

Adaptive Individual Differences

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ABSTRACT Individuals differ in innumerable ways, some adaptive, some maladaptive, and some neutral. Personality theories, we argue, can profit from distinguishing among these importantly different types of individual variation. This article outlines a taxonomy of origins of individual differences—*environmental sources of adaptive differences* (e.g., early environmental calibration), *heritable sources of adaptive differences* (e.g., adaptive self-assessment of heritable qualities), *nonadaptive sources of individual differences* (e.g., incidental by-products of adaptive variation), and *maladaptive sources of individual differences* (e.g., epigenetic trauma). The second section outlines empirical procedures for confirming or falsifying the differing conceptions of individual differences, with a special focus on empirically distinguishing adaptive individual differences from those that are maladaptive or nonadaptive. The final section highlights the importance of individual differences for solving social adaptive problems.

Scientists since Darwin (1859) have known that members of single species show marked differences from one another. A coherent theoretical understanding of the origins and possible functions of individual

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differences, however, has eluded the seemingly disparate disciplines of both personality psychology (e.g., Wiggins, 1996) and evolutionary biology (Tooby & Cosmides, 1990; Wilson, 1994).

Within personality psychology, enduring differences are often regarded as the core phenomena of the discipline (McCrae & Costa, 1996; Saucier & Goldberg, 1996; Wiggins, 1979). Some theoreticians treat heritability as a criterion elevating an individual difference in importance, a marker designating that the difference is a major one (Eysenck, 1981). Precisely why heritable differences should be regarded as more important than nonheritable differences, however, has remained unclear. Other theoreticians ignore issues of heritable or nonheritable origins entirely (e.g., Saucier & Goldberg, 1996) or simply assume that the most important differences arise from experience during ontogeny (e.g., McClelland, 1980).

Some evolutionary biologists have focused on species-typical adaptations, ignoring individual differences except in their role of providing the raw materials on which natural selection operates. Individual differences, *particularly* those that are heritable, are sometimes relegated to secondary status because they are thought to originate primarily through nonselection forces such as random mutation, recombination, or genetic drift (Tooby & Cosmides, 1990; Wilson, 1994). Differences are sometimes viewed as “noise” or “genetic junk” that is maintained within a population precisely because they are presumed to be *unrelated* to the core of the evolutionary process—adaptation and natural selection (Thiessen, 1972). Heritable individual differences are to species-typical adaptations, in this view, as differences in the colors of the wires in a car engine are to the engine’s functional working components—one can vary the wire coloring without affecting the functioning of the engine (Tooby & Cosmides, 1990).

If unity of science is taken to be a reasonable goal, these disparate conceptualizations are difficult to reconcile. Since directional selection tends to reduce genetic variability within populations, why do behavioral genetic studies consistently find moderate heritability to personality dispositions? Is it reasonable for the core of one discipline to be conceptualized as “noise” or “junk” by another? And if individual differences really are independent of adaptation and natural selection, why are individual differences reliably linked to activities closely connected with reproductive success such as survival and sexuality? Individual differences in extraversion, for example, are linked with differences in sexual

access to partners (Eysenck, 1976). Conscientiousness is known to be correlated with work and status attainment (Kyl-Heku & Buss, 1996). Impulsivity is linked with extramarital affairs (Buss & Shackelford, 1997) and higher mortality rates (Friedman et al., 1995). If the individual differences studied by personality psychologists are reliably linked with reproductively relevant phenomena such as status, sexuality, and even survival, perhaps they play a more important role in human evolutionary psychology than previously assumed.

Recently, the possibility that some individual differences are adaptively patterned and themselves products of recurrent selection has been vigorously reexamined within mainstream biology (Clark & Ehlinger, 1987; West-Eberhard, 1989; Williams, 1992) and the newer discipline of evolutionary psychology (e.g., Buss, 1996; Gangestad & Simpson, 1990; Tooby & Cosmides, 1990; Wilson, 1994). Indeed, the emerging field of evolutionary psychology is now grappling with ways to incorporate individual differences and species-typical psychological mechanisms within a unified conceptual framework (e.g., Buss, 1984; Gangestad & Simpson, 1990; MacDonald, 1995; Thiessen, 1994; Wilson, 1994). The goal of this article is to further these integrative efforts by offering a taxonomy of the conceptual models of adaptive and nonadaptive individual differences.

Guiding Premises of Evolutionary Psychology

The evolutionary process creates three sorts of products—adaptations, by-products of adaptations, and noise (see Buss, Haselton, Shackelford, Bleske, & Wakefield, 1998). Adaptations are evolved solutions to recurrent adaptive problems of survival and reproduction. Adaptations, such as binocular vision, specific taste preferences, or desires for particular mates, are often species-typical, characterizing most or all members of a breeding population. They exist in the present because they solved in the past a problem of survival or reproduction recurrently over a sufficiently long span of time to have evolved. As descendants of ancestors who succeeded in reproducing, all humans carry with them the adaptive mechanisms that led to their ancestors' success. There are compelling reasons to believe that human psychological adaptations are many in number, specific in nature, and functional in design (Buss, 1995; Symons, 1987; Tooby & Cosmides, 1992).

Adaptations are sometimes referred to as *evolved strategies*, but this phrase should not be taken to imply a conscious goal state. Taste preferences for substances rich in sugar and fat, for example, can be described as evolved strategies for the problem of food selection, but this does not imply that the person is aware of the adaptive logic of the preferences or the selective process by which they originated.

By-products, the second product of the evolutionary process, refer to phenomena that occur as a result of adaptations, but are not part of their functional design. Light bulbs, for example, produce heat as a predictable by-product. Light bulbs are designed to produce light, not heat, and so the heat is not properly regarded as part of their functional design. In the analysis of human psychological adaptations, it is critical to distinguish between effects that are part of functional design and those that are merely incidental by-products.

Noise is the third product of the evolutionary process. Noise represents random perturbations in evolved design that generally do not affect its functioning. Light bulbs, for example, are designed to have smooth surfaces, but minor imperfections in the process of creating them cause small distortions in the surface. Similarly, human adaptations are presumed to have a residue of random variations due to small imperfections in their development.

In sum, the process of evolution by selection creates adaptations, by-products of adaptations, and a residue of noise. Although evolutionary scientists differ in their estimates of the prevalence of adaptations compared with incidental by-products and noise, most regard adaptations to be the primary product of the selective process (Tooby & Cosmides, 1992).

Evolved psychological mechanisms, therefore, are the primary focus of study for evolutionary psychologists. Psychological mechanisms do *not* represent some mystical level of analysis different from that used by other nonevolutionary psychologists. Rather, they are generally understood in cognitive terms as information processing devices designed to take in certain classes of input, operate on that input with a set of decision rules, and transform it into output in the form of manifest behavior (Buss, 1995). Thus, the cognitive and affective mechanisms studied by evolutionary psychologists are precisely the same as those studied by nonevolutionary psychologists. The difference between psychologists guided by evolutionary frameworks and those not so guided are: (1) an explicit consideration of function—design features as evolved solutions to adaptive

problems; (2) an explicit consideration of the selective process that gave rise to the psychological mechanisms; and (3) guiding premises that evolved psychological mechanisms are likely to be large in number and at least partly domain-specific in nature. It is within this broader evolutionary psychology context that the sources of individual differences can be described.

A Taxonomy of Causal Origins of Individual Differences

Individual differences can emerge from a variety of heritable and non-heritable sources. Evidence from behavioral genetic studies of personality strongly suggests that both are important. Personality characteristics commonly show evidence of moderate heritability, typically ranging from 30% to 50% (Bouchard & McGue, 1990; Loehlin, Horn, & Willerman, 1990; Plomin, DeFries, & McClearn, 1990). Simultaneously, these studies provide the strongest evidence of environmental sources of variance, ranging from 50% to 70%. We offer a conceptual taxonomy of sources of adaptively patterned individual differences based on environmental and heritable sources, as well as interactions between these sources (Table 1). The routes to adaptively patterned individual differences are presented descriptively with illustrative cases that are sometimes speculative. After the conceptual possibilities are presented, we offer some guidelines for empirically testing hypotheses about the routes to adaptively patterned differences. We conclude with a discussion of the role of individual differences as key components of the human “adaptive landscape.”

Early experiential calibration. Individuals who share a common evolved psychology can experience different early environmental events that channel them into alternative strategies. According to this conception, each person comes equipped with two or more potential strategies within that person’s repertoire. From this species-typical menu, one strategy is selected based on early environmental experiences. These early experiences, in essence, “lock in” a person to one strategy to the exclusion of others that could have been pursued had the environmental input been different.

Table 1
Sources of Individual Differences

Environmental Sources of Adaptive Individual Differences

1. Early environmental calibration
2. Enduring situational evocation
3. Strategic niche specialization (including frequency-dependent shifts)

Heritable Sources of Adaptive Individual Differences

1. Adaptive self-assessment of heritable attributes
2. Frequency-dependent adaptive strategies
3. Continuous condition-dependent heritable strategies

Nonadaptive Sources of Individual Differences

1. Neutral variation
2. Incidental by-products of adaptive variation

Maladaptive Sources of Individual Differences

1. Genetic defects
2. Environmental insults (epigenetic trauma)

An evolutionary theory of socialization. Belsky, Steinberg, and Draper (1991), for example, propose the critical event of early father presence versus father absence as a calibrator of alternative sexual strategies. Individuals growing up in father-absent homes during the first five to seven years of life, according to this theory, develop the expectations that parental resources will not be reliably or predictably provided and adult pair-bonds will not be enduring. Accordingly, such individuals cultivate a sexual strategy marked by early sexual maturation, early sexual initiation, and frequent partner switching—a strategy designed to produce a large number of offspring with low levels of investment in each. Extraverted and impulsive personality traits may accompany this strategy. Other individuals are perceived as untrustworthy, relationships as transitory. Resources sought from brief sexual liaisons are opportunistically attained and immediately extracted.

Individuals marked by a reliably investing father during the first five to seven years of life, according to the theory, develop a different set of expectations about the nature and trustworthiness of others. People are seen as reliable and trustworthy, and relationships are expected to be enduring. These early environmental experiences channel individuals toward a long-term mating strategy, marked by delay of sexual maturation, a

later onset of sexual activity, a search for long-term securely attached adult relationships, and heavy investment in a small number of children.

All theories of environmental influence, including this one, ultimately rest on a foundation of evolved psychological mechanisms, whether they are acknowledged as such or not (Tooby & Cosmides, 1990). Contrary to views that perpetuate the false dichotomies of nature/nurture or genetic/environmental, evolved psychological mechanisms are necessarily entailed by theories of environmental influence (Tooby & Cosmides, 1990). In this particular case, the implicit psychological mechanisms are specifically designed to take as *input* information about the presence and reliability of paternal resources, *process* that input via an evolved set of decision rules, *develop* one of two possible psychological models of the social world, and pursue one of two alternative mating strategies as *output* of the mechanisms. It is possible, of course, that mechanisms of this sort may permit three or more alternative strategies from a larger menu of options.

There are two key points to draw from the Belsky et al. (1991) theory of adaptively patterned individual differences. First, the individual variation lies not on a single dimension or trait, but rather represents a coherent constellation of covarying qualities, including reproductive physiology (e.g., early age of menarche), psychological models of the social world (e.g., others as untrustworthy), and overt behavior (e.g., transitory sexual liaisons).

Second, the individual differences that result from early experiential calibration are adaptively patterned, the result of evolved mechanisms that assess the social environment and select one strategy from the menu. In one case, reproductive success historically was attained through a high reproductive rate, with perhaps a concomitant decrease in the survival and reproduction of any one offspring. In the other case, reproductive success historically was attained through a lower reproductive rate marked by heavy investment in the survival and reproduction of fewer offspring. The evolution of these environment-contingent strategies presumably resulted from a long and recurrent evolutionary history in which different individuals confronted radically different rearing environments. Environmental variation over human evolutionary history presumably selected for developmentally flexible mechanisms that take as input the nature of the rearing environment as a key cue to the expected adult environment.

An evolutionary theory of sex-linked socialization. In a survey of 89 cultures, Low (1989) found consistent sex differences in the manner in which parents socialized boys and girls. Boys more than girls were trained to be competitive strivers, presumably as a key male strategy for ascending status hierarchies as a means to attract mates. Girls more than boys were trained to be more restrained in their behavior, with a particular emphasis on sexual restraint. Low suggests that this socialization strategy functions to elevate (or maintain) a woman's mate value by offering potential mates the assurance of paternity certainty.

Cultures vary, however, in the intensity of these socialization practices. The more polygynous the culture, the more intensely parents seem to train boys to be achievement strivers. Polygyny offers men greater opportunities to obtain multiple mates. Simultaneously, polygyny poses greater risks to males of being shut out of mating entirely—if one man monopolizes five women, then four men will be left without mates (assuming an equal sex ratio). Thus, parents may elevate the intensity of their socialization of boys in response to the greater intensity of intrasexual mate competition in polygynous cultures.

Although no data yet exist on the degree to which these early socialization experiences actually create or magnify sex differences and individual differences in mating strategies, the theory nicely illustrates the concept of early experiential calibration. Further research could examine this evolutionary theory of socialization within cultures, as well as between cultures. Boys who may be likely to attract multiple mates even within presumptively monogamous cultures, for example, may be targeted by parents for more intense socialization around competitive striving. And girls within presumptively monogamous cultures who may be especially likely to attract a single high-status male may be especially targeted by parents for more intense socialization around sexual restraint.

Attachment theories of pair-bonds. The proposal that attachment experiences during infancy represent an important source of experiential calibration of adult reproductive strategies has attracted many adherents (e.g., Chisholm, 1996; Hazan & Shaver, 1994; Miller & Fishkin, 1997; Zeifman & Hazan, 1997). But the theorists differ profoundly in their treatment of individual differences.

Zeifman and Hazan (1997) argue that the attachment system represents a set of evolved psychological mechanisms in both mother and infant for the function of increasing the infant's survival. By cultivating a secure

attachment with the mother, the infant maintains proximity to her, avoids the many dangers linked with straying too widely, and hence enhances survival.

In adulthood, this mechanism is hypothesized to be co-opted for the function of establishing a secure pair-bond. According to Zeifman and Hazan (1997), adult attachment serves functions similar to those in infancy—support, protection, and reassurance. But it also serves an additional set of functions—cementing the bond between a man and a woman to enhance the survival and reproduction of children. They argue that without the force of a secure attachment to a woman to keep the man around, the man might stray and hence imperil the survival of offspring. Zeifman and Hazan question whether short-term father involvement with offspring would have improved the survival and reproductive success of those offspring, given the years of protection and assistance offspring need. Thus, “it is doubtful that a short-term bonding mechanism, or serial monogamy, would have been selected for” (1997, p. 251).

Zeifman and Hazan, however, do not address arguments that have outlined the evolution of short-term mating for functions other than the protection and provision of offspring. These include the potential benefits of fertility backup, good genes, mate insurance, immediate resource extraction, and mate manipulation (see Buss, 1994; Buss & Schmitt, 1993; Gangestad & Simpson, 1990; Greiling & Buss, under review; Smith, 1984). And historically, men who successfully pursued a short-term mating strategy would have benefited directly in the currency of increased offspring production. Given the prevalence of short-term mating in human populations, including the physiological, psychological, and behavioral evidence for its occurrence across cultures and over human evolutionary history, comprehensive theories of individual differences cannot ignore short-term sexual strategies.

A clear implication of the Zeifman-Hazan theory is that individual differences, and particularly deviations from secure attachment, represent *maladaptations* rather than alternative adaptive strategies: “dysfunctional early attachment relationships [i.e., those that are not secure] are a common precursor of adult sexual deviance” (1997, p. 255). Furthermore, “If pair-bond members fail in their parenting roles by providing insufficient stability and security [and hence presumably produce insecurely attached offspring], they risk producing progeny who are ill-equipped to meet the challenges of mate competition and retention” (p. 258). Thus, long-term securely attached pair-bonds are regarded as

the primary and most beneficial human sexual strategy, and deviations from them are regarded as maladaptive in posing risks to children in currencies of survival and reproduction.

Miller and Fishkin (1997), following this line of work, seem to concur with Zeifman and Hazan (1997), but are more explicit in claiming that short-term mating and variations from secure attachment represent “‘fall out’ of a *failure* to interface with humans’ adapted for social environment . . . responsive paternal and maternal caregivers” (Miller & Fishkin, 1997, p. 228; emphasis added). Thus, short-term mating is seen as a perturbation or deviation from the preferred species-typical mating strategy, resulting from unnatural and recent sources of variability in parental care that emerged only “after the Pleistocene era” (p. 228).

Unfortunately, this perspective on individual differences runs into several empirical stumbling blocks. Only one will be mentioned here—the prevalence of those who are *not* securely attached. Across a wide array of studies, roughly 45% of adults fail to fall into the securely attached category (Miller & Fishkin, 1997). Is it reasonable to suppose that nearly half of all adult humans have “failed to interface with [their] adapted for environment”? Presumably, this huge percentage represents some radical change in the modern environment compared with human ancestral environments, although no one has articulated precisely what such a change might be or what might have caused it. The only means of addressing this conceptual problem is the assertion that “[u]nfortunately, not all human caregivers today are responsive . . .” (Miller & Fishkin, 1997, p. 216), the implication being that most were in the human ancestral past.

In sum, these attachment theories regard deviations in adult attachment from the secure long-term pair-bonded prototype as maladaptive. Individual differences are seen as maladaptive perturbations from the optimal ideal of secure attachment.

Attachment and life history theory. In sharp contrast, Chisholm (1996) proposes an integration of life history theory and attachment theory that suggests that these individual differences *are* adaptively patterned and likely to reflect the high variability of ancestral child-rearing environments. Chisholm’s argument starts with life history theory, the insight that life cycles constitute evolved adaptive strategies. A core principle of life history theory is effort allocation (Levins, 1968). Individuals have finite time and resources, and decisions must be made about their

allocation to different components of fitness. The components of reproductive success, such as survival, growth, mating, and parenting, are often in conflict with one another. Effort allocated to one component often precludes effort allocated to the other components—there are necessary trade-offs. The effort used to court additional mates, for example, conflicts with time and energy invested in parenting. According to this theory, natural selection would have fashioned decision rules for changing the allocation of effort to these different components, depending upon specific features of context. Strategies are thus “suites of functionally integrated anatomical, physiological, psychological, and developmental mechanisms for optimizing the trade-offs among the components of fitness throughout the life cycle” (Chisholm, 1996; see also Charnov, 1993; Hill, 1993; Stearns, 1992).

One of the most important trade-offs is between current and future reproduction. Increased immediate reproduction occurs at the expense of future reproduction. According to Chisholm, when resources are limited or unpredictable, it may pay to increase fertility and decrease investment in any particular offspring, at least under some conditions. Chisholm further argues that the psychology of attachment constitutes an evolved set of mechanisms for making these allocation decisions.

The ancestral environments in which these mechanisms evolved, according to Chisholm, were neither as rosy or secure as many attachment theorists such as Bowlby, Zeifman, Hazan, Miller, and Fishkin have suggested. Risk and uncertainty come from many sources: unpredictable food supplies, vagaries of climate and weather, diseases, parasites, predators, and, perhaps most important, other conspecifics such as one’s parents. Indeed, Chisholm argues that the parents’ sexual strategy, including the quantity and quality of their investment in offspring, may have provided the most adaptively significant dimension of children’s environments.

Variations from secure attachment, in this view, represent early experiential calibrations to recurrent threats to the child’s survival and growth—the parent’s inability or unwillingness to invest heavily in offspring. Avoidant attachment represents an adaptation to parental *unwillingness* to invest, as when the parent is pursuing a short-term mating strategy rather than investing heavily in offspring. The anxious/ambivalent attachment style, in contrast, represents an adaptation to a parental *inability* to invest—as when the mother herself is irritable, preoccupied, fearful, hungry, or exhausted.

Given the incipient stage of theory-building, the precise nature of the underlying psychological mechanisms has not been articulated. Chisholm presumably does not mean to imply that an infant can literally draw inferences that distinguish between parental intent (unwillingness to invest) and capacity (inability to invest). Rather, the infant presumably detects parental behaviors that are probabilistically linked with these differing states, upon which different attachment styles are activated from the triadic menu. The next decade of research should witness more direct focus on the precise nature of the psychological mechanisms underlying different attachment styles.

Although we view Chisholm's theory of adaptive individual differences as more plausible than the notion that 45% of the population is "maladapted," we note that stringent conceptual and evidentiary standards must be met. Do attachment styles represent early environmental calibration, or do they reflect heritable individual differences as suggested by research by Goldsmith and Harmon (1994)? Are individual differences in attachment stable over the life course? Do the underlying psychological mechanisms of attachment coordinate with the specific features of adaptive problems posed by each alternative strategy? These questions await further conceptual and empirical work.

Early experiential calibration represents only one conceptual possibility for environmentally induced adaptive individual differences. A second possibility is that adaptive individual differences are repeatedly evoked by enduring features of the social environment *currently* occupied.

Enduring situational evocation. Many human adaptations respond to immediately encountered environmental contingencies rather than being "set in plaster" by early environmental events. The physiological mechanism that results in calluses, for example, responds to immediately experienced friction to the skin. Individuals differ recurrently in the degree to which they pursue activities that result in frequent repeated friction to the skin. The stable individual differences in calluses, in this example, are properly understood as adaptively patterned differences stemming from enduring environmental differences in the evocation of the callus-producing mechanism. These enduring individual differences, like those set by early experiential calibration, are the result of a specific form of interaction between environments and evolved mechanisms.

A similar form of adaptively patterned individual differences can occur with psychological factors. Consider a man who is married to a woman

who has higher perceived “mate value” on the mating market than he does (Frank, 1988; Tooby & Cosmides, 1990). Even if his social environment is not populated with interested same-sex rivals, his enduring relationship with his wife may lower his threshold for jealousy compared with the man who is equal to, or higher than, his wife in perceived mate value. As a consequence, the lower mate value man may get jealous more easily, worry about his wife’s activities, and strive to sequester her more intensely (Buss, 1988a; Tooby & Cosmides, 1990; White, 1980). He may become more easily suspicious about her interactions with others and worry more about her potential alternatives.

From an adaptationist perspective, a mechanism for adjusting one’s threshold for jealousy could have resulted from thousands of selective events in the evolutionary past in which a mate value discrepancy, on average, was statistically associated with a greater likelihood of a partner’s infidelity or defection (Hatfield, Traupman, & Walster, 1979; Tooby & Cosmides, 1990; White, 1980). These adaptive problems are more commonly confronted by the lower mate value person within the relationship, and so psychological mechanisms are activated more easily to solve them.

Individual differences in jealousy, in this example, are enduring over time and adaptively patterned. They rest on a foundation of evolved psychological mechanisms shared by all, but differentially activated in some. Were the enduring environment to change—for example, if the man got divorced and remarried a woman of equal or lower mate value—then the enduring pattern of psychology and behavior would change (Hatfield, Traupman, & Walster, 1979; Tooby & Cosmides, 1990).

Mate value theory. Mate value can affect mating strategies not merely through a mate value discrepancy, but also in its relative level within a mating population (Buss, 1987; Symons, 1979; Tooby & Cosmides, 1990). Those who are highest in mate value, more closely embodying the desires of the opposite sex, are better able to carry out their preferred sexual strategy (Buss, 1987; Buss & Schmitt, 1993; Simpson & Gangestad, 1992). Given men’s evolved desire for sexual variety, high mate value may cause men to pursue more short-term or polygynous mating (Symons, 1979).

One piece of empirical evidence that supports this proposition comes from the Aka tribe in Africa (Hewlett, 1991). Aka men who achieve high status and garner many resources during their lives contribute little to the

direct care of their children when they marry. In contrast, Aka men who attain only low status and few resources for a wife and children compensate by spending more time directly caring for the children. One key indicator of a father's investment, for example, is how many minutes a day he spends holding an infant, which is an expensive activity in terms of both metabolic costs and opportunity costs (other activities foregone, such as status striving and courting additional mates). Holding protects the infant from environmental dangers, temperature changes, accidents, and aggression from others. Aka men who maintain positions of status in the group, and hence are highly desired by women, hold their infants an average of 30 minutes per day. Men who lack positions of status, in contrast, hold their infants more than 70 minutes per day. Although women typically prefer men with status and resources, a man's willingness to parent constitutes a valuable resource that can partially compensate for the lack of other qualities.

Thus, low mate value men appear to pursue a high parental investment mating strategy, at least in part in order to attract a single woman. Higher mate value men are more likely to be able to attract multiple mates, and so deploy their efforts less toward the parenting and more toward mating (Gangestad, 1998; Gangestad & Thornhill, 1997; Smith, 1984). Thus far, few empirical tests of mate value theory have been conducted, but the predictions are straightforward and testable. A particularly stringent test would be to examine changes in mating strategy *within* individuals who experience changes in mate value over time. Men who experience a sudden status or resource elevation (e.g., through a large promotion or hunting success) may shift to the pursuit of multiple mates (e.g., Holmberg, 1950).

Sex ratio theory. Similar shifts in mating strategies are predicted to occur when the sex ratio in a circumscribed pool of potential mates changes (Guttentag & Secord, 1983; Pedersen, 1991). Changes in the proportion of men to women may cause predictable changes in men's and women's sexual strategies. The degree of selectivity is the first predicted shift. When there is a surplus of men, fewer men can be highly selective, and they must settle for a less desirable mate than they would otherwise attract if the sexes were more in balance. A deficit of men relative to women, in contrast, restricts women's selectivity, because there are fewer men to choose from. Theoretically, these ratios affect the degree to which both sexes can realize their ideal preferences.

Low proportions of men also appear to cause a destabilization of marriage (Pedersen, 1991). An excess of women relative to marriageable men means that many women lack the ability to secure strong commitments from men. A surplus of women relative to men means that more men can pursue casual sexual liaisons with aplomb and dispatch. Changes in the ratios of men to women within the United States through history confirm this prediction. Periods of increasing divorce, for example, as between 1970 and 1980, correspond closely to periods when there is a surplus of women on the mating market (Pedersen, 1991).

Women in mating environments of few men also appear to intensify their competition with each other by enhancing their appearance, increasing their health-promoting behavior, and even offering sexual resources to attract men (Pedersen, 1991). The sexual revolution in the United States in the late 1960s and early 1970s, for example, involved a change in which many women abandoned their sexual reserve and engaged in sexual relationships without requiring serious commitment from men (Pedersen, 1991).

When there are more men competing for fewer women, the balance of power is predicted to shift to women (Buss, 1994). Women can more easily exact what they want from men, and men in turn become more competitive with each other to attract and retain desirable women. Marriages are predicted to be more stable because men are more willing to offer commitment and are less likely to leave a marriage. When women are scarce relative to men, men have fewer available alternatives and cannot easily pursue casual sexual relationships. Men therefore are predicted to increasingly compete to fulfill women's preferences for a long-term mate, especially by striving for resources and showing a willingness to invest parentally.

The effects of a relatively enduring local environment on sexual strategies are also predicted to affect individual differences within an environment through age, mate value, or local subcultural differences. Cross-culturally, especially in tribal societies, young men often live in a world where available women are in scarce supply, because women prefer mature men with greater status and resources (Buss, 1989a; Chagnon, 1983; Hill & Hurtado, 1995). Young men's strategies appear to reflect these local conditions of female scarcity, because they engage in highly risky competition strategies, committing the vast majority of crimes of sexual coercion, muggings, battery, and murder (Daly & Wilson, 1988). These are risky crimes by men who have trouble attracting women.

As men mature into their thirties and forties, the ratio between the sexes typically tilts in their favor, if they have survived risks and attained positions of reasonable status (Guttentag & Secord, 1983; Pedersen, 1991). They have a wider pool of potential women to choose from, and they often experience a higher value on the mating market than they did in their youth (e.g., Hart & Pilling, 1960; Hill & Hurtado, 1995). Therefore, such men are predicted to be more able to attract multiple mates, whether through casual sex, extramarital sex, serial marriage, or polygyny. Men of any age who have little desirability as mates, however, do not enjoy this advantage, and some men are shut out of mating entirely.

Individual differences observed between local subcultures may also have their origins in the effects of sex ratio on the primary sexual strategy pursued. In many inner city environments, for example, there are heavy surpluses of women due to the greater incarceration, death, and migration of men (Guttentag & Secord, 1983; Pedersen, 1991). Concomitantly, there are more frequent promiscuous matings, fewer long-term relationships, and low levels of male parental investment (Pedersen, 1991). The shift to a short-term mating strategy among those inhabiting inner city environments may reflect the environmental evocation of one choice from the species-typical menu of sexual strategies.

In sum, enduring adaptive individual differences need not stem from early experiential calibration, but instead can result from evocations produced by the enduring situations inhabited. These relatively enduring situations include mate value discrepancy with one's long-term partner (e.g., Tooby & Cosmides, 1990), one's overall desirability as a mate on the mating market (Gangestad & Thornhill, 1997), age (Hart & Pilling, 1960), and the ratio of men to women in the local population (Pedersen, 1991). Future research could profitably explore these and other features of enduring environments as sources of relatively stable individual differences.

Alternative niche picking or strategic specialization. From an evolutionary perspective, competition is keenest among those pursuing the same strategy. As one niche becomes more and more crowded with competitors, success can suffer compared with those seeking alternative niches (Maynard Smith, 1982; Wilson, 1994). Selection can favor mechanisms that cause some individuals to seek niches where the competition is less intense, and hence where the average payoff may be higher.

Mating provides some clear examples. If most women pursue the man with the highest status or greatest resources, then some women would

achieve more success by courting males outside of the arenas in which competition is keenest. In a mating system in which both polygyny and monogamy are possible, for example, a woman might be better off securing all of the resources of a lower status monogamous man rather than having to settle for a fraction of the resources of a high-status polygynous man.

The ability to exploit a niche will depend on the resources and personal characteristics an individual brings to the situation, whether environmental or heritable in origin (see next section on heritable adaptive input). One variable that is *not* heritable is birth order. It is possible that first borns and second borns have faced, on average, recurrently different adaptive problems over human evolutionary history. Sulloway (1996), for example, argues that first borns occupy a niche characterized by strong identification with parents and other existing authority figures. Second borns, in contrast, have less to gain by authority identification, and more to gain by overthrowing the existing order. According to Sulloway, birth order influences niche specialization. Second borns develop a different personality marked by greater rebelliousness, lower levels of conscientiousness, and higher levels of openness to new experiences (Sulloway, 1996). Birth order differences show up strongly among scientists, where second borns tend to be strong advocates of scientific revolutions; first borns tend to strenuously resist such revolutions (Sulloway, 1996).

Whether or not the details of Sulloway's arguments turn out to be correct, the example illustrates strategic niche specialization. Individual differences are adaptively patterned, but they are *not* based on heritable individual differences. Rather, birth order, a nonheritable individual difference, provides input (presumably through interactions with family members) into a species-typical mechanism that canalizes strategic niche specialization.

Heritable individual differences can also provide input into species-typical evolved psychological mechanisms and, in addition, they can also evolve as a consequence of strategic niche specialization—possibilities to which we now turn.

Adaptive self-assessment of heritable qualities. Tooby and Cosmides (1990) coined the term *reactive heritability* to describe evolved psychological mechanisms designed to take as input heritable qualities as a guide to strategic solutions. According to this view, selection operates through

the attainment of goal states. Any feature of the individual's world—including *one's own personal characteristics*—that influences the successful attainment of those goal states may be assessed and evaluated by evolved psychological mechanisms. Evolved mechanisms, in this view, are not only attuned to recurrent features of the external world, such as the reliability of parental provisioning, but can also be attuned to the evaluation of self (Tooby & Cosmides, 1990; Wenegrat, 1984).

Suppose that all men have an evolved decision rule of the form: Pursue an aggressive strategy when aggression can be successfully implemented to achieve goals, but pursue a cooperative strategy when aggression cannot be successfully implemented (modified from Tooby & Cosmides, 1990, p. 58). Evolved decision rules are undoubtedly more complex than this. But given this simplified rule, those who happen to be mesomorphic (muscular) in body build can more successfully carry out an aggressive strategy than those who are ectomorphic (skinny) or endomorphic (round). Heritable individual differences in body build provide input into the decision rule, thereby producing stable individual differences in aggression and cooperativeness. In this example, the proclivity toward aggression is not directly heritable, but rather would be “reactively heritable” in the sense that it is a secondary consequence of heritable body build that provides input into species-typical mechanisms of self-assessment and decision making.

Similar models of heritable adaptive input can be developed for individual differences in mating strategies. One study assessed the physical appearance of teenage boys on two dimensions—the degree to which their faces looked dominant or submissive and physically attractive (Mazur, Halpern, & Udry, 1994). Only photographs were available for the judgments of these features, with a dominant person being defined as someone who “tells other people what to do, is respected, influential, and often a leader” (p. 90). The teenagers who were judged to be more facially dominant and physically attractive were discovered to have had more heterosexual experience with “heavy petting” and sexual intercourse. Furthermore, dominant facial appearance predicted cumulative coital experience, even after statistically controlling for facial attractiveness and puberty development.

Although speculative, these findings may illustrate heritable adaptive input, on the assumption that facial features involved in appearing dominant and attractive are partially heritable. Males could all have an evolved psychological mechanism that takes as input a self-assessment

of the degree to which one appears dominant and attractive: “If high on these dimensions, pursue a short-term sexual strategy; if low, pursue a long-term sexual strategy.” In this example, of course, one cannot rule out third variables, such as testosterone, which may simultaneously produce a more dominant-looking face and a higher sex drive.

According to the conception of adaptive self-assessment of heritable qualities, stable individual differences in the pursuit of short-term and long-term sexual strategies are not directly heritable. But they represent adaptive individual differences based on self-assessment of heritable information (Tooby & Cosmides, 1990).

Frequency-dependent adaptive strategies. In general, the process of directional selection tends to use up heritable variation. Heritable variants that are more successful tend to replace those that are less successful, resulting in species-typical adaptations that show little or no heritable variation in the presence or absence of basic functional components (Williams, 1966, 1975).

There is a major exception to this trend—frequency-dependent selection. In some contexts, two or more heritable variants can be sustained in equilibrium. The most obvious example is biological sex. In sexually reproducing species, the two sexes represent frequency-dependent suites of covarying adaptive complexes. If one sex becomes rare relative to the other, success increases for the rare sex, and hence selection favors parents who produce offspring of the less common sex. Typically, the sexes are maintained in approximately equal ratio through the process of frequency-dependent selection. Frequency-dependent selection requires that the payoff of each strategy decreases as its frequency increases, relative to other strategies, in the population.

Alternative adaptive strategies can also be maintained *within sex* by frequency-dependent selection. Among the bluegill sunfish, for example, three different male mating strategies are observed—a “parental” strategy that defends the nest, a “sneak” strategy that matures to only a small body size, and a “mimic” strategy that resembles the female form (Gross, 1982). The sneakers gain sexual access to the female eggs by avoiding detection due to their small size, while the mimics gain access by resembling females and thus avoiding aggression from the parental males. As the parasitizing strategists increase in frequency, however, their success decreases—their existence depends upon the parentals who become rarer as the parasites become more common, rendering the

parasite strategies more difficult to pursue. Thus, heritable alternative strategies within sex are maintained by the process of frequency-dependent selection. Theoretically, these heritable individual differences can persist in the population indefinitely through frequency-dependent selection, unlike the process of directional selection that tends to drive out heritable variation.

Sociosexuality. Gangestad and Simpson (1990) argue that individual differences in women's mating strategies have been caused (and are presumably maintained) by frequency-dependent selection. They start with the observation that competition tends to be most intense among individuals pursuing the same mating strategy (Maynard Smith, 1982). This lays the groundwork for the evolution of alternative strategies.

According to Gangestad and Simpson, women's mating strategies should center on two key qualities of potential mates—the *parental investment* a man could provide and his *genetic fitness*. A man who is able and willing to invest in her and her children can be an extraordinarily valuable reproductive asset. Similarly, independent of a man's ability to invest, women could benefit by selecting men who are themselves in good condition and are highly attractive to other women. Such men may carry genes for good health, physical attractiveness, or sexiness that are then passed on to the woman's own sons (or daughters—see Baker & Bellis, 1995; Trivers, 1985).

There may be a trade-off, however, between selecting a man for his parenting abilities and selecting him for his genetic fitness. Men who are highly attractive to women, for example, may be reluctant to commit to any one woman. Thus, a woman seeking a man for his genetic fitness may have to settle for a short-term sexual relationship without parental investment.

These different selection foci, according to Gangestad and Simpson (1990), produce two alternative female mating strategies. Women seeking a high-investing mate are predicted to adopt a "restricted" sexual strategy marked by delayed intercourse and a prolonged courtship. This would enable a woman to assess the man's level of commitment to her, detect the existence of prior commitments to other women or children, and simultaneously signal to the man her sexual fidelity and hence assure him of his paternity in future offspring.

Women "seeking" a man for the quality of his genes (no consciousness of goal state is implied by this formulation), on the other hand, have less

reason to delay intercourse. A man's level of commitment to her is less relevant, prolonged assessment of his prior commitments is less necessary, and so there is less need for delaying intercourse. Indeed, if the man is pursuing a short-term sexual strategy, any delay on her part may deter him from seeking sexual intercourse with her, thus defeating the *raison d'être* of the mating strategy.

According to this theory, the two mating strategies of women—restricted and unrestricted—evolved and are maintained by frequency-dependent selection. As the number of *unrestricted* females in the population increases, the number of “sexy sons” also increases. As their numbers increase, the competition between these sons increases, and hence the success of the unrestricted strategy decreases. On the other hand, as the number of *restricted* females in the population increases, the competition for men who are able and willing to invest exclusively in them and their children increases, and the fitness of that strategy commensurably declines.

There are many complicating factors with this theory, and the authors recognize that it must be described and tested more formally. Furthermore, the theory requires evidence that (a) the key elements of each strategy must covary in an organized coherent fashion; (b) the covarying suite of elements must fulfill stringent criteria for adaptation, such as efficiency, economy, and precision for solving the respective adaptive problems; and (c) the adaptive payoff of each strategy decreases as it becomes more common in the population. Pending these further tests, it remains a viable theory of individual differences produced and maintained by frequency-dependent selection.

Mealey's theory of psychopathy. Mealey (1995) proposes a theory of primary psychopathy based on frequency-dependent selection. Psychopathy (sometimes called sociopathy or antisocial personality disorder) represents a cluster of traits marked by irresponsible and unreliable behavior, egocentrism, impulsivity, an inability to form lasting relationships, superficial social charm, and a deficit of social emotions such as love, shame, guilt, and empathy (American Psychiatric Association, 1994; Cleckley, 1982). Psychopaths pursue a deceptive or “cheating” strategy in their social interactions. Psychopathy is more common among men than women, forming roughly 3–4% of the former and less than 1% of the latter (American Psychiatric Association, 1994).

Psychopaths pursue a social strategy characterized by exploiting the reciprocity mechanisms of others. After feigning cooperation, psychopaths typically defect. This cheating strategy might be pursued by men who are unlikely to outcompete other men in a more traditional or mainstream status hierarchy (Mealey, 1995).

According to the theory, a psychopathic strategy can be maintained by frequency-dependent selection. As the number of cheaters increases, and hence the average cost to the cooperative hosts increases, mechanisms would presumably evolve to detect cheating and to inflict costs on those pursuing a cheating strategy. As the prevalence of psychopaths increases, therefore, the average payoff of the psychopathic strategy decreases. As long as the frequency of psychopaths is not too large, it can be maintained amidst a population composed primarily of cooperators (Mealey, 1995).

There is some evidence, albeit indirect, that is at least consistent with Mealey's theory of psychopathy. First, behavioral genetics studies suggest that psychopathy may be moderately heritable, at least as indicated by the MMPI Psychopathic Deviate scale (Willerman, Loehlin, & Horn, 1992). Second, some psychopaths appear to pursue an exploitative short-term sexual strategy, which could be the primary route through which genes for psychopathy increase or are maintained (Rowe, 1995). Psychopathic men tend to be more sexually precocious, have sex with a larger number of women, have more illegitimate children, and are more likely to separate from their wives than nonpsychopathic men (Rowe, 1995). This short-term, opportunistic, exploitative sexual strategy would be expected to rise in populations marked by high mobility, where the reputational costs associated with such a strategy would be least likely to be incurred (Wilson, 1995).

There are several challenges to this theory, such as whether it represents a type or a continuum (Baldwin, 1995; Eysenck, 1995), whether its frequency is sufficiently large to be maintained by frequency-dependent selection, and whether it represents a recently evolved cluster in modern populations or an ancient evolved strategy (Wilson, 1995; but see Mealey's [1995] response to these challenges).

Despite these complications, Mealey's theory of psychopathy and Gangestad and Simpson's theory of sociosexuality nicely illustrate the possibility that heritable alternative strategies can be maintained by frequency-dependent selection. Frequency-dependent selection offers a potential explanation for integrating the cumulative results from behavioral genetic studies (e.g., Willerman, Loehlin, & Horn, 1992) and the findings

on the sexual strategies apparently pursued by psychopaths (Rowe, 1995) with an evolutionary analysis of adaptive individual differences.

Two final comments on frequency-dependent strategies. First, frequency-dependent strategies need not occur through heritable differences. They can occur through local situation-dependent shifts, whereby individuals adjust their strategy according to the frequency of those pursuing various strategies. Second, the logic of frequency-dependent selection does not require typological thinking or discrete strategies. It can also produce continuous heritable variation—a possibility to which we now turn.

Continuous condition-dependent heritable variation. The previous descriptions of environmentally triggered alternative strategies and heritably-based alternative strategies represent relatively pure cases, but a combination is also possible and may be more likely. Individuals whose strategies are condition-dependent, for example, may also show heritable variation in the thresholds or “switch points” for changing from one strategy to another (Dominey, 1984). Different individuals may attend to different cues in switching from one strategy to another, or might switch at different points along a single cue gradient. Thus, there can be continuous heritable variation that is both adaptively patterned and condition-dependent. Just as two alternative strategies can be maintained by frequency-dependent selection, this heritable variation can also be maintained by frequency-dependent selection. Thus far, no researchers studying human populations have proposed models of this type, but it may be a promising route for accounting for the existing evidence that shows both heritability and context-dependence of individual differences in mating strategies.

Nonadaptive Sources on Individual Differences

Not all individual differences are adaptively patterned, and so it is useful to consider the sources of nonadaptive variation (see Williams, 1992).

Neutral genetic variation. Mutations are introduced into the gene pool continuously. Some are deleterious and get weeded out by the process of selection. Others facilitate the solution to an adaptive problem, and so increase in frequency over time. And some are simply neutral with respect to selection. These neutral heritable variants can be maintained in the

population indefinitely unless selection pressures change to favor or eliminate them. Neutral genetic variation is typically random with respect to the basic functioning of complex evolved mechanisms—like the coloring of the wires on the engine of a car, it does not enhance or detract from the normal operation of the mechanisms. It fails to show the hallmarks of adaptation—complexity, design, efficiency, reliability, precision, and coordination with a particular adaptive problem. Phenotypical individual differences based on these neutral heritable variants are nonadaptive (Williams, 1992).

Incidental by-products. The products of the evolutionary process reduce to three—adaptations, by-products of adaptation, and noise (Tooby & Cosmides, 1990). Individual differences, even those that appear coherent, need not represent adaptations. Light bulbs, for example, produce heat as an incidental effect of their design for light production, and light bulbs of different wattage produce predictably different amounts of heat. Similarly, adaptive individual differences can produce by-products or incidental effects that do not constitute adaptive differences.

As a hypothetical example, those who pursue short-term mating strategies may develop stronger leg muscles, not as part of the evolved strategy, but as an incidental effect of having to walk further or dance longer in their pursuit of multiple mates. Individual differences in leg circumference, in this example, would be nonadaptive by-products of sexual strategy and would not be part of the evolved design of the strategy.

A critical part of the search for adaptive individual differences entails distinguishing between differences that are “designed” products of evolved psychological mechanisms and those that are incidental by-products of those mechanisms.

Maladaptive Sources of Individual Differences

Genetic defects. Genetic defects can result from mutation, locally introduced maladaptive genes through migration, or sexual recombination that can produce maladaptive genotypes from two adaptive parent genotypes (Williams, 1992). Homozygote disadvantage, for example, can result from two parents, both of whom are adaptively heterozygous. In these cases, the resulting individual homozygotic variant is maladaptive.

Environmental trauma (epigenetic load). Individual differences can result from traumas inflicted during development, such as poor nutrition, a high parasite load, trace-nutrient scarcity, culturally inherited low social status, or abuse at the hands of a competitor or exploiter (Williams, 1992). These environmental events can perturb the normal operation of evolved psychological mechanisms. As an example, there is some evidence that sustaining severe blows to the head potentiates the sexual jealousy mechanism in men. Boxers with head injury, for example, exhibit a higher incidence of pathological jealousy and delusions of infidelity than boxers who have not sustained head injury (Johnson, 1969). The resulting differences in jealousy, in this example, are presumably not adaptively patterned, but rather are caused by environmental trauma.

An important task in the analysis of individual differences is determining which are adaptively patterned and which are not. Chisholm (1996) argues that individual differences in adult attachment represent early environmental calibration of a menu of adaptive sexual strategies, whereas Zeifman and Hazan (1997) and Miller and Fishkin (1997) argue that deviations from secure attachments represent failures, perturbations, or maladaptations. In each instance, the burden of proof rests with the theorists to propose a specific set of falsifiable predictions based on their models so that the issue can be adjudicated empirically.

Testing Hypotheses About Sources of Individual Differences

Specific evolutionary hypotheses about adaptive, nonadaptive, and maladaptive individual differences must be formulated in a manner that is sufficiently precise to permit empirical testing and potential falsification. Hypotheses can be evaluated individually or in competition with each other by generating specific empirical predictions based on their proposed design features. Since most hypotheses about adaptive individual differences rest on a foundation of evolved psychological mechanisms, either explicitly or implicitly, the design features of those mechanisms must be articulated prior to empirical scrutiny. The theory of early experiential calibration proposed by Belsky, Steinberg, and Draper (1991), for example, implies the existence of an evolved psychological mechanism that takes as input the presence or absence of the father, makes a decision about the future expected mating environment, and produces as output a sexual strategy involving a correlated suite of

features such as the timing of sexual maturation, the onset of sexual intercourse, and a particular set of mate preferences.

Each of these design features—the specific decision rules, the components of output based on the decision rules, and the covariation among the components of output—can be used to generate testable predictions. If women who experience father absence early in life do not reliably pursue a short-term mating strategy later in life, then the Belsky et al. (1991) theory is called into question. If women who reach sexual maturation early do not tend to commence sexual activity early, then the theory is called into question, since these design features are hypothesized to covary positively. As more design features of the hypothesized evolved psychological mechanisms are articulated, more avenues are available for empirical testing and potential falsification. As with all scientific hypotheses, evaluation rests with the cumulative weight of the empirical evidence.

Behavioral genetic methods: Differentiating between heritable and non-heritable adaptive individual differences. Behavioral genetic methods provide a powerful set of tools for evaluating hypotheses of adaptive individual differences, especially when there are two competing theories of the same individual differences, one that invokes heritability and one that does not. Gangestad and Simpson's (1990) theory of sociosexuality, for example, proposes that the pursuit of short-term versus long-term sexual strategies is not predicated on early environmental experiences with the father, but rather is caused by heritable variations maintained by frequency-dependent selection. Pitting this theory against the Belsky et al. (1991) theory of early experiential calibration provides several straightforward means of empirical testing. If individual differences in sociosexuality are highly or even moderately heritable, for example, this constitutes evidence for sociosexuality theory and against the theory of early experiential calibration. In this context, behavioral genetic methodologies offer a set of tools for empirically testing these competing hypotheses.

Longitudinal methodologies: Testing hypotheses about early experience, ontogenetic stability, and context-dependent individual differences. Longitudinal studies provide another set of empirical tools for testing hypotheses about adaptive individual differences. The Belsky et al. (1991) theory implies that individual differences in sexual strategies

are stable over time. Mate value theory, in contrast, implies that ontogenetic increases or decreases in mate value will trigger shifts in sexual strategy (e.g., Holmberg, 1950; Symons, 1979). If a man who is relatively low in mate value, for example, experiences a sudden rise in status and hence mate value, then his sexual strategy may shift more toward multiple mates (Betzig, 1986; Buss, 1994; Gangestad, 1993; Holmberg, 1950). If longitudinal studies discover that these predicted shifts in mating strategy occur, then mate value theory is supported and the Belsky et al. theory is called into question. If individual differences in mating strategy remain stable over time, *despite* ontogenetic shifts in mate value, then mate value theory is called into question and the Belsky et al. theory receives circumstantial empirical support. Thus, longitudinal studies can provide critical empirical data to adjudicate between theories of adaptive individual differences that invoke stability and those that propose change.

Longitudinal studies are also useful for testing any hypothesis that invokes an effect of an early experience on a later strategy. Attachment theories of pair-bonds, for example, typically propose that secure attachment in infancy is necessary for secure, long-term mating strategies in adulthood (e.g., Chisholm, 1996; Miller & Fishkin, 1997; Zeifman & Hazan, 1997). Although retrospective assessments of early attachment have been correlated with current adult attachment styles, no longitudinal study has been conducted to evaluate this central premise of attachment theory. Longitudinal studies provide the most powerful means for evaluating this straightforward empirical prediction.

Experimental methods. Experimental methods offer yet another set of tools for testing hypotheses about adaptive individual differences. According to Sexual Strategies Theory, women pursuing a short-term mating strategy are predicted to be responsive to cues displayed by men that signal *immediate* resources, such as an extravagant lifestyle (Buss & Schmitt, 1993). Women pursuing a long-term mating strategy, in contrast, are predicted to be more responsive to cues that signal *future* resource potential. Stimuli that embody these differing cues—such as photographs depicting a man with a Rolex watch and expensive sports car (cues to extravagant lifestyle) versus the same man described as a promising medical student but wearing a cheap Timex watch and driving an old used car (cues signaling current lack of resources but excellent future resource potential)—could be presented to women previously assessed as pursuing either a short-term or long-term mating strategy. The dependent

measures of attraction, such as pupil dilation, duration of eye gaze, or even subjective assessments of attraction, could then be used to test the hypothesis about individual differences among women.

Physiological procedures have been used experimentally to test evolutionary hypotheses about sex differences (Buss, Larsen, Westen, & Semmelroth, 1992), but they can also be used to test hypotheses about individual differences. Men pursuing a short-term matings strategy, compared with men pursuing a long-term mating strategy, for example, should show greater physiological distress (as indexed by electrodermal activity and brow corrugator contraction) to experimentally induced imagery involving imagining having sex with one *and only one* sex partner for the rest of their lives. Conversely, imagery involving multiple sex partners (e.g., group sex) would be predicted to evoke greater physiological pleasure in men pursuing short-term as contrasted with long-term mating strategies, as indexed by measures of zygomatic contraction (smiling) or penile tumescence. In sum, evolutionary hypotheses about adaptive individual differences are amenable to testing with experimental procedures.

Distinguishing among adaptive, maladaptive, and nonadaptive individual differences. The hypothesis that an individual difference represents an *adaptive* individual difference usually implies the evolution of a complex underlying psychological mechanism containing design features coordinating coherently both with other design features and with the components of the adaptive problems the mechanism was designed to solve. The hypothesis that something is *maladaptive*, in contrast, implies a perturbation or malfunctioning of the evolved mechanism, analogous to the malfunctioning of a car engine. If the component parts fail to do what they were “designed” to do (e.g., spark plug fails to fire), or if they fail to coordinate with the other component parts (e.g., the timing of the firing is wrong and hence fails to mesh with the input of combustible fuel), or if they are activated in contexts in which they were not designed to be activated (e.g., backfires), then these are all signs of maladaptation (the term *malfunction* might be more appropriate). Maladaptation is defined by the *failure* of a mechanism to function in the manner and in the contexts in which it was designed to function, and does *not* correspond with human intuitions about “good” or “appropriate” or “adjusted” or “causing well-being.”

Furthermore, specifying the adaptive function of an evolved mechanism does *not* imply that the mechanism is currently adaptive or currently leads to reproductive success. Our taste preference for fat, for example, was presumably evolved in a fat-scarce environment, and its proper function is to facilitate the consumption of energy-rich high-calorie substances. In the modern environment of fat abundance, with fast-food restaurants multiplying on every street corner, we currently consume too much fat, which leads to clogged arteries and early death (Symons, 1987). In this example, our evolved taste preferences are still functioning properly—they are doing what they were “designed” to do. But because our modern environment is so radically different from the environment in which the mechanism evolved, this particular mechanism may no longer be adaptive. Thus, it is critical to distinguish between a mechanism that is functioning as it was designed to function but is no longer adaptive (i.e., no longer leads to reproductive success) and a mechanism that is malfunctioning (i.e., not doing what it was designed to do). There are strict standards for evaluating each, and human intuitions are relatively poor guides to these forms of scientific evaluation.

To make matters more complex, both adaptive and maladaptive individual differences must be distinguished from those that are *nonadaptive*, such as those based on neutral variation and those that are merely incidental by-products of adaptive variation. Neutral variations, analogous to differences in the colors of the wires on a car engine, should not affect the functioning of other mechanisms (analogous to the spark plug, carburetor, and other functional mechanisms of the car engine). Thus, the discovery that an individual difference does affect, or is causally linked to, mechanisms known to be functional tends to falsify the hypothesis of neutral variation.

As an example, consider individual differences in attachment style. If these differences are unrelated to sexual strategies, then the hypothesis that they represent neutral variation would be supported, since all adult attachment theories reviewed earlier suggest that they should be so linked. If deviations from secure attachment are linked with apparently dysfunctional sexual practices (e.g., pederasty, bestiality), as argued by Zeifman and Hazan (1997), then the hypothesis that they represent maladaptive individual differences is supported. And if individual differences in attachment styles are predictably linked with alternative sexual strategies, as suggested by Chisholm (1996), then the hypothesis of adaptive individual differences is supported.

In sum, by treating the various potential sources of individual differences as alternative hypotheses, empirical tests can be constructed for pitting predictions from each against one another, with the result being a confirmation of one and a falsification of the other. As the field progresses through multiple attempts at empirical confirmation and falsification, cumulative advances can be made in understanding the origins and nature of individual differences.

Coda: Traversing the Social Landscape of Individual Differences

Other individuals compose one of the primary environments within which humans function. Other individuals are crucial for solving adaptive problems. The presence of large individual differences, whether adaptively patterned or not, defines a major part of the human adaptive landscape. Attending to those individual differences can facilitate solutions to adaptive problems. Ignoring those individual differences can be disastrous. Failure to assess differences in whether others are pursuing cooperative or defecting social strategies, for example, can result in resources pilfered, reputations damaged, and pregnancies unwanted.

Over evolutionary time, those individuals who attended to and acted on individual differences in others that were adaptively consequential would have survived and reproduced more successfully than those who were oblivious to adaptively consequential differences in others. It has been proposed that humans have evolved difference-detecting assessment mechanisms that facilitated successful adaptive solutions (Buss, 1989b, 1996).

These mechanisms would have been critical in assessing individual differences for the goals of mate selection, coalition formation, and dyadic alliance building. The formation of these different relationships and the attendant adaptive problems entailed by them may require assessment specificity. That is, different individual differences in the social landscape may be relevant to some problems and irrelevant to others. Individual differences in sexual fidelity, for example, are more critical to assessing the viability of a long-term mate than a coalition partner (Shackelford & Buss, 1996). Despite some degree of domain specificity, some dimensions of individual differences, such as those captured by the five-factor model of personality, may be important because they are relevant to a host of different adaptive problems, and

hence they transcend the particulars of specific relationships (DeKay, Buss, & Stone, in prep.; see also MacDonald, 1995).

Because individual differences are so critical to solving adaptive problems, individuals often attempt to manipulate others' perceptions and reputations of their own and competitors' standings on relevant dimensions of differences. In mate competition, for example, men tend to impugn the surgency, agreeableness, and emotional stability of their rivals (Buss & Dedden, 1990). Thus, derogation of competitors becomes a verbal form of trait usage as manipulation, exploiting the difference-detecting mechanisms of others in the service of mate competition. Simultaneously, men will exaggerate their own positive traits in self-presentation to a woman, striving to appear to fulfill characteristics that she desires in a mate (Buss, 1988b).

Whatever the origins of individual differences—whether they are adaptively patterned or not adaptively patterned—they represent important vectors in the human adaptive landscape. When the individual differences of others in one's social environment are adaptively patterned, however, it may be especially important to detect and act on them because they are more likely to represent coherent and hence predictable suites of covarying qualities rather than randomly varying or single-dimension attributes.

Ultimately, comprehensive theories of personality and individual differences will require accounts of both the adaptive and nonadaptive differences, as well as the difference-detecting mechanisms humans have evolved to grapple with the varying terrain of the human adaptive landscape.

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