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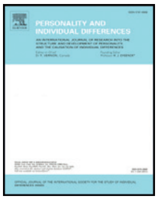

Evidence of contemporary polygenic selection on the Big *G* of national cognitive ability: A cross-cultural sociogenetic analysis

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ABSTRACT

Country-level total fertility rates (TFR) and cognitive ability are negatively correlated, suggesting the existence of a selection pressure that might be reducing *global G*. Also, the cross-population frequencies of several SNPs have been found to predict cognitive ability between countries. This study applies a cross-cultural sociogenetic approach to explore the role of latent factors among cognitive ability measures and these SNPs in moderating the associations among their indicators and TFR. Using a *G* factor constructed from five measures of cognitive ability, positive moderation is found on the TFR*ability relationship ($\rho = 0.251$ $N = 60.6$ countries). Using a metagene common factor among eight SNPs, positive moderation is also found on the TFR*SNP relationship ($\rho = 0.816$, $N = 18$ countries). An inference of *polygenic selection* for lower *G* is supported by the findings of two multivector co-moderation analyses. When controlled for one another, Human Development Index and metagene frequency both independently predicted TFR ($\beta = -0.339$, and -0.678 respectively, $N = 18$ countries). This indicates a joint impact of intelligent fertility control and life history slowing on the distribution of TFR values. Based on these results, polygenic selection might be reducing heritable *G* globally by -0.253 points per decade, highlighting the importance of the Flynn effect as a contributor to global development.

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1. Introduction

The emerging field of *cross-cultural sociogenetics* (Minkov, Blogoev, and Bond, 2015) has led to an abundance of research linking cross-cultural variation in the frequencies of various genes and alleles known or suspected to predict trait variation at the individual differences level, to the cross-cultural distribution of those same traits. Thus far, research in this field has examined the genetic underpinnings of cross-cultural variation in height (Turchin et al., 2012), intelligence and educational attainment (Piffer, 2013, 2015, 2016; Minkov et al., 2015; Minkov, Welzel, and Bond, 2016), life history characteristics and personality (Minkov and Bond, 2015; Minkov et al., 2015), individualism-collectivism (Chiao and Blizinsky, 2010) and subjective wellbeing (Minkov and Bond, 2016). Little attention has been paid to the implications of genetic factors for global patterns of selection operating contemporaneously on these traits however. It is known for example, that substantial differences in total fertility rates (TFR) exist between countries (CIA, 2015). Of particular interest is the observation that these have been found to consistently negatively correlate with country-level differences in cognitive ability (see Lynn and Vanhanen, 2012a, Table 14, p. 231 for an overview of studies). The present study will attempt to establish the role of sociogenetic factors in this relationship utilizing both moderation and regression analyses involving a newly developed cross-cultural genetic index of cognitive ability. These relationships have potentially significant implications for our understanding of the nature of contemporary patterns of phenotypic selection on the future of global cognitive ability.

The introduction is structured as follows; firstly the theoretical and empirical underpinnings of the negative relationship between IQ and fertility, both at the cross-cultural and individual-differences level will be reviewed. Here the *co-occurrence model* as a solution to *Cattell's Paradox*, or the observation that cognitive ability rises over time owing to the Flynn effect, rather than declines, as predicted by genetic selection, will be presented. Secondly, four predictions are made concerning the relationships between cross-cultural sociogenetic factors, TFR and various national-level indicators of cognitive ability.

1.1. The global relationship between cognitive ability and total fertility rates

Whilst several studies have demonstrated the existence of negative correlations between national cognitive ability and TFR (Lynn and Vanhanen, 2012a, 2012b), thus far only two studies have attempted to

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determine the degree to which the potential selection pressure stemming from this association should reduce global 'genotypic IQ' (i.e. the heritable variance component of IQ, or *IQ.h*, following abbreviations developed in Woodley and Figueredo, 2013) across generations. Based on a model that factored in the changing rate of population growth from 1950, projected out to 2050, Lynn and Harvey (2008) estimated a global *IQ.h* decline of 0.86 points between 1950 and 2000 (0.17 points per decade), which increases to 1.28 points between 2000 and 2050 (0.26 points per decade). In a second study, Meisenberg (2009) utilized a more sophisticated model in order to estimate the *IQ.h* change among the young, reproductive aged global population (Lynn and Harvey by contrast provide estimates for the change in the total global population). Meisenberg estimated an *IQ.h* decline of 1.31 points per 28-year generation (0.47 points per decade).

What is the origin of this apparent global selection pressure on cognitive ability? Key to understanding this is the *demographic transition*, or the general decrease in fertility, starting in the West during the Industrial Revolution and now present in the majority of the world's countries (Kirk, 1996). The demographic transition has two principal causes:

i) *Intelligent control of fertility*: Among Western populations, in the period leading up to the late 18th century, fitness among those with higher IQ (as indicated by proxies such as social status) was greater relative to those with lower ability (Clark, 2007; Skirbekk, 2008). A major driver of this fitness difference was selective child mortality, which was concentrated among those with lower social status, and (presumably) also lower IQ (Geary, 2000), and was higher than 50% in some Western populations during the Middle Ages (Volk and Atkinson, 2008). This led to a process of *downward social mobility* whereby the reproductive surplus of the high-socioeconomic status stratum came to gradually replace the reproductively failing lower stratum, as indicated by the increasing prevalence across social classes of formerly elite surnames over time (Clark, 2014). The net result of this would have been more intelligent populations that would have been able to make rational trade-offs between factors such as numbers of children and opportunities to increase their economic competitiveness, such as spending years in education (Kanazawa, 2014; Meisenberg, 2009, 2014). This *intelligent family planning* would have reduced the aggregate fertility of higher-ability Western populations relative to lower-ability populations that were less able to solve the evolutionarily novel 'problem' of fertility regulation.

ii) *Life history speed slowing*: Reductions in factors that cause mortality, such as parasite stress, inadequate nutrition and both intra and inter-group conflict, driven by innovations stemming from rising IQ in Western populations, would have increased social stability (Pinker, 2011). These signals of environmental stability may have encouraged developmental life history speed slowing (i.e. the development of a more K-type life history strategy), which is characterized by the allocation of time and energy into somatic maintenance, the development of lower time preferences and into parenting, rather than into mating (Ellis, Figueredo, Brumbach, and Schlomer, 2009). This would have resulted in reductions in fertility (i.e. fewer numbers of better looked after children), coupled with increases in factors such as body-mass and longevity (Mace, 2000). Increases in standards of living throughout the world might also account for why similar fertility patterns have spread into developing countries (Caldwell, 2001). Nevertheless, adaptive genetic differences in life history strategy between populations (Minkov and Bond, 2015; Rushton, 2000) likely impose limits on the degree to which life history can slow developmentally in response to enhanced environmental stability, which accounts in part, for the persistence of the negative correlations between cognitive ability and TFR between countries, where the latter can be taken as an indicator of life history strategy at the cross-cultural level (Meisenberg and Woodley, 2013; Templer, 2008).

The negative correlation between TFR and cognitive ability measures at the cross-cultural level mirrors the existence of negative associations between these and completed fertility at the individual differences level. These negative associations appear to have been present in many Western countries since the early 1800′s, when wealth/income, occupation/social class and education are utilized as proxies for cognitive ability (Skirbekk, 2008). Presently, these negative associations appear to be nearly worldwide in extent (Lynn, 2011; Meisenberg, 2008; Skirbekk, 2008). Despite the fact that in the West, the demographic transition involved falling fertility levels across socio-economic groups (Kirk, 1996), the impact on the relative fitness of those with high levels of *IQ.h* appears to have been greater than on those with low levels. This was likely a consequence of reduced infant mortality (which fell to <1% in the 20th century; Volk and Atkinson, 2008), stemming from reductions in disease, violence and improvements in nutrition, increasing the overall proportion of children surviving to reproductive age born among those with lower *IQ.h*, coupled with more intensive fertility regulation among those with higher levels, in response to the ever more extensive use of contraceptives and the increasing prevalence of opportunities to delay fertility afforded by further education and longer work hours (Lynn, 2011; Meisenberg, 2010).

It has been estimated that within the UK and US, the selection pressure stemming from the negative IQ-fertility relationship should have reduced heritable general intelligence (i.e. the heritable variance component associated specifically with the *g* factor variance in IQ tests; *g.h*; Woodley and Figueredo, 2013) by around 0.39 points per decade (Woodley of Menie, 2015).

It is important to note that these long-term within and between population selection trends are additive and imply substantial global *IQ.h* losses throughout the 20th century, especially after the second half of the 20th century, when the within-population correlations between fertility and cognitive ability proxies, such as education, became negative for the majority of the world's regions (Skirbekk, 2008). Despite this, measured IQ has actually *risen* throughout the world in this time period at a rate of three points per decade (Pietschnig and Voracek, 2015), this phenomenon having been termed the Flynn effect (Herrnstein and Murray, 1994). Per capita wealth has also been increasing in this period (Maddison, 2007). The Flynn effect is therefore paradoxical, as phenotypic IQ, or measured IQ resulting from both genetic and environmental influences (abbreviated to *IQ.p*; Woodley and Figueredo, 2013) appears to have been rising, when in fact it should have been decreasing – this anomaly was even termed *Cattell's Paradox* (Higgins, Reed, and Reed, 1962), after the psychometrician Raymond B. Cattell, who was vocal in predicting IQ decline due to the low fertility of high-*IQ.p* individuals, yet was among the first to observe the Flynn effect in attempts to test this prediction (Cattell, 1936, 1950).

1.2. The co-occurrence model

A solution to *Cattell's Paradox* is the *co-occurrence model*, which is based on the prediction that genetic selection reduces only *g.h*, whereas environmental improvements boost the levels of the environmentally sensitive variance component of specialized abilities (termed *s.e* by Woodley and Figueredo, 2013, after Spearman's [1904] use of the shorthand '*s*' to collectively denote the non-*g* variance components of each mental ability). Consistent with this prediction, studies using the method of correlated vectors to determine the degree to which the *g* loading of subtests moderates their association with other variables, routinely demonstrate that more *g*-loaded ability measures are not only more heritable (for a review of findings, see: Voronin, te Nijenhuis, and Malykh, 2015), but also negatively correlate more strongly with fertility (Wang, Fuerst, and Ren, 2016; Peach, Lyerly, and Reeve, 2014; Woodley and Meisenberg, 2013; Woodley of Menie and Dunkel, 2015; Woodley of Menie, Figueredo, Dunkel & Madison, 2015; Woodley of Menie, Fernandes, Figueredo & Meisenberg, 2015). Within-populations, genetic selection for lower IQ and heritability are therefore both *Jensen effects* – their effect magnitudes being greatest when g loading is highest (Rushton, 1998). This is consistent with evidence that the *proximate* cause of the high-heritability of g stems from the action of numerous genetic variants with individually small, but pleiotropic (i.e. influencing multiple cognitive abilities simultaneously) effects (Davies et al., 2011; Rimfeld, Kovas, Dale, and Plomin, 2015), this in turn provides selection with a substrate on which it can operate.

A meta-analysis of the results of applying MCV to studies investigating the Flynn effect by contrast revealed the presence of an anti-Jensen effect, i.e. less g–loaded measures of cognitive ability tend to be the ones that are most sensitive to secular gains (te Nijenhuis and van der Flier, 2013). This is consistent with the patterns found for other environmentally mediated cognitive improvements, such as IQ gains due to the Headstart Program (te Nijenhuis, Jongeneel-Grimen, and Kirkegaard, 2014), and those accrued by children due to adoption into higher-IQ families (te Nijenhuis, Jongeneel-Grimen, and Armstrong, 2015). Thus environmental factors seem to primarily influence *s.e* rather than *g.h*.

The idea that *g.h* may actually have declined, despite massive simultaneous gains in *s.e*, may make sense of certain apparently contradictory findings. For example, despite the growth in wealth, worldwide per capita rates of ‘disruptive’ (i.e. world-changing) innovation, along with the eminent individuals responsible for them, have been falling since the mid-19th century (Huebner, 2005; Murray, 2003). Furthermore, there are possible indications of long-term secular declines in the speed with which people process simple visual stimuli (Woodley of Menie, te Nijenhuis & Murphy, 2015), people's capacity to recall digits backwards (Woodley of Menie and Fernandes, 2015), the ability to differentiate among subtle variation in colour hue (Woodley of Menie and Fernandes, 2016), and the usage frequency of difficult-to-learn words sampled across representative collections of text (Woodley of Menie, Fernandes, Figueredo and Meisenberg, 2015). All of these measures relate to basic processes latent in g, such as processing speed and perceptual efficiency (in the case of reaction times and colour discrimination), working memory (in the case of backwards digit span), long-term memory (in the case of vocabulary knowledge) and complex problem solving ability (in the case of innovation and genius), all of which have real world impacts on achievement in everyday life (Kyllonen and Christal, 1990; Rindermann and Neubauer, 2000). The co-occurrence model predicts that each of these trends constitute manifest indicators of an underlying decline in latent *g.h* – this having been termed the *dysgenesis syndrome* by Woodley and Figueredo (2013, p.89).

The growth in wealth could on the other hand be driven purely by increasing ability specialization over time via enhanced comparative advantage. Slow life history is known to be associated with increased cognitive specialization (Woodley, Figueredo, Brown, and Ross, 2013) and also greater wealth (Cabeza de Baca and Figueredo, 2014). Correlations have furthermore been established between the magnitude of Flynn effects across countries and proxies for life history speed slowing (decreasing fertility rates) in addition to wealth growth, making this pattern of causation compelling (Pietschnig and Voracek, 2015). The very factor that initially caused the demographic transition in Western populations, i.e. high *g.h* therefore appears to have led simultaneously to genetic selection against *g.h* coupled with environmental improvements of a sort that encouraged slower life history – and therefore enhanced *s.e* via the Flynn effect. The fact that psychometric measures of life history speed (such as the *K* factor) are virtually uncorrelated with *IQ.p* at the individual differences level (Figueredo et al., 2014; Woodley, 2011; Woodley of Menie and Madison, 2015) lends credence to this model, as within populations, life history speed can slow, ensuring both the continuity of the Flynn effect *despite* simultaneously declining *g.h*.

1.3. Objectives

The Jensen effect on the negative cognitive ability-fertility association has been repeatedly demonstrated using individual differences data, indicating that the g saturation of an indicator positively moderates the magnitude of its association with fertility. As was discussed previously, additive heritability scales positively with the g saturation of ability measures, thus the strength of the selection gradient in part reflects the heritability (which corresponds to the degree to which selection can actually gain traction on a trait) of the ability (this pattern of co-moderation was explicitly demonstrated in Woodley of Menie and Dunkel, 2015). The co-occurrence model predicts that the cross-cultural (i.e. country level) cognitive ability-TFR relationship should also be associated with the Jensen effect. This is because, as with inter-individual variance in IQ (Spitz, 1988), inter-population variance in IQ is typically largest when estimated using highly g-loaded measures (Jensen, 1998; Rushton, 1998, 1999). This accords with evolutionary theories, which posit that the *distal* cause of the high heritability of g stems from it being the primary locus on which selection acted historically and continues to act in the evolution of g (Jensen, 1998; Rushton and Jensen, 2010; Woodley of Menie, Fernandes & Hopkins, 2015).

The availability of data on the frequencies of various Single Nucleotide Polymorphisms (SNPs) that are associated with regions of the genome that code for individual differences in *IQ.p* and proxy phenotypes such as educational attainment (e.g. Davies et al., 2015, 2016; Okbay et al., 2016; Rietveld et al., 2013; Rietveld et al., 2014), permits these evolutionary inferences to be tested. Specifically, analyses can be conducted to look for possible indications of contemporary *polygenic selection* on the cross-cultural distributions of these SNPs. Indications of historical polygenic selection have already been found in the non-random distributions of the cognitive ability SNPs cross-culturally. For example, Piffer (2013) found a strong signal of population-level covariance among the frequencies of 10 SNP hits (i.e. SNPs that are genome-wide significant predictors of variation in a given trait) associated with educational attainment, which replicated across three genomic databases. It was also observed that the common factor score among the frequencies of these SNPs (this is termed a *metagene*) strongly correlated with country-level measures of educational attainment. A more recent study corroborated this finding using a sample of nine SNP hits, some of which have replicated associations with *IQ.p* and related phenotypes in genome wide association studies (Piffer, 2015). Based on the results of three, large GWAS studies with a combined sample size of several hundred thousand individuals (Davies et al., 2016; Okbay et al., 2016; Rietveld et al., 2013), Piffer (2016) identified various loci that have replicated or quasi-replicated (the loci being in linkage disequlibrium across studies, clustered with a threshold $r = 0.5$ in a 500Kb window) associations with *IQ.p* and educational attainment. Based to these criteria, 18 SNPs (nine pairs) were in the same genomic region and one (rs9320913 A) actually directly replicated. A metagene constructed from these hits permitted the recovery of a very strong signal of historical polygenic selection operating on cognitive ability across the populations sampled in the 1000 Genomes Database (The 1000 Genomes Project Consortium, 2012). Critically, Piffer (2015, 2016) also found that null, negative or lower-magnitude positive associations with population-differences in cognitive ability are present when randomly selected SNPs are used instead of the hits, which suggests that the observed distributions and associations were unlikely to be due to chance.

1.3.1. Predictions

Based on the objectives, four predictions are made:

Prediction I) The Jensen effect observed on the negative correlation between completed fertility and measures of IQ.p at the individual differences level should also be present in cross-country data on TFR and convergent indicators of cognitive ability.

Prediction II) Cognitive metagene frequency should negatively predict population differences in TFR.
Prediction III) A Jensen effect should be present on the correlations between the individual SNP frequencies and TFR, when correlated with the vector of the loadings of the metagene onto each of the SNPs. This would provide evidence that the signature of genetic selection, resulting from the confirmation of prediction II, is truly polygenic in nature, as the selection effect would be biggest on those SNPs whose frequencies covary with the overall frequency of the metagene to the greatest extent.
Prediction IV) In order to test for the effects of both intelligent control of fertility and developmental life history slowing on the distribution of TFR, metagene frequency and measures of human development should independently predict TFR when controlled for each other.

The final objective of this analysis will be to utilize the new country-level general intelligence estimates computed in testing *Prediction* 1, along with TFR to generate a new estimate of the predicted global decline in *g.h* due to polygenic selection.

2. Methods

2.1. Phenotypic moderation analysis

Multiple measures of educational achievement and national IQ (collectively national cognitive ability) have been collected for large numbers of countries. It has been found that these measures strongly aggregate into a g-like common factor, termed *Big G* or just *G* (Rindermann, 2007). The 2012 PISA survey (OECD, 2014) measured four distinct cognitive abilities. In addition to mathematics, science and reading literacy in 64 nations, it also measured creative problem solving in 43 nations. Mathematics, science and reading literacy scores have been released for a 65th country, Puerto Rico (Kastberg et al., 2014). Adding to these school achievement indicators the psychometric national IQ estimates published in Lynn and Vanhanen (2012b) will yield a nomologically diverse, five-indicator *G* factor.

For each of these countries, data on 2014 TFR are available from *The CIA World Factbook* (CIA, 2015).

Unit-weighted factor analysis will be used to specify the factor structure a priori, which is essential to the recovery of meaningful factor structure when case and indicator-numbers are low (Gorsuch, 1983). This can be achieved by simply creating a composite average of the standardized ability indicators. The missing data among the creative problem solving scale will be handled using multivariate imputation (Figueredo, McKnight, McKnight, and Sidani, 2000) in SPSS (v.21). The bi-variate correlation between each cognitive ability measure and the *G* common factor yields the factor loadings for those measures. Each measure can be separately correlated with TFR forming an effect size vector, which can then be correlated with the vector of the *G* loadings on each measure, thus determining the presence of a Jensen effect (i.e. indications of positive moderation). Significance of the vector correlations is determined meta-analytically, i.e. based on the assumption that the correct degrees of freedom in MCV correspond to the pooled population of dependent-independent variable pairings, which equals the average sample size across paired vector elements, not the number of vector elements (see: Woodley of Menie, Fernandes, Figueredo and Meisenberg, 2015 for a discussion and demonstration of this). Consistent with this, the vector correlations are estimated using *N* weighted least-squares regressions (in SPSS v.21), where each vector element is weighted based on the number of countries that went into its computation.

The cognitive ability data and TFR values for each country are tabulated in the online Supplement (S.1).

2.2. Genotypic moderation analysis

Thus far, a handful of SNPs have been found to have statistically non-negligible and in some cases, replicable genome-wide associations with *IQ.p* and related phenotypes at the individual differences level. Piffer (2016) utilized population frequency data on the nine SNPs that have been found to have somewhat replicable effects across GWAS studies, obtained from the 1000 genomes database. In the present study, frequency counts are obtained for 18 population-aggregates corresponding to principal country ethnicities. Data on immigrant groups (i.e. populations from one country living in another) are excluded from the analysis on the basis that these populations may self-select for levels of ability that are not representative of their source populations. The SNP frequency values for the Yoruba and Esan populations were furthermore averaged to create a Nigerian composite. One of the nine SNPs identified by Piffer (2016) exhibited a reverse loading on the SNP metagene. It is possible that this SNP may simply be in linkage disequilibrium with SNPs that are causal of *IQ.p* differences in the Western populations in which these association studies have been conducted. If the linkage phase for these SNPs is different in non-Western populations, it may lead to inverse relationships owing to linkage disequilibrium with lower *IQ.p* SNPs in these populations (e.g. Reich et al., 2001). To control for this, in the present analysis, only the SNPs exhibiting associations with population-differences in *IQ.p* that are consistent in direction with their individual differences-level associations will be retained, yielding eight SNPs in total. The standardized frequencies of these SNPs will be aggregated into a unit-weighted metagene. The vector of the metagene loadings on each of the SNPs will then be correlated with the vector of the SNP frequency-TFR correlations in order to test for moderation.

The frequencies of the eight SNPs for each country are tabulated in the online data Supplement (S.1).

2.3. Strengthening the inference of causation via multivector co-moderation analysis

Confirmation of Predictions 1 and 3 alone would not be sufficient to infer the presence of a causal nexus among fertility, the metagene and *G*. In order to test causal inference, it will be necessary to consider also the association between each ability and the metagene frequency, and also the frequencies of each SNP and the *G* factor. Based on the inferred pattern of causation (i.e. selection is operating on *G* via the metagene), it will be necessary to demonstrate positive moderation between the vectors of each ability's *G* loading and the correlation of each of those abilities with the metagene frequency. Similarly, indications of positive moderation should also be present in the association between the vectors of each SNP's metagene loading and the correlation between each SNP and *G*. Thus each indicator of each latent variable can then be shown to associate with the other in proportion to the degree to which the loading of the indicator on its latent factor increases. It should also be possible to use the three vectors computed for each set of indicators (the cognitive and molecular variables) to extract a unit-weighted *multivector common factor*, which should exhibit positive loadings for each vector. All positive loadings in both cases would strengthen the inference of polygenic selection on *G* via the demonstration of *co-moderation* among each of the component vectors. This technique was originally developed by Rushton (1999), who constructed a multivector common factor from various measures of inbreeding depression effects, Black-White ability differentials, subtest *g* loadings and Flynn effect magnitudes obtained for each of the subtests of the WAIS, and found evidence of co-moderation among the first three vectors which was taken to evidence a biological nexus among these variables, and a separate environmental one among the measures of the Flynn effect.

Within our sample, only a small number of countries (China, Colombia, Finland, Italy, Japan, Peru, Spain, UK, USA and Vietnam) had data on both *G* and metagene.

As vectors with different degrees of freedom are being combined in the present analyses, the number of vector elements, which correspond with the numbers of SNPs or abilities, are used as a conservative basis for estimating significance.

2.4. Metagene frequencies and general development as independent predictors of TFR

In the final analysis, multiple-regression (implemented in R 3.2.0) will be used to determine whether metagene frequency and measures of general social development that potentially relate to slowing life history independently predict TFR when controlled for one another. Given the relatively small sample size (18 countries for which SNP-frequencies and national IQ were also available) the analysis will be conducted by standardizing the variables prior to entering them into regression. This yields standardized Beta (β) coefficients in the absence of an intercept, which restores a degree of freedom to the results, boosting statistical power. The most widely used general societal development measure is the Human Development Index (HDI), which is a composite of life expectancy (a proxy for health), education and per capita income. Each of these indicators relates to some aspect of life history speed; life expectancy signals the level of somatic effort being allocated to biological maintenance, education relates to the acquisition of somatic capital and income to time preferences. These data (for 2013) are collected from the United Nations Development Programme *Human Development Report* (2014; data for Puerto Rico were computed separately by Fuentes-Ramírez, 2014) and are included in the online data Supplement (S.1).

3. Results

3.1. Prediction I

Table 1 lists the *G* loadings on the separate cognitive abilities along with the ability*TFR correlations and ability*metagene correlations. TFR was found to exhibit significant skew (skewness magnitude >1) therefore in order to avoid possible issues of non-normality in the residuals it was transformed using a natural logarithm in all analyses. The vector correlations and multivector loadings are all listed as *modular* correlations, i.e. scaled in terms of magnitude rather than direction. The direction of latent variable moderation on the cognitive ability-fertility association is negative in sign owing to the negative-signed selection gradient being largest when latent factor loading is greatest. Rescaling the vector correlations in terms of magnitudes therefore yields the correct direction of moderation.

3.2. Predictions II and III

Table 2 lists the metagene loadings on the separate SNP frequencies along with the individual SNP*TFR correlations and the correlations between SNPs and *G*. The modular vector correlations and multivector loadings are also listed.

3.3. Prediction IV

Table 3 presents the results of multiple regression analysis in which standardized measures of metagene frequency and HDI are used to simultaneously predict TFR in a sample of 18 countries. Regression diagnostics indicate that there is no problematic colinearity present, with Variance Inflation Factor values falling below 2 in both cases. Values below 10 are considered acceptable (Kutner, Nachtsheim, Neter, and Li, 2005).

3.4. Estimating G losses

It should be possible to predict the decline in *G.h* utilizing the common factor *G* score and TFR values for each of the 65 countries to compute a selection differential (S). This can be achieved using Vining's (1982) formula:

$$S = \frac{1}{N}\sum_{i=1}^{N}(X_i - \overline{X})\frac{f_i}{\overline{f}}$$

$\overline{X}$ and $\overline{f}$ are the mean national *G* and TFR of the sample, X_i and f_i are the national *G* and TFR of the individual countries, and N is the sample size. To convert the phenotypic *G* decline predicted on the basis of the selection differential (S) into an estimate of *G.h* decline, the Breeder's equation is employed (Fisher, 1929):

$$R = Sh^2$$

S is the selection differential scaled as a decline in *G* (as computed using the previous equation), h^2 is the world-wide additive heritability of *G*, and R is the responsiveness of the trait to selection, which equates to the expected generational change in *G.h* given the aforementioned parameters. Both Lynn and Harvey (2008) and Meisenberg (2009) assumed that it is the global *IQ.h* variance component that should be declining therefore they correct their projected *IQ.p* declines via multiplication by a guesstimated worldwide IQ heritability of 0.35, which is approximately half of the aggregate additive heritability of IQ found in Western populations (i.e. 0.7). This guestimate is based on the assumption that the larger environmental variance across countries, will suppress the heritability of IQ. An alternative estimate of the degree to which country-level differences in *G* are genetically influenced can be obtained via multiple-regression in which the metagene score and HDI are used to predict national IQ, thus the degree to which the genetic component of national IQ predicts this parameter independently of potential environmental influences stemming from differences in HDI, can be determined. The standardized β coefficient for the metagene is 0.640 ($p < 0.05$, $N = 18$). This value needs to be corrected for psychometric validity (i.e. the degree to which national IQ imperfectly measures *G*), which simply involves dividing it by the *G* loading of national IQ (0.94), yielding a corrected β of 0.680. Squaring the β yields the variance (0.462), which can be multiplied with S in order to rescale this in terms of R, or losses in *G.h*.

A final correction to R can be made on the basis of range restriction. The educational achievement and cognitive ability scores were sampled across the 65 countries that participated in the 2012 PISA assessment wave. None of the countries were sourced from regions with relatively low ability (such as Sub Saharan Africa; Rindermann, 2013) therefore it stands to reason that the decline estimate is attenuated by range restriction. This can be corrected by taking the quotient of the sample standard deviation and a reference standard deviation from a more representative sample. Lynn and Harvey (2008) utilized country-level *IQ.p* data on 192 countries in estimating the decline in *IQ.h*. The standard deviation across their sample is 11.74. The standard deviation value across the countries utilized in the present analysis is 6.43, which is consistent with the presence of substantial range restriction. 6.43 divided by 11.74 yields a correction factor (u) of 0.55. Dividing the *G.h* decline (R) by this u value disattenuates the estimate for range restriction. These estimates are broken down in Table 4.

4. Discussion

Consistent with prediction I, a small magnitude (small = 0.1 to 0.29, moderate = 0.3 to 0.49, large = 0.5 to 1; Cohen, 1988) and also statistically significant Jensen effect was found on the cross-country cognitive ability-TFR association ($\rho = 0.251$), which indicates that ability

Table 1
Loading of G on the abilities, along with TFR*ability correlations and the correlation between abilities and metagene. The modular vector correlations are reported along with the loading of each vector onto a unit-weighted multi-vector common factor.

Ability	G λ (1)	r TFR-*ability (2)	r Ability*metagene (3)
G		**_−0.550*_**	**_0.857*_**
Science	0.982*	−0.523*	0.906*
Mathematics	0.985*	−0.572*	0.915*
Reading	0.980*	−0.507*	0.898*
Creative problem solving	0.952*	−0.534*	0.780*
National IQ	0.940*	−0.523*	0.803*
_1_	**_1.00_**	**_0.251*_**	**_0.944*_**
_2_		**_1.00_**	**_0.191_**
_3_			**_1.00_**
Multivector λ	**_0.888*_**	**_0.633_**	**_0.873*_**

*$P \leq 0.05$ (For *G* λ, and r TFR*ability, $N = 65$ countries per ability, except for CPS, where $N = 43$. For r ability*metagene, $N = 10$ countries per ability, except for CPS where $N = 8$ countries. Vector correlation 1*2 calculated by weighted correlation, therefore $N = 60.4$ countries. All other vector correlations and multivector λ are unweighted, with N equal to the number of vector elements, i.e. 5).

measures on which the *G* factor loads more strongly are somewhat more sensitive to cross-cultural differences in TFR. The Jensen effect is nonetheless smaller than has been observed in some individual differences level studies (effect sizes >0.8, e.g. Peach et al., 2014; Woodley and Meisenberg, 2013). This may stem from low variance among the common factor loadings (SD = 0.020; for comparison, the SD across WAIS subtests from various manuals is 0.128; te Nijenhuis and van der Flier, 2013), which is a known source of effect size attenuation in studies employing MCV (Jensen, 1998).

Prediction II was also confirmed with the finding of a large magnitude and significant negative correlation between metagene frequency and TFR ($r = -0.726$).

The finding of a large magnitude and significant Jensen effect on the association between the SNP frequency*TFR correlation and the loading of the metagene on its constituent SNPs ($\rho = 0.816$) is consistent with prediction III.

In testing Predictions I and III, strong indications of co-moderation are also found in the pattern of correlations among the three vectors, and also in the loadings of these vectors onto their respective multivector common factors, which were of large magnitude in all cases (the smallest value of λ was 0.633 in the case of the *r* TFR*ability vector in Table 1). These findings strengthen the causal inference that polygenic selection is occurring on *G*.

Table 2
Loading of the metagene on the SNP frequencies, along with TFR*SNP frequency correlations and the correlations between SNP frequencies and *G*. The modular vector correlations are reported along with the loading of each vector onto a unit-weighted multi-vector common factor.

SNP	Metagene λ (1)	r TFR*SNP (2)	r SNP*G (3)
Metagene		**_−0.726*_**	**_0.857*_**
rs1008078 C	0.296	−0.370	−0.111
rs11588857 A	0.925*	−0.602*	0.887*
rs12987662 A	0.927*	−0.736*	0.617
rs11712056 T	0.553*	−0.602*	0.186
rs62263923 G	0.846*	−0.625*	0.535
rs13294439 C	0.942*	−0.732*	0.800*
rs12969294 G	0.535*	−0.313	0.718*
rs9320913 A	0.778*	−0.700*	0.564
_1_	**_1.00_**	**_0.816*_**	**_0.812*_**
_2_		**_1.00_**	**_0.385_**
_3_			**_1.00_**
Multivector λ	**_0.991*_**	**_0.831*_**	**_0.829*_**

*$P < 0.05$ (For metagene λ, and r TFR*SNP, $N = 18$ countries per SNP. For r SNP*G, $N = 10$ countries per SNP. Vector correlation 1*2 calculated by weighted correlation, therefore $N = 18$ countries. All other vector correlations and multivector λ are unweighted, with N equal to the number of vector elements, i.e. 8).

Table 3
Multiple regression with metagene frequency and HDI predicting TFR. All variables have been standardized prior to regression and the intercept has been eliminated ($N = 18$ countries).

Standardized predictor (predicting TFR)	β	Standard error	*t*-Value	*p* r(>|*t*|)
Metagene	−0.339	0.122	−2.772	0.014
HDI	−0.678	0.122	−5.540	<0.001
r^2 (adjusted)	0.818			<0.001

Prediction IV was confirmed, as metagene frequency and HDI were modest and large magnitude (respectively) and significant independent predictors of TFR (metagene frequency $\beta = -0.339$; HDI $\beta = -0.678$). This suggests a potential joint role for the metagene and HDI in generating fertility differentials between countries, consistent with the predicted impacts of the intelligent control of fertility and developmental life history slowing hypotheses of the demographic transition.

Taken as a whole, these data not only demonstrate the ecological generalizability of the Jensen effect on the cognitive ability*fertility relationship, but they also indicate for the first time that SNPs, predictive of *IQ.p* at the individual-differences level might presently be under directional polygenic selection globally. This parallels a recent finding at the individual differences level, where an educational attainment polygenic score constructed from the 'hits' reported in Okbay et al. (2016) has been found to inversely predict relative lifetime reproductive success in a large, representative sample of White Americans ($N = 5987$) born between the 1930s and 1950s, indicating the presence of a selection pressure that should reduce educational attainment by approximately 1.5 months of attained education per generation[1] (Beauchamp, 2016).

The present results indicate that *G.h* might be declining globally at a rate of −0.253 points per decade. This parameter is estimated using a similar method to that employed by Lynn and Harvey (2008), thus it represents the decadal change in *G.h* of the total population, however the value was not estimated relative to changing population growth and therefore must be considered a 'snapshot' of the decline in modern populations, which, based on the demographic growth forecasts made by Lynn and Harvey (2008) can be expected to increase in magnitude over the coming decades.

The expectation that genetic selection should favour lower levels of *G.h* worldwide could not contrast more sharply with the co-occurrent and substantial growth in global wealth (Maddison, 2007). The existence of the latter trend is a strong testament to the importance of the Flynn effect, as ability specialization appears to have boosted the comparative advantage of populations in a way that has permitted substantial human development to occur directly in opposition to declining *G.h*.

On this basis, special attention should be paid to recent instances in which the increase in *IQ.p* characteristic of the Flynn effect appears to have slowed (i.e. Pietschnig and Voracek, 2015; Rindermann and Thompson, 2013) or even undergone secular decline (this being the so-called anti-Flynn effect; Dutton and Lynn, 2013, 2015), as such trends might signify a tendency towards reduced cognitive

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[1] Assuming a correlation between *g* and educational attainment of 0.7 (Ceci, 1991) and a standard deviation in years of education of 3.05 years (36.6 months; OECD, 2013), a 1.5 month decline in 'genotypic' attained education per 'standard' 28 year generation, would correspond to a *g.h* decline of 0.885 IQ points per generation, or 0.316 points per decade, which is close to the aggregate decadal loss in *g.h* estimated in Woodley of Menie (2015), i.e. 0.39 IQ points per decade.

Table 4
S: Decadal phenotypic losses in G; R: genotypic losses in $G.h$ per decade and R_u: range restriction corrected decadal losses in $G.h$.

S (phenotypic decline in G per 28 year generation)	S per decade	R (decline in $G.h$ per decade)	R_u (decline in $G.h$ per decade corrected for range restriction)
−0.840	−0.300	−0.139	−0.253

specialization with respect to $s.e$, perhaps ultimately driven by declining $g.h$, and may herald an era of declining human development.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.paid.2016.06.054.

References

Beauchamp, J. P. (2016). Genetic evidence for natural selection in humans in the contemporary United States. *BioRxiv*. http://dx.doi.org/10.1101/037929.

Cabeza de Baca, T., & Figueredo, A. J. (2014). The cognitive ecology of Mexico: Climatic and socio-cultural effects on life history strategies and cognitive abilities. *Intelligence*, *47*, 63–71.

Caldwell, J. C. (2001). The globalization of fertility behaviour. *Population and Development Review*, *27*, 93–115.

Cattell, R. B. (1936). Is our national intelligence declining? *The Eugenics Review*, *28*, 181–203.

Cattell, R. B. (1950). The fate of national intelligence: Test of a thirteen-year prediction. *The Eugenics Review*, *42*, 136–148.

Ceci, S. J. (1991). How much does schooling influence general intelligence and its cognitive components? A reassessment of the evidence. *Developmental Psychology*, *27*, 703–722.

Central Intelligence Agency (2015). *The CIA world factbook 2015*. New York: Skyhorse Publishing.

Chiao, J. Y., & Blizinsky, K. D. (2010). Culture-gene coevolution of individualism-collectivism and the serotonin transponder gene. *Proceedings of the Royal Society B: Biological Sciences*, *277*, 529–537.

Clark, G. (2007). *Farewell to Alms: A brief economic history of the world*. Princeton: Princeton University Press.

Clark, G. (2014). *The son also rises: Surnames and the history of social mobility*. Princeton: Princeton University Press.

Cohen, J. (1988). *Statistical power analysis for the behavioral sciences* (2nd ed.). Hillsdale: Lawrence Erlbaum Associates.

Davies, G., Tenesa, A., Payton, A., Yang, J., Harris, S. E., Liewald, D., ... Deary, I. J. (2011). Genome-wide association studies establish that human intelligence is highly heritable and polygenic. *Molecular Psychiatry*, *16*, 996–1005.

Davies, G., Armstrong, N., Bis, J. C., Bressler, J., Chouraki, V., Giddaluru, S., ... Deary, I. J. (2015). Genetic contributions to variation in general cognitive function: A meta-analysis of genome-wide association studies in the CHARGE consortium (N = 53949). *Molecular Psychiatry*, *20*, 183–192.

Davies, G., Marioni, R. E., Liewald, D. C., Hill, W. D., Hagenaars, S. P., Harris, S. E., ... Deary, I. J. (2016). Genome-wide association study of cognitive functions and educational attainment in UK Biobank (N = 112 151). *Molecular Psychiatry*, *6*, 758–767.

Dutton, E., & Lynn, R. (2013). A negative Flynn effect in Finland, 1997–2009. *Intelligence*, *41*, 817–820.

Dutton, E., & Lynn, R. (2015). A negative Flynn effect in France, 1999 to 2008–9. *Intelligence*, *51*, 67–70.

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*, 204–268.

Figueredo, A. J., McKnight, P. E., McKnight, K. M., & Sidani, S. (2000). Multivariate modelling of missing data within and across assessment waves. *Addiction*, *95*, S361–S380.

Figueredo, A. J., Wolf, P. S., Olderbak, S. G., Gladden, P. R., Fernandes, H. B. F., Wenner, C., ... Rushton, J. P. (2014). 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.

Fuentes-Ramírez, R. R. (2014). An approximation of Puerto Rico's Human Development Index. *Caribbean Studies*, *42*, 253–258.

Geary, D. C. (2000). Evolution and proximate expression of human parental investment. *Psychological Bulletin*, *126*, 55–77.

Gorsuch, R. L. (1983). *Factor analysis*. Hillsdale: Erlbaum Associates.

Herrnstein, R. J., & Murray, C. (1994). *The bell curve: Intelligence and class structure in American life*. New York: Free Press Paperbacks.

Higgins, J. V., Reed, E. W., & Reed, S. C. (1962). Intelligence and family size: A paradox resolved. *Eugenics Quarterly*, *9*, 84–90.

Huebner, J. (2005). A possible declining trend for worldwide innovation. *Technological Forecasting and Social Change*, *72*, 980–986.

Jensen, A. R. (1998). *The g factor: The science of mental ability*. Westport: Praeger.

Kanazawa, S. (2014). Intelligence and childlessness. *Social Science Research*, *48*, 157–170.

Kastberg, D., Chan, J. Y., Roey, S., Lemanski, N., Perkins, R., & Ruess, R. (2014). *Performance of Puerto Rico 15-year-old students in mathematics, science and reading literacy in an international context*. OECD.org.

Kirk, D. (1996). Demographic transition theory. *Population Studies*, *50*, 361–387.

Kutner, M., Nachtsheim, C., Neter, J., & Li, W. (2005). *Applied linear statistical models* (5th ed.). Irwin: McGraw-Hill.

Kyllonen, P. C., & Christal, R. E. (1990). Reasoning ability is (little more than) working memory capacity?! *Intelligence*, *14*, 389–433.

Lynn, R. (2011). *Dysgenics: Genetic deterioration in modern populations (2nd* (revised ed.). London: Ulster Institute for Social Research.

Lynn, R., & Harvey, J. (2008). The decline of the world's IQ. *Intelligence*, *36*, 112–120.

Lynn, R., & Vanhanen, T. (2012a). National IQs: A review of their educational, cognitive, economic, political, demographic, sociological, epidemiological, geographic and climatic correlates. *Intelligence*, *40*, 226–234.

Lynn, R., & Vanhanen, T. (2012b). *Intelligence: A unifying construct for the social sciences*. London: Ulster Institute for Social Research.

Mace, R. (2000). Evolutionary ecology of human life history. *Animal Behavior*, *59*, 1–10.

Maddison, G. (2007). *Contours of the world economy, 1–2030 AD: Essays in macroeconomic history*. New York: Oxford University Press.

Meisenberg, G. (2008). How universal is the negative correlation between education and fertility? *Journal of Social, Political and Economic Studies*, *33*, 205–227.

Meisenberg, G. (2009). Wealth, intelligence, politics and global fertility differentials. *Journal of Biosocial Science*, *41*, 519–535.

Meisenberg, G. (2010). The reproduction of intelligence. *Intelligence*, *38*, 220–230.

Meisenberg, G. (2014). Cognitive human capital and economic growth in the 21st century. In T. Abrahams (Ed.), *Economic growth in the 21st century: New research* (pp. 49–106). New York: Nova Publishers.

Meisenberg, G., & Woodley, M. A. (2013). Global behavioural variation: A test of differential-K. *Personality and Individual Differences*, *55*, 273–278.

Minkov, M., & Bond, M. H. (2015). Genetic polymorphisms predict national differences in life history strategy and time orientation. *Personality and Individual Differences*, *76*, 204–215.

Minkov, M., & Bond, M. H. (2016). A genetic component to national differences in happiness. *Journal of Happiness Studies*. http://dx.doi.org/10.1007/s10902-015-9712-y.

Minkov, M., Blogoev, V., & Bond, M. H. (2015). Improving research in the emerging field of cross-cultural sociogenetics. *Journal of Cross-Cultural Psychology*, *46*, 336–354.

Minkov, M., Welzel, C., & Bond, M. H. (2016). The impact of genes, geography, and educational opportunities on national cognitive achievement. *Learning and Individual Differences*, *47*, 236–243.

Murray, C. (2003). *Human accomplishment: The pursuit of excellence in the arts and sciences, 800 BC to 1950*. New York, NY: Harper Collins.

Okbay, A., Beauchamp, J. P., Fontana, M. A., Lee, J. J., Pers, T. H., Rietveld, C. A., ... Benjamin, D. J. (2016). Genome-wide association study identifies 74 loci associated with educational attainment. *Nature*, *533*, 539–542.

Organization for Economic Co-Operation and Development (2013). *OECD skills outlook 2013: First results from the survey of adult skills*. OECD.org.

Organization for Economic Co-operation and Development (2014). *PISA 2012 results in focus: What 15-year-olds know and what they can do with what they know*. OECD.org.

Peach, H., Lyerly, J. E., & Reeve, C. L. (2014). Replication of the Jensen effect on dysgenic fertility: An analysis using a large sample of American youth. *Personality and Individual Differences*, *71*, 56–59.

Pietschnig, J., & Voracek, M. (2015). One century of global IQ gains: A formal metaanalysis of the Flynn effect (1909–2013). *Perspectives on Psychological Science*, *10*, 282–306.

Piffer, D. (2013). Factor analysis of population allele frequencies as a simple, novel method of detecting signals of recent polygenic selection: The example of educational attainment and IQ. *Mankind Quarterly*, *54*, 168–200.

Piffer, D. (2015). A review of intelligence GWAS hits: Their relationship to country IQ and the issue of spatial autocorrelation. *Intelligence*, *53*, 43–50.

Piffer, D. (2016). Recent polygenic selection on educational attainment: A replication. *Figshare*. http://dx.doi.org/10.6084/m9.figshare.3381439.v2.

Pinker, S. (2011). *The better angels of our nature: Why violence has declined*. New York: Viking Adult.

Reich, D. E., Cargill, M., Bolk, S., Ireland, J., Sabeti, P. C., Richter, D. J., ... Lander, E. S. (2001). Linkage disequilibrium in the human genome. *Nature*, *411*, 199–204.

Rietveld, C. A., Medland, S. E., Derringer, J., Tang, J., Esko, T., Martin, N. W., ... Koellinger, P. D. (2013). GWAS of 126,559 individuals identifies genetic variants associated with educational attainment. *Science*, *340*, 1467–1471.

Rietveld, C. A., Esko, T., Davies, G., Pers, T. H., Turley, P., Benyamin, B., ... Koellinger, P. D. (2014). Common genetic variants associated with cognitive performance identified using the proxy-phenotype method. *Proceedings of the National Academy of Sciences of the United States of America*, *111*, 13790–13794.

Rimfeld, K., Kovas, Y., Dale, P. S., & Plomin, R. (2015). Pleiotropy across academic subjects at the end of compulsory education. *Scientific Reports*, 11713.

Rindermann, H. (2007). The big G-factor of national cognitive ability. *European Journal of Personality*, *21*, 767–787.

Rindermann, H. (2013). African cognitive ability: Research, results, divergences and recommendations. *Personality and Individual Differences*, *55*, 229–233.

Rindermann, H., & Neubauer, A. (2000). Speed of information processing and success at school: Do basal measures of intelligence have predictive validity? *Diagnostica*, *46*, 8–17.

Rindermann, H., & Thompson, J. (2013). Ability rise in NAEP and narrowing ethnic gaps? *Intelligence*, *41*, 821–831.

Rushton, J. P. (1998). The "Jensen Effect" and the "Spearman–Jensen Hypothesis" of Black–White IQ differences. *Intelligence*, *26*, 217–225.

Rushton, J. P. (1999). Secular gains not related to the g factor and inbreeding depression – unlike Black-White differences: A reply to Flynn. *Personality and Individual Differences*, *26*, 381–389.

Rushton, J. P. (2000). *Race, evolution and behavior: A life history perspective* (3rd ed.). Port Huron: Charles Darwin Research Institute.

Rushton, J. P., & Jensen, A. R. (2010). The rise and fall of the Flynn effect as a reason to expect a narrowing of the Black–White IQ gap. *Intelligence*, *38*, 213–219.

Skirbekk, V. (2008). Fertility trends by social status. *Demographic Research*, *18*, 145–180.

Spearman, C. (1904). "General intelligence," objectively determined and measured. *American Journal of Psychology*, *15*, 201–293.

Spitz, H. H. (1988). Wechsler subtest patterns of mentally retarded groups: Relationship to g and to estimates of heritability. *Intelligence*, *12*, 279–297.

te Nijenhuis, J., & van der Flier, H. (2013). Is the Flynn effect on g? A meta-analysis. *Intelligence*, *41*, 802–807.

te Nijenhuis, J., Jongeneel-Grimen, B., & Kirkegaard, E. O. W. (2014). Are Headstart gains on the g factor? A meta-analysis. *Intelligence*, *46*, 209–215.

te Nijenhuis, J., Jongeneel-Grimen, B., & Armstrong, E. L. (2015). Are adoption gains on the g factor? A meta-analysis. *Personality and Individual Differences*, *73*, 56–60.

Templer, D. I. (2008). Correlational and factor analytic support for Rushton's differential-K life history theory. *Personality and Individual Differences*, *45*, 440–444.

The 1000 Genomes Project Consortium (2012). An integrated map of genetic variation from 1,092 human genomes. *Nature*, *491*, 56–65.

Turchin, M. C., Chiang, C. W., Palmer, C. D., Sankararaman, S., Reich, D., Genetic Investigation of Anthropometric Traits, & Hirschhorn, J. N. (2012). Evidence of widespread selection on standing variation in Europe at height-associated SNPs. *Nature Genetics*, *44*, 1015–1019.

United Nations Development Programme (2014). *Human development report 2014: Sustaining human progress: Reducing vulnerabilities and building resilience*. New York: United Nations Publications.

Volk, T., & Atkinson, J. (2008). Is child death the crucible of evolution? *Journal of social, evolutionary, and cultural psychology* (pp. 247–260). Proceedings of the 2nd Annual Meeting of the North Eastern Evolutionary Psychology Society.

Voronin, I., te Nijenhuis, J., & Malykh, S. B. (2015). The correlation between g loadings and heritability in Russia. *Journal of Biosocial Science*, *28*, 1–11.

Wang, M., Fuerst, J., & Ren, J. (2016). Evidence of dysgenic fertility in China. *Intelligence*, *57*, 15–24.

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, M. A., & Meisenberg, G. (2013). A Jensen effect on dysgenic fertility: An analysis involving the National Longitudinal Survey of Youth. *Personality and Individual Differences*, *55*, 279–282.

Woodley, M. A., & Figueredo, A. J. (2013). *Historical variability in heritable general intelligence: It's evolutionary origins and socio-cultural consequences*. Buckingham: The University of Buckingham Press.

Woodley, M. A., Figueredo, A. J., Brown, S. D., & Ross, K. C. (2013). Four successful tests of the cognitive differentiation–integration effort hypothesis. *Intelligence*, *41*, 832–842.

Woodley of Menie, M. A. (2015). How fragile is our intellect? Estimating losses in general intelligence due to selection and mutation accumulation. *Personality and Individual Differences*, *75*, 80–84.

Woodley of Menie, M. A., & Dunkel, C. S. (2015). In France, are secular IQ losses biologically caused? A comment on Dutton and Lynn (2015). *Intelligence*, *53*, 81–85.

Woodley of Menie, M. A., & Fernandes, H. B. F. (2015). Do opposing secular trends on backwards and forwards digit span evidence the co-occurrence model? A comment on Gignac (2015). *Intelligence*, *50*, 125–130.

Woodley of Menie, M. A., & Fernandes, H. B. F. (2016). Showing their true colours: Possible secular declines and a Jensen effect on color acuity – more evidence for the weaker variant of Spearman's other hypothesis. *Personality and Individual Differences*, *88*, 280–284.

Woodley of Menie, M. A., Fernandes, H. B. F., Figueredo, A. J., & Meisenberg, G. (2015). By their words ye shall know them: Evidence of genetic selection against general intelligence and concurrent environmental enrichment in vocabulary usage since the mid 19th century. *Frontiers in Psychology*, *6*, 361.

Woodley of Menie, M. A., Fernandes, H. B. F., & Hopkins, W. D. (2015). The more g loaded, the more heritable, variable and evolvable: Homology with humans in chimpanzee cognitive abilities. *Intelligence*, *50*, 159–163.

Woodley of Menie, M. A., Figueredo, A. J., Dunkel, C. S., & Madison, G. (2015). Estimating the strength of genetic selection against heritable g in a sample of 3520 Americans, sourced from MIDUS II. *Personality and Individual Differences*, *86*, 266–270.

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*, *74*, 270–274.

Woodley of Menie, M. A., te Nijenhuis, J., & Murphy, R. (2015). The Victorians were still faster than us. Commentary: Factors influencing the latency of simple reaction times. *Frontiers in Human Neuroscience*, *9*(452).