

Evolutionary Perspectives on Personality and Individual Differences

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Individual differences are essential to the process of evolution by natural selection. Natural selection is the only known process capable of creating and maintaining adaptations. The properties of inheritance, variation, and differential reproduction are required for evolution of adaptations (see Sela and Shackelford, 2015, for a review). Physiological and psychological traits must be genetically heritable and reliably passed from parent to offspring in order for natural selection to act upon them. Some individuals propagate their genes more successfully than do others, resulting in differential reproduction. Ultimately, the number of successful offspring (and the number of their successful offspring, etc.) determines gene frequency of particular traits in a population. Survival therefore determines fitness to the extent that it contributes to successful gene propagation. Fitness is a term that applies in the context of a specific environment, however, and therefore an individual that is 'fit' in one environment may not necessarily be 'fit' in another. Certain traits may be differentially

beneficial in different environments. Natural selection of physiological and psychological traits is dependent upon organisms' interaction with the environment. Relative consistency of environmental inputs is crucial for significant allele frequency shifts (i.e., evolution) and the construction of adaptations. Consistent environmental variables that pose survival and reproductive challenges over many generations are referred to as *selection pressures*. Selection pressures vary across geographic areas and ecological systems, and consist of both the animate and inanimate natural environments.

The idea that heritable variations of traits provide the raw material upon which selection can act has long been acknowledged in the biological life sciences. Natural selection is typically viewed as a homogenizing force that results in species-typical characteristics. Indeed, application of an evolutionary framework to the study of humans – via a relatively new metatheoretical paradigm called *evolutionary psychology* (Tooby and Cosmides,

1990) – has discovered many such human universals (Buss, 2015). Evolutionary psychology has been a generative scientific endeavor, leading to groundbreaking discoveries in domains such as survival (e.g., evolved navigation; Jackson and Cormack, 2007, 2008), parenting (e.g., adaptations in males to reduce investment when they perceive cues to paternity uncertainty or other mating opportunities; Anderson et al., 1999a,b; Marlowe, 1999), kinship (e.g., altruism preferentially channeled toward kin as a function of degree of genetic relatedness; Jeon and Buss, 2007; Michalski and Shackelford, 2005), cooperation (e.g., discovery of anti-free rider adaptations and cheater-detection; Price et al., 2002; Sugiyama et al., 2002), aggression (e.g., predictable circumstances in which men adopt risky social strategies; Buss and Shackelford, 1997), mating strategies (e.g., universal sex differences in mate preferences; Shackelford et al., 2005), and sexual conflict (e.g., predictable patterns of sexual deception; Haselton et al., 2005).

Evolutionary psychology has traditionally sought to explain species-typical evolved adaptations (Tooby and Cosmides, 1990), with theoretical and empirical advances within evolutionary psychology being achieved primarily at the levels of species-typical and sex-differentiated adaptations. Application of evolutionary theory to the study of human psychology and behavior, however, has given relatively lesser focus to evolutionary explanations of individual differences among humans (Buss, 2009). Historically, individual differences have been viewed as merely noise or error variance to be weeded out (Buss and Hawley, 2011). Only recently have researchers begun to systematically explore personality and individual differences as profound and integral to evolved psychological mechanisms. In this chapter, 1) we review some of the most compelling arguments and evidence for the creation and maintenance of individual differences via the process of evolution by natural selection, cementing the importance of an evolutionary framework to the study of

personality and individual differences; 2) we review the dominant evolutionary approaches used to understand personality and individual differences, including between-sex variation (via theories of sexual conflict and parental investment), developmental approaches (via Life History Theory), and the interplay of genes and environment (via behavioral genetics); and 3) we conclude with practical applications and future research directions for applying an evolutionary framework to investigate personality and individual differences.

NATURAL SELECTION CREATES AND MAINTAINS INDIVIDUAL DIFFERENCES

An interdisciplinary network of evidence supports the perspective that individual differences in a population are created and maintained by natural selection. Research examining individual differences, such as personality dimensions – captured by the five-factor model of personality (Costa and McCrae, 1992; Digman, 1990; Goldberg, 1990) and the six-factor HEXACO model of personality (Ashton and Lee, 2001) – document that individual differences are moderately heritable (e.g., Polderman et al., 2015), stable over time (Plomin et al., 2008) and across cultures (e.g., McCrae et al., 1998), continuous across species (e.g., Gosling, 2001), powerfully predictive of behavior (e.g., Fleeson and Gallagher, 2009), impact evolutionarily relevant aspects of fitness in a trade-off manner (e.g., Nettle, 2005, 2006), and reliably solve adaptive problems (e.g., Buss, 2011). These core features of individual differences suggest that evolution by natural selection is the underlying cause of many observed psychological and behavioral individual differences.

The greatest empirical support for the core features of individual differences comes from the study of personality dimensions – which is arguably the most well-researched aspect

of human individual differences. Several models of personality have emerged in the literature. The five-factor model of personality – or the ‘Big Five’ – assesses the extent to which an individual exhibits characteristics consistent with the five dimensions of Neuroticism (characterized by fearfulness, anxiety, and empathy), Extraversion (characterized by sociability and attention seeking), Agreeableness (characterized by forgiveness, flexibility, altruism, and patience), Conscientiousness (characterized by organization, hard work, and impulse inhibition), and Openness to Experience (characterized by creativity, novelty seeking, and curiosity) (Costa and McCrae, 1992; Digman, 1990; Goldberg, 1990). The six-dimensional model of personality – or the ‘HEXACO’ model – assesses the extent to which an individual exhibits characteristics consistent with the dimensions measured in the Big Five model, with the addition of a sixth personality dimension termed Honesty–Humility – which accounts for morally relevant, pro-social behavior, and represents some aspects of reciprocal altruism (Ashton and Lee, 2007). The malevolent personality traits known as the Dark Tetrad include narcissism (characterized by grandiosity, entitlement, dominance, and superiority), Machiavellianism (characterized by manipulateness and cynicism), psychopathy (characterized by callousness, impulsivity, and lack of empathy, intimacy, and conscience), and sadism (characterized by the enjoyment of hurting others) (see Buckels et al., 2013 or Furnham et al., 2013, for reviews). These models have incorporated evolutionary perspectives (e.g., de Vries et al., 2016; Jonason et al., 2010; Nettle, 2005) to provide empirical support that natural selection creates and maintains individual differences.

One core feature of individual differences is that they are heritable (Polderman et al., 2015). Behavioral genetics research documents heritability estimates of various personality dimensions ranging, on average, from .40 to .50 across various populations

and personality inventories (e.g., Bouchard, 1994; Loehlin, 1992; Tellegen et al., 1988). Research has also shown that individual differences are heritable in nonhuman mammals, such as chimpanzees (Weiss et al., 2000). Behavioral genetics research has converged on the finding that personality dimensions and other individual differences show moderate heritability, solidifying the role – and necessity (Penke, 2011) – of evolutionary genetics within individual differences research (Plomin et al., 2008).

Individual differences are relatively stable across cultures (e.g., Ashton and Lee, 2007; McCrae and Costa, 2008; Saucier, 2009), and have been documented in nonhumans. For example, the five-factor model of personality has been identified across several Western and non-Western cultures, showing that the factors are not specific to any particular language or culture (e.g., McCrae and Costa, 2008; McCrae et al., 1998). Individual differences, such as personality structures, observed in nonhumans reveal meaningful evolutionary continuities among humans and nonhumans (Gosling, 2001). For example, the Big Five personality factors generalize to chimpanzees, as documented in a study employing zoo workers’ ratings of chimpanzees on adjectival personality descriptors (King and Figueredo, 1997). The Big Five factors of personality have been documented in several other species, ranging from octopuses to dogs (see Gosling and John, 1999, for review). Comparative evidence suggests that personality dimensions are not exclusive to humans, and likely have an evolutionary origin predating the emergence of modern humans.

Individual differences powerfully, and consistently, predict manifest behavior. For example, a meta-analysis of 15 experience-sampling studies documented that Big Five personality traits strongly predict trait manifestations in behavior (e.g., trait-level standing on Extraversion predicting average levels of state-level extraverted behaviors of talkativeness, boldness, and assertiveness; Fleeson and Gallagher, 2009). Self-reported standing

on the Big Five predict average levels of manifested behavioral states with moderate to strong correlations between .42 and .56 (Fleeson and Gallagher, 2009). Individual differences of traits likely parallel individual differences of manifest behavior and, therefore, differential survival and reproduction over human evolutionary history as a consequence.

Indeed, individual differences differentially affect evolutionarily relevant outcomes related to survival and reproduction – an essential component for natural selection to operate. Individual differences have been shown to be associated with the domains of survival, mating success, status ascension, offspring production, and parenting (e.g., Buss and Greiling, 1999; Nettle, 2006; Ozer and Benet-Martinez, 2006), to name a few. For example, self-reported degree of Extraversion is positively correlated with one's number of lifetime sexual partners, and one's committed infidelity (Nettle, 2005) – behaviors indicative of short-term mating success. The fitness benefits of a short-term mating strategy, however, are also associated with some fitness costs, such as reduced parental investment (relative to time and resources invested in mating effort), and reduced survival prospects for offspring (Nettle, 2005).

The impact of individual differences for evolutionarily relevant outcomes is particularly evident in the social domain (Buss, 1991, 2011). An individual's personality traits and the personality traits of conspecifics are associated with the creation of, and solutions to, adaptive problems within the social environment (Buss, 2011). Personality and individual differences impact key aspects of an individual's social life, including friendships, rivalries, kinship, and mateships. When selecting a friend or mate, for example, species-typical adaptations, or constants (e.g., bipedalism, upright gait), simply do not inform friendship or mating decisions. Instead, humans are sensitive to the ways in which individuals *differ* in qualities, such as intelligence, attractiveness, or formidability. Individual differences of others with whom

we associate carry significant consequences for outcomes historically associated with reproductive success – such as deferring in competition, cheating in social exchange, free-riding in coalitions, or employing cost-inflicting strategies to get ahead. The ability to identify and predict conspecifics' behaviors would therefore have been advantageous over human evolutionary history. Adaptations dedicated to tracking, identifying, and acting upon individual differences of conspecifics are referred to as *difference-detecting adaptations* (see Buss, 2011).

The above examples illustrate a key concept within the evolutionary study of individual differences: *trade-offs*. Trade-offs refer to the fitness costs and benefits of an individual's standing on any given personality dimension (e.g., Buss and Greiling, 1999; Nettle, 2006). Because there are no universal optimal standings on various personality dimensions, no single personality profile is advantageous in every environment; therefore, individual differences are maintained in the population. For example, extraverted individuals have more sexual partners (fitness benefit), but also more serious bodily injuries (fitness cost) (Nettle, 2005). Further, if two levels of a trait have approximately equal fitness overall, and if changes in the trait augment some component of fitness, then those trait changes also alter other components of fitness (MacDonald, 1995; Nettle, 2006). Benefits produced by changes in a trait also produce associated costs. If this were not the case, no trade-off would occur, and directional selection would select for the higher value of the trait – the evolutionary process observed with many species-typical adaptations (e.g., Tooby and Cosmides, 1990). Differential outcomes and fundamental trade-offs are imperative to the selection, evolution, and maintenance of individual differences.

Various core features of individual differences – non-zero heritability, stability over time and across cultures, cross-species continuity, predictive utility for manifest behavior, associations with components of fitness,

and ability to solve adaptive problems – render tenable the perspective that evolution by natural selection has afforded the creation and maintenance of individual differences. Next, we discuss the ways in which individual differences are empirically studied and theoretically understood within an evolutionary framework.

EVOLUTIONARY APPROACHES TO PERSONALITY AND INDIVIDUAL DIFFERENCES

It is accepted that people vary in personality and behavior. What is less clear, however, is *why* people differ and what factors contribute to phenotypic variance among individuals. Several evolutionary approaches to understanding individual differences have emerged in the literature. Below, we provide an overview of three foundational evolutionary approaches for understanding personality and individual differences between men and women, over development, and from a behavioral genetic perspective. These approaches all provide complementary and profitable avenues of research to investigate human individual differences from an evolutionary psychological perspective.

Between-Sex Variation: Sexual Conflict and Parental Investment

Evolutionary scientists have historically and successfully investigated psychological and behavioral variation between the sexes, with a particular focus on variation in sexual strategies. The foundation for investigating between-sex differences of sexual strategies is Parental Investment Theory (Trivers, 1972). Parental Investment Theory provides a rich and generative framework for the understanding of between-sex variation of sexual strategies that is based on asymmetries of minimum obligatory parental investment for males and females of a given species (Trivers,

1972). In most sexually reproducing species, including humans, internal fertilization and gestation occur in females, rather than males. Males, therefore, may contribute relatively less than females to the production of offspring – a single ejaculate. Females must, at minimum, gestate the offspring until birth and, often, nurse the offspring for a (species-typical) period of time. These biological asymmetries of reproduction – minimum obligatory parental investment – for males and females have profound downstream consequences for sexual strategies, more broadly (Buss and Schmitt, 1993).

Mating strategies can be conceptualized along two dimensions: short-term mating and long-term mating (Jackson and Kirkpatrick, 2007). Individuals who are relatively short-term oriented are motivated to pursue casual, uncommitted sexual relationships with several partners. Individuals who are relatively long-term oriented are more motivated to pursue monogamous, committed relationships with one partner over a long period of time. Because of asymmetries of reproduction and minimum obligatory parental investment between men and women (Trivers, 1972), pursuit of a short-term mating strategy is, on average, more costly for women. Men, relative to women, can potentially benefit more by pursuing a short-term mating strategy. For example, if a man were to copulate with 20 different women over the course of a year, he has the reproductive potential to sire upwards of 20 offspring. If a woman, in contrast, were to copulate with 20 different men over the course of a year, she has the reproductive capacity to carry only a single pregnancy to term. It is this asymmetry in reproductive variance (Bateman, 1948) that affords men, relative to women, greater potential replicative benefits for pursuing a short-term mating strategy (on average). Men are therefore more short-term oriented, and women more long-term oriented, in their mating strategies – on average (Buss and Schmitt, 1993).

Parental Investment Theory explains sex differences of mating strategies, and has

received strong empirical support across various mammalian species, including humans. Trivers (1972) proposed that the more heavily investing sex (typically females) should be more discriminating in their choice of mates, whereas the less investing sex (typically males) should compete more intensely for sexual access to valuable, high-investing individuals of the opposite sex. The consequence of these principles derived from Parental Investment Theory is that reliable sex differences of mating preferences should emerge (e.g., Conroy-Beam et al., 2015). In their foundational theory for human sexual strategies, Buss and Schmitt (1993) outline how differential investment between men and women has shaped adaptations to solve adaptive problems of mating over human evolutionary history. Differential selection pressures on men and women – men and women have some different adaptive problems of mating to solve to optimize their replicative success – have consequently shaped mate preferences and domains of intrasexual competition.

One fundamental problem of mating that has shaped mate preference adaptations is the problem of identifying a suitable mate (Buss and Schmitt, 1993). Because men's replicative success is, ultimately, limited by the number of successful matings with fertile women, sexual selection has shaped men's mating adaptations to prefer mates who display signs of fertility. Men, for instance, tend to prefer mates who are relatively young, because youth signals fecundity and greater reproductive value (Conroy-Beam et al., 2015). Women, in contrast, have a different fundamental problem of mating to solve: because women are the more heavily investing sex, sexual selection has shaped women's mating preferences to prefer mates who display signs of resource holding and acquisition potential. As a result, women tend to prefer mates who have relatively high social status, as status confers greater immediate and potential future resources that could be invested into her offspring (Conroy-Beam et al., 2015).

Given that women are the more heavily investing sex, women are more selective in their mate choice, relative to men (Trivers, 1972). Women's selective mate choice has consequently resulted in men engaging in greater intrasexual competition for access to the limited availability of fertile women (Smuts and Smuts, 1993). Another downstream consequence of asymmetrical parental investment at the population level is that men, as a group, demonstrate greater phenotypic variation of a myriad of psychological traits, relative to women. Most notably, men have greater reproductive variance than do women: over their lifetime, almost all women will have the opportunity to produce offspring, whereas offspring production for men is not guaranteed. However, the potential number of offspring for men is considerably greater than the potential number of offspring for women (Bateman, 1948). In other words, the average number and range of offspring produced by women is relatively low and narrow, whereas, for men, the range of offspring produced is far more variable and, in extreme cases, can be quite large.

With regard to psychological traits, men, on average, tend to occupy the extreme ends of the population distribution for several traits such as intelligence (e.g., mathematical reasoning; Geary, 1996), pathological personality traits (e.g., psychopathy; Cale and Lilienfeld, 2002), and mental disorders (e.g., autism; Baron-Cohen, 2003). One explanation for men, as a group, showing greater phenotypic variation relative to women is because the selection pressures on men with regard to *specific* individual differences are weaker than for women (Arden and Plomin, 2006; Darwin, 1882; Wallace, 1975). Men have to compete intensely for women and, therefore, there is no single male phenotype that reliably confers optimal replicative benefits in the wide variety of ecologies humans have inhabited. Rather, there are numerous phenotypes (i.e., different strategies) that can optimize men's replicative success. In other words, men have a greater variety of 'mate

value niches' that they can potentially occupy to successfully attract a mate (Wallace, 1975). For women, in contrast, there has been a relatively stronger selection pressure over evolutionary history for displaying signs of fertility, in particular, because of the reliable advantages for offspring production and survival. Women therefore have, compared with men, fewer mate value niches to occupy that result in greater probability of high-quality mate acquisition given their reproductive value.

Another consequence of asymmetries of reproduction is paternity certainty, which produced between-sex variation with regard to jealousy and mate retention efforts in the context of romantic relationships. Because internal fertilization and gestation occur in women, ancestral men could not have been certain that they were the genetic sires of their partner's offspring. Ancestral women, in contrast, had maternity certainty. Paternity uncertainty places men at risk for cuckoldry – the unwitting investment of resources into genetically unrelated offspring. Cross-cultural, historical, and behavioral evidence indicate that, over evolutionary history, paternity uncertainty was likely a substantive adaptive problem faced by ancestral men (see Anderson, 2006; Buss, 2000; Daly et al., 1982; Euler and Weitzel, 1996; Goetz and Shackelford, 2006, 2009; Platek et al., 2005; Shackelford, 2003; Shackelford and Goetz, 2007; Thornhill and Gangestad, 2008; Voracek et al., 2008). Because paternity uncertainty was a recurrent adaptive problem over evolutionary history, it is likely that men have evolved psychological mechanisms designed to combat problems associated with paternity uncertainty (Pham and Shackelford, 2014).

Empirical work has demonstrated consistent sex differences with regard to emotional responses of jealousy (Buss et al., 1992). Men, in particular, are more jealous in response to their partner's sexual, rather than emotional, infidelity. Women, in contrast, are more upset about a partner's emotional, rather than sexual, infidelity. This is not to say that men and women are not at all upset by any

form of partner infidelity (they certainly are), but rather, research has documented consistent and robust sex differences with regard to which type of infidelity would be *more* upsetting. That men are more upset by sexual, and women are more upset by emotional, infidelity has been attributed, ultimately, to paternity uncertainty. Men, relative to males in many other species, tend to invest more than the minimum single ejaculate. Thus, female sexual infidelity signals to a man that his resource investment may not 'pay off' if there is a chance that he has been cuckolded. Offspring survival is influenced, in part, by a male partner's investment, and therefore a man's emotional infidelity signals to a woman that her partner may be provisioning time and resources to another woman and her offspring.

Men and women incur sex-specific costs from their partners' sexual or emotional infidelity – men risk cuckoldry from a partner's sexual infidelity (Buss and Shackelford, 1997), and women risk loss of partner-provisioned resources from a partner's emotional infidelity (Schutzwohl and Koch, 2004). Over evolutionary time, sex-specific costs of partner infidelity have produced sex-differentiated mate retention behaviors that appeal to the mate preferences of the opposite sex (Buss, 1988; Buss and Shackelford, 1997; Sela, 2016). Mate retention behaviors are designed to reduce the risk of a partner's infidelity. For men, specifically, mate retention functions to maintain a woman's exclusive sexual involvement and, thus, reduce cuckoldry risk (Buss, 1988; Buss and Shackelford, 1997). Because women prioritize status and resource acquisition potential in their long-term mates, men are more likely (relative to women) to employ mate retention tactics that signal their resources, status, and strength. Because men prioritize youth and fertility in their mates, women are more likely (relative to men) to employ mate retention tactics that increase their perceived reproductive value by focusing on appearance enhancement techniques (Buss, 1988; Buss and Shackelford, 1997; Buss et al., 2008).

In summary, evolutionary approaches to individual differences have most notably focused on between-sex variation, with particular emphasis on mating-relevant psychological traits and manifest behavior. Parental Investment Theory (Trivers, 1972) has been at the foundation of evolutionary psychological approaches to sex differences since its formulation. Because of fundamental asymmetries of reproduction and investment between men and women, we see consistent and, oftentimes, robust sex differences with regard to sexual strategies (Buss and Schmitt, 1993; Jackson and Kirkpatrick, 2007), mate preferences (Conroy-Beam et al., 2015), jealousy (Shackelford et al., 2004), and mate retention (Buss et al., 2008). Next, we turn to questions regarding how these sexual strategies develop, and explanations for the development of between- and within-sex variation.

Developmental Approaches: Life History Theory

Psychological research has historically focused on the development of individual differences. A primary focus of developmental research with regard to individual differences is how and whether experiences throughout the lifespan influence later stages of development and manifest individual differences (e.g., Belsky et al., 1991). Within the evolutionary sciences, life history theory has been leveraged as the dominant approach to understanding the development of individual differences (Del Giudice et al., 2015; Ellis et al., 2009). Situated within a framework of strategic variation (Hagen and Hammerstein, 2005), life history theory addresses how organisms, including humans, allocate finite resources (e.g., time, energy) to conflicting life tasks over the lifespan (Kaplan and Gangestad, 2005; Roff, 2002; Stearns, 1992).

Throughout development, there are three fundamental life history trade-offs to which humans must allocate their resources (Kaplan

and Gangestad, 2005). The trade-off between *present versus future reproduction* entails allocating resources to (1) early reproduction at the cost of continued bodily growth and maintenance, or (2) continued growth and development at the cost of delaying reproduction. The trade-off between *quantity versus quality of offspring* entails allocating resources to (1) producing a greater quantity of offspring, which increases the chances that one or more of these offspring will survive to reproductive age, but at the cost of decreased investment per offspring, or (2) producing higher quality offspring by investing more in each offspring, but at the cost of producing fewer offspring. The trade-off between *mating effort versus parenting effort* entails allocating resources to (1) high mating effort to increase offspring quantity, or (2) high parenting effort to increase offspring quality.

Resource allocation strategies require trade-offs because individuals have limited resources to allocate to such tasks. Strategic resource allocation ‘decisions’ are made throughout the lifespan. These decisions are then reflected as psychological traits and manifest behavior (Kenrick et al., 2010; Simpson et al., 2011). Allocation strategies that optimized the use of resources throughout the lifespan were selected over human evolutionary history (Ellis et al., 2009). Natural selection favored ancestrally adaptive solutions to fundamental life history trade-offs. Strategic resource allocation strategies arise through a combination of genetic variation and phenotypic plasticity (Ellis et al., 2009; West-Eberhard, 2003) whereby psychological mechanisms ‘decide’ how to allocate resources that enhanced ancestral survival and reproduction (Chisholm, 1999).

Life history strategies

The central premise of life history theory as applied to humans, specifically, is that variation of phenotypes can be conceptualized as manifest adaptive strategies that optimize resource allocation decisions throughout development (Del Giudice and Belsky, 2011).

Phenotypic variation, then, reflects adaptive resource allocation strategies, or *life history strategies*, by which an individual optimizes resource use for fundamental life tasks. Although humans are characterized by a species-typical life history strategy that has been relatively successful over evolutionary history (i.e., high dependency in infancy, an extended juvenile period, and a long lifespan; Hawkes, 2004), considerable individual variation of life history strategies is widely recognized within human populations (Gross, 1996; Promislow and Harvey, 1990; Roff, 2002; Stearns, 1992; West-Eberhard, 2003).

Human life history strategies are most commonly conceptualized as a *slow-fast continuum* (Griskevicius et al., 2011; Promislow and Harvey, 1990). Each strategy manifests in distinct sexual, psychological, and behavioral characteristics – prominent outcomes of focus for life history research (Belsky et al., 1991; Del Giudice, 2009; Kaplan and Gangestad, 2005). Relatively slower life history strategies are characterized by greater allocation of resources to somatic effort – growth, maintenance, and parenting. Slow strategists, on average, begin reproduction at a later age, have fewer but more stable and long-lasting romantic relationships, and invest more resources in each offspring. Conversely, relatively faster life history strategies are characterized by greater allocation of resources to mating effort. Fast strategists, on average, begin reproduction at a younger age, have many short-term romantic relationships or many casual sexual relationships, and invest fewer resources in each offspring (Egan et al., 2005; Weiss et al., 2004). The pursuit of a slow or fast life history strategy is largely dependent upon the ecological conditions in which an individual develops (Ellis et al., 2009).

Individual differences of life history strategies are facilitated by psychological mechanisms that are responsive to the local ecology, such that conditional adjustments in strategies resulted in greater ancestral survival and reproduction (Ellis et al., 2009). Variation

of ecological factors (e.g., pathogen load) alter the relative costs and benefits involved with strategic allocation decisions. Current models of human life history strategies (Ellis et al., 2009) focus on two features of extrinsic risk – harshness and unpredictability – that can each (uniquely) result in phenotypic modifications to accelerate human life history strategies (Barbaro and Shackelford, 2017; Ellis et al., 2009; Quinlan, 2007). *Environmental harshness* refers to extrinsic morbidity–mortality rates in the local environment. Higher mortality rates in local environments accelerate life history strategies and are characterized by earlier age at first reproduction (Low et al., 2008; Wilson and Daly, 1997), earlier sexual debut (Ellis et al., 2003; Kotchick et al., 2001), and lesser parental investment per child (Belsky et al., 1991; Ellis et al., 1999). *Environmental unpredictability*, in contrast, refers to stochastic changes in extrinsic morbidity–mortality rates, with greater fluctuations during an individual's development accelerating life history strategies (Ellis et al., 2009). In unstable and unpredictable environments, a generalist strategy is less likely than a specialized strategy to be effective given the variety of possible environmental conditions that may be encountered throughout the lifespan. In such ecologies, life history strategies are accelerated because an accurate estimation of mortality risk cannot be made. Individuals exposed to unpredictable environments report earlier sexual debut, greater number of sexual partners, more aggressive and delinquent behavior (Belsky et al., 2012; Simpson et al., 2012), and invest less in each offspring (Ellis et al., 2009).

Because phenotypes are conceptualized as manifest adaptive strategies for solving fundamental trade-offs, empirical work applying life history theory attempts to identify the patterns of psychological traits and manifest behaviors that comprise relatively fast or slow life history strategies. Life history strategies are often assessed by administering a battery of individual difference measures, the

most common of which is the Arizona Life History Battery (Figueredo et al., 2005) or the Mini-K (Figueredo et al., 2006). Life history strategies as operationalized by the K-factor include traits such as future planning, parental relationship quality, social contact and support, attachment in close relationships, and prosocial behavior. This perspective maintains that these individual differences psychometrically load onto, or cluster, to form a single ‘K-factor’ that represents adaptive patterns of characteristics and behaviors. The K-factor therefore is the foundation from which the slow–fast, unidimensional continuum of life history strategies is derived.

Additional phenotypic correlates of life history strategies have also emerged. Research has mapped various personality traits onto life history strategies, including normative personality features such as the Big Five (Figueredo et al., 2007), ‘dark’ personality traits, such as psychopathy (Jonason et al., 2016), and classes of psychopathologies (Del Giudice, 2016). Other suites of traits have also been identified to map onto life history strategies, such as a ‘covitality’ component representing health and well-being (Figueredo et al., 2007), and physiological correlates including androgens, estradiol, and testosterone (Del Giudice and Angeleri, 2016; Eisenegger et al., 2011; Pollet et al., 2011). Mapping individual differences on the slow–fast continuum of life history strategies has borne enormous empirical fruit for the understanding of adaptive phenotypic variation within humans.

The psychometric structure of human life history strategies has been the subject of debate, however. Traditional psychometric structures have maintained a single factor for which phenotypic variation is ultimately explained by a unidimensional, slow–fast continuum – the K-factor (Figueredo et al., 2006). However, Richardson and colleagues (2017) have challenged the single-factor life history model, and provide empirical evidence for two orthogonal life history factors: the K-factor and a new ‘mating competition’

factor. Evidence of two, rather than one, factors explaining human life history strategies (Richardson et al., 2014, 2016, 2017) may render the unidimensional, slow–fast model untenable and, moreover, the independence of the two factors does not accord with the fundamental trade-offs perspective (Kaplan and Gangestad, 2005) that is a linchpin of human life history theory. Greater evidence is needed to understand and confirm the psychometric structure of human life history strategies – which appear to be more complex in nature than originally proposed (Richardson et al., 2017).

Development of life history strategies

Despite debates concerning psychometrics, most theorists agree on the following propositions about human life history theory: (1) Over evolutionary history, selection favored phenotypes that were best suited to accommodate stochastic environmental fluctuations and optimal resource allocation (West-Eberhard, 2003); (2) The genetic variants associated with phenotypic modifications (or clusters of psychological and behavioral traits that comprise a particular life history ‘strategy’) are then selected over evolutionary time (Kuzawa and Bragg, 2012); and (3) Variation of ecological conditions in tandem with plasticity of psychological mechanisms afford conditional adjustments of individual life history strategies over development. These key features of human life history theory are consequential for the considerable within-species variation of life history strategies observed within and across human populations (Del Giudice and Belsky, 2011; Ellis et al., 2009). With regard to the *development* of life history strategies, however, various models and perspectives have emerged in the literature (Belsky et al., 1991; Del Giudice, 2009).

Traditional developmental life history models focus on the role of the early childhood environment for calibration of life history strategies and, in particular, the first five to seven years of development

(Belsky et al., 1991; Ellis, 2004). From this perspective, parental investment during early development is a primary cue from which children receive information regarding extrinsic risk in their local environment (Belsky, 1999; Chisholm, 1993; Ellis et al., 2009; Simpson and Belsky, 2008). Parental investment therefore varies as a function of extrinsic risk in the local environment, providing an indirect path for which offspring development can either be accelerated or slowed. The proposed logic is that, in less harsh and more stable environments, parents are better able to invest in offspring, whereas parents raising children in harsh and unstable environments are less able to invest in offspring. Offspring can potentially use the degree of parental investment as a cue about the environment that they will probabilistically engage with in the future (Del Giudice and Belsky, 2011).

Several studies have documented associations between early environmental risk and accelerated life history strategies (Albrecht and Teachman, 2003; Belsky et al., 2012; Capaldi et al., 1996; Simpson et al., 2012; Szepeswöl et al., 2015; Woodward et al., 2001; Wu, 1996; Wu and Martinson, 1993). Arguably the most well-researched application of the Belsky et al. (1991) life history model concerns pubertal maturation in girls, specifically as a result of growing up in a home without a father. Proponents of this view maintain that an absent father reliably signals greater environmental risk; if life history strategies are accelerated as a consequence of environmental risk, then girls should achieve puberty at an earlier age. Earlier age at menarche is argued to be indicative of a faster life history strategy in which greater resources are allocated to mating effort via the ability to begin reproduction at an earlier age (Belsky et al., 1991; Ellis, 2004; cf. Barbaro et al., 2017a).

Whether the early environment reliably affects later maturation and psychological development is still debated (e.g., Barbaro et al., 2017a). For instance, early environments may provide valid cues to the

offspring's future for relatively stable features of the environment (e.g., neighborhood crime rate). The long lifespan of humans, however – and, in particular, humans' extended juvenile period – may render information obtained in the first few years of life via parental investment suspect. In other words, information about the local environment obtained via cues of parental investment during the first five years may be unreliable at later stages of development, such as adolescence or adulthood. Several theoretical modifications have been proposed to account for the potential issue of reliability for information obtained early in development.

A key feature of humans' species-typical life history is an extended juvenile period (Hawkes, 2004). Whereas original life history models of development put heavy emphasis on the first few years of offspring development as being instrumental (Belsky et al., 1991), subsequent developmental life history models have targeted middle childhood and early adolescence as pivotal or transitional stages for modulating life history trajectories (Del Giudice, 2009, 2014). Middle childhood begins around six to eight years of age, and is characterized by relatively greater independence from caregivers for feeding and protection, but in which the offspring are not yet sexually mature. Middle childhood is marked by the onset and emergence of sex differences for several individual differences, such as personality traits, attachment styles, and social behavior. The adrenal gland also becomes active during this time – the onset of *adrenarche* – which triggers many of the hormonally mediated sex differences that begin to emerge during this life stage. Middle childhood ends with the transition to adolescence when the offspring begin to produce sex hormones and go through pubertal development changes marked by sexual maturity.

The life stages of middle and late childhood have been incorporated into developmental life history models (Del Giudice, 2009, 2014). The concept of *developmental switch points* (Del Giudice, 2009) has been

implicated as a key feature of life history development. A developmental switch occurs at a specific point in development via regulatory mechanisms by which an organism processes input from the external environment or internal state of the organism to alter individual development to optimize its outcomes. Del Giudice (2014) proposed middle childhood, specifically, as a crucial switch point in development – hormonal changes (e.g., adrenarche, puberty) trigger coordinated activation of various genes that are involved with expressed phenotypes. The primary feature of multi-stage developmental life history models is the integration of environmental information and genetic variation to produce individual differences with regard to physiological development, manifest behavior, and psychological traits. Developmental switch points therefore allow an organism to ‘solve’ the problem of unreliable information about the local environment obtained during the first years of life by ‘updating’ their life history strategy with current information at key life stages (Del Giudice, 2009, 2014).

The concept of developmental switch points was first introduced by West-Eberhard (2003), and is intertwined with the concept of *plasticity* – the ability of an organism to alter its phenotype to accord with the (current) local environment. Life history strategies, therefore, are argued to demonstrate adaptive plasticity (Ellis et al., 2006) by which phenotypes are adjusted within a genetically constrained reaction norm that evolved to optimize replicative success in various ecologies (Del Giudice and Belsky, 2011). Plasticity is posited to be an adaptive solution to the problem of information reliability over development (i.e., whether information obtained early in development is relevant for later life stages). Adaptive plasticity affords organisms the ability to ‘revise’ their life history strategies at key points in development, such as middle childhood.

Subsequent perspectives on adaptive plasticity posit that plasticity itself, however, may be a naturally selected trait (Del Giudice,

2015). That plasticity may be viewed as a psychological trait is a product of the information reliability problem. Because information obtained from the early environment may not be predictive of the future environment, variation in plasticity may have been selected for over human evolutionary history (Del Giudice and Belsky, 2011). The result would be that genetic variation can explain phenotypic variation, with some individuals being relatively more open and responsive to environmental information whereas other individuals may be more ‘fixed’ in their strategies. Greater ecological variability tends to increase phenotypic variation (Roff, 2002). Individuals may therefore vary with regard to the threshold necessary to augment their life history trajectory (West-Eberhard, 2003). Individuals may also vary as to how long they remain open to ‘revising’ their life history strategies (Belsky and Pluess, 2009; Belsky et al., 2007). Finally, various strategies may be successful in the same environment (e.g., different mating strategies).

Closely intertwined with the hypothesis of adaptive plasticity as a trait is the perspective of *differential susceptibility* to extrinsic risk factors (Belsky and Pluess, 2009). Differential susceptibility theory is derived from the observation that some individuals appear to vary with regard to plasticity and the effect that environmental factors have on functioning. In other words, not all individuals respond similarly to the same environmental inputs. Differential susceptibility theory (Belsky and Pluess, 2009) posits that different genotypes are more or less susceptible to environmental information, such that individuals may respond differently to the same environment because of differences in genes (Belsky and Pluess, 2009). The consequence, therefore, is that two individuals exposed to the same environmental risk factors may develop differential solutions to adaptive problems, or different life history strategies.

Life history theory has become the dominant framework for understanding the functionality and development of individual

differences at various stages of the lifespan (Ellis et al., 2009; Kaplan and Gangestad, 2005). Adaptive plasticity (West-Eberhard, 2003) and multi-stage development (Del Giudice, 2009, 2014) are key theoretical concepts of modern perspectives for human life histories that afford emergent individual differences within and between human populations. Apart from the assumption that selection has favored phenotypes that optimize resource allocation strategies over development, explicit integration of genetics with life history theory has yet to be achieved. Given that key life history variables comprising the K-factor are heritable (Figueredo et al., 2004), including personality traits (Bouchard, 2004; Johnson et al., 2008), genetic approaches for the understanding of individual differences can be complementary – and, in fact, necessary (Penke, 2011) – for a comprehensive understanding of individual differences. We next explore behavioral genetic approaches for examining individual differences.

Behavioral Genetics: Interplay of Genes and Environment

Behavioral genetic approaches to understanding phenotypic variation highlight psychological science's movement away from the historic nature *versus* nurture debate, and toward a more accurate recognition of the complex interplay between nature *and* nurture. It is beyond reasonable dispute that human psychology and behavior are (to varying degrees) heritable (Plomin et al., 2016). That all phenotypic traits are heritable is known as the first law of behavioral genetics (Turkheimer, 2000). In accordance with the first law, a comprehensive meta-analysis reported an average heritability estimate of 49% for nearly 18,000 complex human traits (Polderman et al., 2015). For personality traits, specifically, genetic variation between individuals accounts for approximately 50% of phenotypic variation in psychological research (Bouchard, 2004; Johnson et al., 2008). Individual differences of

complex human traits are therefore about 50% attributable to genotypic differences, and approximately 50% attributable to environmental differences.

Not all environments have the same influence on phenotypic variation, however. Behavioral genetic analyses provide insight into the genetic and environmental influences on complex human traits, affording estimates of the phenotypic variation explained by genetic factors and environmental factors (Plomin et al., 2013). Phenotypic variance is composed of three factors, two of which are distinct environmental factors. Genetic variance explaining phenotypic variance is referred to as heritability (h^2), which acts to make two individuals who share more genes more similar to one another than two individuals who share fewer genes. Environmental influences on phenotypic variation are spliced into two components: shared environment (c^2) and nonshared environment (e^2). The environmental components (collectively referred to as *environmentality*, $c^2 + e^2$) refer to phenotypic variance accounted for by environmental experiences. Shared environmental experiences, such as family-level variables, are aspects of the environment that make siblings (or others) reared together similar to one another. Nonshared environmental experiences, such as unique peer groups, are aspects of the environment that make siblings (or others) reared together dissimilar from one another (note that the nonshared component also includes measurement error).

In their meta-analysis, Polderman et al. (2015) document that only 17% of variation across complex human traits is attributable to shared environmental experiences. The relatively trivial effect of shared environmental experiences for explaining phenotypic variation supports what is known as the second law of behavioral genetics: similarities among biological relatives are primarily due to genetic relatedness rather than shared experiences (Turkheimer, 2000). The remaining explanatory variance for complex human traits comes from nonshared, or unique,

experiences. For the majority of human traits, nonshared experiences have substantial explanatory power, oftentimes more than genes or shared experiences – referred to as the third law of behavioral genetics (Turkheimer, 2000). The (unofficial) ‘fourth law’ of behavioral genetics is that complex human traits are influenced by many (hundreds, even thousands or tens of thousands) of genes (Plomin, 2013). Each single gene is likely to have trivial explanatory influence independently ($< 0.5\%$ variance explained), although, additively, genes account for a significant proportion of variance for individual difference traits. Non-zero heritabilities of complex human traits render untenable evolutionary approaches to individual differences that fail to account for genetic variation among individuals (Penke, 2011).

Behavioral genetic approaches are able to identify *sources* of influence for a particular trait in a given population. That is, given a population of individuals, behavioral genetic analyses can estimate what proportion of individual differences within the population for a phenotypic trait – for instance, extraversion – is attributable to genetic variation within the population, and what proportion is attributable to environmental variation (shared and nonshared) within that population. Behavioral genetic approaches estimate the extent to which differences between individuals are due to genetic differences (of any sort) among individuals and to environmental differences (of any sort) among individuals. Naturally occurring ‘experiments’ of twinning and adoption are used for understanding sources of variation underlying complex human traits by partitioning phenotypic variance of a trait into the three components of influence (Plomin et al., 2013).

Gene–environment correlation and gene-by-environment interaction

Partitioning phenotypic variance into three components is a notable goal of behavioral genetic approaches to the understanding of individual differences – to understand the

sources of individual differences (Plomin et al., 2013) or for inferring the intensity of selection on a trait over evolutionary history (Keller et al., 2011), for example. Partitioning of phenotypic variance is only one component of the insights that behavioral genetics can provide for the understanding of individual differences, however. Analyses of trait variation can also bear relevance for the development of traits psychologists have historically researched (Bean and Turkheimer, 2017). Including time as a variable in genetic analyses can inform the complex – and debated – interplay of genetic and environmental influences for human development and adult psychological outcomes.

Both genes and environment produce complex human traits, such as personality and intelligence (the two most researched traits by behavioral geneticists; Plomin et al., 2013). How, exactly, genes and environment interact to produce psychological outcomes, and the implications of such interplay, remain subject to much discussion within the field. The two primary ways for which the interplay between genes and environment is researched is via gene–environment correlation (r_{GE}) and gene-by-environment interactions ($G \times E$).

Gene–environment correlations can account for several fundamental findings of behavioral genetic studies (Kandler and Zapko-Willmes, 2017), as well as provide alternative explanations for mainstream developmental psychology findings (Barbaro et al., 2017a; Barnes et al., 2014). Gene–environment correlation refers to the association between heritable phenotypic characteristics and nonrandom exposure to environmental experiences that are associated with that same phenotypic characteristic (Plomin et al., 1977). In other words, genotypes are expressed in the environment (or outside the organism) via manifest behavior and psychological traits (Kandler and Zapko-Willmes, 2017). This is not to say that behavior is genetically determined, but rather it is to say that environmental experiences are

not random and are prompted by an individual's genotype. That genotypes have a measureable effect on the environment via manifest behavior has several implications for developmental perspectives of individual differences, including minimal effects of the shared environment on most complex traits (Polderman et al., 2015), increasing heritabilities over development (Plomin et al., 2016), heritability of environments (Kendler and Baker, 2007), and genetic confounding of phenotypic associations (Barnes et al., 2014).

Gene–environment correlation (*rGE*) can take several forms (Plomin et al., 1977; Scarr and McCartney, 1983): active, evocative (or reactive), and passive. *Active rGE* occurs when organisms actively seek out, avoid, or modify their environmental experiences that are nonrandomly influenced by their genotype. The environmental experiences can then act to reinforce or stabilize individual differences. For example, extraverted individuals are more likely than introverted individuals to attend social gatherings, which may lead extraverted individuals to be invited to a greater number of subsequent social gatherings, and therefore reinforce the individual's extraverted tendencies.

Evocative rGE occurs when organisms receive responses or evoke reactions from others in their environment that are nonrandomly influenced by their genotype. These evoked reactions can then function to reinforce individual differences responsible for these reactions. For example, an intelligent and motivated student who is eager to participate in the classroom is more likely to receive feedback and support from their teacher; in turn, that student's motivation and eagerness to participate in class will be reinforced.

Passive rGE occurs when the environment that an individual inhabits – such as the neighborhood a child grows up in – is correlated with their genome. Parents endow offspring with an environment in which to live, and a genome comprising half of each (biological) parent's genes, such that the environments children experience are correlated with the

genotypes that they inherit from their parents (Kendler and Baker, 2007). A consequence of passive *rGE* is that the type of parenting or home environment experienced by a child is moderately heritable (i.e., estimates around .40; Kendler and Baker, 2007). For example, two college professors raising their child are likely to endow the offspring with an intellectually rich home environment; the child, however, also inherited her parents' 'intelligence' genes.

The three types of gene–environment correlations described above have implications for the development of individual difference across the lifespan. The dominant type of gene–environment correlation is proposed to change over the course of development (Scarr, 1992). Passive gene–environment correlation has greater explanatory power in infancy and early childhood. Because human infants are heavily dependent on caregivers during the first years of life, evident gene–environment correlations are most likely to be of the passive type given the control caregivers have over children's environments. The importance of active gene–environment correlation increases with age as individual decision making and environmental control also increase. The implications of this change in the dominant type of gene–environment correlation throughout development can, in part, explain the increase in heritability estimates of a myriad of traits (most notably, intelligence) over development (Kandler and Zapko-Willmes, 2017; Plomin et al., 2016).

Gene–environment correlations are foundational components of the ongoing debate about whether and how parenting and early home environments have lasting or meaningful consequences for the development of personality and individual differences, over time (Harris, 1995). Within the field of evolutionary psychology, life history theory is commonly leveraged to explain the development of individual differences. In particular, it is posited that early experiences exert lasting and meaningful effects on (primarily sexual) psychological and behavioral

outcomes (e.g., Belsky et al., 1991). The assumption of this hypothesis is a causal one – early environmental experiences cause observable developmental outcomes. For example, the effect of an absent father in childhood causing early pubertal maturation in girls is a well-researched hypothesis derived from life history theory (see Ellis, 2004, for review). At the level of phenotypic association, the hypothesis has received support. Alternatively, however, the phenotypic association may be confounded to the extent that the genes underpinning both traits are correlated, given that phenotypic correlations are often mediated genetically (Plomin et al., 2016). Empirical research addressing genetic confounding of this phenotypic association, in particular, has yielded support (see Barbaro et al., 2017a, for a review), suggesting the purported causal phenotypic association between father absence and pubertal development may be spurious.

There are several implications of gene–environment correlation for the development of individual differences. As discussed above, gene–environment correlations can result in genetic confounding of phenotypic associations (Barbaro et al., 2017a; Barnes et al., 2014). The dominance of different types of gene–environment correlations (Scarr, 1992) may also explain why shared environmental effects that do exist for some individual differences, such as attachment styles (Barbaro et al., 2017b), are only evident in infancy, with no discernable effects in adolescence and adulthood. An increasing emphasis on active gene–environment correlation during normative development may explain why the heritability of individual differences such as intelligence tend to increase with age (Plomin et al., 2016). As individuals enjoy increasing autonomy over development, small genotypic differences are magnified via active gene–environment correlation as nonshared experiences increase – a process referred to as *genetic amplification* (Plomin and DeFries, 1985). Finally, gene–environment correlations may explain why apparently

environmental factors such as family-level variables are heritable across populations (Kendler and Baker, 2007), further contributing to issues of genetic confounding in developmental research.

Gene-by-environment interactions ($G \times E$) can also explain individual differences. A gene-by-environment interaction refers to a differential effect of the environment on a phenotypic outcome that is dependent on genotypic differences (Gottlieb, 1995; Plomin et al., 1977). In other words, individuals may respond differently to the same environment because of underlying genetic differences. Gene-by-environment interactions have been implicated as a key explanatory concept for differences between siblings: because siblings share only approximately half their genes, the same parenting may differentially affect each child. For example, one child with a genetic propensity for a difficult temperament may be more upset than their sibling with a genetic propensity for an easy temperament, despite receiving the same punishment from their parents.

Gene-by-environment interactions can make siblings either more or less similar depending on whether genes interact with *shared* environmental variables or *nonshared* environmental variables, respectively (Kandler and Zapko-Willmes, 2017). Because shared genes and shared environments both act to make two individuals more similar to one another, a gene-by-shared-environment interaction would act similarly to genetic influences, whereby siblings become more similar as a result. In contrast, interactions between genes and nonshared environmental experiences will function to make two siblings more different from one another. If not statistically modeled explicitly, interactions between genes and shared environments would be masked by genetic main effects, whereas interactions between genes and nonshared environments would be masked by nonshared environmental main effects (Purcell, 2002).

There are, however, criticisms of gene-by-environment interaction approaches for

explaining individual differences. For instance, it has been argued that gene-by-environment interactions are not capable of explaining individual differences of identical twins (Harris, 2011). Given that both twins share the same genetic material, individual differences of identical twins would necessitate a difference of (nonshared) environment only – a main effect. If gene-by-environment interactions did occur for identical twins, in particular, they would be of the shared environment, functioning to make the twins more similar, rather than different (Purcell, 2002). Other issues for gene-by-environment interactions arise with regard to replicability and statistical power (McGue and Carey, 2017). Candidate gene-by-environment interactions, specifically, are difficult to replicate given that most complex traits of interest are influenced by several, rather than a single, gene (Plomin et al., 2016). Each candidate gene may explain only less than .5% of variance in the trait of interest (Park et al., 2010) – an extremely small effect – therefore increasing the likelihood that many published candidate gene-by-environment interactions may be false-positives. Latent variable approaches that use aggregate genetic effects, rather than effects of a single candidate gene, are less susceptible to replicability and power issues (McGue and Carey, 2017).

Finally, the interplay of genes and environment have implications for both the stability and change of individual difference traits over the lifespan. A consistently replicated finding in the field of behavioral genetics is that age-to-age stability is primarily explained by genetics (Plomin et al., 2016). Continuity of individual differences are mainly due to the same genes affecting the trait of interest across the life span (Plomin, 1986). Emergent changes of traits over the lifespan are due to nonshared experiences, and these nonshared experiences are age-specific. That is, nonshared experiences are different at different life stages. That genetics account for developmental stability and nonshared experiences account for change has been shown for personality traits (i.e., 80% of phenotypic

stability is mediated genetically; Briley and Tucker-Drob, 2017; McGue et al., 1993; Turkheimer et al., 2014), psychopathology (Bornovalova et al., 2009; Kendler et al., 2008), and cognitive ability (Cherny et al., 1997). Behavioral genetic approaches have been profitable for understanding sources of individual differences, and for understanding what factors are most influential for the development of individual differences over the lifespan.

CONCLUSIONS AND FUTURE DIRECTIONS

The above discussion provides compelling evidence that evolution by natural selection is responsible for creating and maintaining individual differences. The dominant approaches for the investigation of individual differences highlight the importance and utility of applying an evolutionary framework to the study of between-sex variation (via theories of sexual conflict and parental investment), development (via Life History Theory), and sources of phenotypic variation (via behavioral genetics). We now conclude with a brief discussion of potential future directions for applying evolutionary approaches to the study of personality and individual differences. As with many other areas in the life sciences (including psychology), an evolutionary approach is a powerful framework for interpreting existing findings and for generating novel hypotheses.

An evolutionary approach provides a theoretical framework from which adaptive reasoning can be used to make *a priori*, domain-specific predictions with regard to outcomes of personality (e.g., Denissen and Penke, 2008). From this approach, one can defensibly define and predict how and why some traits (or clusters of traits) accord with some adaptive domains, but not others. The Five Individual Reaction Norms (FIRN) model (Denissen and Penke, 2008),

for example, demonstrates the motivational reaction norms underlying the Big Five. Predictions are made about the specific domains that should be impacted by particular personality dimensions. For example, Agreeableness should be key in situations that entail making a decision between sacrificing resources for the sake of others or maximizing one's own gain, whereas Conscientiousness should be key in situations that entail making a decision between giving up on a goal to pursue attractive short-term options or persisting at a goal-related task (Denissen and Penke, 2008).

Evolutionary perspectives focus on how and whether individual differences are reliably associated with aspects of survival and reproduction, such as health and longevity, close relationships, and social interactions (e.g., Buss and Greiling, 1999; Nettle, 2006; Ozer and Benet-Martinez, 2006). An evolutionary perspective can make predictions with regard to how different levels of a personality dimension may be beneficial in some domains of fitness, but costly in others (e.g., de Vries et al., 2016) – affording novel framing of empirical findings (Nettle, 2005). The situation-affordances model of the HEXACO model of personality (de Vries et al., 2016), for example, demonstrates how each personality dimension at different levels can activate, and be activated by, differing environments to explain how personality functions across situations. These situation-contingent models of personality (Denissen and Penke, 2008; de Vries et al., 2016) provide explanations for the maintenance and functionality of individual differences across populations, and allow for the generation of novel predictions for how individual differences advantageously manifest in different environments.

A debated issue in personality psychology, however, is the useful and accurate definition of personality and other individual difference constructs. Although many personality psychologists use constructs of narrow scope (e.g., facets of the Big Five

dimensions) – which tend to have superior predictive power – these narrow constructs and definitions are data-driven, rather than theory-driven (e.g., Block, 1995; McAdams, 1992). Research, however, also documents that *broad* dimensions of personality have predictive power for behavioral outcomes (Fleeson, 2001; Ozer and Benet-Martinez, 2006). Purely descriptive, data-driven models, such as the Big Five, cannot account for this apparent conflict. An evolutionary perspective can potentially clarify why both narrow and broad individual difference constructs are predictive of manifest behavior: individual differences are domain-specific (i.e., they were selected for their ability to solve specific adaptive problems) but, because there are multiplicative combinations of traits, or types of environments that select for suites of traits, sets of domain-specific traits may become inseparable during development (Nettle, 2011). In other words, levels of a particular individual difference trait may be more likely to be passed on, or coexist, at certain levels of other particular individual difference traits (akin to a correlation). This explanation could also account for observed hierarchical structures proposed for some individual differences, such as personality traits: narrow-domain traits cluster (correlate) together in a predictable manner. These clusters of narrow-domain traits are then conceptualized as broad-domain 'superfactors' (Digman, 1997; Musek, 2007).

An evolutionary approach can guide the framing of novel predictions with regard to the fitness consequences of different *combinations* of traits, or superfactor profiles of individual differences (e.g., general factor of personality, the K-factor). From this approach, novel predictions can be made that the effect of a particular personality profile (i.e., clusters of traits) on fitness will vary with environmental context. For example, Nettle (2011) argues that being high on the imagination aspect of openness is beneficial to the extent that the person also scores highly on the intellect dimension, yielding

the prediction that people high (or low) on imagination and low (or high) on intellect should have less favorable outcomes than those who are either high on both traits or low on both traits. There should be fitness payoffs for cohesiveness among (optimal) superfactor profiles of individual differences.

Whether superfactor profiles of individual differences reflect actual traits that are selected for over human evolutionary history is a debated issue. Superfactors – such as the general factor of personality, the K-factor of life history, or the construct of general intelligence – may simply be a statistical artifact. Arguments for the evolution of superfactors as ‘real’ traits are analogous to arguments for the evolution of domain-general psychological mechanisms (as compared with domain-specific psychological mechanisms). For example, the super K-factor fails to be reliably associated with outcomes of survival and reproduction (Richardson et al., 2017) – findings that are necessary for the validity (and evolution) of the superfactor construct. Concepts from behavioral genetics may explain, in part, the statistical existence of superfactors. Genetic correlations among domain-specific traits may account for the positive manifold for a myriad of superfactors, such as general intelligence. Although superfactors are potentially useful statistically, careful consideration needs to be given when addressing the evolutionary origins of proposed superfactors.

Genetic correlations among traits should also be given careful consideration within research programs aimed at uncovering causal developmental processes. Genetic confounding (akin to the ‘third variable problem’) may render purportedly causal developmental associations spurious (Barbaro et al., 2017a; Barnes et al., 2014). Developmental approaches to the study of individual differences should take into account, or control for, genetic variation, to accurately understand developmental processes. An interesting avenue for developmental research would be the investigation and impact of aggregate environmental experiences for developmental outcomes. Just as

aggregate genetic effects are more predictive of developmental outcomes than are candidate gene effects (Park et al., 2010), aggregate environmental effects may be informative. The pressing issue, however, concerns how to accurately and reliably measure aggregate environmental effects, given that experiences are age-specific (Plomin et al., 2016), unlike genes (which are constant). Behavioral genetics has the potential to substantively inform evolutionary approaches to developmental psychology – a necessary future direction for research (Barbaro et al., 2017a; Penke, 2011).

In summary, theoretical arguments and empirical evidence support the perspective that natural selection both creates and maintains individual differences in the population. Core features of individual differences – non-zero heritability, stability over time and across cultures, cross-species continuity, predictive utility for manifest behavior, associations with components of fitness, and ability to solve adaptive problems – provide compelling support for evolutionary perspectives on individual differences. Evolutionary approaches for the study of individual differences – theories of sexual conflict, parental investment, Life History Theory, and behavioral genetics – have made considerable contributions to the field of psychology. These scientific successes foreshadow a promising future for an evolutionary psychology of individual differences.

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