



Consilience and Life History Theory: From genes to brain to reproductive strategy

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Abstract

We describe an integrated theory of individual differences that traces the behavioral development of life history from genes to brain to reproductive strategy. We provide evidence that a single common factor, the K-Factor, underpins a variety of life-history parameters, including an assortment of sexual, reproductive, parental, familial, and social behaviors. We explore the psychometrics and behavioral genetics of the K-Factor and offer a speculative account of the proximate mediation of this adaptive patterning of behavior as instantiated in well-established functions of specific areas of the human brain, including the frontal lobes, amygdala, and hippocampus. We then apply Life History Theory to predict patterns of development within the brain that are paedomorphic (i.e., development begins later, proceeds at a slower rate, and has an earlier cessation) and peramorphic (i.e., development begins early, proceeds at a faster rate, and has a later cessation).

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We describe and extend a research program (Figueredo, Sefcek, Vasquez, et al., 2005; Figueredo et al., 2005c) which, using latent variable modeling, has identified a single common factor, the K-Factor, that underlies a variety of life-history parameters. We first describe Life

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History Theory and derive some testable predictions, including the existence of the K-Factor, as indicated by the positive associations among an assortment of sexual, reproductive, parental, familial, and social behaviors. We then relate the K-Factor to an observed positive manifold or “cluster” of comorbid and socially problematical behaviors as reported in the literature. We go on to explore the psychometric validation and multivariate behavioral genetics of the K-Factor, reviewing much of our own recent empirical work on this topic. Finally, we examine the proximate mediation of this adaptive patterning of behavior as instantiated in brain function and propose an integrated theoretical model that traces the behavioral development of individual life history from genes to brain to reproductive strategy.

Life History Theory as a unifying principle

Life History Theory is a mid-level theory from evolutionary biology that describes the strategic allocation of bioenergetic and material resources among different components of fitness (e.g., calories and nutrients devoted to growth vs. reproduction). Somatic Effort anchors one end of the first dimension of this trade-off whereas Reproductive Effort anchors the other. *Somatic Effort* refers to resources devoted to continued survival of the individual organism whereas *Reproductive Effort* refers to resources devoted to production of new organisms as vehicles for survival of the individual’s genes. The second dimension of this trade-off further partitions Reproductive Effort. Mating Effort anchors one end of this continuum whereas Parental Effort and Nepotistic Effort jointly anchor the other. *Mating Effort* refers to resources devoted to obtaining and retaining sexual partners whereas *Parental/Nepotistic Effort* refers to resources devoted to enhancing the survival of existing offspring and other genetic relatives. Thus, a life-history strategy allocates an individual’s bioenergetic and material resources among the competing demands of survival and reproduction (Shennan, 2002).

Life History Theory is the basis of a number of studies describing consistent correlations among pace of maturation, length of lifespan, encephalization (i.e., relatively large brains), reproductive effort, and degree of social cohesion (Barash, 1982; Eisenberg, 1981; Rushton, 2004; Wilson, 1975). The r/K continuum proposed by Life History Theory represents a covarying range of reproductive behavior patterns inversely relating life-history traits such as fecundity and parental investment (Bogaert & Rushton, 1989; Mac Arthur & Wilson, 1967). The endpoints of this continuum range from extreme r (e.g., maximum egg output and no parental care) to extreme K (e.g., minimal birth rate and elaborate parental care).

According to Pianka (1970), Life History Theory predicts that, all things being equal, species living in unstable (e.g., fluctuation in food availability) and unpredictable (e.g., high predation) environments tend to will evolve clusters of “r-selected” traits associated with high reproductive rates, low parental investment, and relatively short intergeneration times. In contrast, species living in stable and predictable environmental conditions tend to evolve clusters of “K-selected” traits associated with low reproductive rates, high parental investment, and long intergeneration times. In reference to human evolution, Geary (2005) emphasizes whether the environment is relatively unexploited and resource-rich and can therefore facilitate rapid population expansion, which favors r-selection and entails the production of numerous but inexpensive offspring. In contrast, when the environment is relatively saturated (has reached a high conspecific population density) and therefore occasions more intraspecific competition for limited resources, this favors K-selection and entails sufficient parental investment to produce less numerous but more competitive

offspring. As a model of ecological causation, Pianka's (1970) version of r/K theory has been extensively elaborated and revised since the 1980s (Stearns, 1992; Reznick, Bryant, & Bashey, 2002), but as an organizing principle for empirical description, the general patterning of life-history traits has gained continued support (e.g., Rushton, 2004).

The literature describes many different species with stereotypical life-history strategies. For example, rabbit sexual development is rapid, they are highly fertile, they produce a number of offspring at a time, and they suffer high infant mortality because they provide little parental care; in fact, given multiple predation risks, they may have little ability to protect their offspring and thus there is little opportunity for high levels of parental care to evolve. After reaching maturity, rabbits are short-lived. In contrast, elephant sexual development is slow, they produce few widely spaced offspring, and they experience low infant mortality because they provide extensive parental care. For example, Asian elephant parental care may last up to 14 years (until sexual maturity), even though most young are weaned from suckling after 18 months. High initial parental investment results in larger and healthier offspring; this, in turn, reduces predation risks and increases probability of successful maturation (Clutton-Brock, 1991). Furthermore, even after reaching maturity, elephants are long-lived. For example, Asian elephants may live as long as 70 years.

A K-selected life-history strategy allocates an individual's bioenergetic and material resources preferentially to Somatic Effort over Reproductive Effort, and to Parental and Nepotistic Effort over Mating Effort, emphasizing the survival of individual organisms (whether self, offspring, or kin) over the production of new ones. Generally, humans appear to be highly K-selected. Human sexual development is slow, they generally produce only one or two offspring at a time, and they experience relatively low infant mortality rates because, even though human infants are born helpless, adults invest a substantial amount of parental care in their offspring. As a result, human infants have a higher survival rate than our closest relative, the Chimpanzee, even among contemporary human hunter-gathers (Hill et al., 2001).

Several evolutionary theorists, however, have demonstrated there is a substantial degree of individual variation in the life-history strategy of humans. Because, compared to many other species, humans are highly K-selected, Life History Theory, when applied to humans, is often referred to as "Differential K" Theory (Rushton, 1985). There is lively theoretical debate regarding the degree of environmental and genetic contributions to these individual differences (Belsky, Steinberg, & Draper, 1991; Chisholm, 1996; Rowe, 2000). For example, theorists assuming strong environmental influences on human life-history strategy propose that a father's absence from the home during childhood biases an individual toward a lower-K life-history strategy. Belsky et al. proposed that experiences occurring during the first five to seven years of life provide an experiential history upon which individuals later base their reproductive strategy. Those who experience close interpersonal relationships and predictable resources are more likely to experience delayed puberty, whereas those who experience unstable environments and support are more likely to experience early puberty. Ellis (2004), in a comprehensive review of the literature, indicated that father-absent girls were significantly more likely to experience menarche by age 12 than their peers. The age of menarche experienced by these father-absent girls correlated with the number of years of father absence, the time fathers spent taking care of daughters during the first five years of life, and the affection observed in parent-child relationships. The time a stepfather was present in the home also correlated with age of puberty: girls who experienced longer exposure to a non-related male tended to experience menarche earlier.

In contrast, theorists who assume strong genetic influences on human life-history strategy predict that a voluntarily absent father passed along genes biasing offspring toward a shorter-term life-history strategy. Rowe (2000) reported heritabilities of .44 for menarchal age and .40 for pubertal timing, with a negligible effect of shared environment. Kirk et al. (2001) reported heritabilities of .50 for age at menarche, .23 for age at first reproduction, and .45 for age at menopause. Kirk and colleagues also reported substantial heritable variation in fitness, .39 of the variance attributable to additive genetic effects and most of the remainder attributable to the effects of non-shared environment. Rodgers et al. (2001) reviewed both the theory and the evidence for heritable differentials in human fertility, attributing much of this influence to genetically mediated behavioral precursors. Significant heritabilities have been reported for many of these behavioral precursors to differential fertility such as sexual behavior, marriage and divorce, fertility desires, fertility ideals and expectations, age of first explicit attempt to get pregnant, completed family size, and parenting behavior.

Thus, the biological correlates of the father-absence effect include a cluster of characteristics associated with relatively rapid sexual development and increased fertility. For men and women, psychological correlates include relatively lower adult attachment to romantic partners and greater manipulative and exploitative social attitudes. Behavioral correlates include less parental care devoted to one's own offspring and greater risk-taking behavior, social aggression, sexual promiscuity, and preference for sexual variety.

Life history and psychosocial characteristics

Research based on Differential K theories of human development and related behavioral genetic work describes substantial individual differences in biological and behavioral characteristics indicative of differences in life-history strategy (Belsky et al., 1991; Chisholm, 1996; Rowe, 2000). In addition to basic biological characteristics, such as longevity and fecundity, Life History Theory predicts that many psychosocial traits will accumulate non-randomly. The theory suggests that, due to natural and sexual selective pressures, these psychosocial traits will combine into functional composites representing coadapted reproductive strategies. Applied to human behavior, Life History Theory claims that natural and sexual selection shape many aspects of an individual's approach to adaptive problems presented by the physical and social environment causing specific psychosocial traits to intertwine intimately and hence to appear in clusters (e.g., Rushton, 1985; Thornhill & Palmer, 2004).

The core psychological characteristics clustering toward the low end of the Differential K continuum entail a focus on short-term gains at the expense of long-term costs, numerous mates, and little parental investment. Within modern society, these low-K characteristics could manifest as impulsivity, short-term thinking, promiscuity, low female parental investment, little or no male parental investment, little social support, disregard for social rules, and extensive risk-taking (Bogaert & Rushton, 1989; Ellis, 1988; Figueredo et al., 2005d; Rushton, 1985, 1987; Geary, 2002; Rushton & Bogaert, 1988; Thornhill & Palmer, 2004). The core psychological characteristics at the high end of the Differential K continuum entail long-term considerations, selective mating, and high parental investment. Within modern society, these high-K characteristics could manifest as long-term thinking, monogamy, extensive parental investment, substantial social support structures, adherence to social rules (e.g., cooperation, altruism), and careful consideration of risks.

Hence, Life History Theory predicts that people who are high in K will have fewer offspring, will invest more time and energy into those offspring, will be more committed to long-term relationships, will think more in terms of long-term benefits rather than short-term gain, will plan more for their offspring's future (e.g., by amassing more resources or providing avenues to enhance their children's social status), and will adhere to the social norms of modern industrialized societies more closely than those who are low in K. Theoretically, individuals in possession of an evolutionary history associated with either end of the Differential K continuum will possess value systems and personality characteristics that bias them toward these characteristics. Of course, the degree to which these characteristics manifest themselves will depend on developmental and extant environmental circumstances such as monetary wealth, cultural influences, immediate social institutions, and physical constraints (Heath & Hadley, 1998).

Hence, Life History Theory predicts that multivariate correlational techniques, such as factor analysis and structural equation modeling, will detect functional cognitive, affective, and behavioral composites representing coherent and integrated reproductive strategies. In spite of these massively multivariate predictions, most of the extant literature examining predictions derived from Differential K Theory in humans test specific causal hypotheses (e.g., Quinlan, 2003) using univariate correlational analyses. Hence, they do not detect, fully describe, or explain the wider pattern of correlations among variables predicted by Life History Theory. In other words, the combination of Life History Theory and sophisticated analytic approaches has the potential to reveal reproductive biases, personality, cognitive, and other traits that cluster together and thus describe individual differences in how people approach sexual and social relationships, how they treat their children, and other important social behaviors (e.g., lawfulness).

Relationship of life-history strategy to “social problem” behaviors

The dominant norms in many industrial and technologically advanced societies tend to designate low-K strategies as undesirable and high-K strategies as socially favored, presumably because these norms were created largely by high-K individuals who tend to rise in social status and influence. Even within modern industrialized and technological societies, however, there is a wide range of social and ecological niches within which individuals may adaptively practice different reproductive strategies. It is therefore not surprising that we observe life-history strategies ranging from low-K to high-K strategies in our own and in related societies. We know that humans do not all implement one simple and species-typical reproductive life-history strategy. We also know there is a wide range of costs and benefits associated with different strategies. As we have demonstrated, both an individual's genetic history and current ecological situation influence the manifestation of specific reproductive strategies. Therefore, it is incorrect (and scientifically untenable) to view one strategy as globally “better” than another strategy. This applies directly when discussing the differences between low-K and high-K life-history strategies. For example, there are always trade-offs between time and resources invested parental effort and those invested in mating effort (Gangestad & Simpson, 2000). Alternative mating strategies, representing differential allocations, may be maintained indefinitely in a single population through frequency-dependent selection (Gangestad & Simpson, 1990; Rowe, 1996, 2002); different modal mating strategies might also be favored by different populations or subpopulations within varying sociocultural and ecological contexts (Lumsden & Wilson, 1981).

Ethnographic examples may illustrate how differences in local ecology can influence a normatively “good” or “bad” reproductive strategy. For example, the Canela people of Brazil are a matrilineal society (where resources are passed along the female lineage) and the women are sexually unrestricted. There are community ceremonies where women are encouraged to copulate with multiple partners other than their mate. Men support this and it is socially inappropriate for a man to show jealousy of his wife’s extramarital copulations (he may experience jealousy but must suppress this). A suggested ecological explanation is that when resources are scarce and males experience high mortality (as is the case with the Canela), that women seeking extramarital relationships may be wise in that this results in several men who will invest in or protect her children (Hrdy, 1999). The sexual promiscuity, the uncertainty about future resources, and the high rates of mortality are characteristics suggestive of a low-K life-history strategy.

Nevertheless, even among other horticulturalists, having fewer children provides some leeway when resources are scarce—relieving siblings of the necessity of competing with one another for basic resources. Among the Yanomamo people of Venezuela, during a particular harsh season where food became scarce, parental investment and sibling competition were important factors in how well children fared. Girls with more relatives in the village suffered the least due to high investment from kin. Boys whose father had fewer offspring and fewer wives, and who was currently married to the boy’s mother fared better than other boys did. These boys had both more of their fathers’ attention and resources and less competition from siblings (Hagen, Hames, Craig, Lauer, & Price, 2001). Geary (2000) reviews the relation between paternal investment and child mortality risks and concludes that the effects can be quite large and are consistent across societies, at least before the demographic shift.

Furthermore, the prevalence of matrilineal systems appears to decrease and to be replaced by patrilineal organizations (where resources are passed along the male lineage) when a subsistence economy based on intensive agriculture (as opposed to a foraging or horticultural subsistence economy) is introduced. It is argued that when patrilineal systems can control and monopolize wealth, it is then that women will prefer to marry for material resources (Hrdy, 1999). Patrilineal organization places more emphasis on male paternity certainty and stronger male kin alliances. When males invested more resources in offspring, they became more concerned with paternity certainty (Hrdy, 1999). The increased predictability of resources due to intensive agriculture and the greater paternal investment in offspring is characteristic suggestive of a high-K life-history strategy.

Some of the expected costs and benefits of high-K and low-K life-history strategies can also be assessed for modern industrial societies. An increase in a country’s gross national product has been demonstrated to allow for an increase in parental investment, but cannot necessarily account for individual differences in parental investment by that country’s citizens (Barber, 2002). An increase in resources available seems to provide multiple parental investment choices, but is not predictive of which choice any given individual may make (cf., Geary, 2000).

Among the relative benefits of a high-K life-history strategy is that through delaying reproduction and intensifying investment in fewer offspring, one would expect to decrease the likelihood of both infant mortality and adverse health events and increase access to resources via enhanced educational opportunities (e.g., Figueredo, 2000). Investing in somatic effort should also increase an individual’s likelihood to have an extended lifespan and possibly increase inclusive fitness through grandparenting later in life by contributing

to the viability of genetically related infants (Hrdy, 1999). Another expected benefit of a high-K life-history strategy in modern industrial society is the probable outcome of increasing socioeconomic status and its attendant benefits, including the affordance of increased parental investment in offspring. According to one study that compared four major cosmopolitan cities, elevated infant mortality occurred when there was both low income and a stable birth rate in an area. These areas also reported exceptionally high percentage of unintended pregnancies (Rodwin & Neuberg, 2005). Geary (2000) has reviewed the relation between socioeconomic status and child mortality risks and found that the relation is very strong cross-culturally in societies that have not undergone the demographic shift.

Women who seek higher education often put off having children and devote their energies to their careers (e.g., Figueredo, 2000). In contrast, if adolescence is cut short by a pregnancy early in life, an individual may lose future economic opportunities. Women who have young children often have fewer resources available to devote to educational opportunities, and may be at risk of losing those opportunities altogether. Teenage mothers have lower incomes as adults and are more likely to be dependent on welfare (Coley & Chase-Lansdale, 1998). They are also more likely to experience medical complications themselves and have less healthy babies. Teenage mothers also experience higher divorce rates than later-life mothers, and though they are more likely to marry early, they are less likely to be married in their 20s and 30s than later-life mothers (Coley and Chase-Lansdale). This marriage pattern would decrease the overall paternal investment they could expect from any males, including the infant's father.

The social and behavioral literature indicates that many behavioral traits commonly considered "social problems" in modern industrial society occur in such clusters. A number of independent literatures consistently describe a positive manifold of correlations among many common human behavioral traits considered "social problems." Theories derived from the Standard Social Science Model do not fully account for this positive manifold or cluster of "social problems," but Life History Theory does because it instead construes such clusters to be coordinated arrays of contingently adaptive life-history traits.

The literature examining teen pregnancy describes an entire cluster of what are considered "social problems" in modern industrial society. Teen pregnancy is predictive of both welfare dependence and the intergenerational transmission of poverty (Bonell, 2004; Gueorguieva et al., 2001; Smith, 2000; Spencer, 2001). Also, simply belonging to a group identified as high-risk sexually active teens (defined as teens who have had sexual intercourse six or more times in the past six months and rarely or never used birth control) predicts low socioeconomic status, sexual intercourse before the age of 15, non-use of birth control, and having multiple sexual partners (Kivisto, 2001). These same behaviors occur concurrently with poor school performance, alcohol and illicit substance use, and having friends in gangs (Kivisto, 2001). Reports from males indicating a history of impregnating others, multiple sexual partners, presence of an STD, drug abuse, and unreliable condom use indicate strong positive correlations among these variables (Guagliardo, Huang, & D'Angelo, 1999).

The parenting literature consistently documents a comparable cluster of "social problems." Young fathers as well as fathers who do not support their children or their relationship with the child's mother tend to exhibit criminal behavior and substance abuse, are of low socioeconomic status, unemployed, and drop out of high school (Cochran, 1997; Weinman, Smith, & Buzi, 2002). Moreover, father-absence tends to co-occur with low

socioeconomic status, family life stressors, conduct problems, dysfunctional parental relationships, sexual precociousness, early pregnancy and young motherhood, and poor parenting, as well as poor academic performance, mood and anxiety disorders, suicide attempts, and violent offending (Ellis et al., 2003). Similar clusters have been identified and described in the divorce literature (Amato & Keith, 1991; McLanahan & Booth, 1989; O'Connor, Thorpe, Dunn, & Golding, 1999; Amato, 1996), the child-abuse literature (Rodgers et al., 2004; Widom, 1994; Perkins & Jones, 2004; Moran, Vuchinich, & Hall, 2004; Dong et al., 2004), the psychopathology literature (Rodgers et al., 2004; Lindsay et al., 2004; Mangina, Beuzeron-Mangina, & Grizenko, 2000) as well as literatures examining unwell motherhood, welfare dependency, learning disabilities, and delinquency (Allen, Philliber, & Herrling, 1997; Voydanoff & Donnelly, 1990; Murphey & Braner, 2000).

The literatures on criminality, delinquency, and drug abuse also document a cluster of analogous "social problems." For example, people who exhibit criminal and delinquent behaviors also tend to abuse legal or illegal substances, experience familial problems, such as familial distress, father absence, unemployment or underemployment, drop out of school, and exhibit social distress, teen pregnancy, and psychopathology. Criminal and delinquent behavior, along with juvenile recidivism (Cottle, Lee, & Heilbrun, 2001), gang involvement, dropping out of school, and poor parental support and supervision (Hunt et al., 2002) tend to co-occur, as do abuse of alcohol (Fischbein & Folklander, 2000) and drugs, risky sexual behavior, impulsivity, low self-esteem, a propensity for general risk-taking (Lejuez, Simmons, Aklin, Daughters, & Dvir, 2004), as well as prior family violence, and violent behaviors (Albus, Weist, & Perez-Smith, 2004). Examination of more specific traits within this literature demonstrates strong positive relations among impulsive sensation seeking and alcohol problems, alcohol use, failure to use condoms, and cigarette smoking (Robbins & Bryan, 2004). Moreover, there are strong positive associations among substance abuse, sexual risk-taking, and STDs including HIV (Sharma, Aggarwal, & Dubey, 2002), as well as adolescent emotional and behavioral problems, sexual and physical abuse, life stress, impaired family relationships, and school drop-out (Friedrich, Lysne, Sim, & Shamos, 2004; Hubbard & Pratt, 2002). Similarly, delinquency is positively associated with an unusually large number of sexual partners and early age of first intercourse (Jessor & Jessor, 1977), as well as drug abuse, teen parenthood, father-absence, being a recipient of poor parenting and supervision, broken homes, and poverty (Bulow & Meller, 1998).

Rowe and Rodgers (1989) accounted for such patterns by proposing a partially heritable and unitary trait disposition toward social deviance in general, which they called "d," in the spirit of Spearman's "g." This common factor accounts for the genetic covariance between sexual motivation, including adolescent promiscuity, and antisocial motivation, including an array of twenty-five delinquent acts "from drug abuse to vandalism" (p. 60). One of the two competing explanations advanced for the existence of this factor was indeed reproductive life-history strategy. Ellis (1988) proposed a similar view, pointing to the utility of the *r/K* concept in explaining why race and socio-economic status correlate with criminal behavior. In a subsequent study, Rowe and Flannery (1994) created a predictive latent variable called "delinquency proneness" that loaded positively and saliently on impulsivity, deceitfulness, rebelliousness, and peer delinquency, but also loaded negatively and saliently on mother affection, father affection, value placed on academic achievement, and parental encouragement of achievement. These latter four negative loadings are additional theoretical links to Life History Theory. Rowe, Vazsonyi, and Figueredo (1997)

provided another direct link to Life History Theory, reporting that juvenile delinquency correlated significantly to Mating Effort both within individuals and across siblings. Again, heritable individual differences in life-history strategy were offered as one possible explanation of these effects.

Recent empirical work

Our ongoing program of research (Figueredo, Sefcek, & Jones, 2005; Figueredo et al., 2005c) involves developing a series of latent variable models—analytic techniques that can be used to identify traits that cluster together—that have identified a single common factor, the K-Factor, underlying a variety of life-history parameters, including clusters of sexual, reproductive, parental, and social behaviors.

Latent variable modeling

The central idea of latent variable modeling is that an observation involves the measurement of some hypothetical attribute that is not itself operationally defined or otherwise directly measured. The approach assumes that a multiplicity of observed behaviors, called “manifest indicators,” more accurately reflect the postulated attribute, called a “latent construct.” The intended focus is on this postulated attribute rather than on the observed behaviors, scores on criterion variables, or results dependent on the particular method that is used. The convergent validity of the different manifest indicators of a given latent construct is the correlation of each indicator to that construct, or, indirectly, the correlations of these indicators to each other (Campbell & Fiske, 1959). Thus, one obtains an operationalization of each construct based on multiple measures rather than an operational definition arbitrarily based upon a single measure. Factor analysis is a major tool of for the validation of multivariate hypothetical constructs (Gorsuch, 1983; Loehlin, 2004).

Psychometric studies of life-history strategy

To test the hypothesis that a single psychometric latent common factor underlies variation in human life-history strategy, we first created a battery of measures that sampled several central behavioral indicators of life-history strategy. We then administered the battery to a sample of 222 University of Arizona undergraduates. A factor analysis of these measures produced a single common factor that explained 92% of the reliable variance in attachment to and investment from the biological father, attachment to and investment from any father figure other than the biological father, adult romantic partner attachment, mating effort, Machiavellianism, and risk-taking propensity. Based on the traits assessed in the study and Life History Theory, we called this factor the K-Factor (Figueredo et al., 2005d).

The study of the individual differences in personality has been a widely explored topic of research. Because no consensus on the exact dimensions that comprise all of human personality has been reached, we used three major personality inventories on the same sample of undergraduates to explore the relationship of the K-Factor to traditional personality dimensions: the NEO-FFI, which describes personality variation with the dimensions of Openness to Experience, Conscientiousness, Extraversion, Agreeableness, and Neuroticism (or Emotionality) (Costa & McCrae, 1992); the EPQ, which describes personality using the

dimensions of Extraversion, Psychoticism, and Neuroticism (Eysenck & Eysenck, 1975); and the ZKPQ, which describes personality on the dimensions of Impulsivity/Sensation-Seeking, Neuroticism-Anxiety, Aggression-Hostility, Activity, and Sociability (Zuckerman, Kuhlman, Joireman, Teta, & Kraft, 1993). These inventories have been used extensively with little cross-cultural variation in the core components of personality. Although differing on specific dimensions, each of these inventories shares the ability to tap into three of the same major constructs: Neuroticism, Extraversion, and Psychoticism.

We used factor analysis to create common factors that cut across the particular personality inventories and obtained three common higher-order factors, Big N (for Neuroticism), Big E (for Extraversion), and Big P (for Psychoticism), which accounted for virtually 100% of the reliable variance on the personality measures. This result essentially replicated results published previously by Zuckerman et al. (1993). Big N loaded positively on NEO-FFI Neuroticism, EPQ Neuroticism, and ZKPQ Neuroticism/Anxiety; Big E loaded positively on NEO-FFI Extraversion, EPQ Extraversion, and ZKPQ Sociability; Big P loaded negatively on NEO-FFI Conscientiousness and NEO-FFI Agreeableness, but loaded positively on EPQ Psychoticism, ZKPQ Impulsivity/Sensation Seeking, and ZKPQ Aggression/Hostility. In latent variable modeling, a higher-order factor stands in the same relation to its lower-order factors as a lower-order factor does to its manifest indicators; the higher-order factor thus explains the common variance among the lower-order factors just as a lower-order factor explains the common variance among its indicators (Gorsuch, 1983).

In our study, the bivariate correlations of the K-Factor with higher-order personality factors were negative with Big N, positive with Big E, and negative with Big P. The correlations were statistically significant for Big N and Big P and approached significance for Big E. An especially high negative correlation of the K-Factor with Big P also supported Zuckerman and Brody's (1988) prediction that Psychoticism is more relevant to K than Neuroticism or Extraversion. Furthermore, the bivariate correlation of the K-Factor was negative with Sex, denoting generally lower K-Factor scores for males, but did not relate to Age in this restricted age-range sample. The lower mean on the K-Factor for males is consistent with theoretically predicted and empirically well-documented sex differences in reproductive strategy (Trivers, 1972; Geary, 2002; Geary, Vigil, & Byrd-Craven, 2004).

In another study of 193 University of Arizona undergraduates (Sefcek, Figueredo, & Miller, 2005, 2005), we expanded the K-Factor test battery to include several scales derived from the National Survey of Midlife Development in the United States (the MIDUS Survey; Brim et al., 2000) in combination with several other published measures of contact and support with friends and family (Figueredo et al., 2001). This replication of the K-Factor loaded positively on parental investment as a child from the biological mother as well as from the biological father, secure adult romantic partner attachment, family social contact and support, friends' social contact and support, and altruistic feelings and behavior toward non-kin. We also performed a constructive replication (Tal, Hill, Figueredo, Frias-Armenta, & Corral-Verdugo, 2005) in Northern Mexico (Hermosillo, Sonora) with a sample of 164 adults with their own children. Again, we used several scales derived from the MIDUS Survey—translated, with permission, into Spanish—in combination with the other published measures of contact and support with friends and family. These scales included parental investment as a child from both mother and father, parental investment in their own children, family social contact and support, friends' social contact and support, general altruism, and long-term planning propensity. As before, a single common

factor explained 92% of the reliable variance. In all, these preliminary small-sample analyses demonstrated the presence of a single psychometric latent common factor underlying individual variation in human life-history strategy as measured by our instruments. Moreover, the analyses demonstrated that the K-Factor shows some cross-cultural validity.

The composition of the K-Factor suggested that high-K individuals possess attitudes and beliefs that support sexual restraint (e.g., Rushton, 1985). Hence, high-K individuals are more likely to delay sexual activity and, once initiated, are less likely to engage in risky sexual behaviors. Walsh, Brumbach, and Figueredo (2005) examined baseline sexual attitudes, beliefs and behaviors of over a statewide sample of 10,958 adolescents, 12–19 years old, from schools and detention centers participating in a program promoting sexual abstinence until marriage. Again, we detected a single common factor, which we called Sexual Restrictedness, hypothesized to be a dimension of the K-Factor that underlies a variety of self-reported sexual beliefs and attitudes. Salient positive indicators of the Sexual Restrictedness Factor included religiosity, endorsed value reasons to refrain from sex, endorsed health reasons to abstain from sex, perceived refusal skills regarding sex, sexual decision-making ability, positive attitudes toward teenage abstinence, perceived subjective norms about pre-marital sex, intentions to abstain from sex, and prosocial behaviors. Salient negative indicators of the Sexual Restrictedness Factor included endorsement of positive aspects of sex and non-sexual risk behaviors. This single common factor explained 89% of the reliable variance. Moreover, the number of parents in the home, even when controlling for age, predicted the Sexual Restrictedness Factor: youth from two-parent homes were more likely to be sexual restricted than those from one-parent homes. Perhaps most importantly, the level of Sexual Restrictedness Factor inversely predicted self-reported sexual activity, even when statistically controlling for age.

Secondary analysis of the MIDUS survey

In a more recent study (Figueredo, Vásquez, Brumbach, & Schneider, 2005a), we selected data taken from a subsample of 2095 individuals (who were currently parents) from the MIDUS (Brim et al., 2000) singleton (non-twin) data. We used 20 scales constructed from MIDUS items that corresponded to dimensions we hypothesized to be indicators of the K-Factor, each of which had acceptable internal consistency (as measured by Cronbach's alpha). The scales used included Mother Relationship Quality, Father Relationship Quality, Marital Relationship Quality, Children Relationship Quality, Family Support, Altruism Toward Kin, Friends Support, Altruism Toward Non-Kin, Close Relationship Quality, Communitarian Beliefs, Religiosity, Financial Status, Health Control, Agency, Advice Seeking, Foresight/Anticipation, Insight Into Past, Primary Control/Persistence, Flexible/Positive Reappraisal, and Self-Directedness/Planning. Factor analysis revealed a single common factor that explained 70% of the reliable variance in these measures.

Life History Theory predicts that high-K individuals allocate more to parenting, as well as to their health and well being and that of their children. High-K individuals, in contrast to low-K individuals, should therefore be more individually viable on a variety of indicators of general health, developmental stability, and mental and physical function. With these predictions in hand, we constructed another common factor, the "Covitality" Factor (Weiss, King, & Enns, 2002), from MIDUS scales to measure these predicted effects of increased Parental and Somatic Effort. The Covitality Factor was constructed from scales

for Subjective Well-Being, Negative Affect, Positive Affect, General Health, and Medical Symptoms. Furthermore, Fitness Indicator Theory (Miller, 2000) predicts that increased “Covitality” should also be behaviorally displayed in the manifestation of sexually selected mental traits, that is, traits that aid in competition for mates or increase one’s attractiveness as a mate (e.g., conscientiousness). We therefore performed a factor analysis on the MIDUS scales for the “Big Five” personality factors to obtain a higher-order personality construct, composed of scales for Openness to Experience, Conscientiousness, Extraversion, Agreeableness, and Neuroticism.

We note two relevant but previously unrelated empirical facts: (1) ostensibly established personality models such as the Five-Factor Model (Costa & McCrae, 1992) and the ‘Gigantic Three’ (Eysenck & Eysenck, 1975) generate higher-order personality dimensions (Digman, 1997; Zuckerman et al., 1993), and (2) certain profiles of traditional personality factors may indeed reflect the mating preferences and the reproductive life-history strategies of individuals (Buss, 1989, 1991, 1997, 1999). For example, when the self-report of a person’s personality is subtracted from the description of their “ideal romantic partner,” this ideal romantic partner is rated significantly higher than the self on Conscientiousness, Extraversion, and Agreeableness, and significantly lower than the self on Neuroticism (Figueredo, Sefcek, Vasquez, et al., 2005; Figueredo, Sefcek, et al., 2005). In a related study, Vasquez (2004) found that a higher-order factor reflecting this pattern can be found using the NEO-FFI (Costa & McCrae, 1992), loading saliently and positively on Conscientiousness, Extraversion, and Agreeableness, and saliently and negatively on Neuroticism. Furthermore, Vásquez also found that the Mate Value Inventory (Kirsner, Figueredo, & Jacobs, 2003), a measure of self-reported mate value, correlated significantly and positively (.50) with this general personality construct. These results confirm that a higher-order personality factor indicates perceived mate value, as predicted by theory. Moreover, the higher-order personality construct we derived from the MIDUS scales for the “Big Five” closely converges with this “ideal romantic partner” personality profile and higher-order factor found in previous research. In short, an ideal mate would be high on Conscientiousness, Extraversion, and Agreeableness, and low on Neuroticism.

The K-Factor, Covitality factor, and general Personality factor correlated significantly. To determine whether the Covitality Factor and this general Personality Factor were all extended indicators of Life History Strategy, as suggested by these theoretical considerations, we factor analyzed them along with the K-Factor and obtained a single higher-order factor, which we called the “Super-K” Factor, which explained virtually all of the reliable variance among them. This finding supported the hypothesis that a high-K life-history strategy predicts the physical and mental health consequences of high somatic effort and parental and nepotistic effort received and is also manifested in the behavioral display of sexually selected personality and behavioral traits.

Life History Theory further predicts significant and positive correlations among the K-Factor and other socially important variables. To investigate this prediction, we correlated the K-Factor to a set of variables theoretically expected to covary with it. Several authors, for example, claim that the childhood presence or absence of an individual’s biological father affects adult life-history strategy (Belsky et al., 1991; Chisholm, 1996; Rowe, 2000). Upon analyzing our data, we found that the K-Factor correlated significantly and positively with the presence or absence of the biological father during childhood. This finding is consistent with previous results investigating the effects of father absence on various mating strategies. Moreover, it supports the prediction that childhood involvement and

interaction with the biological father affects life-history strategies in adulthood, although these studies do not exclude shared genes affecting both parental and child behavior.

Social privilege

Because of such significant correlations of life history with social and familial variables, it is important to address “Social Privilege Theory” (Gottfredson, 2005) as an alternative hypothesis for both the existence of and the associations among these clusters of life-history traits. Social Privilege Theory is the sociological view that sociocultural factors such as social stratification according to sex, race, and class may determine characteristics such as variance in mental abilities and health status normally attributed by differential psychologists to individual differences (Arrow, Bowles, & Durlauf, 2000; Kawachi, Kennedy, & Wilkinson, 1999; Gottfredson, 2005; Kerckhoff, 2000; Wilkinson, 1996). For example, the “Family Advantages” version of Social Privilege Theory maintains that factors present in more or less advantaged families provide greater or lesser opportunities during development. These variations in opportunities function to transmit social class advantages and disadvantages. Advocates of this view predict that equalizing social opportunities will dissolve the observed links between parent and child outcomes.

To control the possible effects of stratification on such sociocultural factors, hierarchical regression models were used to residualize (statistically adjust) all of the 30 targeted life-history traits on respondent sex, race, total financial earnings of the self, spouse, and all other family members for the past 12 months, and the highest degree of education achieved to date by both the self and spouse. We then repeated the entire series of factor analyses reported above on these residualized variables.

Although virtually every multiple regression model based on the “Social Privilege Theory” was statistically significant for this set of socioeconomic and demographic predictors, the amount of variance collectively accounted for by each entire regression model was always less than 10% and usually much less than that. Furthermore, the factor loadings for the K-Factor, the Covitality Factor, and the Personality Factor on the residualized life-history traits were not appreciably attenuated by this statistical manipulation, nor were the correlations among them or with the higher-order Super-K Factor. Finally, the factor model parameters were either virtually unchanged or slightly improved. For example, the variance accounted for by the K-Factor itself actually increased from 70% to 72% as a result of this procedure. In short, Social Privilege Theory cannot explain either the K-Factor itself or any of the additional correlations with Covitality and Personality that constitute the Super-K Factor. If anything, removing several possible sources of extraneous variance improves the multivariate model fit to the data. In other words, the basic K-related clustering of dimensions of personality, parenting, sexual behavior, and so forth are found independent of the factors associated with Social Privilege Theory. This does not mean that K-related dimensions do not vary across sex or social class, for instance, but rather the same clusters are found within as well as across these groups.

Behavioral genetic studies of life-history strategy

We recently replicated these results using the genetically informative MIDUS subsample of Monozygotic (MZ) and Dizygotic (DZ) twins (Figueredo, Vásquez, Brumbach, & Schneider, 2005b). Constructed the same way as for the singleton data, at first ignoring the

fact that the respondents were twins, the 20-scale K-Factor accounted for 72% of the reliable variance in the twin data. The 5-scale Covitality Factor and the 5-scale Personality Factor also replicated, accounting for virtually all of the reliable variance in their component scales. The significant bivariate correlations among the K-Factor, the Covitality Factor, and the Personality Factor also replicated with the twin data, as did the higher-order Super-Factor that included all three of these common factors. The model parameters for the twin data were virtually identical to those obtained using the singleton data. The evaluation of Social Privilege Theory by residualization on the set of socioeconomic and demographic predictors described above also replicated in the twin data, with identical results. Again, Social Privilege Theory, as an alternative hypothesis, did not account for the patterns of correlations among these life-history traits in the twin data.

Using only the data from 309 same-sex DZ twins for maximal comparability to the data from 333 necessarily same-sex MZ twins reared together for at least the first 12 years of life, the Falconer (1989) formula was applied to estimate both univariate and bivariate heritabilities. We then subjected the genetic variance–covariance matrix obtained to factor modeling. The Genetic K-Factor accounted for 61% of the variance of its component scales, the Genetic Covitality Factor accounted for 85% of the variance of its component scales, and the Genetic Personality Factor accounted for 55% of the variance of its component scales. The estimated heritability of the K-Factor was .65, that of the Covitality Factor was .52, and that of the General Personality Factor was .59. Furthermore, there were significant and very high genetic correlations among the Genetic K-Factor, the Genetic Covitality Factor, and the Genetic Personality Factor; these correlations suggest the same genes may contribute to the traits assessed by each of these factors. The Genetic Super-K Factor accounted for 82% of the variance of its component scales. The estimated heritability of the Genetic Super-K Factor as a whole was .68. The residual environmentality thus leaves plenty of room for the variance explained by Social Privilege Theory.

Generally, the genetic factor loadings were greater than the phenotypic factor loadings. Moreover, the heritability estimates of the individual scales were substantial but those for the genetic common factors were appreciably greater. These results suggest that the same set of pleiotropic genes (i.e., genes having multiple effects) influence each of the measured life-history traits considerably. This finding supports the hypothesis that life-history strategy is predominantly under the control of regulatory genes that coordinate the expression of an entire array of life-history traits. Presumably, common genetic control is necessary to integrate these individual tactical elements into a coherent and internally consistent reproductive strategy.

The hypothesized existence of such higher-order regulatory genes does not rule out adaptive interaction with the environment. It is quite probable that the expression of these regulatory genes is conditional, that is, subject to environmental triggers. Natural and sexual selection presumably favor enough developmental plasticity in the control of life-history strategy to respond appropriately to an array of adaptive contingencies reliably present in human evolutionary history. Our results are consistent with this assertion, indicating that expression of a substantial portion of the variation in life-history traits is under environmental control, although individuals may differ in the likelihood of expressing a high- or low-K strategy even when exposed to similar environments.

These results point to the existence of a single, highly heritable latent psychometric common factor (the K-Factor) that, as predicted by evolutionary ecological theory, underlies both the phenotypic and genetic covariances among a wide array of behavioral and

cognitive life-history traits. In addition, these results indicate the K-Factor is significantly associated with a composite of both mental and physical health outcomes (“Covitality”), significantly correlates with a general factor derived from the “Big Five” dimensions of personality,¹ and correlates significantly to the quality of one’s relationship to one’s biological father and perhaps other childhood experiences. Furthermore, these results indicate that a substantial portion of these phenotypic correlations is genetic in nature, although expression of these genes is likely influenced to some extent by the environment.

Social deviance

To relate Life History Theory to the empirical data regarding the comorbidity of “social problem” behaviors more directly, we performed another small-sample study explicitly relating the K-Factor to such a complex of traits (Figueredo et al., 2005c; Wenner, Figueredo, & Jacobs, 2005). We presented a battery of questionnaires measuring a set of related theoretical constructs to a sample of 35 University of Arizona undergraduates. We used a short form measure of Delinquent Behavior, the D-20, largely drawn from a much larger pool of items used by Charles and Egan (2005). Those data were used to select the best items by means of an “extension analysis,” beginning with the most common core characteristics of delinquency identified by an experienced Forensic Psychologist (Professor Vincent Egan of Glasgow Caledonian University). We supplemented this with a revised measure of Risk Taking Behaviors, based on the Life Experiences Questionnaire (LEQ), originally developed by Zuckerman and Kuhlman (2000). This measure sampled risk-taking behavior in various domains, including drinking, smoking, drug-taking, risky sexual activity, reckless driving, and gambling. We also created a purified measure of Impulsive Behaviors by sorting items from several existing questionnaires, including the Self-Control Schedule (Rosenbaum, 1980), the Self-Control Questionnaire (Rehm, 1988), and the Barrett Impulsivity Scale (Barrett, 1983) into two composite lists of Impulsive Behaviors (*sensu stricto*) and Impulse Control items, respectively. This also produced a separate measure of Impulse Control, as distinct from Impulsive Behavior *per se*.

The measures of Delinquent Behaviors, Risk-Taking Behaviors, and Impulsive Behaviors were then aggregated into a single unit-weighted common factor. We labeled this the Risk Factor, consistently with criminological theory (Gottfredson & Hirschi, 1990). The content of the Risk Factor is extremely similar to the multivariate construct previously labeled “d” (Rowe & Rodgers, 1989). We then related the Risk Factor to a 20-item short form measure of the K-Factor, which we called the Mini-K, based on all of the previous work reported on the convergent indicators of Life History Strategy. We found that, as predicted by Life History Theory, the Risk Factor significantly and negatively correlated with the K-Factor. The Risk Factor also significantly and negatively correlated with the separate measure of Impulse Control that was produced by our sorting of items from existing questionnaires. In addition, as predicted by theory, the K-Factor significantly and highly positively correlated with this separate and purified measure of Impulse Control.

The complete Mini-K short form is provided in Appendix A for reference. Mini-K has an internal consistency (Cronbach’s alpha) reliability of about .70 and a test–retest

¹ Perhaps reflecting the perceived characteristics of a high-mate value or “ideal” romantic partner.

reliability of about .70 as well. The Mini-K is currently being validated on a variety of samples (Brumbach, Figueredo, & MacDonald, 2005; Sefcek et al., 2005; Sefcek, Figueredo, & Miller, 2005; Vásquez, Sefcek, Douglas, & Figueredo, 2005; Wenner et al., 2005; Wolf, Vásquez, Frias-Armenta, Corral-Verdugo, & Figueredo, 2005), and it correlates positively with the K-Factor battery as a whole, with the Rand SF-36 Short Form Health Survey, with the Mate Value Inventory, with Openness to Experience, with Extraversion/Dominance, with Agreeableness/Nurturance, and with Conscientiousness. The Mini-K correlates negatively with Neuroticism and with both Anxious and Avoidant Romantic Partner Attachment. Furthermore, the Mini-K has significant assortative mating and interrater reliability coefficients in both same-sex friends and romantic partners.

In addition, we created a purified measure of Impulsivity, loosely based on the Seven Deadly Sins (i.e., Pride, Sloth, Gluttony, Wrath, Envy, Lust, and Greed), which we called the “Jake’s Temptation” scale. This scale asked respondents to estimate the number of times in the past two weeks they were *tempted* to engage in impulsive behavior, regardless of whether or not they acted on their impulses. We defined *temptations* as all behaviors producing relatively small short-term gains but relatively large long-term costs. The addition of this scale permitted us to construct and test a general linear model for predicting impulsive, risky, and delinquent behaviors based upon the presumed opponent processes of raw impulsivity and impulse control. Running a hierarchical general linear model of the Risk Factor with Jake’s Temptation, Impulse Control, and their two-way interaction as predictors, we obtained significant and opposing main effects of behavioral excitation and inhibition. There was no significant statistical interaction between the presumed opponent processes.

Furthermore, these analyses allowed us to test for the incremental validity of the K-Factor over Impulse Control. Hierarchically entering Impulse Control before the Mini-K into the general linear model, we obtained a significant *incremental* effect of the K-Factor over Impulse Control in predicting the Risk Factor. This indicated that the K-Factor had a *direct effect* upon the Risk Factor that was not mediated by Impulse Control. Impulse Control may represent just one more characteristic, among others, of high-K individuals and might correlate spuriously, at least in part, to the Risk Factor. Partial mediation remains possible, but a residual direct effect of the K-Factor remains that high Impulse control does not entirely explain.

Going one step further, we tested the incremental validity of Impulse Control over the K-Factor. Hierarchically entering the Mini-K before Impulse Control into the general linear model, we again obtained a significant main effect of the K-Factor, but *no* significant incremental main effect of Impulse Control in predicting the Risk Factor. That indicated that the K-Factor might be *directly* suppressing impulsive, risky, and delinquent behaviors and that this effect is more than an indirect effect of Impulse Control. The most parsimonious regression model with only Jake’s Temptation and the Mini-K predicting the Risk Factor explained 37% of the variance. The effect of Jake’s Temptation was positive and that of the Mini-K was negative in predicting the Risk Factor and both were statistically significant and substantial in magnitude.

This study confirmed that a high-K life-history strategy is a major protective factor against a positive manifold or “cluster” of correlated socially problematic behaviors and is highly associated with the theoretically important construct of impulse control. Most recently, Frias-Armenta et al. (2005) conducted a study of 56 delinquent and 80

non-delinquent Mexican juveniles between 11 and 15 years of age that related executive functions to social deviance. A Deviance Factor was constructed which loaded positively on antisocial behavior, self-control problems, impulsivity, and risk-taking, and loaded negatively on both susceptibility to peer pressure and future orientation, accounting for 99% of the reliable variance. Performance on two measures of executive functions correlated significantly and negatively with the Deviance Factor: the Wisconsin Card Sort (−.28) and a modified version of the Stroop Test (−.25) that emphasized set-shifting abilities. Executive functions include the abilities entailed in planning for the future, inhibiting or delaying responding, initiating behavior, and shifting between activities flexibly. The ability to set goals, plan, sequence, prioritize, organize, initiate, inhibit, pace, shift, monitor, control, and complete actions all involve executive functions (cf., [Lezak, Howieson, & Loring, 2004](#)).

Life History Theory and neuropsychology

In humans, the frontal lobes are essential for impulse control and delay of gratification, factors central to synthetic reasoning (the combination of ideas into a complex whole), abstract thought, and the organization of independent behaviors in time and space (e. g., speech, decision-making, and willed action; [Goldman-Rakic, 1984](#); [Davison, Neale, & Kring, 2004](#)). Damage to the prefrontal areas causes a variety of problems including difficulties planning, forming, or implementing behavioral rules and strategies. Individuals with prefrontal damage also have difficulty inhibiting their own behaviors, likely because they have difficulty using social or self-generated rules to guide their actions ([Reisberg, 2002](#), p. 34). In addition, patients with unilateral prefrontal damage have specific impulse control problems in simple tasks such as standardized maze learning. A primary problem in these simple tasks appears to be a failure to comply with task instructions. For example, these individuals consistently disregard a buzzer signaling an error, thereby continuing on an incorrect path and triggering further error signals. This rule-breaking behavior disappears spontaneously after a few trials only to appear again on the next novel task ([Cavanaugh, 1983](#); [Milner, 1964](#); [Milner & Petredez, 1984](#)).

The ability to control impulses is central to most major accounts of personality (including our developing account based on the K Factor); whereas difficulties with impulse control are a feature of many accounts of mental disorders ([Moeller, Barratt, Dougherty, Schmitz, & Swann, 2001](#)). For example, children with impulse control problems often present with attention-deficit disorder, inattention, hyperactivity, oppositional-defiant disorder, or child conduct disorder ([APA, 1994, 2000](#)). Similarly, adults with impulse control problems often present with anti-social personality disorder, borderline personality disorder, or substance abuse. In addition, paraphilias, pyromania, kleptomania, and intermittent explosive disorder tend to involve problems with impulse control ([APA, 1994, 2000](#)).

Theoretical and empirical research on impulse control converges on a set of cardinal features: Engaging in behavior too quickly, lacking deliberation before action, and failing to consider the consequences of action ([Patton, Stanford, & Barratt, 1995](#)). Impulsive behavior reflects failed inhibitory control, short-latency decisions, minimal task persistence, susceptibility to boredom, and sensation seeking. Criminal offenders are likely to exhibit this cluster and the existence of such a cluster predicts re-offending ([Craig, Browne, Beech, & Stringer, 2004](#)). The neuropsychological and impulse control literatures converge

to suggest that information-processing deficits exist in offenders. Both literatures point toward deficits in three areas; Executive functioning in circuits of the prefrontal cortex,² executive emotional processing in circuits in the orbito-frontal cortex (associated with the limbic system), and emotional processing in circuits in the Amygdala. Circuits in each of these areas are central to the cluster of emotions and behaviors exhibited in this population (Blair & Frith, 2000). Moreover, similarities between many aspects of the emotions and behaviors exhibited by this population and the emotional and behavioral effects of surgically placed damage to specific parts of the brain in nonhuman animals—including damage to the Septum, the Hippocampus, and the Frontal Cortex—have led many to propose that a key element in this cluster is heightened impulsivity related to diminished frontal and temporal lobe functioning (Gorenstein & Newman, 1980; Metcalfe & Jacobs, 1998; Metcalfe & Mischel, 1999; Metcalfe & Jacobs, 2000).

These facts add a proximate and mechanistic dimension to our thinking about the causes of the cluster of behaviors we identified as life-history traits. We propose that the coordination of Life History Strategy provides the ultimate adaptive functions behind the proximate brain mechanisms of impulsivity and impulse control. Moreover, we propose that, properly done, results from ecologically valid neuropsychological tests, as well as brain imaging studies will serve as one centerpiece of the personality theory we are developing.

Traditionally, a proper interpretation of a neuropsychological profile rests on the assumption that the brain is a plastic organ that continuously grows and changes in response to its genetic programs and to successful (and unsuccessful) solutions of adaptive problems. By this assumption, the brain, as well as the cognition and behavior it produces, holds both innate and acquired knowledge about itself, the physical body, and the outside world. The view suggests that, in the natural conditions of an individual's life, a specific genetic blueprint and an array of specific experiences combine in idiosyncratic patterns. The resulting unique circumstances in turn lead to a unique pattern of cognitive, affective, and behavioral characteristics that characterize a person's psychological repertoire. The neuropsychological profile reflects both that repertoire and the product of individual differences in brain organization, functions, and ability to adapt to change. It follows that the use of standardized neuropsychological examinations may help us understand the proximate mechanisms of process mediation by which the complex of behaviors that constitute an integrated and coordinated life-history strategy are controlled and implemented by the brain.

This work predicts that results from standardized neuropsychological testing will provide theoretically and clinically useful idiographic profiles of people exhibiting characteristics of the trait-clusters we described. By characterizing extant cognitive, affective, and behavioral patterns that are a product of natural and sexual selection (which provides the raw material), ecological demands (which fashioned the raw material), and the extant environmental demands (which shape the raw material into the form it exhibits in a given situation), such a profile permits a comparison of an individual profile to normative data, which in turn permits the neuropsychologist to determine the cognitive strengths and weaknesses of any person. One may then use this interpretation to relate individual differ-

² Asahi, Okamoto, Okada, Yamawaki, and Yokota (2004), for example, report that difficulties with impulse control reflect hypoactivity of the right prefrontal cortex.

ences in these capacities to specific areas of the brain. Conversely, one may use these profiles to tailor intellectual or psychological interventions to the specific needs of a person.

The theoretical approach that we are taking, coupled with the empirical data we have outlined, predicts that a low-K individual will exhibit a neuropsychological profile indicating low-normal performance on tests sensitive to prefrontal and temporal function (e.g., planning, set shifting, long-term memory, and the ability to “contextualize” or recognize and discriminate both physical and social situations).

An integration of ultimate, proximate, and developmental models

The course of brain development is particularly susceptible to perturbation during periods of rapid change. As brain–hormone interactions during the adolescent brain ‘growth spurt’ are integral to behavioral maturation, temporal dissociations between gonadal maturation and adolescent brain development are likely to have consequences for adult behavior. For example... precocious puberty results in exposure of the brain to steroid hormones in early childhood. Will premature organizing effects of steroids alter the developmental trajectory of the brain? Animal models predict they would. At the very least, variations in the temporal sequence of gonadal maturation and adolescent brain development would...contribute to individual differences in adult behavior and risk for sex-biased psychopathologies. (Sisk & Foster, 2004, p. 1045)

Risk taking and novelty seeking are hallmarks of typical adolescent behavior. Adolescents seek new experiences and higher levels of rewarding stimulation, and often engage in risky behaviors without considering future outcomes or consequences....Brain pathways that play a key role in emotional regulation and cognitive function undergo distinct maturational changes during this transition period. (Kelly, Schochet, & Landry, 2003, p. 27)

One focus of evolutionary developmental psychology has been the development of a functional explanation of the extended juvenile period in humans. Many authors (e.g. Flinn, this issue; Geary, 2005; Bjorklund & Rosenberg, 2005) conclude that need for this extended childhood and adolescence resulted, at least in part, from the social complexity of human groups. More specifically, the need for a large brain, required to deal with the demands of the increasing size and complexity of human societies (cf., Dunbar, 1998), caused selective pressure for an extended juvenile period. Furthermore, the variability of human environments also necessitated developmental plasticity and the ability to deal with novel situations (Bjorklund & Rosenberg, 2005; Figueredo, Hammond, & McKiernan, 2005; Geary, 2005).

Adolescence is a time of turmoil. Some argue that the turmoil relates to gonadal hormones associated with gonadarche (puberty). In contrast, we hypothesize that this turmoil is less dependent on increases in adolescent hormones than a developmentally adaptive state of neural development occurring during adolescence.

Prominent developmental changes in the Frontal Cortex and the Limbic System occur during adolescence, which we, for our purposes, define as roughly between the ages of 12 and 18 years of age—occasionally extending as early as 8 years of age and as late as 25 years of age in humans. Defined this way, adolescence is a temporally ambiguous phase during which one makes a transition from childhood to adulthood. In contrast, gonadarche is a temporally discrete phase, usually occurring between 8 and 12 years of age, during which one attains sexual maturation. Hence, gonadarche is simultaneously part of and

contained within the transitional phase known as adolescence (but see Giedd et al., 1999 for a longitudinal MRI study of brain development).

Perhaps the most substantial behavioral characteristics occurring during adolescence are in the arenas of risk taking, Impulsivity, novelty seeking, reward sensitivity, decision-making, social interactions, and play fighting. In addition, humans show a behavioral profile of seeking novel experiences involving drugs and sexual behavior and a period during which a substantial majority of adolescents see risky behaviors as exciting and rewarding. Hence, adolescents exhibit unusual characteristics in emotional expression, cognitive and attentional function, and reward sensitivity. Brain areas that show both profound developmental change and appear deeply involved in these cognitive, affective, and motivational systems involve corticolimbic circuitry, including the circuits in the Frontal Cortex, the Amygdala, the Hippocampus, the Nucleus Accumbens, and the dopaminergic innervation of these structures (see e.g., Spear, 2000 for a comprehensive review and Sisk & Foster, 2004 for a brief, but more recent review). A variety of neuroanatomical, neurohormonal, and hormonal changes occur in these circuits during adolescence. These changes reflect dramatic differences in the behavioral strategies and tactics exhibited by humans in childhood or adulthood.

The frontal cortex

As outlined above, the cognitive capacities related to the production of behaviors that depend upon the integrity of this part of the brain include executive functions such as working memory, rule governance, impulse control, delay of gratification, attention, decision making, and effort after meaning. When damage, loss of myelin, or changes in neurotransmitter/hormonal concentrations disrupt the Frontal Cortex we consistently observe changes in personality that include disorganized, impulsive, stimulus-driven behavior. As the Frontal Cortex, the Hippocampus, the Amygdala, and related structures develop, we observe more adult-like behavior in the natural environment accompanied by a continuing increase in the ability to perform on neuropsychological tasks dependent on the normal function of these structures.

During adolescence, substantive changes occur in the human Frontal Cortex (Giedd et al., 1999). For example, the Frontal Cortex of the adolescent primate brain loses, by some estimates, as many as 30,000 synapses *per second* (e.g., Rakic, Bourgeois, & Goldman-Rakic, 1994). This may partially account for a loss in gross volume in the human Frontal Cortex during adolescence. Consequently, complete myelination of the Frontal Cortex occurs late in adolescence and well into adulthood. Indeed, the Frontal Cortex is the last area of the brain in to complete myelination (see e.g., Spear, 2000).

Because the Frontal Cortex plays a central role in decision-making, emotional regulation, behavioral inhibition, and delay of gratification, all of which are essential for cost-benefit based decisions based on weighing risk/reward trade-offs, the cognitive, emotional, and motivational substrate of adolescent behavior very likely involves a still immature substrate consisting of the Frontal Cortex. In addition, developmental changes occurring in the Hippocampus (related to cognitive mapping, autobiographical memory, and behavioral flexibility), the Amygdala (related to expression and recognition of emotion), the Ventral Striatum (Nucleus Accumbens), and the Ventral Tegmental Area (related to sensitivity to positive and negative motivation, reward, the incentive value of sensory stimuli.) appear to play a role in the profound behavioral changes seen during adolescence (see below for details).

The hippocampus

The cognitive capacities related to behavior—and that depend upon the integrity of this part of the brain include the ability to contextualize rules, differentiate situations, seek novelty, explore, exhibit behavioral flexibility, acquire and use situational awareness, and to form episodic memories (memories localized in space and time). When damage, loss of myelin, or changes in neurotransmitter/hormonal concentrations disrupt the Hippocampus, we consistently observe an inability to map space, disabilities in differentiating situations, and profound difficulties with long-term memory; in contrast, short-term or “working” memory appears unaffected. As the Hippocampus and related structures develop, we observe more adult-like behavior in spatial ability, autobiographical memory, and the ability to differentiate both physical and social situations, which are abilities necessary for normal social intercourse (see O’Keefe & Nadel, 1978 for an early review; and Duvernoy et al., 2005 for a more recent review).

A substantial pruning of glutamate receptors occurs in the human Hippocampus during adolescence, accompanied by a loss of up to 25% of *N*-methyl-D-aspartate (NMDA) receptors in the same region (demonstrated, thus far, only in rats). Over and above dramatic changes in NMDA receptors, observable changes occur in the GABA/BDP receptor complex and endogenous cannabinoid systems during this period of life. Myelination continues in portions of this structure throughout adolescence and may continue well into adulthood. In addition, some believe that during this period, not only are neurons generated in this region, but also massive pruning of synapses occur simultaneously.

The amygdala

The cognitive capacities related to behavior—and that depend on the integrity of this part of the brain—include the ability to express and recognize emotion, “mind read” other humans (e.g., infer certain affective and motivational states of another human being on the basis of their movement, posture, and facial expression), and to detect and appropriately respond to environmental threats to the individual (e.g., LeDoux, 1998, 2000).

A biologically based heightened reactivity to emotionality arousing material (including fearful, sexual, and appetitive stimuli such as food and drink) is suggested by fMRI studies indicating age-specific differences in Amygdala activity in adolescent versus adult humans in the presence of emotionally ‘hot’ material (e.g., Killgore & Yurgelun-Todd, 2004). Coupled with this is the fact that the neural basis of feedback loops (to which the Amygdala and the Hippocampus contribute a great deal) regulating HPA-based stress responses changes dramatically during adolescence—at least partially through changes in connectivity occurring in this structure. This suggests that adolescents produce not only developmentally specific neural responses to challenging stimuli; their peripheral reactions are substantially different from those of adults.

Other changes

In addition to the changes we briefly sketched, other maturational changes occur during adolescence. The cognitive capacities that appear to rely on the integrity of the Nucleus Accumbens and Ventral Tegmental Area include sensitivity to reward and reinforcement and are likely to influence incentive value (the “appeal”) of sensory stimuli. Massive

changes occur in dopamine projections to (and concentration in) the Frontal Cortex and mesolimbic brain regions occur by way of developmental changes occurring in these structures. In addition, both overproduction and pruning of synapses in these regions occur during adolescence. These changes appear to be responsible for a shift in balance from subcortical toward a greater prominence of cortical dopamine in early adolescence. Because these dopaminergic systems are involved in modulating the reward value of reinforcers, we find systematic changes in subjective ‘taste,’ the incentive value of stimuli, and sensibility throughout adolescence.

In addition, because of regional differences in myelination and other factors, there is a striking change (increase) in the independent information-processing capacity—and possibly information processing specialization—of the two cerebral hemispheres during adolescence. MRI imaging data suggest that the gross anatomy of many areas of the human cortex do not approximate average adult levels until about 20 years of age in humans (e.g., Giedd et al., 1999). Furthermore, measures of brain activity show developmental hypermetabolism until about 20 years of age in humans at which time metabolism settles to adult levels. Finally, gonadal steroids act to organize circuits in the primary optic sensory cortex, the Hippocampus, and the Amygdala throughout adolescence.

Although the developmental changes we have described are by no means complete, the list is complete enough to illustrate the dramatic changes occurring in various parts of the human brain between the ages of about 12 and 25, the ages normally considered to encompass human adolescence. In short, the adolescent brain is in flux, undergoing numerous regressive and progressive changes in mesocorticolimbic regions. Gonadarche introduces a unique set of adaptive problems that interact with adaptively appropriate neural development in personally, socially, and clinically important ways.

Adaptive individual differences in brain development

There are documented individual differences in the rates and degrees of development of all of these brain areas. At the same chronological ages, individuals may differ appreciably in the degree of development that has taken place. Furthermore, not all individual brains continue these developmental patterns to the same degree.

We hypothesize that these observed individual differences are more than mere random errors of development. We propose that they instead relate to individual differences in life-history strategies documented by our group and others. Just as others suggest that speed of maturation and pubertal development are a life-history trait of evolutionary significance, we suggest that both the speed and the eventual extent of brain development also represent life-history traits. By this view, individual differences in life-history strategies find their proximate mediation in varying rates and degrees of brain development as well as adrenal and gonadal development. Life-history strategies represent the ultimate adaptive functions and heterochrony in brain development represent the proximate mechanisms by which they are instantiated.

Hence, we suggest there are three levels of adaptive heterochrony at work. One is the heterochrony or interindividual variability in brain development among individuals; another is the heterochrony or discrepancy between brain development and gonadal development. A third stems from differences in developmental rates between different parts of the brain. We advance the hypothesis that these differences are adaptive and represent design features of different reproductive life histories.

The heterochrony of high-K with respect to low-K individuals is therefore parallel to the heterochrony of humans as compared to other great apes. MacNamara (1997) suggests that humans have a combination of paedomorphosis and peramorphosis as compared to the other great apes. Similarly, we predict that high-K humans have a mixture of paedomorphosis and peramorphosis with respect to low-K individuals. In *paedomorphic* heterochrony, development begins later, proceeds at a slower rate, and has an earlier cessation. In *peramorphic* heterochrony, development begins early, proceeds at a faster rate, and has a later cessation. To summarize our predictions for the relations among different forms of heterochrony and organs affected by differential life-history strategy, we expect that for high-K individuals (as compared with low-K individuals): (1) the development of the Amygdala, the Nucleus Accumbens, and the Ventral Tegmental Area is paedomorphic; (2) the development of the Hippocampus and the Frontal Cortex is peramorphic.

These hypothesized developmental patterns predict that, at the behavioral level, high-K individuals will experience sexual feelings and attractions later than will low-K individuals. The full range of human emotionality (associated with development of the Amygdala complex)—and interest in intersexual and intrasexual competition associated with changing incentive values related to secondary sex characteristics and fitness indicators (associated with development of the Nucleus Accumbens and Ventral Tegmental Area) will appear later in these individuals.

Conversely, faster and earlier development of the Hippocampus predicts greater behavioral flexibility, greater exploration, earlier lifting of infantile amnesia, and a greater ability to discriminate among physical (and perhaps social) situations/contexts in high-K individuals. Finally, the faster and earlier development of the Frontal Cortex predicts a greater working memory capacity, rule governance, impulse control, and delay of gratification in high-K individual. In addition, highly organized attention, decision-making, and effort after meaning (i.e., making adaptive sense of situations and events) should appear in these individuals.

Relating this directly to the development of sexual behavior, we expect high-K individuals to be interested in all things sexual, including intersexual and intrasexual competition, short-term mating strategies, mate retention, and parenthood later in life than low-K individuals. Once sexual interest develops in high-K individuals, we expect that interest to manifest differently than in low-K individuals. For example, we expect high-K individuals to be less spontaneous, adventurous, outgoing, or overtly emotional in situations involving either intersexual or intrasexual competition. In addition, we expect high-K behavior to be, by contemporary middle-class North American standards, more situationally appropriate, subtle, and, skillful.

An integrated theoretical model

Our theoretical model includes four major phenotypic constructs: (1) Frontal Function, (2) Amygdala Function, (3) Hippocampal Function, and (4) Personal/Social Function. Neuropsychologically, the extent of Frontal Function can be estimated by measures of self-regulation, rule breaking, verbal fluency, working memory, block construction that requires planning, and related executive functions (see Lezak et al., 2004 for a description of specific tasks). Estimates of Hippocampal Function can include measures of spatial cognition, long-term memory, configural learning and memory, and other functions related to

contextualization and the discrimination of situations (e.g., Jacobs and Schenk, 2003; Jacobs and Nadel, 1985, 1998, 1999; Nadel and Hardt, 2004; Nadel and Jacobs, 1998; Sweatt, 2004). Estimates of Amygdala Function can be made through measures of emotionality, conditioning, sensitivity to both positive and negative social stimuli (e.g., facial expressions), and other indicators of normal ranges of affect (e.g., LeDoux, 2000). Each of these measures is a well-validated indicator of the functional status of these brain areas (Kolb & Whishaw, 2003). Measures of Personal/Social Function can be taken through the cognitive and behavioral indicators of the K-Factor identified in our previous studies, including individual, familial, and social behaviors related to Life History Strategy. Measures of the anatomical development of the brain may be taken through the use of modern imaging technology (e.g., Giedd et al., 1999).

We have chosen to focus on frontal and medial temporal (i.e., amygdala, hippocampus) lobes for two reasons. First, in humans, factors that interfere with frontal lobe function produce a broad range of characterological changes including changes in personality, self-awareness, memory, self-control, language, behavioral spontaneity, planning, response inhibition, and both social and sexual behavior. Factors that interfere with temporal function produce profound difficulties with long-term memory, spatial cognition, the discrimination of physical and social situations, and extraordinary levels of behavioral and verbal stereotypy. Factors that interfere with Amygdala function include disruptions of aspects of the ability to ‘mind read’ (read the intentional or emotional states of others), to read the facial expressions of others, to detect positive, negative, or neutral consequences of one’s actions, to respond emotionally to physical or social stimuli or situations, and seriously disrupted species typical social behavior (e.g., Adolphs et al., 2005; Aggleton, 2000). Second, there are anatomical reasons to believe that interactions among these areas are central to their normal function (and hence to normal social behavior).

Other factors will influence performance on neuropsychological tests and in the day-to-day life of these individuals. In humans, various sub-areas of the Frontal cortex, the Hippocampus, and the Amygdala are interconnected directly, densely, and reciprocally. Disruption of these interconnected pathways produces Disconnection Syndromes, which range from emotional insensitivity to aversive stimuli to difficulties adjusting to the social (or sexual) demands of various situations (see e.g., Darby & Walsh, 2005; Kolb & Whishaw, 2003). Given these long-standing data, there is little doubt that each of these brain areas contribute to normal, day-to-day social functioning. Furthermore, there is little doubt that variations in the way in which these areas function, or interconnect, has profound effects on the cognitive and behavioral strategies used throughout one’s life history.

Hence, this integrated theoretical model, although speculative, is based on testable hypotheses. First, we predict a common set of additive and pleiotropic regulatory genes (“K-Factor Genes”) underlies all four phenotypic composite factors (see Fig. 1). Second, we predict an extended neuropsychological feedback loop with interactions among Frontal, Hippocampal, and Amygdala Function (see Fig. 2). Third, we predict the three neuropsychological phenotypic composites partially mediate the Personal/Social Function phenotypic composite or “K-Factor” (see Fig. 3). Taken together, these hypotheses describe a system of causal influences that trace the proximate causation from genes through neuropsychological function to the cognitive and behavioral life-history traits of the K-Factor (see Fig. 4). Although the anatomical and functional interactions among the Frontal cortex, the Hippocampus, and the Amygdala are densely reciprocal, we have simplified these interactions to illustrate some of the causal pathways we predict to be important.

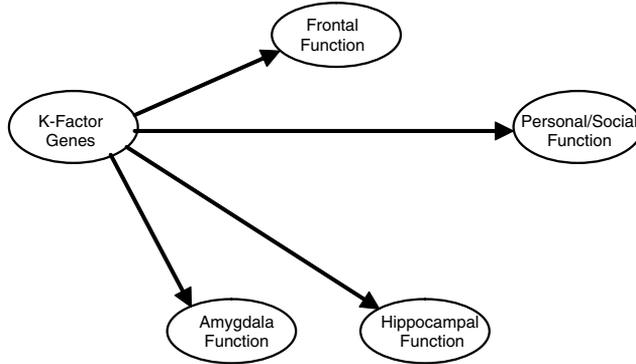


Fig. 1. Pleiotropic Effects of K-Factor genes.

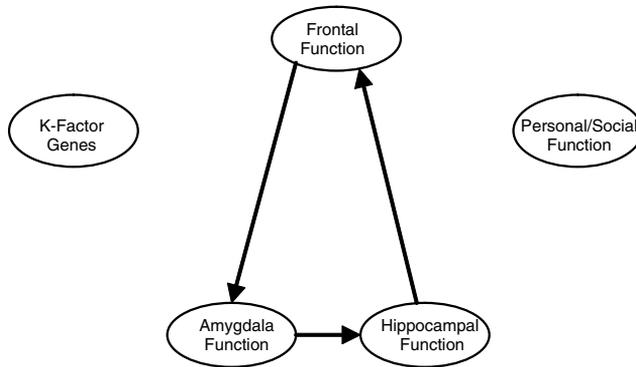


Fig. 2. Relations among brain functions.

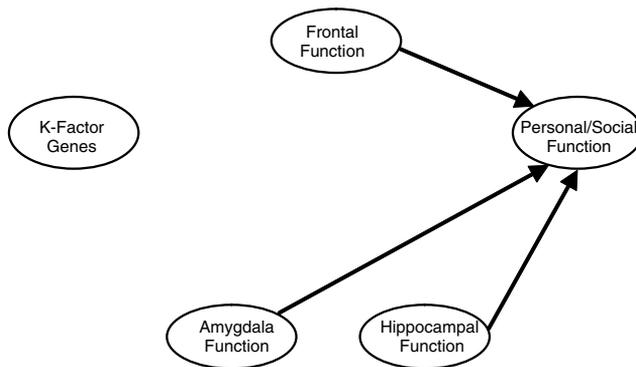


Fig. 3. Effects of brain on behavior.

This conceptual model essentially suggests that the behavioral effects of the pleiotropic genes identified in our behavioral genetic studies are causally mediated by heterochronies in brain development. These heterochronies affect neuropsychological function and are ultimately expressed in the differential manifestation of the life history traits associated with the K-Factor.

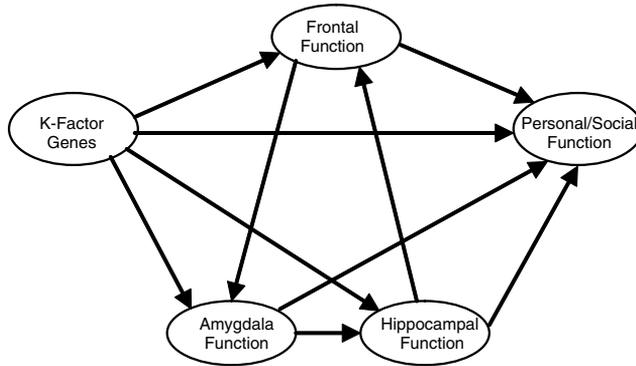


Fig. 4. Full structural model.

Conclusion

We first described Life History Theory and derived certain testable predictions, including the existence of a single common factor, the K-Factor, underlying a variety of life-history traits, including an assortment of sexual, reproductive, parental, familial, and social behaviors. We then related the K-Factor to a positive manifold or “cluster” of comorbid and socially problematical behaviors that has been repeatedly reported in the literature. We went on to explore the psychometrics and behavioral genetics of the K-Factor, reviewing much of our own recent empirical work on this topic, describing a research program (Figueredo, Sefcek, Vasquez, et al., 2005; Figueredo et al., 2005c) that applied latent variable modeling to the identification and construct validation of the K-Factor. Finally, we examine the proximate mediation of this adaptive patterning of behavior as instantiated in brain function and propose an integrated theoretical model that traces the behavioral development of individual life history from genes to brain to reproductive strategy.

A fundamental idea guiding this integrated theoretical model is “consilience.” Wilson (1998) and Whewell (1840) over 150 years prior, wrote of consilience—the unification of knowledge. They proposed that theoreticians, researchers, and other thinkers integrate their knowledge base to best understand and explain an idea or natural phenomena. As such, the optimal course toward minimizing causal uncertainty of human behavior involves an interfield alliance of scientific endeavors. Thinkers within fields such as anthropology, psychology, biology, and molecular behavior genetics need not be “diverse,” but rather ought to share the common goal of synthesizing knowledge to create a common platform of information. With consilience in mind and in practice, we have used this idea to guide our attempt to create a conceptual unity in which an appreciation of proximate and ultimate causes of human behavior coincide with an appreciation of phylogenetic and ontogenetic histories to create a conceptual and data-based whole.

Acknowledgments

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Appendix A. The Mini-K

Please indicate how strongly you agree or disagree with the following statements. Use the scale below and write your answers in the spaces provided. For any item that does not apply to you, please enter “0.”

Disagree Strongly	Disagree Somewhat	Disagree Slightly	Don't Know / Not Applicable	Agree Slightly	Agree Somewhat	Agree Strongly
-3	-2	-1	0	+1	+2	+3

	1. I can often tell how things will turn out.
	2. I try to understand how I got into a situation to figure out how to handle it.
	3. I often find the bright side to a bad situation.
	4. I don't give up until I solve my problems.
	5. I often make plans in advance.
	6. I avoid taking risks.
	7. While growing up, I had a close and warm relationship with my biological mother.
	8. While growing up, I had a close and warm relationship with my biological father.
	9. I have a close and warm relationship with my own children.
	10. I have a close and warm romantic relationship with my sexual partner.
	11. I would rather have one than several sexual relationships at a time.
	12. I have to be closely attached to someone before I am comfortable having sex with them.
	13. I am often in social contact with my blood relatives.
	14. I often get emotional support and practical help from my blood relatives.
	15. I often give emotional support and practical help to my blood relatives.
	16. I am often in social contact with my friends.
	17. I often get emotional support and practical help from my friends.
	18. I often give emotional support and practical help to my friends.
	19. I am closely connected to and involved in my community.
	20. I am closely connected to and involved in my religion.

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