

Original Article

**MULTIPLE SUCCESSFUL TESTS OF THE STRATEGIC
DIFFERENTIATION-INTEGRATION EFFORT (*SD-IE*)
HYPOTHESIS**

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Abstract

The Strategic Differentiation-Integration Effort (*SD-IE*) hypothesis predicts regulation by life history speed (*K*) of the magnitudes of the correlations among its components, such that individuals with slower life history strategies exhibit life history traits that are less correlated with each other than individuals with faster life history strategies. This conative differentiation among high-*K* individuals is proposed to arise due to the elevated social competition in stable, predictable environments faced by these individuals and to facilitate mutualistic rather than antagonistic social interaction strategies via social-ecological niche-splitting and domain-specific resource allocation. We tested the predictions of *SD-IE* regarding relations among life history traits using the Continuous Parameter Estimation Method on data from two college student convenience samples, one all-female sample ($N=382$) and one mixed-sex sample ($N=205$), as well as two nationally-representative samples of the US population, the *MIDUS* (*National Survey of Midlife Development in the United States*, $N=2080$) and the *NLSY* (*National Longitudinal Survey of Youth*, $N=5082$). The predicted *SD-IE* effects were statistically significant and in the expected negative direction among most indicators of the lower-order slow life history factors and among all indicators of the single higher-order slow life history *Super-K* factor.

Keywords: Life history strategy, polymorphism, polyethism, character displacement, niche-splitting, MIDUS, NLSY, Continuous Parameter Estimation Method

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Introduction

The Strategic Differentiation-Integration Effort (*SD-IE*) is a new evolutionarily based hypothesis relating individual differences in organization of life history traits to life history strategy. *SD-IE* predicts regulation by life history speed (*K*) of the magnitudes of the correlations among its components, such that individuals with slower life history strategies exhibit life history traits that are less correlated with each other than individuals with faster life history strategies. In this paper we examine *SD-IE* predictions regarding individual differences in the organization of conative (e.g. psycho-social, behavioral, attitudinal, and personality) traits. Essentially, it is predicted that high-*K* individuals should be *conatively differentiated* whereas low-*K* individuals should be *conatively integrated* with respect to their life history traits.

Fundamentals of Life History Theory

Life History (LH) theory describes the ways in which organisms allocate resources to maximize fitness given the context of either a stable or an unstable environment. Between taxa, LH strategies are conceptualized as being distributed along an *r-K* continuum, with *r* denoting the maximum population growth rate and *K* denoting the carrying capacity of the environment (MacArthur & E. O. Wilson, 1967; Pianka, 1970). At the *K*-selected end of this continuum, *slow* LH strategists maximize the *quality* of relatively small numbers of offspring. Slow LH or *K*-strategists (such as elephants) typically live at the carrying capacity of their stable environments. In contrast, at the *r*-selected end of this continuum, *fast* LH strategists maximize the *quantity* of relatively large numbers of offspring. Fast LH or *r*-strategists (such as rabbits), tend to overshoot the carrying capacity of their environments by evolving very high reproductive rates as a means of buffering against the high mortality associated with environmental instability. Significant population and individual differences in LH strategy also exist within species. This dimension is conceptualized as LH “speed” owing to the theoretical and empirical relationships between LH strategy and the rates of maturation, reproduction, and longevity (Figueredo, Vásquez, Brumbach, & Schneider, 2004, 2007; Figueredo, Cabeza de Baca & Woodley, 2013). Thus, LH theory is fundamentally an evolutionary-economic theory of *resource allocation* among different *components of fitness*: (1) a *descriptive* proximate-level theory in which the various life history tradeoffs are organized into coherent life history strategies, which may be modeled as latent multivariate constructs (such as the *K*-Factor); and (2) a *causal* ultimate-level theory of the evolutionary pressures selecting among different life history strategies are modeled.

The major components of fitness contribute multiplicatively: (1) *longevity*, or the probability of individual survival, at any given point in time; (2) *fertility*, or the number of offspring produced, at each successive time point; and (3) the coefficient of genetic relatedness between parent and offspring. This product is then integrated over the number of successive bouts of reproduction in which an individual engages over its lifespan. Many different combinations of these three components are possible that jointly yield the same fitness result when integrated over time. Furthermore, the simultaneous achievement of both *survival* and *reproduction* may pose a resource allocation problem to organisms with limited resources. Survival and reproduction both require the expenditure of resources, placing them in competition as subordinate objectives. Nevertheless, reducing either parameter to zero also

reduces their product, overall fitness, to zero – genetic extinction. LH theory is the dominant framework within theoretical biology used to model the process presumed to maximize overall fitness through optimal allocation of these resources to both survival and reproduction under varying environmental conditions.

LH *Parameters*, or LH *Traits*, are the basic *descriptive units* used within LH theory. Some mammalian examples of LH traits include: (1) Spacing of Births; (2) Length of Gestation; (3) Weight at Birth; (4) Size of Litters; (4) Length of Lactation; (5) Length of Juvenile Dependency; (6) Postnatal Growth Rates; (7) Age at Sexual Maturity; (8) Adult Body Size; and (9) Length of Lifespan. Life History *Tradeoffs*, on the other hand, are the basic *tactical elements*: (1) Parental Survival versus Current Reproduction; (2) Parental Growth versus Current Reproduction; (3) Current versus Future Reproduction; (4) Current versus Future Offspring Quantity; (5) Current versus Future Offspring Quality; and (6) Current Offspring Quantity versus Quality. At the highest level of this hierarchy, LH *Strategies* represent *coevolved, coordinated patterns* of optimal resource allocation. LH *Tradeoffs* are the component tactical elements that are coadapted by selection into coherent LH *Strategies*; these LH *Strategies* generally follow internally consistent and synergistic *functional patterns*.

These functional patterns of resource allocation can be partitioned among two major categories: (1) *Somatic Effort*, the resources devoted to the continued survival of the individual organism; and (2) *Reproductive Effort*, the resources devoted to the production of new organisms as vehicles for survival of the individual's genes. Further subdivisions are also possible and often useful. For example, within the category of Reproductive Effort, we may define the following two subclasses: (1) *Mating Effort*, the resources devoted to obtaining and retaining sexual partners; and (2) *Parental/Nepotistic Effort*, the resources devoted to enhancing survival of offspring produced by self or kin. Using these preferential allocations as descriptive, organizing principles, the “speed” of life history can be characterized as follows: (1) *Fast (“r-Selected”)* Life History Strategies allocate resources preferentially to Reproductive Effort over Somatic Effort, and Mating Effort over Parental/Nepotistic Effort, emphasizing the *production* of new offspring over the *survival* of existing ones, including self, offspring, or genetic relatives; whereas (2) *Slow (“K-Selected”)* Life History Strategies allocate resources preferentially to Somatic Effort over Reproductive Effort, and Parental/Nepotistic Effort over Mating Effort, emphasizing the *survival* of self, offspring, or genetic relatives over the *production* of new ones (Figueredo et al., 2006).

At the individual differences level it has been found that diverse conative indicators exhibit a common source of variance stemming from the existence of a latent life history speed construct called *K* (Figueredo, Vásquez, Brumbach, & Schneider, 2004, 2007). This *K*-factor is substantially heritable ($h^2 \sim .65$; Figueredo, Vásquez, Brumbach, & Schneider, 2004; Figueredo & Rushton, 2009), and furthermore exhibits evidence of having undergone recent directional selection (Figueredo & Rushton, 2009).

The SD-IE Hypothesis

Fast LH strategies are naturally selected in unstable, unpredictable environments, in which sources of mortality are predominantly *extrinsic*, and hence uncontrollable by genetically-influenced developmental processes, leading to highly variable population densities and reinforcing this selective effect. Slow LH strategies are naturally selected in

stable, predictable environments, in which sources of mortality are predominantly intrinsic, and hence controllable by genetically-influenced (and hence evolvable) developmental processes, leading to highly stable population densities and reinforcing this selective effect (Ellis et al., 2009).

It therefore follows theoretically that the effects of the predictability and controllability of the environment over time will not only be reflected by patterns of resource allocation in general, but also in the optimization of niche fitting, impacting the distribution of life history traits. Individuals evolving and developing in predictable, controllable environments are *socially selected* to become more *socio-ecologically specialized* as a consequence of heightened social competition. Individual “realized niches” will have lesser *micro-niche breadth* and will be less extensive than species-typical “fundamental niches” due to their more temporally reliable persistence. Slow LH individuals should become more *strategically differentiated* in behavior to adapt to stable and specific socio-cultural micro-niches. Such *strategic differentiation* permits the long-term allocation of resources among components of fitness that have higher fitness “return on investment”, where these patterns possess sufficient temporal stability. Different LH “traits” are therefore emphasized over others by conspecific individuals in different *micro-niches* and different LH “tradeoffs” are made. This strategic differentiation leads to socio-ecological specialization among individuals (*individuation*; Jung, 1969/1950) in *conative* dimensions.

Conversely, individuals evolving and developing in unpredictable, uncontrollable environments are *socially selected* to become more *socio-ecologically generalized* to allow contingent *switching* among unstable socio-cultural niches. Individual “realized niches” will have great *micro-niche breadth* and may thus be more co-extensive with the species-typical “fundamental niche” due to their ephemeral, precarious existence. Fast LH individuals should become more *strategically integrated* in behavior to maximize flexibility in migrating between socio-cultural micro-niches. Such *strategic integration* permits the rapid reallocation /redeployment of resources among alternative components of fitness with changing fitness “return on investment,” where these patterns lack sufficient temporal stability. No LH “traits” are therefore permanently emphasized over others by conspecific individuals in different environments and no permanent LH “tradeoffs” are made. This strategic integration leads to socio-ecological *generalization* and hence similarities among individuals (*convergence*) in *conative* dimensions.

The CD-IE Hypothesis

An interesting anomaly in the LH schema concerns the observation that the general factor of intelligence (*g*) does not correlate significantly with the *K*-factor (Woodley, 2011), despite the long standing prediction that they ought to do so owing to theoretical associations between brain size and somatic effort allocation (Rushton, 2004). This has led to the suggestion that the underlying dimension of genetic quality tapped by *g* within a population is in fact distinct from life history as, unlike life history, variability in this dimension results from mutation-selection balance rather than balancing selection (as is likely the case for *K*; Woodley, 2011). A logical implication of the *SD-IE* hypothesis, however, is that individuals at high levels of *K* should not just be more differentiated on the sorts of *conative* traits at the heart of *K*, but should also be more *cognitively* differentiated in terms of decreased strength of the positive correlations amongst the various abilities which constitute *g*. Thus, *K* might

also control the strength of the correlation amongst *mental* abilities as a means of adapting people to the level of environmental stability.

In high stability environments, it is predicted that individuals evolving and developing in predictable, controllable environments are *socially selected* to become more *cognitively specialized* as a consequence of heightened social competition, whereas individuals evolving and developing instead within unpredictable uncontrollable environments are *socially selected* to become more *cognitively generalized* to allow contingent *switching* among unstable socio-cultural niches (Woodley, 2011). This CD-IE hypothesis has been supported with data from student convenience samples, the nationally representative National Longitudinal Survey of Youth and in ethnic differences data. In all cases, CD-IE effects manifest on the correlation between abilities and *g* as a function of *K*, even when there are no correlations between *K* and *g* in the data (Woodley, Figueredo, Brown & Ross, 2013).

Broader Implications and Evidence

This capacity for specialism should allow for the development of distinct complexes of traits, which would permit resource polymorphism in the context of a high competition environment (Figueredo et al., 2010; Woodley, 2011). An implication of this is that there are various alternative ways of being a high-*K* strategic specialist, whereas there are relatively fewer ways of being a low-*K* strategic generalist.

Evidence for this comes from the observation that those with autistic-like personalities exhibit many high-*K* traits (such as high stability preference and longer-term time preferences; Del Giudice, Angeleri, Brizio & Elena, 2010), however, they also exhibit unique traits differentiating them markedly from non-autistic individuals who exhibit similarly high-*K* characteristics. For example, those with autistic-like personalities are very low on emotional intelligence (Baron-Cohen & Wheelright, 2004). This contrasts with those who are high on *K* and who do not have autistic-like personalities who are typically high on emotional and social intelligence (Figueredo, Cabeza de Baca, & Woodley, 2013). It is often stated that autism and autistic-like personality are pathological, so how could this constitute a strategy? It has been observed that high-functioning autism is associated with high levels of competency in domains requiring high-level visuo-spatial and quantitative abilities such as engineering and mathematics (Baron-Cohen, Wheelright, Stott, Bolton, & Goodyear, 1997; Fitzgerald, 2002); therefore, autistic-like personality could permit certain types of high-*K* individuals to specialize with respect to engineering and mathematical niches.

By the same token, it could be argued that individuals who are high-*K* and who exhibit high social and emotional intelligence are specialists with respect to social niches. These two alternative phenotypes could therefore be considered as different “morphs” of slow LH strategy, although the differences between phenotypes may be graded instead of discrete, as among the different so-called “castes” in many species of ant (e.g., Götsch, 1965; E. O. Wilson, 1953). Recall that “caste” polymorphism in most eusocial insects is determined by environmental influences experienced during larval development, rather than genetic differences among individuals, and serves the function of role specialization in social cooperation (Wheeler, 1991). More generally, such graded polyethisms, polyphenisms, or polymorphisms might be maintained within high-*K* populations via a combination of assortative mating and balancing selection. This possibility suggests that *strategic*

differentiation-integration effort may be an important and thus far unrecognized element of human life history strategies. *Strategic* polymorphism in LH traits would thereby serve to reduce social competition within a high-*K* population, which in turn would further raise the effective carrying capacity of the environment.

The graded polymorphism predicted by the SD-IE hypothesis is also consistent with the *coral reef model* of personality diversification, as derived from selectionist models of evolution and development (e.g., Figueredo et al., 2005b; Figueredo, Vásquez, & Sefcek, 2008; Figueredo, Gladden, Vásquez, Wolf, & Jones, 2009; Figueredo et al., 2010; Figueredo, Jacobs, Burger, Gladden, & Olderbak, 2011). In this model, social competition serves as the centrifugal force that disperses individuals against the otherwise centripetal force of the species-typical optimum or norm of reaction. This model predicts that personality differentiation (*individuation*) represents a product of intraspecific character displacement, selected with the adaptive function of promoting the intraspecific splitting of the fundamental species-typical niche by partitioning it into the realized socio-cultural micro-niches of individuals.

What the SD-IE hypothesis adds to this more general model is the necessary specification that the ecological conditions must possess sufficient temporal stability to permit long-term adaptation and specialization to such restricted centroids (*hypervolumes*) within the multidimensional space that defines the breadth of the ecological niche. According to the SD-IE hypothesis, this necessary condition can only be met by the specific set of environmental conditions that are known to favor slower LH strategies. The SD-IE hypothesis therefore predicts that the expected patterns of strategic differentiation should *only* be characteristic of slower LH strategists. Conversely, possessing highly integrated and internally consistent reproductive strategies might provide a contrary advantage to fast LH (low-*K*) individuals coping with either unpredictable natural, social, and sexual selective pressures (such as those that might be encountered in a short term mating market), as integrated mental abilities allow for highly generalized tactics (such as the development of a multi-dimensional fitness indicator display for use in the short-term mating market) to be contingently transferred from one socio-cultural micro-niche to another.

Another set of predictions made jointly by the SD-IE and CD-IE hypotheses is that both strategic and cognitive differentiation function to do more than just to ameliorate *social competition*, as predicted by the coral reef model. In highly social species, such as humans and many hymenopterans, adaptive specialization also facilitates *social cooperation*. The coral reef model was originally developed in the context of explaining the evolution of individual differences among non-human animals in comparative psychology, and was only secondarily applied to human personality variation. This model correctly predicted that the majority of species of non-human animals in which individual differences in personality (or systematic behavioral predispositions, by any other name) had been identified were *social* species. This principle was generally satisfied by the published data then available (see Figueredo et al., 2005), with the exception of certain species of cephalopods, such as the octopus. Just recently, however, the researcher that first documented octopus personality variation has reported a probable link between such variation in individual behavior and trophic specialization occasioned by social competition for resources (Mather et al., 2012). Generalist species (such as *Octopus vulgaris*, *Octopus cyanea*, and *Enteroctopus dofleini*) can therefore be composed primarily of specialist individuals that each concentrates their foraging behavior upon a limited variety of prey species with respect to the broader range of prey

normally taken by the species as a whole. Although direct social interactions between individuals are not required by this evolutionary mechanism, the behavioral differentiation still purportedly serves the ultimate adaptive function of *competitive release*.

At an intermediate level on this spectrum of competitive release to fully developed cooperation are the majority of social mammals, such as may be illustrated by the case of the non-human primates. Monkeys, for example, are not known for their spectacular feats of social cooperation. Most primatologists believe that monkey sociality evolved primarily for the purpose of antipredator vigilance and some degree of antipredator defense in larger and more powerful species. Other than the specific behaviors serving those functions, such as the well-documented alarm calls of vervet macaques (Cheney & Seyfarth, 1990) and some alloparental behaviors (Hrdy, 1977) within matrilineal groups, most monkey species do not typically coordinate their behaviors cooperatively to achieve many common goals, such as the cooperative prey capture observed in chimpanzees. Many of the purportedly “cooperative” acts documented are instead attack coalitions where more than one individual monkey will coordinate a joint attack upon another.

Humans and many eusocial insects, however, are remarkable in the sophisticated levels of cooperation exhibited. Even the alloparenting observed in many non-human primates is much more greatly developed in humans (Hrdy, 1990). The CD-IE and SD-IE hypotheses further jointly predict that, among humans, those with slower LH will, as a result of the division of labor facilitated by the cognitive and strategic differentiation among individuals, be both: (1) more cognitively preadapted to perform the divergent tasks required by increasingly complex forms of social cooperation (Woodley & Figueredo, 2013); and (2) more conatively disposed to do so given the generally more altruistic and prosocial behaviors associated with slow LH in humans (Figueredo, Cabeza de Baca, & Woodley, 2013).

Methods

In this study, we tested the most basic level of prediction possible from *SD-IE*, the life history strategy dependent distribution of life history traits. Specifically, we examined individual differences in conative traits in humans using data from both student and US population representative samples. The following subsections are broken down by sample because the measures administered and the measurement models estimated for the constructed latent variables vary by specific sample and analysis. A variety of different measures of the theoretically-specified constructs of interest were used to show the generality of the SD-IE effect, in that detecting it was not dependent upon the use of any specific set of measures or particular sampling of respondents. As this is a set of secondary analyses, details of the data collection procedures are cited from the original sources rather than reproduced in their entirety here.

Samples

Two convenience samples were collected from student volunteers at a Southwestern U.S. University. *Student Sample 1* was comprised of 382 female undergraduates, and these data were collected entirely online; *Student Sample 2* was a mixed-sex, heterosexual sample of 205 undergraduates, and the data collection was partially online and partially in person (for complete description of procedures, see Ross, 2010; Brown, 2011). Samples from two

national surveys that were more representative of the U.S. population were obtained from publicly available databases. *Population Sample 1* was comprised of a subsample of 2080 Adults (ages 25-75) sourced from Wave 1 (1995-1996) of the Survey of Midlife Development in the United States (MIDUS; Brim et al., 2000), on which previous LH analyses had been performed (Figueredo et al., 2004, 2007), and *Population Sample 2* was comprised of a subsample of 5082 Adolescents (ages 12-16) sourced from the National Longitudinal Survey of Youth (NLSY79), on which a selection of LH-related variables were available.

Measures

For *Student Sample 1*, data on the *K*-Factor, measuring LH speed, were obtained using the full 199-item Arizona Life History Battery (ALHB; Figueredo, 2007); data on the Covitality Factor were obtained using the MOS Short Form Health Survey (SF-36; Ware & Sherbourne, 1992); and data on the Personality (GFP) Factor were obtained using the Ten-Item Personality Inventory (TIPI; Gosling, Rentfrow, & Swann, 2003).

For *Student Sample 2*, data on the *K*-Factor were obtained using the Mini-K, a 20-item short form of the ALHB (Figueredo et al., 2006); data on Covitality Factor were again obtained using the 36-item MOS Short Form Health Survey (SF-36; Ware & Sherbourne, 1992); and data on the Personality (GFP) Factor were obtained using the 60-item NEO Five Factor Inventory (NEO-FFI; Costa & McCrae, 1992).

For *Population Sample 1*, we reconstructed the same 30 subscales that had been used in previous studies on LH strategy using the MIDUS Survey data (Figueredo et al., 2004, 2007; Figueredo & Rushton, 2009). Collectively, these scales covered a wide breadth of psycho-social, attitudinal, behavioral, health and personality domains, and were associated with three broader factors: the *K*-factor, the Covitality Factor, and the General Factor of Personality. These three factors have been found to share a common source of genetic variance stemming from the existence of an overarching higher-order *Super-K* factor, which accounted for the preponderance of the phenotypic and genetic covariance amongst the three principal lower-order factors (Figueredo et al., 2004; Figueredo & Rushton, 2009).

For the purpose of direct quantitative comparison to the student samples, the 20 subscales of the MIDUS *K*-Factor were theoretically assigned to be distributed among the 7 corresponding subscales of the ALHB; the 5 subscales of the MIDUS Covitality Factor were theoretically assigned to be distributed among the 2 corresponding major subscales of the SF-36, respectively representing *Mental Functioning* and *Physical Functioning*; and the 5 subscales of the MIDUS Personality Factor were theoretically identified as directly corresponding to the 5 lower-order personality factors (*Openness to Experience*, *Conscientiousness*, *Extraversion*, *Agreeableness*, and *Emotional Stability*, which is reverse-scored *Neuroticism*) of either the TIPI or the NEO-FFI. The specification of this consilient measurement model is displayed on Table 1, along with the part-whole correlations between each of the MIDUS *K*-Factor indicators and the ALHB component to which it was assigned.

Table 1. Correspondence and Reallocation of MIDUS K-Factor Indicators among the Subscales of the ALHB

<u>ALHB SUBSCALES</u>	<u>MIDUS K-FACTOR SCALES</u>	<u>λ(ALHB)</u>
Insight, Planning, and Control	<i>Financial Status</i>	.503*
	<i>Agency</i>	.614*
	<i>Foresight/Anticipation</i>	.724*
	<i>Self-Directedness/Planning</i>	.731*
	<i>Insight Into Past</i>	.655*
	<i>Primary Control/Persistence</i>	.758*
	<i>Flexible/Positive Reappraisal</i>	.709*
Romantic Partner Attachment	<i>Marital Relationship Quality</i>	1.000*
Mother and Father Relationship Quality	<i>Mother Relationship Quality</i>	.877*
	<i>Father Relationship Quality</i>	.877*
Family Social Contact and Support	<i>Family Support</i>	1.000*
Friends Social Contact and Support	<i>Friends Support</i>	1.000*
General Social Altruism	<i>Close Relationship Quality</i>	.591*
	<i>Children Relationship Quality</i>	.651*
	<i>Altruism Towards Kin</i>	.663*
	<i>Altruism Towards Non-Kin</i>	.709*
	<i>Communitarian Beliefs</i>	.614*
Religiosity	<i>Religiosity</i>	1.000*

Note: * $p < .05$

Thus, as with human intelligence (Carroll, 1993), specific LH traits are arranged into a three-stratum hierarchy. The objective of these quantitative comparisons was to determine if statistically equivalent SD-IE effects occur among of the following strata of the LH hierarchy: (1) the convergent correlations among the 14 major “Stratum I” indicators (defined by the 7 ALHB, 2 Covitality, and 5 GFP subscales) and the 3 major “Stratum II” lower-order common factors, as represented by the factor loadings from the *K*-, Covitality, and Personality Factors on these 14 indicators; and (2) the convergent correlations among these 3 major “Stratum II” lower-order common factors and the single “Stratum III” higher-order common factor, as represented by the factor loadings from the Super-*K* Factor on the 3 lower-order factors.

For *Population Sample 2*, an “alternative” *K*-factor was constructed that could not be structured in a parallel way from the following psychosocial indicators of Slow LH that had been sampled in the 1979 wave of the National Longitudinal Survey of Youth (NLSY79): (1) *Self-Esteem*, measured using the Rosenberg scale, averaged between 1980 and 1987 (Rosenberg, 1965); (2) *Happiness* or *Subjective Well-Being*, which was simply reverse-scored depression, as measured using the Center for Epidemiological Studies depression scale, averaged between 1992 and on reassessment of individuals over 40; (3) *Delay of Gratification*, which corresponds to “time preferences” assessed using interest rates on deferred receipt of \$1,000 for a month and for a year; (4) *Sociability*, which was based on a question administered in 1985 asking the adult respondents to rate their shyness vs. outgoingness; (5) *Trust*, which is based on a measure of the degree to which the respondent often trusts others; (6) *Self-Concept*, using the Pearlin Mastery Scale (Pearlin, Lieberman, Menaghan, & Mullan, 1981); and (7) *Internal Locus Of Control* (Rotter, 1966). All of these psychosocial indicators have been found to correlate with *K* and/or its constituent factors, such as the GFP, indicating that their arrangement into a *K*-factor is theoretically justified (Figueredo, de Baca & Woodley, 2013; Woodley, Figueredo, Brown & Ross, 2013).

Despite its reduced nomological breadth as compared with the *K*-factor extracted using the ALHB, this alternative NLSY *K*-factor has been successfully used in prior research (Woodley, Figueredo, Brown & Ross, 2013) to identify CD-IE effects on the 10 subtests of the Armed Services Vocational Aptitude Battery (a measure of *g* in the NLSY). Furthermore, if it can be demonstrated that SD-IE manifests on an “imperfect” *K*-factor, this suggests additional robustness to the phenomenon.

Statistical Analyses

Common Factor Modeling. As the samples used varied in size considerably, ranging from $N > 100$ to $N > 5000$, unit-weighted factor scoring was applied, which avoided the well-documented sample-specificity of factor scoring coefficients produced by standard errors of inconsistent magnitudes across the different samples (Gorsuch, 1983). The unit-weighted factor structures presented are therefore no more than the part-whole correlations between the latent composites constructed and each of their component indicator measures. Although some of the samples were of sufficient size to reliably estimate differentially-weighted factor scores and factor loadings, this one method was applied throughout for the sake of consistency.

Identifying SD-IE via CPEM. The Continuous Parameter Estimation Method (CPEM; Gorsuch, 2005) was employed. This model permits the change in the strength of the correlation between two variables (such as a multivariate construct like *K* and a constituent indicator variable) to be determined throughout the full range of a third variable (such as the overall level of *K*). For all LH domains sampled, correlation coefficients were estimated at the individual level by taking the cross-product of the standardized (*z*) scores of each individual’s performance on the relevant subscales.

Pearson’s Product-Moment Correlation Coefficient is defined as the mean cross-product of the standardized (“*z*”) scores:

$$\Sigma(Zx*Zy)/N$$

It follows that the group mean of these individual-level cross-products automatically becomes the correlation coefficient for each group under consideration. This is mathematically inevitable by definition. Therefore, the cross-product itself ($Zx*Zy$) can be used as the individual-level “raw score” in CPEM to estimate the varying amount of strategic integration or differentiation “effort” in each group. Thus, computing and comparing the group means of these cross-products using ANOVA automatically calculates and compares group-level Pearson Correlation Coefficients. This tests the degree to which the strength of this relationship varies between any discreet groups.

When using more traditional methods for identifying changes in the strength of the correlation coefficient between groups, it is necessary to acquire samples of at least 75-100 respondents in each group, so as to stabilize the correlation coefficients for comparison. However, as a graded method, CPEM does not require the polytomization of continuous distribution, by potentially problematic methods such as the median split (e.g. Cohen & Cohen, 1983; MacCallum, Zhang, Preacher, & Rucker, 2002). Furthermore, CPEM permits one to regress the individual cross-products of the z -scores on continuous as well as categorical predictor variables, facilitating the application of this method to multiple regression/correlation (MRC) analyses as well as ANOVAs.

Another recent criticism leveled against studies considering similar *manifold inconstancy effects*, such as Spearman’s Law of Diminishing Returns (the tendency for the manifold of g to be weaker at higher levels of g ; Spearman, 1927) in intelligence research, is that both the directionality and magnitude of these effects might be contingent upon the magnitude and direction of any skew in the distributions of the indicator variables, such as subtest scores (Murray, Dixon, Johnson & Bouchard Jr., 2011). In the realm of LH, indicator skew also might be an important source of error in comparing LH traits across domains that are further removed from the self, like immediate family, extended family, and community, such as was conceptualized by the *circles of mutual influence* model (Bronfenbrenner, 1979). The further removed from the self, the greater the potential level of K -Factor “difficulty” (in the language of IQ testing), in that higher levels of bioenergetic and material investment are required to achieve high scores on each successive level. It therefore requires more effort allocation to practice group-level altruism than to care for one's own direct offspring, which entails the presence of floor and ceiling effects in measures of K .

Skew is defined as the mean cube of the standardized scores of any variable: $\Sigma(Zx^3)/N$. Skew can be operationalized using CPEM by statistically controlling the other model parameters for any effects of subtest skew by including the cube of the standardized subtest scores (Zs^3) as an additional predictor in the regression equations predicting the individual-level cross-products. Instead of simply controlling for raw subtest skew, however, we statistically controlled for the differences in skew between the manifest indicator and the latent common factor. This was done by taking the cube of the difference between the corresponding standardized scores: $(Zs-Zf)^3$. This provides an estimate of the skew of the *residuals*.

Contrary to popular misconception, parametric statistics does not assume that the raw data need be normally distributed: the normality assumption applies exclusively to the *residuals*. Otherwise, methods such as ANOVA would automatically violate normality by employing categorical (non-normal) predictors. For the residuals to be normally distributed, it is only necessary that the distributions of the predictor(s) and criterion be of the same form (*isomorphic*), meaning that if the former is skewed then the latter should be similarly skewed

and subtracting the weighted predictor(s) from the criterion score will leave nothing but a symmetrical pattern of random errors, centered around zero. This makes sense if one variable, which happens to be skewed, is in fact causally influencing the other. The skew of the residuals therefore reflects any mismatch between the distribution forms of the criterion with respect to the predictor(s), and is probably a more important indicator of a potential problem than the separate skew of either of the two raw distributions (in the present case, those of the subtest and factor scores). We thus controlled statistically for the influence of the resultant skew on the component domains of each composite common factor (such as *K*) by taking the cube of the differences among the *z*-scores of each indicator from that of each common factor, and then statistically controlling the SD-IE effects for this potential confound by directly including this extra term within each multiple regression model.

An unrelated criticism leveled against many psychological studies that rely even partially on samples of convenience (such as samples of University student volunteers) and thereafter attempt to draw species-typical conclusions is the issue of the relative generalizability (or lack thereof) among demographically different populations. The focus of an important subset of our analysis was therefore to determine the degree to which the estimated SD-IE effects were comparable between student and population samples when assessed using the same or similar measures of *K*. This was done, not just by “eyeballing” the results and judging them as similar (sometimes called the *inter-ocular trauma* method, because it purportedly “hits you right between the eyes”), but by conducting formal quantitative null-hypothesis tests for systematic differences in the relative magnitudes of the observed effects among the samples.

Results

The results of the analyses are tabulated in Tables 1-9. Tables 2-5 and Table 10 show various relations between the component (“Stratum I”) *indicator* scales (listed in the first columns) and their corresponding lower-order (“Stratum II”) common *factors* (used as the headings of the first columns); Tables 6-9 show various relations between constituent (“Stratum II”) *lower-order* common factors (listed in the first columns) and their corresponding *higher-order* (“Stratum III”) common factors (used as the headings of the first columns). To save space and summarize all the statistical information as concisely as possible in the minimal number of tables, the results of two different analyses are shown on each table: a *measurement* model and a corresponding *structural* model. A more general schematic for these structural relations is displayed in Figure 1, which integrates these hierarchical levels of aggregation within a single diagram. The curved, single-headed arrows leading from the higher-order constructs to the straight, single-headed arrows representing their factor loadings on their corresponding lower-order components, from Stratum III to Stratum II and then from Stratum II to Stratum I, depict the moderating SD-IE effects predicted.

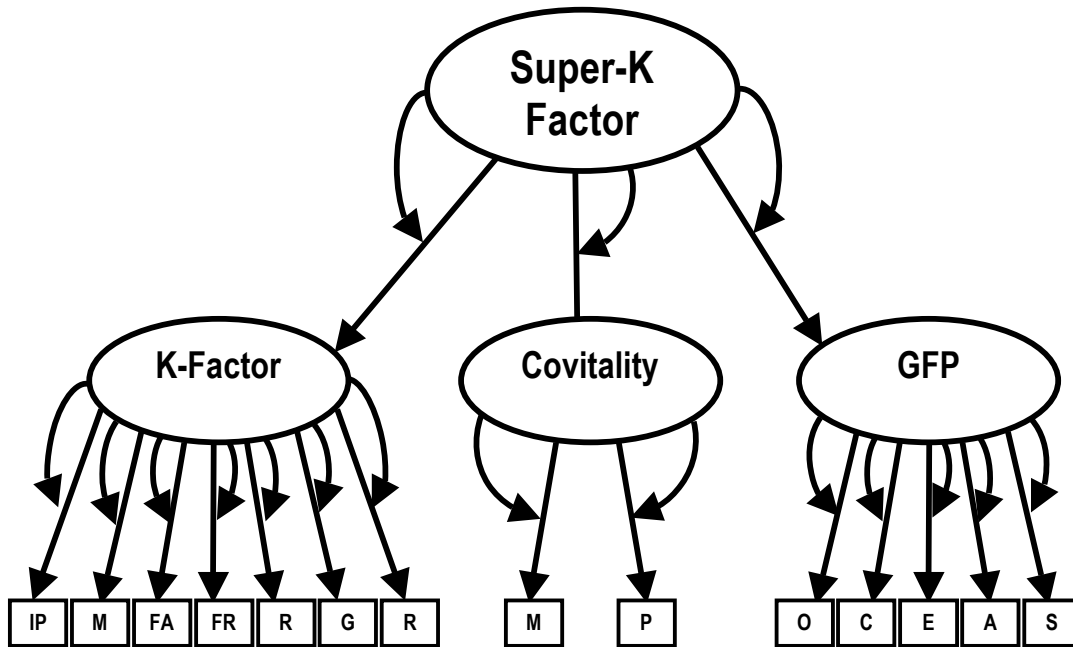


Figure 1. The hierarchical organization of life history traits.

First, we describe the measurement models for each multivariate construct. In the case of Tables 2-5 and Table 10, the second column lists the unit-weighted factor loading (essentially a part-whole correlation of the component indicator scores to the composite factor scores) of each component (“Stratum I”) indicator scale from its corresponding lower-order (“Stratum II”) common factor; in the case of Tables 6-9, the second column lists the unit-weighted factor loading of each constituent (“Stratum II”) lower-order common factor from its corresponding higher-order (“Stratum III”) common factor, which always happens to be Super-K in these analyses.

Second, we describe the structural model for each multivariate construct. The remaining columns on each table (the third column and above, where applicable), present the regression coefficients obtained by regressing the cross-products of the standardized (z) scores of each lower-order term (e.g., convergent indicator) with each higher-order term (e.g., common factor) upon each of various hypothesized predictor variables. These regression coefficients indicate the effect that each of those predictors are estimated to have on the magnitude of the raw correlation coefficient between each lower-order term and each corresponding higher-order term: a positive regression weight would indicate a systematic *increase* in the correlation coefficient and a negative regression weight would indicate a systematic *decrease* in the correlation coefficient and with any *increase* in the value of the predictor.

Thus, in the third columns of each table, we list the size of the effect associated with differences in skew, $\beta(\Delta Z)^3$, between each common factor and each indicator, in the context of each multiple regression. The skew effects are operationalized as the regression coefficient of the *cubed differences* among the z -scores of each lower-order term (e.g., convergent

indicator) from that of each higher-order term (e.g., common factor) upon the *cross-products* of the *z*-scores of each lower-order term (e.g., convergent indicator) with each higher-order term (e.g., common factor).

In the fourth columns of each table, we list the magnitudes of the estimated SD-IE effects when statistically controlled for any contamination stemming from differences in skew. The SD-IE effects are operationalized as the regression coefficient of the level of each higher-order term (e.g., the common factor score) upon the cross-products of the *z*-scores of each lower-order term (e.g., convergent indicator) with each higher-order term (e.g., common factor). For example, a negative regression coefficient estimate for $\beta(K)$ would indicate that as the level of the common factor (*K*) increases, the indicator is becoming less strongly correlated with the latent factor, as would be consistent with the SD-IE hypothesis; conversely, a positive regression coefficient estimate for $\beta(K)$ would indicate the opposite effect.

In the fifth columns of Tables 4, 7, and 9, we compare samples for significant differences among corresponding CPEM effects by including a “dummy” or binary (meaning 1 or 0) variable called “Sample” within each multiple regression that distinguishes among the samples being compared. Hence, the extra column labeled $\beta(\text{Sample})$ contains the regression coefficient associated with that possible difference, along with an indication as to whether that difference is statistically significant at the $p \leq .05$ level or not (denoted with an asterisk). Because what is being regressed upon these dummy variables are the cross-products of the *z*-scores of each lower-order term (e.g., convergent indicator) with each higher-order term (e.g., common factor), a significant regression coefficient would indicate a significant difference among the corresponding correlation coefficients of the samples being compared.

Table 2. Lower-Order Factors for Student (All-Female) Sample 1

<i>K</i>-Factor (<i>K</i>) Indicators	$\lambda(K)$	$\beta(\Delta Z)^3$	$\beta(K)$
<i>Insight, Planning, and Control</i>	.543*	-.001	-.102
<i>Mother and Father Relationship Quality</i>	.587*	.053	-.261*
<i>Family Social Contact and Support</i>	.685*	-.144*	-.372*
<i>Friends Social Contact and Support</i>	.434*	-.084	-.107
<i>Romantic Partner Attachment</i>	.600*	-.157*	-.256*
<i>General Social Altruism</i>	.638*	-.157*	-.188*
<i>Religiosity</i>	.478*	.093	.059
<i>Covitality (COV) Indicators</i>	$\lambda(COV)$	$\beta(\Delta Z)^3$	$\beta(COV)$
<i>Mental Functioning</i>	.821*	-.277*	-.550*
<i>Physical Functioning</i>	.821*	-.363*	-.661*
<i>Personality (GFP) Indicators</i>	$\lambda(GFP)$	$\beta(\Delta Z)^3$	$\beta(GFP)$
<i>Openness to Experience</i>	.644*	-.198*	-.287*
<i>Conscientiousness</i>	.592*	-.183*	-.312*
<i>Extraversion</i>	.431*	-.141*	-.236*
<i>Agreeableness</i>	.597*	-.092	-.160*
<i>Stability</i>	.671*	.038	-.218*

Note: * $p < .05$

Table 2 indicates that with respect to the all-female University student sample, all but one of the effects (*Religiosity*) trended in the direction expected by the SD-IE hypothesis.

Furthermore, even when statistically controlled for differences in skew, the majority of these SD-IE effects remained statistically significant (11 out of 14).

Table 3. Lower-Order Factors for MIDUS (Mixed-Sex) Population Sample 1

K-Factor (K) Indicators	$\lambda(K)$	$\beta(\Delta Z)^3$	$\beta(K)$
<i>Insight, Planning, and Control</i>	.590*	-.134*	-.203*
<i>Mother and Father Relationship Quality</i>	.530*	-.075*	-.180*
<i>Family Social Contact and Support</i>	.593*	-.094*	-.265*
<i>Friends Social Contact and Support</i>	.655*	-.122*	-.210*
<i>Romantic Partner Attachment</i>	.619*	-.198*	-.284*
<i>General Social Altruism</i>	.749*	-.091*	-.262*
<i>Religiosity</i>	.475*	-.007	-.066*
Covitality (COV) Indicators	$\lambda(COV)$	$\beta(\Delta Z)^3$	$\beta(COV)$
<i>Mental Functioning</i>	.858*	-.166*	-.581*
<i>Physical Functioning</i>	.858*	-.470*	-.497*
Personality (GFP) Indicators	$\lambda(GFP)$	$\beta(\Delta Z)^3$	$\beta(GFP)$
<i>Openness to Experience</i>	.707*	-.074*	-.188*
<i>Conscientiousness</i>	.640*	-.201*	-.290*
<i>Extraversion</i>	.764*	-.124*	-.250*
<i>Agreeableness</i>	.698*	-.218*	-.310*
<i>Stability</i>	.477*	-.058*	-.002

Note: * $p < .05$

Table 3 indicates that with respect to the adult MIDUS Survey sample, arguably more representative of the US population than our all-female University student convenience sample, all but one of the SD-IE effects (*Religiosity*) also trended in the expected direction. When statistically controlled for differences in skew, all but one of the SD-IE effects remained statistically significant (13 out of 14).

Table 4. Lower-Order Factors for Student (All-Female) Sample 1 Versus MIDUS (Mixed-Sex) Population Sample 1

K-Factor (K) Indicators	$\lambda(K)$	$\beta(\Delta Z)^3$	$\beta(K)$	$\beta(Sample)$
<i>Insight, Planning, and Control</i>	.582*	-.114*	-.197*	.022
<i>Mother and Father Relationship Quality</i>	.592*	-.044*	-.170*	-.045*
<i>Family Social Contact and Support</i>	.660*	-.100*	-.271*	-.022
<i>Friends Social Contact and Support</i>	.515*	-.118*	-.210*	.039
<i>Romantic Partner Attachment</i>	.616*	-.192*	-.281*	.003
<i>General Social Altruism</i>	.732*	-.100*	-.269*	.047*
<i>Religiosity</i>	.475*	.002	-.064*	.310
Covitality (COV) Indicators	$\lambda(COV)$	$\beta(\Delta Z)^3$	$\beta(COV)$	$\beta(Sample)$
<i>Mental Functioning</i>	.853*	-.169*	-.614*	.117*
<i>Physical Functioning</i>	.853*	-.460*	-.512*	-.011
Personality (GFP) Indicators	$\lambda(GFP)$	$\beta(\Delta Z)^3$	$\beta(GFP)$	$\beta(Sample)$
<i>Openness to Experience</i>	.697*	-.100*	-.192*	-.033
<i>Conscientiousness</i>	.632*	-.195*	-.284*	-.021
<i>Extraversion</i>	.712*	-.114*	-.238*	-.012
<i>Agreeableness</i>	.682*	-.185*	-.297*	.036
<i>Stability</i>	.507*	-.050*	.000	-.099*

Note: * $p < .05$

Table 4 indicates that when the all-female University student and the MIDUS Survey samples are combined and systematically compared, all but one of the variables (*Stability*) exhibit effects that are statistically significant and directionally consistent with SD-IE, even when statistically controlled for differences in skew. In comparing between the magnitudes of the effects between the two demographically discrepant samples, 10 of the 14 are not significantly different from one another.

Table 5. Higher-Order Factors for Student (All-Female) Sample 1

<i>Super-K Factor (SKF) Indicators</i>	$\lambda(SKF)$	$\beta(\Delta Z)^3$	$\beta(SKF)$
<i>K-Factor (K)</i>	.754*	-.241*	-.345*
<i>Covitality (COV)</i>	.787*	-.254*	-.416*
<i>Personality (GFP)</i>	.834*	-.106*	-.301*

Note: * $p < .05$

Table 5 indicates the presence of significant SD-IE effects on all three lower-order components of the higher-order *Super-K* Factor in the all-female University student sample, when statistically controlled for differences in skew.

Table 6. Higher-Order Factors for Student (Mixed-Sex) Sample 2

<i>Super-K Factor (SKF) Indicators</i>	$\lambda(SKF)$	$\beta(\Delta Z)^3$	$\beta(SKF)$
<i>K-Factor (K)</i>	.737*	-.142*	-.309*
<i>Covitality (COV)</i>	.754*	-.129	-.381*
<i>Personality (GFP)</i>	.842*	-.020	-.220*

Note: * $p < .05$

Table 6 indicates the presence of significant SD-IE effects on all three lower-order components of the higher-order *Super-K* Factor in the mixed-sex University student sample, when statistically controlled for differences in skew.

Table 7. Higher-Order Factors for Student (All-Female) Sample 1 Versus Student (Mixed-Sex) Sample 2

<i>Super-K Factor (SKF) Indicators</i>	$\lambda(SKF)$	$\beta(\Delta Z)^3$	$\beta(SKF)$	$\beta(Sample)$
<i>K-Factor (K)</i>	.748*	-.197*	-.311*	-.032
<i>Covitality (COV)</i>	.775*	-.214*	-.411*	.004
<i>Personality (GFP)</i>	.837*	-.079*	-.295*	.373

Note: * $p < .05$

Table 7 indicates the presence of significant SD-IE effects on all three lower-order components of the higher-order *Super-K* Factor in the combined student samples, when statistically controlled for differences in skew. Furthermore, none of the differences among the two convenience samples were statistically significant.

Table 8. Higher-Order Factors for MIDUS (Mixed-Sex) Population Sample 1

<i>Super-K Factor (SKF) Indicators</i>	$\lambda(SKF)$	$\beta(\Delta Z)^3$	$\beta(SKF)$
<i>K-Factor (K)</i>	.826*	-.109*	-.272*
<i>Covitality (COV)</i>	.775*	-.241*	-.372*
<i>Personality (GFP)</i>	.823*	-.071*	-.242*

Note: * $p < .05$

Table 8 indicates the presence of significant SD-IE effects on all three lower-order components of the higher-order *Super-K* Factor in the MIDUS Survey sample, when statistically controlled for differences in skew.

Table 9. Higher-Order Factors for MIDUS Versus Student (COMBINED) Sample

<i>Super-K Factor (SKF) Indicators</i>	$\lambda(SKF)$	$\beta(AZ)^3$	$\beta(SKF)$	$\beta(Sample)$
<i>K-Factor (K)</i>	.809*	-.131*	-.275*	-.021
<i>Covitality (COV)</i>	.775*	-.236*	-.384*	.013
<i>Personality (GFP)</i>	.826*	-.072*	-.240*	-.019

Note: * $p < .05$

Table 9 indicates the presence of significant SD-IE effects on all three lower-order components of the higher-order *Super-K* Factor in the combined student and MIDUS Survey samples, when statistically controlled for differences in skew. Furthermore, and perhaps most strikingly, none of the tested differences among these demographically discrepant samples were statistically significant.

Table 10. Lower-Order Factors for NLSY (Mixed-Sex) Population Sample 2

<i>K-Factor (K.NLSY) Indicators</i>	$\lambda(K.NLSY)$	$\beta(AZ)^3$	$\beta(K.NLSY)$
<i>Self-Esteem</i>	.487*	-.055*	-.102*
<i>Happiness (Reversed Depression)</i>	.456*	-.234*	-.304*
<i>Delay of Gratification</i>	.412*	-.671*	-.251*
<i>Sociability</i>	.395*	-.225*	-.156*
<i>Trust</i>	.508*	-.061*	-.150*
<i>Rotter Self-Concept</i>	.486*	-.049*	-.058*
<i>Pearlin Locus of Control</i>	.504*	-.076*	-.059*

Note: * $p < .05$

Table 10 indicates the presence of significant SD-IE effects on all seven convergent indicators identified within the NLSY sample as LH indicators. All effects trended in a direction consistent with SD-IE, and were furthermore statistically significant when controlled for differences in skew.

Finally, we address the question of whether and in what direction the SD-IE effect might be sensitive to the relative magnitudes of the common factor loadings on the various indicators. We addressed this by using the method of correlated vectors (Jensen, 1998), which involved simply correlating the rank-order of the magnitudes of the common factor loadings of the lower-order LH factors on the different indicators with that the rank-order of the magnitudes of their associated SD-IE effects. To maximize robustness and reduce the probability of Type 1 error, the vectors were correlated using Pearson's Product Moment correlation, but the level of statistical significance of the association was determined using Spearman's ρ (Jensen, 1998). Consistent with the direction of the expected effect, we reversed the signs of the regression coefficients on the common factors, such that negative (SD-IE) effects became positive and positive (anti-SD-IE) effects became negative. By applying this method, we observed the following vector correlations: $r(12) = .831$ ($p < .05$) for the all-female student sample, $r(12) = .861$ ($p < .05$), for the MIDUS sample, and $r = .879$ ($p < .05$) in both samples combined. These findings indicate the presence of high-magnitude

and significant positive vector correlations between the common factor loadings from the lower-order LH factors and the relative magnitudes of the SD-IE effects.

Discussion

Summary of Empirical Results

As described above, for both of the University student samples, three lower-order and one higher-order slow LH factors were constructed from the component scales of the ALHB (constituting the *K*-Factor), those of the SF-36 (constituting the Covitality Factor), as well as those of both the TIPI and the NEO-FFI (constituting the General Factor of Personality or *GFP*). Parallel lower-order and higher-order slow LH factors were constructed from selected scales of the MIDUS Survey in which it had previously been shown that both their genetic and phenotypic covariances yielded an essentially equivalent latent structure (Figueredo et al., 2004, 2007). In these three samples, the same set of domain-specific manifest indicators of the three lower-order LH factors as well as the single higher-order LH factor (*Super-K*) was constructed and tested parametrically for factorial invariance. A conceptually related general slow life history factor was constructed from a selection of psychosocial indicators from the *NLSY* data.

Systematic effects upon the magnitudes of the bivariate correlations of each of these manifest indicators with their latent lower-order common factors and those of the lower-order latent common factors with their corresponding higher-order latent common factors were also estimated by applying the Continuous Parameter Estimation Method (*CPEM*). By using the level of each higher-order term as a predictor of such correlation coefficients, the predicted *SD-IE* effects were found to be statistically significant and in the expected negative direction among *most* indicators of the lower-order slow life history factors (11/14 in the combined student sample; 13/14 in the *MIDUS* population sample; 7/7 in the *NLSY* population sample) and among *all* of the indicators of the single higher-order slow life history *Super-K* factor (3/3 in all samples tested). These results were also statistically controlled and tested for significant differences between each higher- and lower-order term in the skew of their distributions.

Another interesting observation concerned the SD-IE effects on *Emotional Stability* and *Religiosity*. The SD-IE effects on *Religiosity* exhibited heterogeneous directionalities between the all-female student sample (+0.059^{ns}) and the MIDUS sample (-0.066, $p \leq .05$), whereas the SD-IE effects on *Emotional Stability* were in the expected direction in both the all-female student sample (-0.006^{ns}) and in the MIDUS sample (-0.002^{ns}), but were of very low magnitude. Nevertheless, by applying the method of correlated vectors (Jensen, 1998), we found that SD-IE effects are monotonically related to the strength of the common factor saturation of the indicator on which it manifests, suggesting that SD-IE occurs principally on the speed of *LH* itself, rather than on the specific sources of variance in each indicator that might be unrelated to *LH* strategy. This finding provides an explanation for the apparent anomalies presented by *Religiosity* and *Emotional Stability*, which in comparison with the other subscales, are comparatively much less loaded on by their respective LH factors.

This finding is consistent with comparable results found in intelligence research, where it is well-established that some effects exhibit a high affinity with *g*, in that they are most pronounced on more *g*-saturated subtests than on less *g*-saturated ones. Examples include subtest heritabilities and inbreeding depression scores (Jensen, 1998). Other effects

have greater affinity with sources of variance in cognitive performance that are independent of g , and are hence most pronounced on less g -saturated subtests relative to more g -saturated ones. Examples include the Flynn effect (the secular increase in IQ over time; te Nijenhuis & van der Flier, 2013) and IQ gains via retesting (te Nijenhuis, van Vianen & van der Flier, 2007).

Finally, and most strikingly, we found that most of the differences in model parameters tested in the planned comparisons between these demographically diverse samples were statistically non-significant. In other words, the reported effects were generally *parametrically equivalent* within our degree of statistical precision to discriminate between them, indicating a high degree of generalizability for SD-IE effects across these populations.

Implications and Future Directions

Predicted *SD-IE* effects on the distribution of conative life history traits were found across all samples used in our analyses and to be highly generalizable. Given this initial evidence in support of the *SD-IE* hypothesis, future research applying its predictions regarding the integration or differentiation of traits and the costs and benefits potentiated by these distributions at both the individual and group level is needed.

In the introduction, we suggested that those on the autistic-like personality spectrum and those with “normal” social intelligence might represent distinct morphs of slow LH, specializing with respect to “systemizing” and “empathizing” socio-cultural micro-niches respectively. This leads to the explicit prediction that the dimensions of *empathizing* and *systemizing*, identified by Baron-Cohen (2009) as significant determinants of autistic-like versus “normal” personality, may themselves be a source of “horizontal” variance in life history, and therefore dimensions of SD-IE. This could be tested by examining the placement of high-scorers on both of these dimensions with respect to the level of K , and in the context of CPEM analysis, which could be used to determine the degree to which these strategies differentiate as a function of increasing K and are hence SD-IE effects.

The costs and the benefits to the individual and to the group of the proposed differentiation and integration achieved by the *SD-IE* effect deserve further exploration, and can be illustrated by analogous phenomena in different species. Some examples of the way these costs and benefits can be adaptively manipulated are demonstrated in the eusocial Hymenoptera (including thousands of species of ants, bees, and wasps). In these species, colony controlled developmental switches trigger developmentally plastic responses through differential feeding and housing (O’Donnell, 1998). In this way, social control is exerted over the number of individuals expressing a specific behavioral or physical morphology. Exercise of this control creates the adaptive problem of how to produce an optimal number of different alternative phenotypes and an optimal ratio among individuals who possess each of those alternative phenotypes, given the variability in ecological contingencies. Different eusocial insects have evolved different general strategies to confront the adaptive problems posed by environmental variability (Oster & E. O. Wilson, 1978).

One of these strategies, called *tychophobic* (“risk-fearing”), is to create as many distinct morphs (the so-called “castes”) as there are tasks or adaptive problems in their local ecology, a potential parallel to strategic differentiation. Each morph becomes highly specialized and increases the ergonomic efficiency of the colony in confronting these specific adaptive problems. Any individuals that develop into a morph that is currently without such a

specific task, due to the temporary lack of environmental affordances, become an ergonomic drain on the colony. Such individuals, however, are nonetheless produced as a form of “bet-hedging” against the uncertain contingencies of environmental fluctuation. High caste differentiation thus occasions the problem commonly known as “structural unemployment” in human economics because these species are eusocial and “unemployed” workers are still fed. The entire colony shares both the costs and the benefits of ergonomic efficiency or lack thereof, but the social benefit offsetting this cost is that the colony as a whole is better prepared for a variety of resource contingencies.

A contrary evolutionary *tychophilic* (“risk-loving”) strategy taken by many other social insects is to produce *fewer* discrete morphs composed of less-specialized individuals, essentially paralleling strategic integration. The social benefit of this strategy is that the colony supports fewer idle workers, increasing the ergonomic efficiency of the group. As with Ricardo's *Law of Comparative Advantage* (Ricardo, 1891) in human economics, however, less-specialized individuals contribute less to the ergonomic efficiency of the society. Nevertheless, this strategy persists in the face of selection because of environmental variance. Although there is a quantifiable risk that the specific resources that each morph is equipped to exploit will become temporarily unavailable, a low degree of individual differentiation permits the full colony workforce to exploit the available resources.

We believe that the general form of this adaptive problem is, at least in principle, completely isomorphic to the challenges faced by both human individuals and societies in *r*-selecting and *K*-selecting environments, given that the critical differences in the documented effects of such environments on LH evolution and development translate directly into the quantitative balance between intrinsic and extrinsic risks of morbidity and mortality at different stages of life (Ellis et al., 2009). Whether the costs and the benefits of differentiation or integration accrue to the individual or to the group in humans, and whether the adaptations that we are describing are the product of individual selection (see Figueredo, 1995; Figueredo et al., 2005), group selection (see D. S. Wilson, 1994), or some combination of both, is a problem that can be best addressed by multilevel selection models (Woodley & Figueredo, 2013) and are thus beyond the scope of the present paper.

Nevertheless, it is perhaps worth noting that the dimension representing the long-term *stability*, *predictability*, and hence, potential *controllability* of the environment by evolved developmental mechanisms (*the SPC gradient*) is not the only selective pressure governing the evolution of LH strategies. A more comprehensive taxonomy of ultimate- and proximate-level causal influences has been detailed and illustrated graphically elsewhere (Ellis et al., 2009), indicating the theoretically-specified effects of each. As expounded upon more fully in that previous work, the term most commonly used in evolutionary biology to describe the main driving force of LH evolution is *extrinsic* morbidity and mortality, which denotes probabilities of disease and death that are inherently uncontrollable by evolved adaptive mechanisms, as opposed to *intrinsic* morbidity and mortality, which denotes those which are potentially controllable. However, the SPC gradient is believed to be the key mechanism underlying the SD-IE effect. We are therefore not predicting that all factors known to influence LH evolution are predicted to also generate SD-IE effects. We instead predict that this particular gradient represents the specific correlate of LH that is most likely to give rise to the SD-IE phenomenon. Because other factors may indeed affect LH evolution, this implies that the association between LH and SD-IE is not expected by our theory to be

perfect, and our empirical results show that the correlation falls far short of perfect determination.

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