

16 Evolutionary theories of personality

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Integration with evolutionary theory could enhance personality theory by generating original predictions about the mechanisms governing personality. Novel hypotheses about how personality works can be derived from theories about the ultimate function of personality traits. Personality psychology currently describes and explains how personality is structured and how the mechanisms that produce such differences in behavioural patterns work. Personality theorists observe how personality differences develop and explain the proximate ('how it works') causes of these individual differences, but generally do not address ultimate ('why it works') causes. Ultimate explanations address why human personalities are structured in the precise manner that they are, why specific environmental inputs affect individuals in the way that they do, why the specific epigenetic rules that dictate how an individual responds to different environmental input exist and why other rules do not, as well as why personality traits are responsive to the environment at all and what adaptive function personality characteristics may serve. By adopting a framework for answering these questions about evolved function, personality theory would become enriched with novel hypotheses.

Evolutionary psychology views all psychological phenomena through the lens of the theory of evolution, in the hope that by asking why specific psychological mechanisms originally evolved, previously unidentified psychological mechanisms and new aspects of known psychological mechanisms will be illuminated. Evolution by natural and sexual selection is the only coherent framework that can explain why complex, adaptive psychological mechanisms exist and what adaptive problems they are designed to solve (Tooby and Cosmides, 1992). The standard social science model (SSSM) offers no explicit meta-theory to direct the investigation of personality. This leaves personality researchers to follow intuition or trial and error to direct their discovery of new psychological phenomena (Tooby and Cosmides 1992). This may impede significant progress in understanding the mechanisms underlying personality differences and the development of those characteristics.

Although evolutionary psychologists agree that evolution is relevant to all psychological mechanisms, there has been very little research done on personality from an evolutionary perspective. Evolutionary psychologists have generally been interested solely in what Tooby and Cosmides (1992) have termed the *psychic unity of mankind*. Therefore, they have been primarily concerned with human nature rather than individual differences. Consequently, much of evolutionary personality

psychology research has focused on universally-shared psychological mechanisms that result in phenotypic plasticity due to varying environmental input without regard to genetic variability or heritable traits.

However, the vast behavioural genetics literature on personality traits indicates strong genetic components for differences in all of the Big Five personality traits (Loehlin, McCrae, Costa and John 1998). The genetic variability of such traits is dismissed or explained by some evolutionary psychologists as selectively neutral or as genetic 'noise' (Tooby and Cosmides 1990). But the argument that personality differences are selectively neutral is unable to account for the fact that our closest living relative, the chimpanzee, exhibits similar versions of the Big Five personality traits (plus Dominance) (King and Figueredo 1997). Evolutionary psychology's focus on the shared genetic endowment of the human species has thus created what is, in our view, an artificial barrier between evolutionary psychology and individual differences psychology (including behavioural genetics), especially as it applies to personality. In our view, ultimate causation ('why') questions can be applied as well to genetically variable traits, such as personality traits, as they can to more species-typical human traits.

Strong ties with evolutionary theories of ultimate function can lead to novel predictions that could facilitate the discovery of new proximate mechanisms governing personality. Theories of evolutionary adaptive significance provide a framework that can inform personality theorists about (a) whether there are adaptive functions for the genetic differences that influence variation in personality characteristics and what those functions are; (b) potential new aspects of mechanisms governing personality structure; (c) what aspects of an individual's developmental environment should be expected to affect that individual; (d) how and to what degree individuals should be affected by different environments; and (e) why personality traits are responsive to environmental modulation.

Evolutionary theory provides an additional way in which to supplement and enrich current personality theory. Data on non-human primate (and other animal) personality structures and the ecological and social conditions associated with the evolutionary development of those personality traits could provide reliable predictions about new aspects of human personality. The current data on animal personalities and the selective pressures responsible for producing those traits is far too sparse to properly contribute to human research. But this information could be important to facilitate the discovery of unforeseen aspects and mechanisms of human personality and this line of inquiry should be pursued vigorously.

A more detailed and specific explanation addressing ultimate questions about evolved function can and is already beginning to inform personality research. We review what we currently know about personality as viewed in the light of evolutionary theory and provide a model for the future study of personality from an evolutionary point of view.

Tooby and Cosmides (1990) have claimed that traits that are heritable and variable, such as the Big Five personality traits that are heritable by a margin of .3 to .5 (MacDonald 1995), cannot be the result of adaptation. Nevertheless, most

evolutionary personality psychologists have generally concluded that individual differences in personality traits are adaptive in nature (see Figueredo, Sefcek, Vasquez *et al.* 2005 for a review). Those in the majority include David Buss (e.g. 1991, 1997; Buss and Greiling 1999) whose personality theory suggests that individual differences lead to differences in the effectiveness with which people can adopt different strategies in our complex social groups. Furthermore, Buss has suggested that people are especially aware of personality variation among group members because it is something that must be noticed and contended with in order to be successful in our daily interactions. MacDonald (e.g., 1995, 1998) has taken a similar approach to explaining the adaptive nature of personality differences and expanded it a step further. He proposed that, in addition to needing to manage the personality differences of others and the ability we have to adopt different strategies, personality variation is important because there are a wide variety of continuously graded niches within our social, ecological and physical environments. Personality differences allow different individuals to be suited to particular niches that others would not be suited for. This is adaptive because it leads to decreased competition, due to greater specialization, and renders the various personality characteristics optimal under differing local conditions.

Wilson (1994) and Figueredo (1995) have suggested that the diversification of individual traits to fit different social niches might be ultimately due to frequency-dependent selection. In this view, social competition drives individuals into different social niches and filling these diverse niches offers partial release from competitive pressure from conspecifics. In support of this view, Figueredo (see also Figueredo, Sefcek, Vasquez *et al.* 2005; Figueredo and King 2001) observed that the variation in personality reported in the non-human animal literature appears to be almost exclusively a characteristic of social species; applying concepts from behavioural ecology suggests that intraspecific 'niche-splitting' leads to intraspecific 'character displacement'. Niche-splitting is the fragmentation of the ecological space into more specialized niches, and character displacement is the differentiation of individual traits to adapt to these different niches. According to this model, the cost of deviating from the species-typical optimum is compensated by the benefit of competitive release. The species-typical optimum is the evolved norm of response in any given situation, and competitive release is the relief from intraspecific competition achieved by the displacement of individual behaviour from that modal norm of response. The result is an 'ideal free distribution' of alternative behavioural phenotypes where the balance of costs and benefits are equalized among different individuals. This centrifugal dispersion of individuals will create bell-shaped curves around the modal norm of response along different dimensions of personality (Figueredo, Sefcek, Vasquez *et al.* 2005).

There are essentially three solutions to the problem of adaptation to environments that are variable or heterogeneous in either time or space (including 'ecological space'): (1) developmental plasticity, (2) genetic diversity, and (3) spatial migration. According to Brunswikian Evolutionary Developmental (BED) theory, ecologies that are variable over evolutionary time select for organisms that

are phenotypically plastic enough to adapt by means of learning over developmental time (Figueredo, Hammond and McKiernan 2006). However, such behavioural development depends critically on the existence of reliable and valid cues that signal which alternative phenotype is optimal under each set of localized conditions in time, space and ecology; in the absence of such reliable and valid cues, the solution to either environmental temporal variability or spatial heterogeneity is the production of genetically diverse individuals that are dispersed along the expected distribution of locally optimal trait values (West-Eberhard 2003). However, as BED theory elucidates, ecological cues are typically neither completely reliable and valid nor unreliable and invalid; they are instead characterized by some ecological validity coefficient ranging between zero and one. Under those conditions, a hybrid theory would predict that organisms would show a combination of developmental plasticity and genetic diversity to collectively fill the available ecological niche space. Interestingly enough, the partial heritability and partial environmentality of personality variation in humans conforms precisely to the predictions of this synthetic model.

One seemingly paradoxical suggestion derivable from evolutionary psychology is that, while personality differences are likely adaptive, they also constrain individuals' behavioural flexibility. MacDonald (1998) suggested that different personality traits are best suited for the occupation of different social and ecological niches. Viewed differently, this means that individuals may be constrained in their behavioural repertoires based on the particular suite of personality characteristics that they possess, due to heredity and environmental factors. This may, at first, seem extremely maladaptive because it does not allow individuals fully to exploit the range of possibilities inherent in the different situations that they might encounter. In fact, according to some psychologists who favour the situation side of the person-situation debate (e.g., Mischel, Shoda and Smith 2004), the very definition of a personality disorder is unchanging personality in the face of the changing environmental contexts that a person encounters. In contrast, we propose that the biological preparedness for and the developmental plasticity of certain behaviours can and do vary independently of each other (Figueredo, Hammond and McKiernan 2006). In our view, personality traits represent dispositions to respond to environmental contingencies in certain ways, and to seek out environments in which prepared behaviours are suitable, but they do not represent the unalterable necessity to behave in the predisposed manner.

Interestingly, when we consider the actual behaviour of humans, the paradox no longer seems to hold. For example, in keeping with the idea that personality does constrain behaviour, in a naturalistic observation study by Mehl and Pennebaker (2003), which required participants to wear recording devices that recorded examples of conversation and any other aspect of quotidian life that a person might engage in at intervals of approximately twelve minutes, a remarkable amount of temporal and behavioural stability was encountered within subjects. Furthermore, as hypothesized by both MacDonald and Figueredo, they found that individuals possessing different personality types actually did gravitate toward

different niches that seemed to suit their personalities best. This indicates that, while human behaviour may be constrained by individual personality traits, the cost of these constraints can be overcome by the benefits entailed in the selection of suitable social niches for the personality traits that each individual possesses. This is also an example of how genetic diversity can work synergistically with migration within ecological niche space to solve the problem of environmental heterogeneity.

To put these evolutionary models of personality into perspective, one must consider the natural history of human evolution. The past 3.5 million years have been a rapidly varying timeframe when it comes to global climate (for a review see Lisiecki and Raymo 2005; Zachos, Pagani, Sloan *et al.* 2001). These global fluctuations translated into ecological variability, be it in specific African basins (Wynn 2004) or the waxing and waning of the northern hemisphere's ice sheets. When it comes to human evolution the story starts in Africa and ends with the current worldwide distribution. A complicating factor when considering this timeframe is the onset of the Holocene. During the Holocene, farming and herding were developed, and with it came larger population densities. These larger populations blur the distinction between when, where and why adaptations evolved by increasing the complexity of the problem. These complicating factors, along with others, present difficulties for even the most inclusive evolutionary models.

When considering the paleontological record, evidence suggests that it is likely that organisms which do not adapt to ecological variability by evolving a degree of adaptive plasticity tend to become extinct. Migration to ecologically supportive environments (a form of 'niche picking'), however, can also solve the adaptive problems associated with ecological variability. At the global level, rarely does a specific ecological niche disappear entirely, making it possible for a species to continue existing by merely moving to an appropriate habitat. Examples of the power of migration or niche picking as an adaptive response to the changing world comes from the animals adapted to the glacial environments of the northern hemisphere. Although the last glacial maximum is dated at approximately 15,000 years ago, many species that were adapted to glacial conditions survived well into the warmer climates of the Holocene, with the woolly mammoth surviving in parts of Siberia until approximately 4,000 years ago (Pastor and Moen 2004). Although there are examples of migration successfully working as a solution to variability, this particular example shows that this adaptive tactic does not always work. There are times when other adaptations are necessary if a species is to survive the change or disappearance of an ecosystem. If the change in environment is slow enough, a transition from one set of adapted phenotypes to another is possible. However, depending on the speed of the change, this form of adaptation may not be fast enough and may lead to extinction, as was the case with many large mammals during the late Pleistocene. As mentioned previously, another possible solution to variability is the evolution of versatile phenotypes capable of solving adaptive problems in a diverse array of ecologies. Although measuring behavioural adaptations over evolutionary time is difficult,

evidence coming from the study of morphology suggests that whole taxonomic families, including Hominids, evolved more versatile phenotypes in response to increases in variability during both the Pliocene and the Pleistocene (Potts 1998; Wynn 2004).

Geary (2005) has classified the selective pressures on ancestral humans into three basic types: (1) climactic, (2) ecological, and (3) social. After reviewing much of the available evidence, he concludes that the major selective pressures on both recent human ancestors and modern humans have been social in nature. While we agree that social selection provides the most immediate and constant set of adaptive problems needing to be solved by humans, we disagree about the relative lack of importance assigned to the climactic and the ecological forces. Instead, as proposed by Richerson and Boyd (2000) we take the view that changes in social structure were likely an adaptive solution to selective pressures originating with climactic and ecological variability. By solving these adaptive problems through social behaviour, novel adaptive problems arose linked directly to social selection. A more inclusive model would be that climate changes produce ecological changes and these, in turn, exacerbate social competition over resources. For example, migration of some groups out of habitats rendered uninhabitable by climate change into still-habitable habitats ('refugia') already inhabited by other groups set the occasion for conflict both between and within groups over limited resources. Thus, Geary is probably correct in proposing social selection as the most immediate and constant promoter of human evolution, but changes in climate and ecology ultimately heighten social competition.

What all this evolutionary history suggests is that, in accounting for the manifest variation in human personality traits, we should probably observe a strategic mix of adaptive plasticity, genetic diversity, niche picking/migration, and local adaptations to the recently stabilized Holocene climate. This combination of selective pressures accounts for the observed much-debated combination of partial heritability and partial environmentality in human personality traits.

We argue that personality variation is important in guiding the social and sexual relationships of individuals. Personality is an important factor when making friends or finding a romantic partner. What it means to say that someone has a 'great personality' remains unclear, but there is some consensus on what is a desirable personality in a romantic partner (Figueredo, Sefcek and Jones 2006). Variation in personality is likely to drive individuals into different kinds of relationships and to seek and obtain different kinds of friends and lovers. In social and ecological niches that demand particular approaches to relationships, it is likely that different personalities have been selected for and are more likely to enable an organism to survive and reproduce.

Many personality traits seem to predict relationship outcomes across time and across different relationships. Further, research suggests that individual differences in personality are better predictors of relationship outcomes than other factors such as compatibility, similarity and honesty (Eysenck and Wakefield 1981). For example, lower levels of self-esteem (Swann 1996), higher levels of

neuroticism (Donnellan, Larsen-Rife and Conger 2005, Eysenck and Wakefield 1981; White, Hendrick and Hendrick 2004;), higher levels of psychoticism (Diener and Seligman 2002; Eysenck and Wakefield 1981), and insecure attachment (see Simms 2002, for review) all predict 'poor' relationship outcomes. If part of the function of personality is to guide our social relationships, one may wonder how such variations in these traits would have been passed on if they were maladaptive.

One explanation deals with the relationship goals of the individual. In highly competitive or harsh environments, it is likely to be adaptive for an individual to be hypervigilant and aggressive. For example, neuroticism is related to increased levels of romantic jealousy in a relationship (Melamed 1991). While jealousy can drive a relationship apart, it can also be a very useful mechanism in keeping a partner from straying in a relationship (Buss 2000). Thus, in environments where hypervigilance or aggressiveness is adaptive, individuals who are neurotic may be more effective in protecting themselves from negative outcomes such as infidelity.

Some individual differences may also interact or co-evolve with other characteristics of individuals to aid in adaptation to a given environment. For example, individuals who are at a competitive disadvantage (e.g., lower intelligence, poor genetic quality) in friendships and reproduction may benefit from having higher levels of mating effort in harsh environments. Such impulsive and sensation-seeking individuals will try harder, and more often, to get romantic partners, and display attributes such as toughness to friends or partners in order to serve short-term interests (Rowe, Vazsonyi and Figueredo 1997). It would also lead the individual to focus on short-term opportunistic encounters, which would be more attainable for someone in a disadvantaged position, rather than long-term meaningful relationships. Further, Brown and Moore (2002) have demonstrated that individuals with higher levels of fluctuating asymmetry report higher levels of dispositional jealousy. Therefore, it seems that individuals who are less attractive have certain traits that lead them to be vigilant against the increased risk of infidelity in a partner.

Individuals also differ in their desire for multiple partners and for sexual contacts (Buss and Schmitt 1993; Figueredo, Sefcek, Vasquez *et al.* 2005; Simpson and Gangestad 1991; Rowe, Vazsonyi and Figueredo 1997). This, too, leads to a variety of social and romantic relationship outcomes. The demands of the environment and the costs posed by relationships can lead individuals to be careful in choosing which relationships to invest in and how much to invest in them. In harsh and unpredictable environments, where extrinsic mortality is high, it is important for individuals to produce many low-maintenance offspring rather than invest heavily in a smaller number of offspring (Figueredo, Sefcek, Vasquez *et al.* 2005). As a result, we would expect relationship satisfaction to interfere with such a strategy, since it is likely to impede moving from one sexual partner to another. Research has indeed confirmed that shared traits such as lower levels of mating effort and a generally 'slower' life history strategy significantly predict romantic partner and relationship satisfaction and commitment (Olderbak 2007).

Similarly, those who are altruistic and build long-term, reciprocal friendships may experience higher levels of fitness in environments where it is favourable to do so. However, in harsh and unpredictable environments that favour short-term social relationships, such traits and behaviours may pose severe costs to an individual. Thus, individuals who are less likely to trust others and more willing to exploit others may be best suited in environments where short-term encounters are the norm and immediate extraction of resources is necessary.

In conclusion, we propose that sociality is the major cause of personality variation in humans. Specifically, adaptation to different micro-niches within the overall social ecology of the species is what leads to the differentiation of personality traits among individuals. Climactic and ecological fluctuations during repeated Ice Ages may have historically provided much of the initial impetus by exacerbating social competition, but the larger population densities occasioned by the Neolithic Revolution in human subsistence economies (e.g., farming, herding, industrial and now information-based) have largely taken their place in recent human history. We suggest that this complex combination of selective pressures accounts for the strategic mix of heritability and environmentality observed in human personality development. These selective pressures serve as the ultimate causes of adaptive personality variation and provide some unique predictions regarding these proximate causes of personality. Further, these predictions are not limited to the adaptive aspects of personality. Predictions about by-products and trade-offs that result from pursuing one adaptive personality strategy over another are also derivable. Thus, personality variation retains its adaptive significance even to this day.

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