

Slow and Steady Wins the Race: K Positively Predicts Fertility in the USA and Sweden

Michael A. Woodley of Menie^{1,2} · Tomás Cabeza de Baca³ · Heitor B. F. Fernandes⁴ · Guy Madison⁵ · Aurelio-José Figueredo⁴ · Mateo Peñaherrera Aguirre⁶

Published online: 16 November 2016
© Springer International Publishing 2016

Abstract Nothing is presently known about the relationship between individual differences in fertility and life history (LH) speed, as measured by the K -Factor. To examine this relationship, the correlation between LH speed and the number of children was examined in two, large samples (MIDUS II and the Swedish STAGE dataset). Their association was positive and statistically significant in both cross-national samples. The association was robust with respect to statistically controlling for participant age. Nested model comparison of a Model looking only at linear effects with a second Model incorporating a quadratic term did not improve model fit in any instance, suggesting directional selection for slower LH. The heritability of the indicators comprising the K -Factor positively moderated the strength of selection, while K -Factor loading weakly negatively moderated selection strength, suggesting that K -Factor variance, as a multivariate latent construct, is not the primary target of selection. These results are consistent with *fertility intentions* data indicating positive correlations between slower LH and *desired* numbers of children.

In modern environments, higher mating effort does not appear to result in more offspring, likely because of *strategic interference* suppressing the fertility of those with fast LH, stemming from influences that may be either endogenous (i.e., contraceptive usage) or exogenous (i.e., the presence of laws, such as alimony) to the individual.

Keywords Fertility · Life history theory · Selection · Strategic interference

Introduction

Human reproduction, especially in modern, industrialized populations, is a complex phenomenon with multiple causal determinants. Certain antecedents of reproductive success have been extensively studied, such as education and general intelligence, where research consistently reveals negative relationships in modern populations (e.g., Woodley of Menie 2015). By contrast, virtually nothing is known about the relationship between life history (LH) strategy and reproductive outcomes in modern, industrialized populations.

Life History Theory

Life history theory describes the variation that exists among species, among populations within species, and among individuals within populations, in the ways that bioenergetic and material resources are allocated towards different components of fitness under different environmental conditions. These allocations are subject to *tradeoffs*, where resources expended on raising fitness in one domain necessarily reduce resource expenditures in other fitness domains. There exists an adaptive logic to these tradeoffs, whereby complementarity exists among

✉ Michael A. Woodley of Menie
Michael.Woodley@vub.ac.be

¹ Department of Psychology, Technische Universität Chemnitz, Chemnitz, Germany

² Center Leo Apostel for Interdisciplinary Studies, Vrije Universiteit Brussel, Brussels, Belgium

³ Department of Psychiatry, University of California San Francisco, San Francisco, CA, USA

⁴ Department of Psychology, University of Arizona, Tucson, AZ, USA

⁵ Department of Psychology, Umeå University, Umeå, Sweden

⁶ Department of Psychology, University of New Brunswick, Fredericton, NB, Canada

the domains that characterize different LH strategies. For example, species (such as rabbits) that are highly fertile are also short lived and are characterized by precocial development, where the offspring mature rapidly and require little parental investment. Other species (such as elephants) instead exhibit low fertility, are extremely long lived, and are characterized by altricial development, with the young requiring long periods of gestation and subsequent parental investment. Consistent with the adaptive logic of these tradeoffs, there exists a latent source of covariance among these domains, described by the r/K continuum, which broadly corresponds to the degree to which the strategy favors rapid reproduction (r) as opposed to one that limits reproduction to track the carrying capacity (K) of the environment (MacArthur and Wilson 1967; Pianka 1970; Rushton 2004). A major determinant of a species' or populations' positioning along this continuum stems from a phylogenetic or evolutionary history of exposure to environmental harshness (i.e., the *absolute level* of extrinsic mortality) and predictability (i.e., the *variance* or *stochasticity* in extrinsic mortality), with high levels of both harshness and unpredictability typically favoring more r -selected life history strategies and low-levels favoring more K -selected strategies (Del Giudice et al. 2015; Ellis et al. 2009).

Life history theory was extended to understanding the covariance that exists among seemingly distinct human behavioral and conative (i.e. personality) traits in the 1980s, when Rushton (1985) proposed that the tendency for individual differences in future-oriented behaviors and personality traits to correlate stems from an underlying LH common factor produced by K -selection. Examples of such traits are impulse control, low time preferences, and reproductive restraint. In contemporary LH theory, the opposing poles of this continuum tend to be labelled *fast* and *slow* rather than r and K , due to subsequent discoveries concerning the antecedents of LH evolution having eclipsed the original models that were based primarily on population density dynamics. The existence of the latent multivariate K -Factor as a source of individual differences across many different behavioral domains was corroborated by Figueredo et al. (2004). These researchers also identified an even higher order common factor, reflecting a broader source of covariance, termed *Super-K*, which exists among the K -Factor, the *General Factor of Personality* (GFP), and a General Health Factor, termed *Covitality*. Genetic correlations exist among these sources of variance in addition to indications of *criterion validity* (i.e., the ability to predict salient life outcomes), which indicates that the LH theoretic approach to understanding patterns of covariance among human individual differences exhibits considerable robustness and validity (Figueredo et al. 2013a).

Pleistocene and Holocene Selection Favoring Slower Life History Speed

Slower LH speed is expected to be favored when environmental mildness and/or predictability is high (Ellis et al. 2009). During the Pleistocene, more northerly latitudes are believed to have been characterized by *predictable harshness* owing to the presence of systematic seasonal variability in temperature and resource abundance. This environmental predictability is believed to have favored slower LH speeds among the ancestors of contemporary Western European and East Asian populations, as the ability to cope with colder winters would have favored dispositions towards planning, insight, and control type behaviors (Rushton 1985, 2000). The decreased parasite prevalence produced by colder winters might also have played a role in reducing certain sources of extrinsic morbidity and mortality. Subsequent transitions into sedentarism and agriculture, starting around 10,000 BC, would have furthermore favored higher levels of the sorts of slow LH traits that predisposed towards cooperative behavior and the formation of *high trust* societies (Cochran and Harpending 2009; MacDonald 2001).

Historical data indicate that prior to the 19th century in Western Europe, individuals belonging to the *bourgeoisie* (i.e., who had wealth and a degree of status) were at a fitness advantage relative to the peasantry (i.e., those who relied on working the land for subsistence), in terms of both numbers of surviving children and the relative genetic contribution to subsequent generations (as measured by the increasing prevalence of formerly rare surnames) (Clark 2007, 2014). It has been proposed that this period of *survival of the richest* (Clark and Hamilton 2006) involved selection for certain dispositions associated with wealth creation and retention, such as impulse control and low time preferences. Figueredo (2009) argued that the *embourgeoisement* of Western populations may therefore have been an outcome of selection for slow LH speed. A critical component of this process is that slower LH is associated with enhanced *ecological control*—an example of which would include the formation of cooperative social networks, which permit populations to locally exceed the environmental carrying capacity via niche splitting stemming from divisions of labor (e.g., Figueredo et al. 2013b; Woodley 2011). Such networks of cooperating slow LH strategists can also exert *strategic interference* upon fast LH strategists, via the generation of cultural free-rider controls such as criminal law and religious injunctions that normalize slow LH ecological preferences and penalize fast LH ones (MacDonald 2009). Thus, via the establishment of *manipulative* gene-environment covariances (Buss 1987), slow LH populations were able, via culture-gene co-evolution, to maintain and intensify selection pressures favoring the fitness of their slower LH phenotypes. An excellent historical example of strategic interference is the liberal use of capital

punishment in cases of violent criminality during the period of *embourgeoisement* in the West, which appears to have removed violent criminality from the population at a rate commensurate with actual measured historical declines in violent criminality (Frost and Harpending 2014). Note that violent criminality is strongly correlated with poor impulse control and high time preferences, both components of fast LH strategy; Dunkel and Beaver, 2013; Figueredo et al. 2013a, b).

Advances in technology would have given slow LH populations even greater control over their environments and therefore the sorts of selective pressures operating on subsequent generations. A prominent result of technological advances, especially in the domains of public hygiene and medicine, has been to massively reduce the degree of extrinsic mortality in Western populations, especially as it pertains to infant and child death (Volk and Atkinson 2008). A response to this was the *Demographic Transition* in which fertility levels started to decline across social groups (Kirk 1996), likely in part as an adaptive response to the reduced mortality of offspring, thus lowering the requisite threshold for replacement fertility (Lawson et al. 2012). In addition to fertility, industrialized populations appear to be developing slower LH speeds with respect to many other dimensions of LH strategy, such as increased height, mass, and longevity. This pattern is suggestive of increasing somatic effort (e.g., Mace 2000). It also includes prolonged educational activity, which is associated with an opportunity to acquire somatic capital (i.e., knowledge and specialized abilities or *cognitive differentiation effort*; Woodley 2011), and the existence of a complex web of increasingly global economic relationships, requiring ever-greater divisions of labor to sustain and grow them.

The impact of the demographic transition and modernity on general intelligence is fairly well characterized, with longer fertility delays and higher rates of contraceptive usage among the highly intelligent, especially among women, tending to favor the fitness of those with lower levels of general intelligence (e.g., Meisenberg 2010). Nevertheless, the effect of modernity on the relationship between LH speed and fertility remains poorly understood. Although LH appears to have slowed since the advent of the demographic transition, this may have been in response to the effects of improved environments on ontogeny, encouraging the behavioral development of slower LH strategies, rather than via selection. One indication that slow LH may still nonetheless be associated with higher relative fitness in modern populations, and that *K*-selection may therefore be continuing to operate on these populations, comes from the work of Brase (2013), who found that slow LH speed and short-term mating orientation both predicted (inversely in the case of the latter) more total desired numbers of children, in addition to less negative and more positive assessments of babies and also less focus on the perceived tradeoffs associated with raising children. Whether or not this leads to higher *achieved fitness* (completed fertility)

among those with slower LH strategies remains an open question. If this is indeed the case, then it hints at the continuing influence of strategic interference mechanisms on the fertility of those with faster LH strategies.

Strategic Interference

It is important to recall that historical selection favoring slower LH in human populations has been concomitant with selection for greater proficiency in environmental manipulation of a sort that has generated culture-gene co-evolutionary pressures favoring slower LH speeds (Figueredo 2009). The use of technology for niche manipulation by slower LH populations can therefore be seen as a source of *exogenous* (to the individual) *strategic interference* on the fitness of those with faster LH strategies. By removing a catalyst for *r*-selection, slower LH strategists are necessarily favoring their own LH strategy. An example of exogenous strategic interference in modern populations would be the existence of cultural controls, such as laws, that interfere with the fitness of faster LH individuals. These would include alimony laws, which mandate that delinquent fathers allocate parenting effort (in the form of finances) to their offspring. Laws mandating that a certain minimum amount of time be allocated to education can also be considered a source of exogenous strategic interference, as relatively more precocious individuals with fast life histories are being encouraged to trade mating effort against the acquisition of somatic capital, a situation that inherently favors those with slower LH. The presence of these sources of exogenous strategic interference on the fitness of faster LH individuals is also consistent with the normative association of slower LH with *social desirability* (Sherman et al. 2013).

Another source of strategic interference can be termed *endogenous* (to the individual) and encompasses self-imposed fertility constraints stemming from the use of contraceptives and other birth control techniques (such as abortions). As faster LH individuals desire having children less and appraise them more negatively than do slower LH individuals, it stands to reason that they should be more willing to utilize birth control techniques to achieve their desired, low numbers of children, and that they may well have experienced higher fertility (in terms of total numbers of children ever born) historically prior to the advent and wide-scale utilization of birth control techniques, even though they experienced commensurately higher rates of infant and child mortality. This may seem contradictory, as LH Theory proposes that faster LH individuals and species produce more offspring. However, this is not the same as saying that they *desire* having offspring or have positive appraisals of offspring and parental activities. They desire sexual activity and engage in intercourse not with the *intention* of having offspring and caring for them. On the other hand, slower LH individuals invest time and bioenergetic resources on their offspring, not being negatively orientated

towards them. This is in line with self-report findings reported by Brase (2013): among humans, those with higher scores on the Mini-K desire children more than those with lower scores, whereas the latter exhibit higher mating effort and practice short-term mating strategies.

It is also worth noting that general intelligence positively predicts contraceptive usage (Kanazawa 2005), whereas it does not correlate substantially with LH speed (Figueredo et al. 2014a, b; Woodley 2011; Woodley of Menie and Madison 2015). Thus, there are large numbers of individuals with faster-than-average LH speed and higher-than-average general intelligence, who are perfectly capable of solving the *abstract problem* of fertility control via the application of contraception, despite possessing poor insight, planning, and control at the conative level.

Hypothesis

Although it might superficially appear paradoxical that slower LH strategy should be expected to correlate positively with increased fertility in modern populations, this hypothesis is nevertheless consistent with the evolutionary psychological perspective that individual organisms are *adaptation executors* rather than *fitness maximizers* (Tooby and Cosmides 1992). For example, during the historical period of the early modern era described above as that of *embourgeoisement* in Western populations, faster LH strategists continued to produce large numbers of offspring, consistent with their evolved adaptations. The high rates of morbidity and mortality associated with harsh environmental conditions of the contemporaneous “Little Ice Age,” however, are what translated high levels of mating effort allocation into a lower number of *surviving* offspring giving a fitness advantage to slow LH strategists, based on the greater inclinations and abilities among these individuals to provide the heightened levels of parental effort required to buffer their offspring against the elevated risks. The ability of evolved adaptations to moderate the environmental hazards rendered the morbidity and mortality partially *intrinsic* rather than completely *extrinsic* (Ellis et al. 2009), thus favoring slower LH. Similarly, we are proposing that faster LH strategists in modern populations continue to engage in high-mating-effort behaviors, consistent with their evolved adaptations. Nevertheless, the availability of contraceptives and other sources of strategic interference permits fast LH strategists to engage in heightened sexual activity while avoiding the otherwise natural consequences of fertility.

We aim to test this hypothesis with two samples from modern, industrialized societies.

Methods

Samples and Measures

MIDUS

Sample 1 was comprised of a nationally representative sample of 2257 individuals (aged 35–86 years) from Wave 2 (2004–2006) of the *Survey of Midlife Development* in the USA (the MIDUS Survey; Brim et al. 2000). The MIDUS Survey consisted of a telephone interview and two follow-up mail surveys given to a nationally representative sample, collected in two longitudinal data collection waves; the first wave over a 1-year period from 1995 to 1996 ($N=7108$) and the second wave over a 2 year period from 2004 to 2006 ($N=4963$).

The MIDUS (I & II) *K*-Factor (Figueredo et al. 2004, 2006, 2013a, b) was used as a measure of LH speed in the present analysis. This lower order factor of the *Super-K* construct was chosen because it correlates only very weakly with general intelligence (in the range of .02 to .07, the correlations furthermore exhibit high-heterogeneity, with several studies having yielded indications of negative correlations in meta-analysis; Woodley 2011; Figueredo et al. 2014a, b). As was mentioned previously, general intelligence is reliably negatively correlated with fitness outcomes in modern, industrialized populations (Woodley of Menie 2015), so it was important to minimize this potential source of extraneous variance in our analyses. *g* is in fact much more substantially correlated with the GFP (Dunkel 2013) and with measures of general health (Deary 2012), than with *K*, which makes these other *Super-K* components less suitable for the proposed analysis.

This sample was limited to English speakers in the USA. The MIDUS surveys contain items that measure total numbers of children. This variable includes adopted and stepchildren in addition to biological ones and cannot be disaggregated. Given that adoption is relatively rare, it is unlikely to substantially compromise the results of subsequent analyses.

MIDUS II (which was employed in the main analysis) descriptive statistics for age and fertility are reported (for both the combined and sex-specific samples) in Table 1.

The STAGE Sample

Data on fertility and LH speed were collected from a large sample of twins from the *Swedish Twins Registry*—also known as the STAGE cohort (Lichtenstein et al. 2006) with approximately 32,000 twins born between 1959 and 1985. Life history speed was evaluated using a web survey implementation and Swedish language translation of the Mini-K. The Mini-K exhibits satisfactory reliability (.73) and high validity (.91) as a measure of the broader *K*-Factor (Figueredo et al. 2014a, b). Fertility was evaluated via a question that asked about numbers of children.

Table 1 Descriptive statistics for MIDUS II and STAGE cohorts. *K* descriptives not reported as this indicator was standardized (hence, mean = 0 and SD = 1 in all samples)

	MIDUS II (USA)			STAGE (Sweden)					
	Total sample	Male	Female	Total sample (Twin 1)	Total sample (Twin 2)	Twin 1 Male	Twin 1 Female	Twin 2 Male	Twin 2 Female
Age (SD)	55.84 (12.76)	55.6 (12.66)	56.03 (12.86)	40.16 (7.82)	40.16 (7.82)	40.11 (7.70)	40.19 (7.90)	40.11 (7.70)	40.19 (7.90)
Numbers of children (SD)	2.49 (1.74)	2.42 (1.71)	2.55 (1.77)	2.38 (1.20)	2.41 (1.18)	2.34 (1.24)	2.40 (1.19)	2.42 (1.17)	2.40 (1.17)

An invitation was sent via surface mail to 32,000 twins, 11,543 of whom completed at least one instrument in a web questionnaire via the Internet. After excluding incomplete answers to either fertility or the Mini-K, the final sample consisted of 1521 twin-pairs (3042 individuals), 1178 men and 2257 women, aged between 27 and 54. The analysis was run on each twin from a pairing separately, so as to avoid potential issues associated with pseudo-replication involving genetically identical individuals. This yielded two subsamples of 1521 individuals (the Twin 1 and Twin 2 samples, respectively). An advantage of this design was that by splitting the twins into two subsamples of twin-singletons, the second twin set could be used to replicate and validate the regression parameters derived from the first set of singletons.

The age and fertility descriptive statistics for both sets of twins (combined and separated by sex) are reported in Table 1.

Analyses

Two separate analyses were performed on these data. In the first analysis, an attempt was made to determine the nature of any selection operating on LH speed using the *Chicago School* approach to modelling phenotypic selection (e.g., Kingsolver and Pfennig 2007). This approach involves the use of linear and quadratic relations among data on the level of traits and fitness outcomes, in order to discriminate between directional selection (i.e., where fitness increases or decreases as a function of the level of the trait under selection), stabilizing selection (where fitness is reduced at the extremes of the distribution) and disruptive selection (where fitness at the extremes of the distribution is raised relative to the mean). The latter two forms of selection are sometimes collectively referred to as *quadratic selection*, being best described by negative and positive quadratic regression terms, respectively (Kingsolver and Pfennig 2007).

A nested model comparison regression analysis was performed, incorporating three steps: (I) the linear term was entered first along with age as a control; (II) sex and a *K*-factor by sex interaction term were added to the model; and (III) the mean-centered quadratic term was added afterward along with its interaction term with sex. Age

was also included as a covariate, as age is a proxy for the degree to which fertility is complete. To determine the validity of an inference of non-directional selection, the quadratic term must be both statistically significant and must also add significantly to model fit. As count data were used as the criterion variable (numbers of children), negative binomial regression analyses were performed using “Proc Genmod” in SAS 9.3.

A second analysis involving the Method of Correlated Vectors was conducted in order to determine whether the *K*-loading (i.e., the strength of the relationship between the *K*-factor and each of its indicators, representing how central each indicator is to the *K* construct) and the indicator-level additive heritabilities positively moderate the strength of selection operating on each indicator. If *K* variance is the target of selection, then we would expect a positive vector correlation between selection strength and *K*-loading. Similarly, the finding of positive vector correlations between the heritable variance associated with the indicators and strength of selection would be consistent with a selection effect, as genetic additivity and the responsiveness of a trait to a given degree of selection are positively associated (Fisher 1929). Thus, for this analysis, the vector correlations are computed between (1) the vector of age-controlled correlations between scores on *K*-factor indicators and fertility, (2) the vectors of *K*-loadings for each indicator, and (3) their respective additive heritability estimates. All indicator-level associations are obtained from MIDUS Wave 1, as the complete indicator-level structure could be obtained only from this MIDUS wave. Despite the fact that the cohorts in MIDUS I are at a less advanced stage of having completed their fertility (typically mid-40s for both males and females; Fieder and Huber 2007), and hence the strength of the indicator-fertility correlation will likely be weaker (owing to higher-*K* individuals postponing child birth until later in life), we nonetheless rely upon the fact that the relative magnitudes of these indicator-fertility relationships would remain the same at completed fertility. Hence, the method of correlated vectors can still yield valuable information about the pattern of moderation despite the limitations of using a younger sample that is at incomplete fertility (MIDUS I).

Results

Analysis 1

The results presented for MIDUS II in Table 2 were obtained using negative binomial regressions. Model fit was determined using the Akaike Information Criterion (AIC). A decreased value indicates a more parsimonious model fit. The differences in AIC values between models were tested for significance using their constituent log-likelihood values and degrees of freedom. The model incorporating Steps I and II exhibited a better fit than the one including only Step I (Chi-squared = 5.92, *df* = 2, *p* < .05). Age, the *K*-Factor, and the *K*-Factor by sex interaction (indicating a weaker effect of *K* upon fertility in women than in men) significantly predicted fertility. However, the addition of the quadratic term and its interaction with sex in Step III did not improve the fit of the model (Chi-squared = .17, *df* = 2, *p* > .05), suggesting that the relationship of life history speed with fertility is linear in MIDUS II.

Similar tests were conducted on the Swedish STAGE data, and results are displayed in Table 3. As twins were involved in the data collection for this sample, two sets of results are reported: one for each set of twins, separating them. For both sets of twins, the model including only Step I was the most parsimonious according to AIC values, with the sex differences and interactions introduced in Step II not adding to model fit (Chi-squared = .74 and .09 for the first and second sets of twins, respectively; *df* = 2, *p* > .05). The fit of the model including Step III was not different from that including Steps I and II (Chi-squared = 1.21 and .31 for the first and second sets of

Table 2 Negative binomial regression model parameters and model fit in American MIDUS II subjects

Predictor	Model AIC	<i>b</i>	s.e.
Step I	8408.81		
Age		.01*	.00
<i>K</i>		.11*	.04
Step II	8406.85		
Age		.01*	.00
<i>K</i>		.19*	.06
Sex		-.02	.04
Sex* <i>K</i>		-.16*	.08
Step III	8410.68		
Age		.01*	.00
<i>K</i>		.16	.11
<i>K</i> ²		-.03	.10
Sex		-.01	.04
Sex* <i>K</i>		-.10	.15
Sex* <i>K</i> ²		.05	.13

Fertility is the dependent variable
**p* < .05

Table 3 Negative binomial regression model parameters and fit in Swedish STAGE twins

Predictor	Twin 1			Twin 2		
	Model AIC	<i>b</i>	s.e.	Model AIC	<i>b</i>	s.e.
Step I	4761.99			4777.18		
Age		.03*	.00		.03*	.00
<i>K</i>		.06*	.03		.06*	.02
Step II	4765.25			4781.09		
Age		.03*	.00		.03*	.00
<i>K</i>		.07*	.02		.06*	.02
Sex		.02	.04		-.01	.04
Sex* <i>K</i>		-.02	.04		-.01	.04
Step III	4768.04			4784.78		
Age		.03*	.00		.03*	.00
<i>K</i>		.07	.02		.06	.02
<i>K</i> ²		.02	.02		.01	.02
Sex		.03	.04		-.01	.04
Sex* <i>K</i>		-.00	.04		.00	.04
Sex* <i>K</i> ²		-.00	.03		.00	.02

Fertility is the dependent variable
**p* < .05

twins, respectively; *df* = 2, *p* < .05), again indicating that the relationship of LH speed and fertility is not quadratic.

Analysis 2

Vector correlations are computed between the vectors of *K*-factor indicator*fertility correlations, *K*-factor loadings, and additive heritabilities (Table 4). Vector correlations are a relatively simple form of moderation analysis that in this instance tells us the extent to which both the loading of *K* onto the indicator and the indicator-level additive heritability predicts the strength of selection. Statistical significance of vector correlations is a function of participant numbers associated with the dependent variable, as each vector element (i.e., each effect size 1* effect size 2 pairing) is weighted by the size of the participant pool—thus, the vector correlation is functionally equivalent to an *N*-weighted correlation, deriving its degrees of freedom accordingly (see: Woodley of Menie et al. 2015b). The vector correlation between (1) age-controlled *b* estimates for the effect of *K*-Factor indicators upon fertility and (2) *K*-loadings of the same indicators was -.06 (*p* < .05), whereas that between (1) *b* estimates and (2) the heritability of the indicators was .28 (*p* < .05), indicating that the more heritable an indicator of *K* is, the stronger is its relationship with fertility.

The results of analysis 1 indicated a positive and statistically significant age-controlled linear relationship between life history and fertility in both MIDUS II and in the STAGE samples. These results were robust to the addition of a

Table 4 Vectors of K -factor indicator*fertility correlations (all controlled for age), indicator K -loadings, and indicator-level additive heritabilities (h^2). N for vector 1 = 2257, N for vectors 2 and 3 = 642

K -factor indicator	b (indicator*fertility)	K -loading	h^2
Insight, planning, and control	-.00	.54*	.62
Romantic partner attachment	.00	.60*	.35
Mother and father relationship quality	-.00	.59*	.46
Family social contact and support	.05*	.69*	.22
Friends social contact and support	-.02	.43*	.04
General social altruism	-.02	.64*	.33
Religiosity	.10*	.48*	.52

quadratic term (to detect non-directional selection), indicating that the K -factor is under directional selection, with slower life history speeds being selected. No sex differences were found in this effect in the Swedish sample, whereas in the American sample, the relationship was stronger among men—even though it was observed to be positive in both sexes. That both sets of Swedish twins yielded highly congruent estimates of the K -fertility correlation indicates that the STAGE results replicate well.

The apparent generalizability of the finding of a positive correlation between K and fertility, using two different operationalizations of K , is further evidence for the *validity* of the Mini- K as a short-form measure of the K -factor (Figueredo et al. 2014a, b). Age was a consistently significant and positive predictor of fertility in all models, independent of K . This is consistent with the expectation that individuals continue to produce offspring up to the point at which fertility is complete.

The results of the moderator analysis (Analysis 2) indicate a small-to-moderate magnitude (Cohen 1988), but statistically significant, positive vector correlation between the indicator-fertility association and indicator-level additive heritability ($\rho = .28$). This suggests that indicator heritability positively moderates the strength of selection operating on each indicator. This finding can be tentatively interpreted as evidencing the substantiveness of the selection effect, as increasing amounts of genetic additivity should increase the degree of traction that selection has on a trait. This is consistent with the Breeder's equation, where the responsiveness of a trait to selection (R) is proportional to both the strength of selection operating on the trait (S) and the additive heritability (h^2) of the trait ($R = S * h^2$; Fisher 1929). The existence of a very small magnitude negative vector correlation between indicator K -loading and selection strength ($\rho = -.06$) indicates that the common K -Factor variance is *not* the principal target of selection, as selection directly upon the K -Factor itself would be expected to produce stronger selection gradients on the indicators that are more K loaded.

The parameter S from the Breeder's equation can be calculated by averaging across the parental levels of K and then taking a weighted average using the numbers of children as a

weighting term. The difference between the two values yields the degree to which the trait should change over the course of a single generation (all else being equal, i.e., assuming 100% heritability, no multivariate selection and ignoring interactions between trait level and age of first birth). For the MIDUS II sample, when the aggregate level of the K -Factor is scaled using "Mini- K " units, i.e., an IQ-like interval scale with a mean of 0 and a standard deviation of 13—derived from the scoring system of the Mini- K , K should be increasing by around .55 units per generation. When this value of S is multiplied by the additive heritability of the MIDUS K -factor ($h^2 = .65$ from Figueredo et al. 2004), we get an R value of .36 K units per generation or .03 of a standard deviation increase. In the case of the STAGE sample, the heritability of the Mini- K is lower ($h^2 = .33$; Woodley of Menie and Madison 2015), thus when averaging the S values derived from the two twin subsamples, we get a lower value of R for the STAGE sample (.27 K units, or .02 standard deviation units per generation).

Discussion

The Contemporary Effects of Strategic Interference

These results are highly consistent with Brase's (2013) findings of positive correlations between a measure of slow LH speed and desired numbers of children, as not only do slower LH individuals desire to have greater numbers of children (and indeed find children more desirable in general), they actually produce greater numbers as well, consistent with theoretical expectations.

Accelerating LH Slowing and Differentiation

The selection pressure favoring slower LH, while positive, is small in both populations, and cannot account for the relatively large apparent slowing of life history experienced by Western populations post-demographic transition, as evidenced by increases in somatic effort factors, such as height and body mass, increased longevity, decreased fertility,

increased somatic capital (i.e., more time spent in education), etc. (e.g., Mace 2000). A potential solution to this observation of apparent runaway LH slowing in modern populations is based on the observation that slower LH is positively associated with developmental plasticity (Woodley of Menie et al. 2015a, b), thus genetic changes favoring slower LH might rebound, via their effects on environmental harshness and predictability, on LH speed in developmental, or *ontogenetic* time, eliciting ever slower LH strategies via the operation of a *social multiplier* (e.g., Dickens and Flynn 2001; cf. Del Giudice 2016).

As the multivariate *K*-Factor score increases, the apparent independence and modularity of its components increase also—this being the *Strategic Differentiation-Integration Effort* (SD-IE) effect (Figueredo et al. 2013a, b). The observation that selection appears to be largely indifferent to the *K*-loading of indicators might therefore result in the slowing of life history in the aggregate but may also contribute simultaneously to the weakening of the manifold integrity of the *K*-Factor over time. This latter proposition could be tested via cross-sectional comparisons of the amount of variance accounted for by the principal factor among LH indicators in two samples separated by decades. Not all of the components of slower LH are under directional selection favoring higher levels either, with the “friends, social contact and support” subscale being one prominent example of an indicator exhibiting an oppositely directed selection gradient ($b = -.02$). These indicators may share variance with general intelligence (possibly via *altruism* in the case of friend support; Millet and Dewitte 2007). Decreased general intelligence stemming from selection favoring those with lower levels of the trait may therefore contribute to the further weakening of the *K* manifold, as those components that share variance with general intelligence can be expected to pull-away from *K* relatively rapidly owing to antagonistic selection operating on the two sources of variance.

Conclusion

For nearly a century, studies of the relationship between cognitive ability measures and fertility have revealed negative relationships—indicating the existence of a selection pressure disfavoring high general intelligence (Woodley of Menie 2015). This has recently been substantiated utilizing genetic markers of general intelligence, which also negatively predict fertility outcomes (Beauchamp 2016; Woodley of Menie et al. 2016). Much trepidation has accompanied these findings—revolving around the idea that the “dumbing down” of society will have severely negative consequences for future generations (Galton 1869; Lynn 1996). The present results however indicate a fundamentally different evolutionary trajectory among Western populations for LH traits, as high *K*—a prospectively highly socially desirable trait—seems to be favorable to fitness outcomes, implying that future generations may

enjoy more of it than present ones. These findings should give those interested in the patterns of contemporary or *anthropocene* selection pause for thought, as it is clear that humans micro-evolution is not simply favoring one trajectory, but many, some of which involve the promotion of so-called socially desirable traits, whereas others are disfavoring them.

Acknowledgements The MIDUS I study (Midlife in the U.S.) was supported by the John D. and Catherine T. MacArthur Foundation Research Network on Successful Midlife Development. The MIDUS II research was supported by a grant from the National Institute on Aging (P01-AG020166) to conduct a longitudinal follow-up of the MIDUS I investigation. TCDB was supported by a National Institute of Mental Health grant T32MH019391.

References

- Beauchamp, J. P. (2016). Genetic evidence for natural selection in humans in the contemporary United States. *Proceedings of the National Academy of Sciences U S A*, *113*, 7774–7779.
- Brase, G. (2013). Do life-history strategies and mating orientation translate into desires for children? Oral Presentation given at the 25th Annual Meeting of the Human Behavior and Evolution Society.
- Brim, O. G., Baltes, P. B., Bumpass, L. L., Cleary, P. D., Featherman, D. L., Hazzard, W.R., & Kessler, R.C., et al. (2000). National survey of midlife development in the United States (MIDUS), 1995–1996 [Computer file]. ICPSR version. Ann Arbor, MI: DataStat, Inc. /Boston, MA: Harvard Medical School, Dept. of Health Care Policy [producers], 1996. Ann Arbor, MI: Inter-university Consortium for Political and Social Research [distributor].
- Buss, D. M. (1987). Selection, evocation, and manipulation. *Journal of Personality and Social Psychology*, *53*, 1214–1221.
- Clark, G. (2007). *A farewell to alms: a brief economic history of the world*. New Jersey: Princeton University Press.
- Clark, G. (2014). *The son also rises: surnames and the history of social mobility*. New Jersey: Princeton University Press.
- Clark, G., & Hamilton, G. (2006). Survival of the richest: the Malthusian mechanism in pre-industrial England. *The Journal of Economic History*, *66*, 1–30.
- Cochran, G., & Harpending, H. (2009). *The 10,000 year explosion: how civilization accelerated human evolution*. New York: Basic Books.
- Cohen, J. (1988). *Statistical power analysis for the behavioral sciences* (2nd ed.). Hillsdale: Lawrence Erlbaum Associates.
- Deary, I. J. (2012). Looking for ‘system integrity’ in cognitive epidemiology. *Gerontology*, *58*, 545–553.
- Del Giudice, M. (2016). The evolution of interaction shape in differential susceptibility. *Child Development*. In press.
- Del Giudice, M., Gangestad, S. W., & Kaplan, H. S. (2015). Life history theory and evolutionary psychology. In D. M. Buss (Ed.), *The handbook of evolutionary psychology—Vol 1: foundations* (2nd ed., pp. 88–114). New York: Wiley.
- Dickens, W. T., & Flynn, J. R. (2001). Heritability estimates versus large environmental effects: the IQ paradox resolved. *Psychological Review*, *108*, 346–369.
- Dunkel, C. S. (2013). The general factor of personality and general intelligence: evidence for a substantial association. *Intelligence*, *41*, 423–427.
- Dunkel, C.S., & Beaver, K. (2013). Life history theory and the general theory of crime: Life expectancy effects on low self-control and criminal intent. *Journal of Social, Evolutionary, and Cultural Psychology*, *7*, 12–23.
- Ellis, B. J., Figueredo, A. J., Brumbach, B. H., & Schlomer, G. L. (2009). Fundamental dimensions of environmental risk: the impact of harsh

- versus unpredictable environments on the evolution and development of life history strategies. *Human Nature*, 20, 204–298.
- Fieder, M., & Huber, S. (2007). The effects of sex and childlessness on the association between status and reproductive output in modern society. *Evolution and Human Behavior*, 28, 392–398.
- Figueredo, A. J. (2009). Human capital, economic development, and evolution: a review and critical comparison of Lynn & Vanhanen (2006) and Clark (2007). *Human Ethology Bulletin*, 24, 5–8.
- Figueredo, A. J., Vásquez, G., Brumbach, B. H., & Schneider, S. M. R. (2004). The heritability of life history strategy: the K-factor, covitality, and personality. *Social Biology*, 51, 121–143.
- Figueredo, A. J., Vásquez, G., Brumbach, B. H., Schneider, S. M. R., Sefcek, J. A., Tal, I. R., et al. (2006). Consilience and life history theory: from genes to brain to reproductive strategy. *Developmental Review*, 26, 243–275.
- Figueredo, A. J., Cabeza de Baca, T., & Woodley, M. A. (2013a). The measurement of human life history strategy. *Personality and Individual Differences*, 55, 251–255.
- Figueredo, A. J., Woodley, M. A., Brown, S. D., & Ross, K. C. (2013b). Multiple successful tests of the strategic differentiation-integration effort (SD-IE) hypothesis. *Journal of Social, Evolutionary & Cultural Psychology*, 7, 361–383.
- Figueredo, A. J., Cabeza de Baca, T., & Black, C. (2014a). No matter where you go, there you are: the genetic foundations of temporal stability. *Journal of Methods and Measurement in the Social Sciences*, 5(2), 76–106.
- Figueredo, A. J., Wolf, P. S., Olderbak, S. G., Gladden, P. R., Fernandes, H. B. F., Wenner, C., et al. (2014b). A meta-analytic validation of the Mini-K short form of the Arizona Life History Battery. *Evolutionary Behavioral Sciences*, 8, 148–185.
- Fisher, R. A. (1929). *The genetical theory of natural selection*. Oxford: Clarendon.
- Frost, P., & Harpending, H. C. (2014). Western Europe, state formation, and genetic pacification. *Evolutionary Psychology*, 13, 230–243.
- Galton, F. (1869). *Hereditary genius*. London: Macmillan.
- Kanazawa, S. (2005). An empirical test of a possible solution to “the Central Theoretical Problem of Human Sociobiology”. *Journal of Cultural and Evolutionary Psychology*, 3, 249–260.
- Kingsolver, J. G., & Pfennig, D. W. (2007). Patterns and power of phenotypic selection. *BioScience*, 57, 561–572.
- Kirk, D. (1996). Demographic transition theory. *Population Studies*, 50, 361–387.
- Lawson, D. W., Alvergne, A., & Gibson, M. A. (2012). The life-history trade-off between fertility and child survival. *Proceedings of the Royal Society B: Biological Sciences*, 279, 4755–4764.
- Lichtenstein, P., Sullivan, P. F., Cnattingius, S., Gatz, M., Johansson, S., Carlström, E., et al. (2006). The Swedish twin registry in the third millennium: an update. *Twin Research and Human Genetics*, 9, 875–882.
- Lynn, R. (1996). *Dysgenics: genetic deterioration in modern populations*. Westport: Praeger.
- MacArthur, R. H., & Wilson, E. O. (1967). *The theory of island biogeography*. Princeton: Princeton University Press.
- MacDonald, K. (2001). An integrative evolutionary perspective on ethnicity. *Politics and the Life Sciences*, 20, 67–79.
- MacDonald, K. B. (2009). Evolution, psychology, and a conflict theory of culture. *Evolutionary Psychology*, 7, 208–233.
- Mace, R. (2000). Evolutionary ecology of human life history. *Animal Behavior*, 59, 1–10.
- Meisenberg, G. (2010). The reproduction of intelligence. *Intelligence*, 38, 220–230.
- Millet, K., & Dewitte, S. (2007). Altruistic behaviour as a costly signal of general intelligence. *Journal of Research in Personality*, 41, 316–326.
- Pianka, E. R. (1970). On r- and K-selection. *American Naturalist*, 104, 592–596.
- Rushton, J. P. (1985). Differential K theory: the sociobiology of individual and group differences. *Personality & Individual Differences*, 6, 441–452.
- Rushton, J. P. (2000). *Race, evolution and behavior: a life history perspective* (3rd ed.). Port Huron: Charles Darwin Research Institute.
- Rushton, J. P. (2004). Placing intelligence into an evolutionary framework, or how g fits into the r-K matrix of life history traits including longevity. *Intelligence*, 32, 321–328.
- Sherman, R. A., Figueredo, A. J., & Funder, D. C. (2013). The behavioral correlates of overall and distinctive life history strategy. *Journal of Personality and Social Psychology*, 105, 873–888.
- Tooby, J., & Cosmides, L. (1992). The psychological foundations of culture. In J. H. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: evolutionary psychology and the generation of culture* (pp. 19–136). Oxford & New York: Oxford University Press.
- Volk, T., & Atkinson, J. (2008). Is child death the crucible of evolution. *Journal of Social, Evolutionary, and Cultural Psychology, Proceedings of the 2nd Annual Meeting of the North Eastern Evolutionary Psychology Society*, 247–260.
- Woodley, M. A. (2011). The cognitive differentiation-integration effort hypothesis: a synthesis between the fitness indicator and life history models of human intelligence. *Review of General Psychology*, 15, 228–245.
- Woodley of Menie, M. A. (2015). How fragile is our intellect? Estimating losses in general intelligence due to both selection and mutation accumulation. *Personality and Individual Differences*, 75, 80–84.
- Woodley of Menie, M. A., & Madison, G. (2015). The association between g and K in a sample of 4246 Swedish twins: a behavior genetic analysis. *Personality and Individual Differences*, 75, 80–84.
- Woodley of Menie, M. A., Figueredo, A. J., Cabeza de Baca, T., Fernandes, H. B. F., Madison, G., Wolf, P., et al. (2015a). Strategic differentiation and integration of genomic-level heritabilities facilitate individual differences in preparedness and plasticity of human life history. *Frontiers in Psychology*, 6, 422.
- Woodley of Menie, M. A., Figueredo, A. J., Madison, G., & Dunkel, C. S. (2015b). Estimating the strength of genetic selection against g in a sample of 3520 Americans, sourced from MIDUS II. *Personality and Individual Differences*, 86, 266–270.
- Woodley of Menie, M. A., Schwartz, J. A., & Beaver, K. M. (2016). How cognitive genetic factors influence fertility outcomes: a meditational SEM analysis. *Twin Research and Human Genetics*. In press.