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Original Article

Personality and long-term reproductive success measured by the number of grandchildren

Venla Berg [a,*], Virpi Lummaa [b], Mirkka Lahdenperä [c], Anna Rotkirch [a], Markus Jokela [d]

[a] Population Research Institute, Väestöliitto, Helsinki, Finland
[b] Department of Animal and Plant Sciences, University of Sheffield, Sheffield, UK
[c] Department of Biology, Section of Ecology, University of Turku, Turku, Finland
[d] Institute of Behavioural Sciences, University of Helsinki, Helsinki, Finland

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ABSTRACT

Personality, that is, individual behavioral tendencies that are relatively stable across situations and time, has been associated with number of offspring in many animals, including humans, suggesting that some personality traits may be under natural selection. However, there are no data on whether these associations between personality and reproductive success extend over more than one generation to numbers of grandchildren. Using a large representative sample of contemporary Americans from the Health and Retirement Study ($n = 10{,}688$; mean age 67.7 years), we studied whether personality traits of the Five Factor Model were similarly associated with number of children and grandchildren, or whether antagonistic effects of personality on offspring number and quality lead to specific personality traits differently maximizing short and long-term fitness measures. Higher extraversion, lower conscientiousness, and lower openness to experience were similarly associated with both higher number of children and grandchildren in both sexes. In addition, higher agreeableness was associated with higher number of grand-offspring only. Our results did not indicate any quality–quantity trade-offs in the associations between personality and reproductive success. These findings represent the first robust evidence for any species that personality may affect reproductive success over several generations.

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1. Introduction

Personality – defined as suites of correlated behavioral tendencies of individuals that are relatively stable across situations and time – has been linked to reproductive outcomes in humans and many non-human animals (Dijkstra & Barelds, 2009; Gurven, von Rueden, Stieglitz, Kaplan, & Eid Rodriguez, 2014; Jokela, Kivimäki, Elovainio, & Keltikangas-Järvinen, 2009; Jokela, Hintsa, Hintsanen, & Keltikangas-Järvinen, 2010; Jokela, Alvergne, Pollet, & Lummaa, 2011; Reis, Doernte, & von der Lippe, 2011; Skirbekk & Blekesaune, 2013; Smith & Blumstein, 2008). In humans, a larger number of children and higher probability of parenthood have been associated with extraversion and related traits, such as sociability and leadership in both sexes (Alvergne, Jokela, & Lummaa, 2010; Bailey et al., 2013; Dijkstra & Barelds, 2009; Jokela & Keltikangas-Järvinen, 2009; Jokela et al., 2009; Jokela et al., 2011), although not all studies have found evidence of these associations (Mealey & Segal, 1993; Nettle, 2005; Perkins et al., 2013). Agreeableness, particularly in women, has also been associated with higher reproductive outcomes (Dijkstra & Barelds, 2009;

Jokela et al., 2011). Neuroticism, and its temperamental counterparts high emotionality and harm avoidance, on the other hand, have been associated with lower number of children, delayed parenthood and decreased probability of childbearing (Jokela et al., 2009, 2010, 2011; Reis et al., 2011; Gurven et al., 2014) but see (Dijkstra & Barelds, 2009), except in a high-fertility and high-mortality population, where neuroticism appeared to increase number of offspring in women (Alvergne et al., 2010). In addition, one study found that combinations of high neuroticism and low extraversion, or low neuroticism and high extraversion, were associated with higher number of children (Eaves, Martin, Heath, Hewitt, & Neale, 1990).

The two other central personality traits of the widely used Five Factor Model of personality (John, Naumann, & Soto, 2008), conscientiousness and openness to experience, have also been linked to reproductive outcomes, although these findings are fewer in number and less consistent. In different studies, openness to experience has been found to be positively (Gurven et al., 2014, in men), negatively (Jokela et al., 2011), or not at all related to reproductive outcomes (Dijkstra & Barelds, 2009; Alvergne et al., 2010). Conscientiousness and related traits such as persistence have been found both to decrease (Jokela et al., 2010, 2011) and increase (Dijkstra & Barelds, 2009; Gurven et al., 2014) offspring number. In addition, the negative association between openness to experience and number of children, and the negative association between

* Corresponding author. Population Research Institute, Väestöliitto, P.O. Box 849 (Kalevankatu 16), 00101 Helsinki, Finland. Tel.: +358 9 2280 5138.
E-mail address: venla.berg@helsinki.fi (V. Berg).

conscientiousness and number of children in women, appear to have become evident only in cohorts born in wealthy countries in the latter part of the 20th century (Jokela, 2012), suggesting that environmental conditions may moderate the fitness consequences of personality traits. In sum, although several findings on personality and reproductive success have been documented, the specific fitness consequences of different personality traits are yet unclear, and seem to be at least partly associated with differences in the socio-economic development of the studied populations (i.e., high-fertility, high-mortality vs. low-fertility, low-mortality societies).

Most studies on personality traits and reproductive success in humans have focused on offspring quantity. However, life history theory states that individuals may decrease the number of progeny in order to improve their quality (Hill & Kaplan, 1999), that is, increase the survivorship of the offspring or, especially in the case of contemporary Western humans, increase the reproductive success of the offspring. Personality traits have been associated with parental investment styles, e.g. warmth, gentle behavioral control and support for autonomy (Prinzie, Stams, Dekovic, Reijntjes, & Belsky, 2009), and they may influence the reproductive quality of offspring. Thus, the hypothesis is that if personality traits work to steer parental investment toward focusing either on quantity or quality of offspring, the associations between personality and number of children could be nullified or reversed in the generation of the grandchildren. There is some preliminary evidence to support this hypothesis of personality effects on quality–quantity trade-off in non-human animals, although results so far have been mixed. For example, exploratory behavior was not associated with chick provisioning in great tits (*Parus major*; Patrick & Browning, 2011), whereas more explorative great tits defended their nests with more alarm calls (Hollander, Van Overveld, Tokka, & Matthysen, 2008). In one study with captive minks (*Neovison vison*), less active females had smaller litters but faster growing kits, suggesting parental investment in the quality of offspring rather than quantity (Meagher, Bechard, & Mason, 2012).

Three studies in humans have tackled the question of personality and quality–quantity trade-offs. In a high-fertility and high-mortality human population, female neuroticism was associated with more offspring but also with lower body condition of the offspring, but this trade-off was only evident in women with low access to resources (Alvergne et al., 2010). Among Tsimane forager-horticulturalists, higher extraversion, conscientiousness and openness to experience, and lower neuroticism in men were associated with higher number of children, but there was no association with personality and children dying before age 15 (Gurven et al., 2014), suggesting no quality–quantity trade-offs. A study of contemporary Americans found interaction effects between offspring number and parental personality on child education: parental neuroticism was detrimental to child education only in large families and parental openness to experience only to later born children (Jokela, Alvergne, Rotkirch, Rickard, & Lummaa, 2014). To date, however, no studies have documented how personality simultaneously predicts offspring quantity and quality in contemporary low-fertility populations when this is assessed in terms of reproductive success in the second generation. Therefore, we do not know how selection acts on personality traits when "fitness" is considered across more than one generation. If personality has antagonistic effects on offspring quality and quantity, the number of children alone may not be enough to assess long-term fitness consequences of different personality traits. Thus one needs to investigate how personality traits are related to number of children *and* number of grandchildren—which combines both offspring number (quantity) and their survival and reproductive output (quality) into one measure.

We used a large ($N = 10,688$) representative sample of American women and men in their 60s and 70s to study how personality traits of the Five Factor Model (FFM) were related to number of children and number of grandchildren. The FFM is one of the most widely accepted

personality models in humans, and consists of extraversion (sociability, talkativeness, outgoingness), neuroticism (the opposite end of emotional stability), agreeableness (kindness, willingness to cooperate with others), conscientiousness, and openness to experience (intellect, creativeness) (John et al., 2008). These data allowed us to investigate (i) how personality is related to number of children, (ii) whether and how personality is related to number of grandchildren, and (iii) whether there are differences in the relations between number of children and number of grandchildren that could be indicative of the existence of quality–quantity trade-offs. In addition, we tested whether sex affected the above mentioned associations in order to determine whether personality is under similar selection in both sexes.

2. Methods

2.1. Participants

The data were derived from the Health and Retirement Study (HRS), which is a nationally representative longitudinal study of more than 30,000 individuals representing the U.S. population older than 50 years (Juster & Suzman, 1995). Telephone or in-person interviews are conducted every second year, administered under the National Institute of Aging (NIA) and the University of Michigan's Institute for Social Research. As of 1992, the HRS consists of many different sources of data collection, and several new subsamples have been included in the study as the original cohorts have aged. In the case of married couples, both spouses (including spouses who would otherwise not be age-eligible for the study) have been interviewed. The Health Sciences Institutional Review Board at the University of Michigan approved the HRS. For complete information on the HRS, see (Juster & Suzman, 1995). The present sample (6245 women and 4434 men) consisted of persons who had information on number of grandchildren (from 1998 to 2002, including those with no children and/or no grandchildren) and personality (from either 2006 or 2008), and were at least 55 years old at the time data on the number of their grandchildren was collected.

The data thus include US men and women born between 1900 and 1947, who mostly had their children during the 1920s–1970s. During this time the US population first experienced a decline in fertility, briefly reversed by post-war "baby boom" in the 1950s, but followed by a steady decline to around replacement levels in the late 1970s (average cohort fertility was 2.9 per woman in 1920, around 2.5 in 1930 and 1940, 2.8 in 1950, 3.0 in 1960, 2.4 in 1970 and 2.0 in 1980) (Schoen, 2004). Until the 1940s, the US population was ethnically divided mainly into whites (around 86%) and blacks (around 14%), after which the proportion of blacks has remained constant, while the proportion of Hispanics and other ethnicities has increased to around 6%, and the proportion of whites diminished to around 80% toward the 1970s (Sandefur, Martin, Eggerling-Boeck, Mannon, & Meier, 2001). The descriptive statistics of the present sample are shown in Table 1, and correspond closely to the national US averages at the time.

2.2. Measures

Because of the complex data collection structure of the HRS, *number of children and number of grandchildren* were obtained from the streamlined family datasets preprocessed by the RAND Corporation, which combine information collected over the study waves. The RAND HRS Family data (respondent-level file), which includes the derived variables for number of children and grandchildren, consist of data from waves in 1998, 2000, and 2002 (http://hrsonline.isr.umich.edu). Over 98% of our sample had information on the number of children and grandchildren from 2002, 1.5% from 2000 and 0.2% from 1998. The mean age of participants at the time of data collection for number of grandchildren was 67.7 years (SD 8.1, range 55–102).

Table 1
Descriptive statistics.

	Women	Men
N	6245	4434
Number of children, mean (SD)	2.89 (1.86)	2.78 (1.79)
0, *n* (%)	490 (7.9%)	390 (8.8%)
1	699 (11.2)	468 (10.6)
2	1745 (27.9)	1327 (29.9)
3	1450 (23.2)	1044 (23.6)
4	895 (14.3)	596 (13.4)
5+	966 (15.5)	609 (13.7)
Number of grandchildren, mean (SD)	5.81 (5.60)	5.21 (5.21)
0, *n* (%)	862 (13.8%)	748 (16.9%)
1–3	1613 (25.8)	1244 (28.1)
4–6	1658 (26.6)	1107 (25.0)
7–10	1169 (18.7)	768 (17.3)
11–15	577 (9.2)	371 (8.4)
16+	366 (5.9)	196 (4.4)
Personality (scale: 0–3)		
Extraversion, mean (SD)	2.24 (.55)	2.14 (.56)
Neuroticism	1.32 (.68)	1.19 (.67)
Agreeableness	2.63 (.42)	2.38 (.51)
Conscientiousness	2.42 (.46)	2.35 (.47)
Openness to experience	1.91 (.56)	1.91 (.55)
Race		
White/Caucasian, *n* (%)	4912 (78.7%)	3624 (81.7%)
Black	797 (12.8)	439 (9.9)
Hispanic	433 (6.9)	287 (6.5)
Other/unknown	103 (1.7)	84 (1.9)
Education, mean (SD; in years)	12.35 (2.88)	12.68 (3.25)
Age, mean (SD)	67.71 (8.35)	67.66 (7.70)

Number of children was top-coded at 10 for those with 10 or more children (35 participants had more than 10 children) and number of grandchildren was top-coded at 30 (42 participants had more than 30 grandchildren).

Personality was measured using a self-reported instrument adapted from the MIDUS study (Lachman & Weaver, 1997) with 5 items for extraversion ($\alpha = 0.74$), 4 items for emotional stability ($\alpha = 0.63$), 5 items for agreeableness ($\alpha = 0.78$), 5 items for conscientiousness ($\alpha = 0.63$), and 7 items for openness to experience ($\alpha = 0.79$), rated on a 4-point scale. The personality instrument was administered to half of the sample in 2006 and to the other half in 2008. Mean scores for personality scales were calculated for individuals with a maximum of 1 missing item in the scale. The scores for agreeableness and conscientiousness were negatively skewed and were therefore corrected with cubic transformations. Because reproductive output in the study population is strongly related to ethnicity (Sandefur et al., 2001), we controlled for such variation in our analyses. Data on *race/ethnicity* was based on participants' self-reports and was coded as white/Caucasian, black, Hispanic, or other/unknown. *Educational level* was determined as years of education (range 0–17). Information about education was missing in 33 persons.

2.3. Statistical analyses

The associations between personality and number of children and number of grandchildren were examined with linear regression analysis. Regression coefficients are shown for standardized personality scores (mean = 0, SD = 1) but the outcome variables of numbers of children and grandchildren were not standardized in the main analyses. In each analysis, three types of models were run: one for the whole study group and two separate models for men and women. To examine the independent associations of personality traits, all personality traits were mutually adjusted, i.e., entered in the regression models simultaneously. Moreover, all models were adjusted for race/ethnicity and participant's age (in 1998, 2000 or 2002 depending on which year the participant had information on the

number of grandchildren), and for sex in models including the whole study group. To examine sex differences in the associations, we also tested for the interaction effects between sex and personality traits: these models included the basic covariates, all personality traits, and their interactions with sex. We also tested for possible non-linear associations between personality and numbers of children and grandchildren by fitting regression models including categorized personality scores with participants divided into four groups (quartiles) and basic covariates as independent variables, and models including all personality traits, their quadratic terms, and basic covariates as independent variables.

The associations between personality and number of offspring were then further elaborated by adjusting for education, which correlates with personality and reproduction (Kohler & Rodgers, 2003; Poropat, 2009). We also tested the effect of income (measured on the same year as personality) on the associations, but controlling for income instead or in addition to education did not change our conclusions (data not shown). In the case of associations between personality and number of grandchildren, number of children was included as an additional covariate to examine to what extent the associations with number of grandchildren was accounted for by number of children. The possible effect of the birth cohort on the associations between personality and number of offspring was examined by dividing the study sample into four birth cohorts (1900–20, 1921–30, 1931–40, 1941–47), and testing for birth cohort by personality traits interactions (adjusting for the basic covariates, and number of children in the grandchild model). Finally, to test whether the personality traits' regression coefficients on number of children and number of grandchildren were different in magnitude, we plotted the standardized betas and their 95% confidence intervals against each other (adjusting for the basic covariates). The difference is statistically significant if the confidence interval of one beta does not overlap the other beta estimate.

All analyses were carried out with Stata 13.1 (StataCorp, 2013). Because of skewness in the distributions of descendants, we used robust standard errors (sandwich estimator) throughout all analyses. Since we were primarily interested in the associations with grandchildren, tables detailing the results on the grandchild analyses are presented here, whereas those concerning the numbers of children are presented in the online supplementary material.

3. Results

3.1. Number of children

Higher extraversion, lower conscientiousness, and lower openness to experience were associated with higher numbers of children in both sexes (Supplementary Table S1), with no sex differences in any of the associations (all interactions between sex and personality traits were non-significant, *p*-values > .05). Compared to people with low extraversion (-1 standard deviation, SD, below the mean), people with high extraversion ($+1$ SD above the mean) had 0.15 (5.6%) more children; compared to people with low conscientiousness, people with high conscientiousness had 0.11 (3.9%) fewer children; and compared to people with low openness to experience, people with high openness to experience had 0.24 (8.2%) fewer children.

There was no evidence of marked non-linearity in the associations between personality traits and number of children in either sex, so that intermediate personality levels would have been associated with higher or lower number of children than either of the extremes (Supplementary Figure S1). Also, none of the quadratic personality terms were significant (data not shown). Birth cohort effects on the associations were not significant, except for openness and the latest cohort (1940s) in women. Openness to experience was not associated with number of children in the earlier cohorts ($B = .06$, 95% CI $-.16$,

Table 2
Linear regression of number of grandchildren on personality.

	All			Women			Men		
	B	95% CI	p	B	95% CI	p	B	95% CI	p
Extraversion	.24	.11, .37	.000	0.15	−.03, .32	.110	.38	.18, .57	.000
Neuroticism	−.07	−.17, .04	.220	−0.11	−.25, .03	.134	−.01	−.16, .15	.950
Agreeableness	.17	.05, .30	.008	0.21	.03, .38	.024	.12	−.06, .30	.194
Conscientiousness	−.26	−.37, −.14	.000	−0.32	−.47, −.16	.000	−.17	−.34, −.00	.044
Openness to experience	−.37	−.49, −.24	.000	−0.34	−.51, −.17	.000	−.40	−.59, −.20	.000

Note. All models adjusted for age and race, and the model for the whole sample additionally adjusted for sex. Personality traits are standardized and entered simultaneously.
CI = confidence interval.
All sex–personality trait interactions were statistically non-significant, $p > .05$.

.29; $p = .598$), but it did decrease the number of children in women born in the 1940s ($B = −.23$, 95% CI −.34, −.13; $p < .001$).

Controlling for education attenuated the associations between extraversion and openness to experience and number of children, rendering the latter association non-significant (Supplementary Table S2), whereas it strengthened the association between neuroticism and number of children to a statistically significant level.

3.2. Number of grandchildren

Higher extraversion, higher agreeableness, lower conscientiousness, and lower openness to experience were associated with higher number of grandchildren in both sexes (Table 2). Again, there were no sex differences in these associations (for the interaction terms, all p-values > .05). Compared to people with low extraversion (−1 SD), people with high extraversion (+1 SD) had 0.48 (9.1%) more grandchildren; compared to people with low agreeableness, people with high agreeableness had 0.35 (6.5%) more grandchildren; compared to people with low conscientiousness, people with high conscientiousness had 0.52 (8.9%) fewer grandchildren; and compared to people with low openness to experience, people with high openness to experience had 0.74 (12%) fewer grandchildren.

Again, we investigated non-linear associations between personality and numbers of grandchildren by using categorized personality scores with participants divided into four groups (Supplementary Figure S2). For extraversion, there was a larger difference between the lowest quartile versus the others than among the three highest quartiles in both sexes. The opposite pattern was observed for men's conscientiousness, with only the highest quartile having fewer grandchildren than others. There was also evidence of a non-linear association for women's neuroticism, with the lowest and highest quartiles being indistinguishable from each other and women in the middle having the smallest numbers of grandchildren. There were no other marked non-linear associations between personality traits and number of grandchildren. However, none of the quadratic personality terms were significant (data not shown).

When adjusting for number of children to determine the independent effects of personality on number of grandoffspring, the association with number of grandchildren was attenuated by 60% for

extraversion, by 25% for agreeableness, by 41% for conscientiousness, and by 62% for openness to experience (Table 3). However, the association between extraversion and number of grandchildren was the only one to lose statistical significance in this adjustment. When number of children was taken into account, compared to people with low agreeableness (−1 SD), people with high agreeableness (+1 SD) had 0.26 (4.8%) more grandchildren; compared to people with low conscientiousness, people with high conscientiousness had 0.30 (5.3%) fewer grandchildren; and compared to people with low openness to experience, people with high openness to experience had 0.28 (4.5%) fewer grandchildren.

The associations between personality traits and number of grandchildren were attenuated when controlling for education (Table 4) and openness to experience and agreeableness lost statistical significance in this adjustment. Finally, when controlling for both number of children and education in the same model (Table 5), only conscientiousness remained a significant predictor of number of grandchildren.

There were no significant birth cohort effects on the detected associations between personality and number of grandchildren.

3.3. Comparing associations with children and grandchildren

The regression coefficients from three regression models, predicting (a) number of children (Table S1), (b) number of grandchildren (Table 2), and (c) number of grandchildren, adjusted for number of children (Table 3) by personality traits (and basic covariates) were standardized and are illustrated in Fig. 1. The 95% confidence intervals of the standardized betas from the first grandchild model overlap the estimates from the child model (and vice versa), which means that all personality traits were similarly associated with number of children and number of grandchildren. This also holds for agreeableness: the difference in the coefficients was not statistically significant, although the coefficient for number of grandchildren differed significantly from zero and the coefficient for number of children did not. Thus, the standardized effect sizes between personality and reproductive success did not attenuate over two generations. When adjusting for number of children, extraversion and openness to experience were less strongly associated with number of grandchildren than with

Table 3
Linear regression of number of grandchildren on personality, adjusted for number of children.

	All			Women			Men		
	B	95% CI	p	B	95% CI	p	B	95% CI	p
Extraversion	.10	−.00, .19	.057	.06	−.07, .18	.395	.17	.01, .32	.032
Neuroticism	−.02	−.10, .06	.647	−.02	−.12, .08	.689	−.01	−.13, .11	.902
Agreeableness	.13	.04, .22	.007	.13	.00, .26	.045	.12	−.02, .26	.086
Conscientiousness	−.15	−.24, −.07	.001	−.14	−.25, −.03	.012	−.16	−.29, −.02	.023
Openness to experience	−.14	−.23, −.04	.005	−.12	−.24, .00	.064	−.17	−.33, −.01	.036
Number of children	1.90	1.85, 1.96	.000	2.00	1.92, 2.07	.000	1.75	1.66, 1.85	.000

Note. All models adjusted for age and race, and the model for the whole sample additionally adjusted for sex. Personality traits are standardized and entered simultaneously.
CI = confidence interval.

Table 4
Linear regression of number of grandchildren on personality, adjusted for education.

	All			Women			Men		
	B	95% CI	p	B	95% CI	p	B	95% CI	p
Extraversion	.16	.03, .29	.017	.06	−.11, .24	.484	.30	.11, .49	.002
Neuroticism	−.14	−.24, −.04	.008	−.19	−.33, −.06	.006	−.07	−.22, .09	.403
Agreeableness	.08	−.05, .20	.220	.15	−.02, .32	.089	−.01	−.19, .17	.916
Conscientiousness	−.21	−.32, −.10	.000	−.30	−.45, −.16	.000	−.09	−.26, .08	.286
Openness to experience	−.00	−.13, .13	.982	.04	−.13, .21	.635	−.05	−.25, .15	.593
Education (in years)	−.42	−.46, −.38	.000	−.47	−.53, −.41	.000	−.36	−.42, −.31	.000

Note. All models adjusted for age and race, and the model for the whole sample additionally adjusted for sex. Personality traits are standardized and entered simultaneously. CI = confidence interval.

number of children, whereas the other traits were not differently associated with number of children and number of grandchildren.

4. Discussion

We found that personality traits of the Five Factor Model were similarly associated with both number of children and number of grandchildren in a large sample of contemporary U.S. citizens. Larger number of children and grandchildren were associated with higher extraversion, lower conscientiousness and lower openness to experience. In addition, higher agreeableness was associated with larger number of grandchildren, but not with number of children, but the difference between these associations was not statistically significant. Although there were some differences in the regression coefficients between men and women, these differences were not statistically significant.

Not all the present findings are in agreement with previous studies on this topic (e.g., Jokela et al., 2011). We did not observe the previously reported association between neuroticism and number of offspring, and the previously reported association between agreeableness and offspring number was here observed only for the number of grandchildren, but not for the number of children. These differences with earlier studies may reflect various methodological differences between studies, such as the specific instruments used to assess personality, the age at which personality is measured, birth cohort effects, and differences in the socio-demographic composition of populations.

Our current results extend previous findings of personality and reproductive success by demonstrating the long-term fitness associations of personality in a modern society. We used a large, nationally representative dataset with the Five Factor Model personality traits, which is one of the most accepted personality models in psychology (John et al., 2008). Few caveats of this study need to be mentioned, though. First, not all the participants' children had completed their reproductive span, which may have biased the associations between personality and number of grandchildren, as some personality traits may be associated with earlier or later timing of having children (Jokela et al., 2011). As far as personality would have only timing effects on reproduction, e.g. more conscientious people starting

reproduction later but eventually reaching the same quantity as the less conscientious, the results of this study would be misguided. However, previous studies have found similar associations when using timing of parenthood and when using number of children as an outcome, e.g. more extraverted people start having children earlier and end up with more children (e.g., Jokela et al., 2011), and the associations between personality and reproduction seem to reach significant levels early on in the reproductive career (Berg, Rotkirch, Väisänen, & Jokela, 2013). Secondly, personality was measured in adulthood, which raises the possibility of reverse causality (i.e., number of children, or grandchildren, may affect personality development). Data that would enable a prospective design on personality and number of grandchildren are difficult to obtain because this would require a very long follow-up time. However, one study that investigated the associations between personality and number of children both prospectively and retrospectively found no differences between the approaches (Jokela et al., 2010). Personality in humans has also proven to be relatively stable throughout lifetime (Caspi, Roberts, & Shiner, 2005), and furthermore, in our study the associations between personality traits and number of grandchildren remained similar, although attenuated, when number of children was statistically controlled for. Thus, it seems unlikely that the retrospective nature of our study would have substantially confounded the main findings.

Personality traits may channel individual's parental investment toward either higher number of offspring or higher quality of offspring. Our study had no information on child characteristics, so we could not assess other measures of "offspring quality" besides number of grandchildren. Yet the associations between personality traits and number of children were replicated very closely by associations between the traits and number of grandchildren. In other words, associations between personality traits and lower number of children did not improve the offspring's "quality" in any such way that would have been beneficial for parents' long-term fitness. And vice versa, associations between personality traits and higher number of children did not lessen the offspring's "quality" in a manner that would have been detrimental for parents' long-term fitness.

The associations of personality with number of grandchildren may be partly explained by the strong genetic correlations between number of children and grandchildren that have been reported in

Table 5
Linear regression of number of grandchildren on personality, adjusted for number of children and education.

	All			Women			Men		
	B	95% CI	p	B	95% CI	p	B	95% CI	p
Extraversion	.05	−.05, 15	.302	.02	−.11, .15	.749	.12	−.04, .27	.317
Neuroticism	−.06	−.14, .02	.116	−.06	−.16, .04	.213	−.05	−.17, .07	.408
Agreeableness	.08	−.01, .17	.090	.11	−.02, .23	.092	.04	−.10, .18	.608
Conscientiousness	−.13	−.21, −.04	.003	−.14	−.25, −.03	.012	−.11	−.24, .03	.123
Openness to experience	.06	−.04, 16	.218	.05	−.07, .18	.404	.07	−.09, .22	.418
Number of children	1.85	1.79, 1.90	.000	1.94	1.87, 2.01	.000	1.71	1.62, 1.80	.000
Education (in years)	−.24	−.27, −.21	.000	−.22	−.27, −.18	.000	−.25	−.29, −.21	.000

Note. All models adjusted for age and race, and the model for the whole sample additionally adjusted for sex. Personality traits are standardized and entered simultaneously. CI = confidence interval.
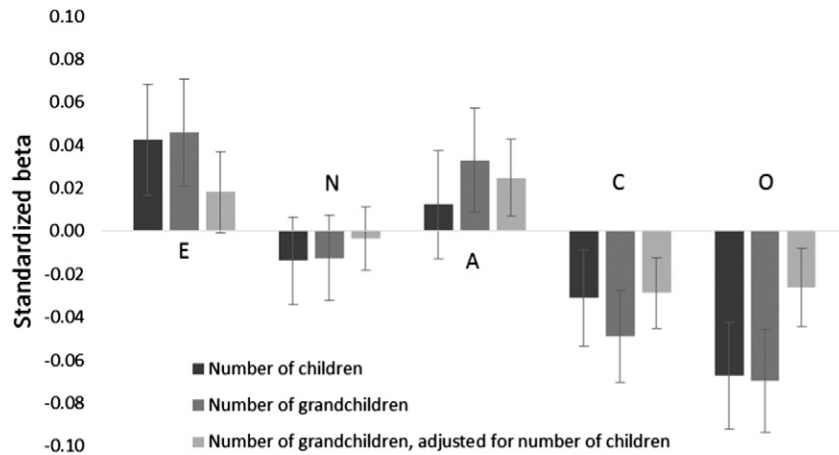
Fig. 1. Standardized betas and 95% confidence intervals from the regressions of number of children and number of grandchildren on personality traits, adjusted for race/ethnicity, age, and sex, and in the second grandchild-model, additionally for number of children. E = extraversion; N = neuroticism; A = agreeableness; C = conscientiousness; O = openness to experience.

contemporary societies(Zietsch, Kuja-Halkola, Walum, & Verweij, 2014). Thus, number of children appears to be a good predictor of long-term fitness in societies in mature stages of the demographic transition (Goodman & Koupil, 2009). In these societies, reducing offspring number does not necessarily translate into higher reproductive success of those offspring (Goodman, Koupil, & Lawson, 2012; Lawson & Mace, 2011). However, there is some evidence that during the first phases of the demographic transition to smaller family sizes, quantity–quality trade-offs would play a role, especially in people with high socio-economic status (Lawson & Mace, 2010; Lawson, Alvergne, & Gibson, 2012; Liu, Rotkirch, & Lummaa, 2012). Based on our results, personality is not involved in quantity–quality trade-offs that would hold for long-term fitness in developed contemporary societies.

The associations between personality traits and number of grandchildren were similar to their corresponding associations with number of children (Fig. 1). That is to say, that not only did we not find evidence of the associations with personality and number of children reversing or nullifying in the next generation, we also found personality effects to be similar in magnitude for number of children and grandchildren. This is somewhat surprising, as one might expect that an individual's personality is more important for the individual's own fertility than for the fertility of the individual's children. When controlling for the number of children in the grandchild regression models, and comparing the effect sizes (Fig. 1) of personality on number of children and grandchildren, the standardized effects of extraversion and openness to experience on grandchildren were smaller than on children. Conscientiousness, however, still predicted number of children and number of grandchildren with a similar effect magnitude, and agreeableness was still associated with number of grandchildren. Two conclusions can be drawn from this. First, some of the effects of personality on number of grandchildren result from the associations between personality and number of children. Extraversion in particular, which was not a significant predictor of number of grandchildren when number of children was controlled for, did not have an independent effect on number of grandchildren apart from its associations with the size of the first generation.

Secondly, all of the other personality traits (apart from neuroticism) were associated with number of grandchildren independently of number of children. This is an interesting finding, because the personalities of parents and children correlate only weakly ($r = .10$–$.30$; Bratko, Butkovic, Vukasovic, Kerešteš, & Brkovic, 2014), despite moderate levels of heritability in personality traits (Bouchard & Loehlin, 2001). Therefore, the reasoning that, for example, more conscientious people would have on average more conscientious children, who in turn would have on average fewer

children than people less prone to high conscientiousness, would probably explain only a small part of the similarity in these associations. A plausible, yet often neglected explanation for inter-generational continuities would be common genetic factors that affect both reproductive outcomes and personality (Zietsch et al., 2014). Conscientiousness, for example, has been found to be more pro-nounced and associated with the level of sex steroids in infertile men (Conrad et al., 2002), and extraversion with testosterone production (Campbell et al., 2010). In fact, one study found that the association between extraversion and neuroticism and number of offspring was solely mediated by genetic factors (Berg et al., submitted for publication). Such genetic effects could account for the associations between personality and grandchildren, because the genes may be inherited even if their behavioral expression (i.e., personality traits) changes between generations.

Some of the associations between personality and number of grandchildren could be mediated by grandparental effects. Grandpa-rental support, especially from grandmothers, has been related to higher reproductive success of children in pre-industrial societies (Lahdenperä, Lummaa, Helle, Tremblay, & Russell, 2004), and to beneficial outcomes of grandchildren also in modern societies (Coall & Hertwig, 2011). Personality traits might influence the amount and quality of grandparental support, and thereby influence children's fertility decisions. Agreeableness, in particular, might be associated with greater willingness to provide grandparental support, and in the present study agreeableness seemed to be more strongly related to number of grandchildren than to number of children. However, while grandparental effects vary with both sex and kin lineage, so that maternal grandmothers have the most beneficial effects and paternal grandfathers the least also in contemporary populations (e.g., Coall & Hertwig, 2011), we found no sex differences in the associations between personality and number of grandchildren. The effect of personality on the quantity and quality of grandparental aid needs to be addressed in more detail in future studies.

In conclusion, we have shown for the first time in any species that personality is associated with reproductive success over generations, making it a more likely target for natural selection. All central human personality traits were similarly associated with both number of children and number of grandchildren. Our study did not provide support for the hypothesis concerning quality–quantity trade-offs in terms of personality and reproduction, so that personality associa-tions with the number of children would have been reversed or nullified in the next generation. The evolutionary origins and maintenance of personality variation is currently under vigorous study (e.g., Dingemanse & Wolf, 2010; Penke, Denissen, & Miller, 2007). Our study adds to the growing evidence that at least in the case

of modern humans "counting babies" is a good indicator of selective pressures acting on various characteristics, including personality traits. Thus, studies using numbers of children as an outcome measure provide valuable information when contemplating the evolution of personality.

Acknowledgments

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