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Paternal age negatively predicts offspring physical attractiveness in two, large, nationally representative datasets

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ABSTRACT

The effect of paternal age on offspring attractiveness has recently been investigated. Negative effects are predicted as paternal age is a strong proxy for the numbers of common *de novo* mutations found in the genomes of offspring. As an indicator of underlying genetic quality or fitness, offspring attractiveness should decrease as paternal age increases, evidencing the fitness-reducing effects of these mutations. Thus far results are mixed, with one study finding the predicted effect, and a second smaller study finding the opposite. Here the effect is investigated using two large and representative datasets (Add Health and NCDS), both of which contain data on physical attractiveness and paternal age. The effect is present in both datasets, even after controlling for maternal age at subject's birth, age of offspring, sex, race, parental and offspring (in the case of Add Health) socioeconomic characteristics, parental age at first marriage (in the case of Add Health) and birth order. The apparent robustness of the effect to different operationalizations of attractiveness suggests high generalizability, however the results must be interpreted with caution, as controls for parental levels of attractiveness were indirect only in the present study.

1. Introduction

Paternal age is an extremely strong proxy for the presence of common *de novo* Single Nucleotide Polymorphism mutations in the genomes of offspring. Each additional year of paternal age results in an average of two new mutations being added to the haploid genomes of sperm cells. At age 35, males typically bequeath around 70 new mutations to their offspring (Kong et al., 2012). It is estimated that a little over two of these mutations will have deleterious effects (Keightley, 2012). Establishing relationships between paternal age and offspring traits is therefore potentially highly informative in terms of estimating the sensitivity of those traits to the effects of common and mildly deleterious mutations, which in turn serves as an index of the degree to which the trait may be under mutation-selection balance (e.g. Arslan, Penke, Johnson, Iacono, & McGue, 2014). Paternal age effects also permit predictions from Fitness Indicators Theory to be tested. This theory predicts that pleiotropic mutations create genetic correlations among distinct sources of physical and psychological individual differences causing them to cohere into a latent general Fitness (F) factor (Houle, 2000; Miller, 2000; Penke, Denissen, & Miller, 2007). Phenotypic levels of this latent factor are reflected in *developmental stability*, which relates to the degree to which the effects of genetic and environmental disturbances interfere with the development of a trait (Penke et al., 2007; Waddington, 1942). Traits that are sensitive to mutations will develop optimally in the presence of a low load of deleterious mutations and abnormally in the presence of a high load, thus the levels of such traits can potentially serve as honest phenotypic signals of underlying fitness in sexual selection (Houle, 2000; Miller, 2000; Penke et al., 2007).

Consistent with this model, relationships have been established between paternal age and offspring levels of traits believed to signal neurodevelopmental stability, such as autism (Kong et al., 2012), schizophrenia (Brown et al., 2002) and attention deficit/hyperactivity disorder (D'Onofrio et al., 2014). Offspring general intelligence on the other hand does not appear to be sensitive to paternal age, contrary to predictions from Fitness Indicators Theory (Arslan et al., 2014; D'Onofrio et al., 2014).

One phenotypic trait that is expected to be highly sensitive to deleterious mutations is physical attractiveness. Attractiveness is believed to relate in part to the property of *symmetry* (Grammer & Thornhill, 1994), which is a highly general indicator of developmental stability (van Valen, 1962). Thus far, two studies have investigated the association between paternal age and physical attractiveness yielding mixed results. Huber and Fieder (2014) utilized a large mixed-sex sample ($n = 10{,}317$) drawn from the Wisconsin Longitudinal Study (WLS) for

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which data on facial attractiveness (evaluated using multiple, convergent ratings of attractiveness based on high school photographs) and both paternal and maternal age at birth were available. The bivariate correlation between facial attractiveness and paternal age was found to be −0.071, and the correlation with maternal age was found to be −0.029 (both were statistically significant). General Linear Models were constructed to evaluate the effect of controlling for various confounds, including subject's birth year, sex, father's age at birth of subject's eldest sibling and time to subject's birth (the last two control for the potential confounding effects of paternal attractiveness on the basis that less attractive males may take longer to find mates and produce offspring). Two separate models were run, one in which maternal age at subject's birth was controlled, and a second model in which the paternal physical attractiveness proxies were used as controls instead of maternal age. Both models yielded significant, negative effects of paternal age on offspring facial attractiveness ($b = -0.021$ in the case of Model 1, and −0.011 in the case of Model 2), consistent with the theory that advanced paternal age should reduce offspring attractiveness. Model 1 also found an independent significant *positive* effect of advanced maternal age on offspring attractiveness ($b = 0.013$), however additional analysis (involving different model specifications) indicated an inconsistent effect.

The only other study to investigate this question was that of Lee et al. (2016). This study utilized a relatively smaller mixed-sex sample ($n = 1823$) of monozygotic and dizygotic twins and their siblings to investigate the genetic architecture of the correlation between facial attractiveness (evaluated using convergent ratings of attractiveness) and facial averageness (evaluated using computer aided geometric morphometric analysis). Multiple regression analysis was used to determine whether there was any effect of paternal and maternal age on both facial attractiveness and facial averageness, after controlling for sex, the year in which the photograph was taken and subject's age. Neither paternal nor maternal age exhibited a significant effect on facial averageness ($\beta = -0.03$ and −0.01 respectively), however a significant *positive* effect of paternal age on facial attractiveness was found ($\beta = 0.09$), which runs contrary to Huber and Fieder's (2014) finding.

In the present study, we will revisit the question of whether or not there is a paternal age effect on offspring physical attractiveness utilizing two, large and representative, datasets (Add Health and the National Child Development Study) that are sourced from two different countries (the US and UK respectively). These datasets contain data on physical attractiveness and paternal age, along with a variety of covariates.

2. Methods and data

2.1. Add Health

The National Longitudinal Study of Adolescent Health (Add Health) is a large, nationally representative, and prospectively longitudinal study of young Americans. A sample of 20,745 adolescents were personally interviewed in their homes between 1994 and 1995 (Wave I; mean age = 15.6). They were again interviewed in 1996 (Wave II; $n = 14{,}738$; mean age = 16.2), in 2001–2002 (Wave III; $n = 15{,}197$; mean age = 22.0), and in 2007–2008 (Wave IV; $n = 15{,}701$; mean age = 29.1). Additional details of sampling and study design are provided at: http://www.cpc.unc.edu/projects/addhealth/design.

2.1.1. Dependent variable: physical attractiveness

At the conclusion of the in-home interview at each wave, the Add Health interviewer rated the respondent's physical attractiveness on a five-point ordinal scale (1 = very unattractive, 2 = unattractive, 3 = about average, 4 = attractive, 5 = very attractive). We performed a factor analysis with the four attractiveness scores given by four different interviewers at four different times spanning 12 years, yielding a *longitudinal* physical attractiveness measure. To compute the factor score, a Unit-Weighted Factor analysis was performed in which each participant's attractiveness ratings for each time-point were standardized – the average of the ratings across all four time-points yielded the unit-weighted longitudinal composite physical attractiveness measure for the participants. By specifying the common factor *a priori*, unit-weighting the indicators avoids the well-documented sample and indicator-specificity of factor scoring coefficients produced by standard errors of inconsistent magnitudes across different samples, and is considered to be the only method suitable for isolating common factor variance when either indicator of case numbers are low, as in the present study (Gorsuch, 1983). The loadings of each indicator onto the unit-weighted common factor can be computed by simply correlating each indicator with the common factor score (Gorsuch, 1983). Doing so reveals high-magnitude loadings of the unit-weighted longitudinal attractiveness score onto each of its component indicators (Wave $I = 0.646$, Wave II = 0.661, Wave III = 0.611, Wave IV = 0.581). We used the unit-weighted factor, with a mean of 0 and a standard deviation of 1, as the dependent variable in an Ordinary Least Squares (OLS) regression (implemented in SPSS v.22.0.0.2).

2.1.2. Independent variables

Our main independent variable was father's age at respondent's birth measured at Wave 1. Potential confounds that were controlled included mother's age at the respondent's birth (in order to control for potentially independent effects of maternal age on offspring attractiveness), the respondent's birth year (in order to control for potential secular trends in physical attractiveness, as noted by Huber & Fieder, 2014) and the respondent's sex (0 = female, 1 = male; in order to control for potential dimorphic effects on ratings of subject attractiveness). The respondent's race was measured with three dummy variables for Black, Asian and Native American (with White as the reference category) in order to control for the effects of race on perceived attractiveness (e.g. Lewis, 2011). Parent's income and respondent's earnings were included in the model (these were transformed using a natural logarithm in order to compensate for skewness) to control for the potential effects of socio-economic status on offspring attractiveness, on the premise that low socio-economic status may reduce the condition of the offspring or influence their perceived attractiveness. Parental socioeconomic characteristics furthermore serve as indirect controls for parental attractiveness, as robust positive associations have been observed between attractiveness and earnings (e.g. Hamermesh & Biddle, 1994; Scholz & Sicinski, 2015). Parental age at first marriage was also included as an indirect control for parental attractiveness on the basis that less attractive parents may take longer to find mates (in the same vein as Huber and Fieder's use of father's age at birth of subject's eldest sibling and time to subject's birth). Finally subject's birth order was included as a covariate on the basis that there may be within-family influences on physical attractiveness, perhaps via maternal immunoreactivity or post-natal discriminative parental solicitude with respect to earlier-born offspring (e.g. Zajonc & Sulloway, 2007). Consistent with this possibility, there are indications of birth-order effects on one component of attractiveness, i.e. symmetry (Lalumière, Harris, & Rice, 1999). The latter control is especially important as, if it can be shown that the effect is due to *between* rather than purely *within* family influences, it strengthens the case for it being mutagenic in origin, especially when considered in the context of the other covariates (e.g. Arslan et al., 2014; D'Onofrio et al., 2014). The covariates were also measured at Wave I.

2.2. NCDS

The National Child Development Study (NCDS) is an on-going large-scale prospectively longitudinal study, which has followed a *population* of British respondents since birth for more than half a century. The study included *all* babies ($n = 17{,}419$) born in Great Britain (England, Wales, and Scotland) during one week (03–09 March 1958). The respondents were subsequently reinterviewed in 1965 (Sweep 1 at age 7; $n =$

15,496), in 1969 (Sweep 2 at age 11; $n = 18{,}285$), in 1974 (Sweep 3 at age 16; $n = 14{,}469$), in 1981 (Sweep 4 at age 23; $n = 12{,}537$), in 1991 (Sweep 5 at age 33; $n = 11{,}469$), in 1999–2000 (Sweep 6 at age 41–42; $n = 11{,}419$), in 2004–2005 (Sweep 7 at age 46–47; $n = 9534$), and in 2008–2009 (Sweep 8 at age 50–51; $n = 9790$). There were more respondents in Sweep 2 than in the original sample (Sweep 0) because the Sweep 2 sample included eligible children who were in the country in 1969 but not in 1958. In each sweep, personal interviews and questionnaires were administered to the respondents, to their mothers, teachers, and doctors during childhood, and to their partners and children in adulthood. The vast majority (97.8%) of the NCDS respondents were White.

2.2.1. Dependent variable: physical attractiveness

At ages 7 and 11, the teacher of each NCDS respondent was asked to describe the child's physical appearance by choosing up to three adjectives from a highly eclectic list of five: "attractive," "unattractive or not attractive," "looks underfed or undernourished," "abnormal feature," and "scruffy or slovenly and dirty." Dichotomous coding was employed whereby a participant was assigned a value of 1 if they were rated as "attractive" and 0 for all other ratings. As with Add Health, a longitudinal composite attractiveness measure was computed via unit-weighted aggregation of participant attractiveness ratings taken at both ages 7 and 11 (the correlation between the two ratings is 0.411, $p < 0.001$, $n = 6687$), which yielded a four-level measure of attractiveness. The highest and lowest levels of attractiveness correspond to those who were consistently rated as either attractive (i.e. 1) or unattractive (i.e. 0) across both measurement occasions. The middle levels resulted from the fact that a subset of the sample were inconsistently rated as being either attractive or unattractive across measurement occasions, with the mean attractiveness of the sample having decreased very slightly in the older cohort (the difference in the percentage of subjects rated as attractive across Waves was −4.02%), hence those rated as being unattractive initially, but attractive subsequently receive a slightly lower unit-weighted score than when the permutation is reversed.

2.2.2. Independent variables

As with Add Health, father's age at the respondent's birth, mother's age at the respondent's birth, the respondent's sex (0 = female, 1 = male) and race (with four dummies for Black, South Asian, other Asian, and other race, with White as the reference category) were controlled. Parental class (measured with a 7-point ordinal scale) was also included to control for parental socioeconomic characteristics. This control is particularly important as two of the five sets of adjectives that we treat as indicators of unattractiveness (specifically "looks underfed or undernourished" and "scruffy or slovenly and dirty") might be confounded with the participant's socioeconomic circumstances – which as children they necessarily share with their parents. Thus controlling for parental class should reduce the degree to which our attractiveness measure is confounded with participant socioeconomic characteristics. It must be noted however that all of our substantive conclusions presented below remained identical if we excluded the small number of respondents described as either "looks underfed or undernourished" or "scruffy or slovenly and dirty." A birth order variable was furthermore computed for each participant. All variables were measured at Sweep 0, except for birth order, which was measured at Sweep 3. Note that the birth year in NCDS was a constant (1958 in all cases) and was therefore not included in the analysis.

3. Results

Presented in Figs. 1 and 2 are scatter plots illustrating the bivariate relationship between paternal age and offspring attractiveness, broken out by sex, for the Add Health and NCDS samples respectively.

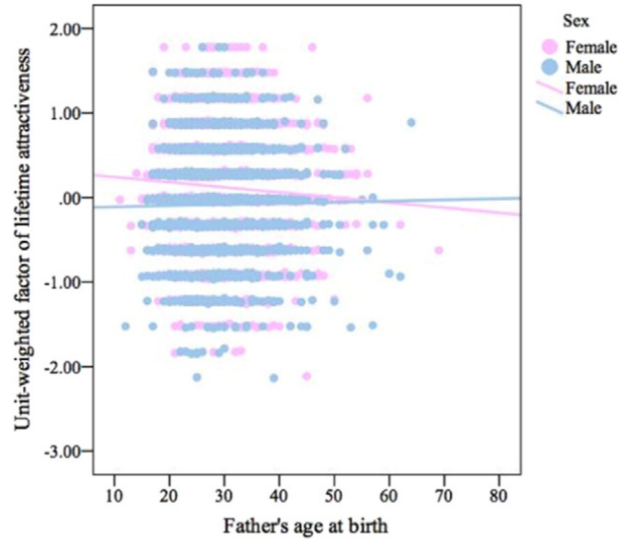

Fig. 1. Father's age at subject's birth predicting their longitudinal attractiveness in Add Health. Pink = females ($n = 5579$); blue = males ($n = 2834$). Female bivariate $r = -0.058$, $p < 0.001$, male bivariate $r = 0.015$, *ns*.

Figs. 1 and 2 indicate negative bivariate correlations between paternal age and offspring longitudinal attractiveness, except in the case of the Add Health males.

In the next set of analyses the robustness of these associations will be determined via the use of regression analysis involving several covariates. The descriptive statistics and correlations among each indicator used in this analysis are appended in the supplemental Tables S1 (Add Health) and S2 (NCDS).

Table 1 presents the results of the OLS regression analysis involving the Add Health cohort.

Table 2 presents the results of the OLS regression using the NCDS cohort. All of our substantive results remained identical, however, if we used ordinal regression instead.

The possibility that collinearity among the covariates may be confounding these effects was investigated via the computation of Variance Inflation Factor (VIF) values for each indicator. In all cases these values

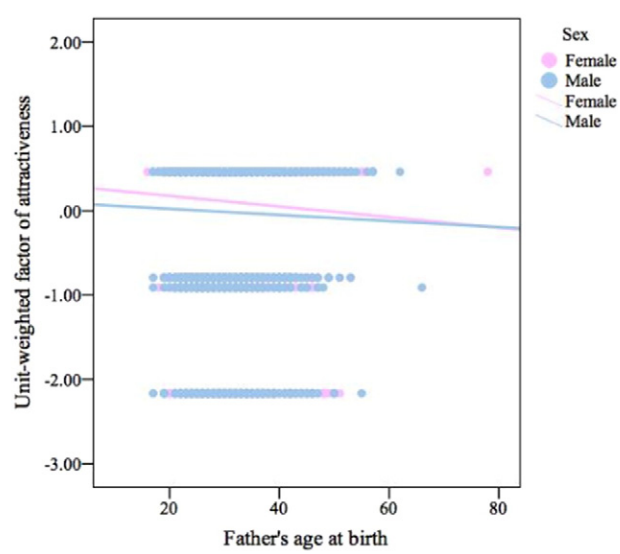

Fig. 2. Father's age at subject's birth predicting their longitudinal attractiveness in NCDS. Pink = females ($n = 3408$), blue = males ($n = 2852$). Female bivariate $r = -0.053$, $p < 0.01$; male bivariate $r = -0.027$, *ns*.

Table 1
National Longitudinal Study of Adolescent Health (Add Health), United States Ordinary Least Squares Regression.

Father's age at birth	−0.007**
	(0.002)
	−0.065
Mother's age at birth	0.006
	(0.003)
	0.048
Birth year	−0.009
	(0.006)
	−0.023
Sex	−0.228***
	(0.019)
	−0.182
Race	
Black	−0.018
	(0.029)
	−0.009
Asian	0.018
	(0.038)
	0.008
Native American	−0.119*
	(0.052)
	−0.034
ln (parents' income)	0.022***
	(0.006)
	0.054
ln (respondent's earnings)	0.009***
	(0.003)
	0.054
Parent's age at first marriage	0.003
	(0.003)
	0.018
Birth order	−0.008
	(0.009)
	−0.015
Constant	18.152
	(11.853)
R^2	0.041
Number of cases	4231

Main entries are unstandardized coefficients.
(Entries in parentheses are standard errors.)
Entries in italics are standardized coefficients.
* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

Table 2
National Child Development Study (NCDS), United Kingdom Ordinary Least Squares Regression.

Father's age at birth	−0.008**
	(0.003)
	−0.067
Mother's age at birth	0.019***
	(0.004)
	0.132
Sex	−0.099***
	(0.024)
	−0.063
Race	
Black	−0.028
	(0.195)
	−0.002
South Asian	0.176
	(0.337)
	0.008
Other Asian	0.562
	(0.753)
	0.011
Other race	0.192
	(0.251)
	0.012
Parent's social class	0.112***
	(0.014)
	0.127
Birth order	−0.123***
	(0.010)
	−0.220
Constant	−0.202
	(0.073)
R^2	0.070
Number of cases	4015

Main entries are unstandardized coefficients.
(Entries in parentheses are standard errors.)
Entries in italics are standardized coefficients.
* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

were found to be <4, with the larger values being associated with the race dummy variables in NCDS, owing to the fact that there are relatively few non-Whites in the sample. VIF values of <10 are considered indicative of non-problematic collinearity (Kutner, Nachtsheim, Neter, & Li, 2005).

4. Discussion

The results of the present analysis are consistent with the findings of Huber and Fieder (2014), as significant negative effects of paternal age at subject's birth were found on offspring physical attractiveness in both cohorts ($b = -0.007$ in the case of Add Health and -0.008 in the case of NCDS). Our pattern of controls did not precisely match those employed by Huber and Fieder (2014). However, in the case of the Add Health sample, it was possible to control for parental age at marriage, which, while not a significant independent predictor of offspring attractiveness, nonetheless serves a similar function to the variables utilized as proxies for parental attractiveness by Huber and Fieder (2014). More importantly, we employed a larger variety of controls than did Huber and Fieder, and were nonetheless able to detect the effect.

While the effect of maternal age at subject's birth was positive in both of our analyses, it was statistically significant in only one cohort (Add Health, $b = 0.019$). Note that Huber and Fieder (2014) also found a significantly positive effect of maternal age on offspring attractiveness in their first model, however the effect did not withstand additional robustness checks.

Subject's age in Add Health did not independently predict variation in attractiveness, which suggests no secular trend with respect to attractiveness in this sample. Huber and Fieder (2014) found indications of positive effects of subject's age on attractiveness (suggesting increasing attractiveness over time) in their female, but not their male sample.

Parent's income (in Add Health) and social class (NCDS) both independently and positively predicted offspring attractiveness, however the effect of paternal age on attractiveness persisted, which indicates that the ratings of attractiveness are not confounded by socioeconomic status – this is especially significant in the case of the NCDS ratings which were based on adjectives that may have been confounded with low socio-economic status. It also needs to be restated that parental attractiveness serves as an indirect measure of parental attractiveness – given the existence of positive correlations between attractiveness and earnings (e.g. Hamermesh & Biddle, 1994; Scholz & Sicinski, 2015). Offspring income in the Add Health dataset furthermore had a positive, independent effect on attractiveness ratings.

Sex independently negatively predicts offspring attractiveness (meaning that females are rated as more attractive than males) in both samples. In the Add Health data it was furthermore found to interact significantly with the effect of paternal age on offspring attractiveness ($b = 0.164$), meaning that the paternal age effect was more pronounced in females than in males. No interactions were found in the NCDS data, however ($b = 0.002$).

Controlling for race revealed effects on offspring attractiveness in only one instance from the Add Health data, where being assigned to the Native American category had a significant and negative effect on offspring attractiveness ($b = -0.119$).

Finally, birth order did not confound the effect of paternal age on offspring attractiveness. In NCDS it had a significant independent negative effect on attractiveness ($b = -0.123$; meaning that laterborn subjects were less attractive), which is consistent with the prediction that there may be certain uniquely within-family sources of variance that influence phenotypic condition beyond the influence of paternal age. A significant effect of birth order was not present in the Add Health sample, however the sign of the effect was in the theoretically expected direction (i.e. negative).

Aside from the larger array of covariates employed in the present analysis, another key difference between our own analysis and that of Huber and Fieder (2014) concerns our operationalization of the attractiveness variable, which was quite different from that used by Huber and Fieder (2014). They employed panel ratings of facial attractiveness based on photographs of the participants taken while in high school. In Add Health, a longitudinal measure of overall physical attractiveness was constructed by creating a unit-weighted factor score among multiple attractiveness ratings of each participant across a span of 12 years. In NCDS a longitudinal unit-weighted factor score was also created from ratings of overall physical attractiveness obtained at two different time points, using a somewhat different rating criterion to that employed in Add Health. The variable was also dichotomously, rather than polytomously coded. The fact that an apparent effect of paternal age on offspring attractiveness could be replicated in these data, despite the differences in the nature of the attractiveness ratings indicates that the effect has a potentially high *generalizability*, as it is apparently indifferent to differences in trait operationalization (Cronbach & Meehl, 1955).

This raises the question as to why Lee et al. (2016) were unable to identify the effect in their own sample. One potential issue is that the effect magnitude appears to be quite small. This suggests that it will be sensitive to sampling error, which is necessarily higher when small sample sizes are employed. Lee et al. (2016) employed only 1823 individuals in their analysis, which is far fewer than the numbers used in both the present analysis and that of Huber and Fieder (2014). This might be exacerbated by the fact that their sample was not representative of the population from which it was drawn, whereas the WLS, Add Health and NCDS cohorts are.

The results presented here are both consistent with those reported by Huber and Fieder (2014), and furthermore suggest that the paternal age effect on offspring attractiveness might be robust to both the use of a larger array of covariates and to different operationalizations of the dependent variable. However, a major limitation of all studies of the paternal age effect on offspring attractiveness conducted to date (including the present effort) is the availability of direct measures of potentially important confounds, such as paternal attractiveness. This is an important control as high attractiveness could make it easier for individuals to find mates and start families earlier, thus older fathers might produce less attractive offspring simply by virtue of being less attractive themselves. Variables, such as parental socioeconomic characteristics and the age at which parents married can only obliquely control for parental attractiveness. The 'perfect' sample for investigating the effect would therefore contain direct measurements of paternal and maternal levels of physical attractiveness, in addition to providing data on sibling trait levels. This would allow for the use of a sibling comparison design (Lahey & D'Onoffrio, 2010) as a means of thoroughly separating the effects of between- from within-family variance. These results must therefore be considered merely indicative of the effect of paternal age on offspring attractiveness, rather than definitive, until such time that they can be replicated in better datasets that are amenable to the use of more sophisticated methods.

Finally, Lee et al. (2016) contend that there is no theoretical reason to expect an effect on attractiveness from relatively small numbers of paternally derived *de novo* mutations accumulated over a limited range of years. This is however inconsistent with the theory that purifying selection against deleterious mutations in human populations works (or at least historically worked) in part through *relative fitness differentials* among individuals subject to sexual selection (Lesecque, Keightley, & Eyre-Walker, 2012), and that physical attractiveness seems (in some populations) to positively influence fitness outcomes (e.g. Jokela, 2009). To play this role in sexual selection, traits such as attractiveness might have adapted in such a way that makes them highly sensitive to even relatively small numbers of mutations. Thus our results, and those of Huber and Fieder (2014) suggest that attractiveness might actually serve as a *cue* rather than merely a signal of underlying fitness in sexual selection.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.paid.2016.11.003.

References

Arslan, R. C., Penke, L., Johnson, W., Iacono, W. G., & McGue, M. (2014). The effect of paternal age on offspring intelligence and personality when controlling for paternal trait levels. *PloS One*, *9*(5), e97370.

Brown, A. S., Schaefer, C. A., Wyatt, R. J., Begg, M. D., Goetz, R., et al. (2002). Paternal age and risk of schizophrenia in adult offspring. *American Journal of Psychiatry*, *159*, 1528–2533.

Cronbach, L. J., & Meehl, P. E. (1955). Construct validity in psychological tests. *Psychological Bulletin*, *52*, 281.

D'Onofrio, B. M., Rickert, M. E., Frans, E., Kuja-Halkola, R., Almqvist, C., Sjölander, A., Larsson, H., et al. (2014). Paternal age at childbearing and offspring psychiatric and academic morbidity. *JAMA Psychiatry*, *71*, 432–438.

Gorsuch, R. L. (1983). *Factor analysis*. Hillside, NJ: L. Earlbaum Associates.

Grammer, K., & Thornhill, R. (1994). Human (*Homo sapiens*) facial attractiveness and sexual selection – The role of symmetry and averageness. *Journal of Comparative Psychology*, *108*, 233–242.

Hamermesh, D. S., & Biddle, J. E. (1994). Beauty and the labor market. *American Economic Review*, *84*, 1174–1194.

Houle, D. (2000). Is there a *g* factor for fitness? In G. R. Bock, J. A. Goode, & K. Webb (Eds.), *The nature of intelligence* (pp. 149–170). Chichester: Wiley Ltd.

Huber, S., & Fieder, M. (2014). Advanced paternal age is associated with lower facial attractiveness. *Evolution and Human Behavior*, *35*, 298–301.

Jokela, M. (2009). Physical attractiveness and reproductive success in humans: Evidence from the late 20th century United States. *Evolution and Human Behavior*, *30*, 342–350.

Keightley, P. D. (2012). Rates and fitness consequences of new mutations in humans. *Genetics*, *190*, 295–304.

Kong, A., Frigge, M. L., Masson, G., Besenbacher, S., Sulem, P., Magnusson, G., et al. (2012). Rate of de novo mutations and the importance of father's age to disease risk. *Nature*, *488*, 471–475.

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

Lahey, B. B., & D'Onoffrio, B. M. (2010). All in the family: Comparing siblings to test causal hypotheses regarding environmental influences on behavior. *Current Directions in Psychological Science*, *19*, 319–323.

Lalumière, M. L., Harris, G. T., & Rice, M. E. (1999). Birth order and fluctuating asymmetry: A first look. *Proceedings of the Royal Society B: Biological Sciences*, *7*, 2351–2354.

Lee, A. J., Mitchem, D. G., Wright, M. J., Martin, N. G., Keller, M. C., & Zeitsch, B. P. (2016). Facial averageness and genetic quality: Testing heritability, genetic correlation with attractiveness, and the paternal age effect. *Evolution & Human Behavior*, *37*, 61–66.

Lesecque, Y., Keightley, P. D., & Eyre-Walker, A. (2012). A resolution of the mutation load paradox in humans. *Genetics*, *191*, 1321–1330.

Lewis, M. B. (2011). Who is the fairest of them all? Race, attractiveness and skin color sexual dimorphism. *Personality and Individual Differences*, *50*, 159–162.

Miller, G. F. (2000). Mental traits as fitness indicators: Expanding evolutionary psychology's adaptationism. *Annals of the New York Academy of Sciences*, *907*, 62–74.

Penke, L., Denissen, J. A., & Miller, G. F. (2007). The evolutionary genetics of personality. *European Journal of Personality*, *21*, 549–587.

Scholz, J. K., & Sicinski, K. (2015). Facial attractiveness and lifetime earnings: Evidence from a cohort study. *The Review of Economics & Statistics*, *97*, 14–28.

van Valen, L. (1962). A study of fluctuating asymmetry. *Evolution*, *16*, 125–142.

Waddington, C. H. (1942). Canalization of development and the inheritance of acquired characters. *Nature*, *150*, 563–565.

Zajonc, R. B., & Sulloway, F. J. (2007). The confluence model: Birth order as a within family or between-family dynamic. *Personality and Social Psychology Bulletin*, *33*, 1187–1194.