology, within evolutionary psychology, and within the broader field of psychology writ large.

Evolutionary personality psychology provides a unifying framework within which both important approaches—individual differences and species-typical characteristics--can be successfully integrated.

We argue that evolutionary psychology cannot ignore important individual differences because they are omnipresent, somewhat stable over time, show moderate heritability, and have known empirical links to components of functioning that recurrently contribute to reproductive fitness. At the same time, the field of personality psychology cannot afford to ignore evolutionary psychology: It provides the only cogent meta-theory for the broader field of psychology and provides a powerful set of conceptual tools, such as life history theory and evolutionary genetics, for transforming personality psychology into an explanatory rather than merely descriptive science.

Advances in evolutionary personality psychology afford a reformulation of units of analysis long considered fundamental to the field. First, it offers a non-arbitrary formulation of *fundamental human motives*—a domain historically plagued by different and incommensurate frameworks with no basis for adjudication. Second, it provides a functional analysis of *personality traits* anchored in motivational individual reaction norms and adaptive individual differences that enable the field to move beyond the important descriptive advances currently achieved.

Third, evolutionary personality psychology furnishes a novel formulation of *situations*, which historically have been arbitrary and almost completely ad hoc: Adaptive problems define situations. Evolved psychological mechanisms are calibrated to the statistical design features of recurrent adaptive problems (situations), such as mate selection, cheater detection, hierarchy negotiation, intrasexual competition, coalition

formation, and many others. More broadly, a person's developmental life history environment is defined by the distribution, salience, and sequencing of adaptive problems encountered over time.

Finally, evolutionary personality psychology provides a unique formulation of *person-situation interactions*. Person-situation interactions come in two well-defined forms: (1) the ways in which person variables, through processes such as selection, evocation, and manipulation, influence non-random exposure to different suites of adaptive problems, and (2) adaptive individual differences in the strategies that people deploy toward solving the problems to which they are non-randomly exposed.

In sum, evolutionary personality psychology offers a crisp non-arbitrary functional formulation of the fundamental units of analysis in the field, and in so doing yields a common framework for currently disparate and incommensurable programs of research within the field.

Although evolution by selection tends to produce species-typical traits that characterize human nature, genetics research over the past few decades has revealed a surprising reservoir of individual differences within many species, including humans. Some differences are not heritable and might be best explained by different forms of conditional adaptation. Others are genetic in origin on most likely not neutral to selection, but best explained by mutation-selection balance and different forms of balancing selection. Conceptual advances within evolutionary theory itself provide powerful tools for understanding the origins of both non-heritable and heritable individual differences.

Although the molecular genetics and genomics of personality are relatively new fields, new and cheaper techniques are coming on-line to permit finer-grained testing of competing theories about the evolutionary genetic origins of personality.

The personality traits of others inhabiting an individual's social environment create non-random exposure to adaptive problems. Because evolutionary personality psychology defines "situations" as adaptive problems, this framework provides a novel means of conceptualizing the environments to which individuals are non-randomly exposed.

At the same time, one's personality traits may reflect habitual individual differences in strategies for solving adaptive problems. We suggest that humans have evolved personality assessment adaptations, or difference-detecting mechanisms, precisely for navigating the social landscape of adaptive problems posed by others, which are influenced in part by their personality traits.

More generally, evolutionary personality psychology provides a conceptual framework for addressing some of the most important foundational issues in the field: How can the key units of analysis such as motive, trait, and situation be conceptualized? How can person-environment interaction be conceptualized? What are the evolutionary origins of personality? And how can the field of personality psychology be theoretically integrated with the broader field of psychology and with foundational knowledge in the rest of the life sciences?

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