

Personality and reproductive success in a high-fertility human population

Alexandra Alvergne^{a,b,1}, Markus Jokela^c, and Virpi Lummaa^a

^aDepartment of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, United Kingdom; ^bDepartment of Anthropology, University College London, London WC1H 0BW, United Kingdom; and ^cDepartment of Psychology, University of Helsinki, 00014 Helsinki, Finland

Edited by Richard E. Nisbett, University of Michigan, Ann Arbor, MI, and approved May 12, 2010 (received for review February 12, 2010)

The existence of interindividual differences in personality traits poses a challenge to evolutionary thinking. Although research on the ultimate consequences of personality differences in nonhuman animals has recently undergone a surge of interest, our understanding of whether and how personality influences reproductive decisions in humans has remained limited and informed primarily by modern societies with low mortality–fertility schedules. Taking an evolutionary approach, we use data from a contemporary polygynous high-fertility human population living in rural Senegal to investigate whether personality dimensions are associated with key life-history traits in humans, i.e., quantity and quality of offspring. We show that personality dimensions predict reproductive success differently in men and women in such societies and, in women, are associated with a trade-off between offspring quantity and quality. In women, neuroticism positively predicts the number of children, both between and within polygynous families. Furthermore, within the low social class, offspring quality (i.e., child nutritional status) decreases with a woman's neuroticism, indicating a reproductive trade-off between offspring quantity and quality. Consistent with this, maximal fitness is achieved by women at an intermediate neuroticism level. In men, extraversion was found to be a strong predictor of high social class and polygyny, with extraverted men producing more offspring than their introverted counterparts. These results have implications for the consideration of alternative adaptive hypotheses in the current debate on the maintenance of personality differences and the role of individual factors in fertility patterns in contemporary humans.

Big Five dimensions | life-history traits | polygyny

Individual personality differences [also termed behavioral syndromes, temperament, or coping styles (1)] are rapidly becoming one of the most frequently studied factors underlying phenotypic variation within animal populations (2). The existence of persistent variation in personality traits poses the question of how natural selection acts on those traits and how the alternative phenotypes can coexist (3). A number of studies in nonhuman animals (>30, reviewed in ref. 4) indicate that differences in individual personality traits are associated with fitness outcomes that vary according to the individual characteristics or environments, suggesting that adaptive explanation for the interindividual variation in animal personality may be likely. In contrast, although human sciences have a long history of investigating individual personality differences from a psychological and neurobiological perspective (5), surprisingly few empirical studies have examined the ultimate causes of variation in personality dimensions in humans to date (6–9). Such knowledge, however, is critical to understanding how natural selection could shape interindividual differences in response to socioecological pressures not only from an evolutionary biological perspective but also from that of the human sciences perspective. Indeed, deciphering the individual-level determinants of reproductive decisions is key to the current debate on the role of individual vs. social factors in explaining recent fertility changes with the industrialization of societies (10).

Although increasing knowledge of the evolutionary dynamics of personality traits in animal populations has provided significant insights for the human studies, such as understanding the origins of leadership in economics and business (11), it has inspired few examinations of the role of personality differences in fertility patterns. Nevertheless, personality has been linked to several social behaviors potentially related to reproductive success in humans (e.g., mate access, sexual behavior, and survival). For example, extraversion (i.e., sociality) has been positively linked to the number of sexual partners in both men and women, and low neuroticism (i.e., high emotional stability and low anxiety) has been associated with increased longevity (although evidence is mixed). Conscientiousness (i.e., being organized, careful, and task-oriented) has been found to predict adherence to healthy behaviors (reviewed in refs. 12 and 13). However, to date all studies have been conducted on humans living in post-demographic transition environments characterized by recent and drastic cultural changes, thus complicating the understanding of the evolutionary significance of human personality traits. For example, although extraversion is positively linked to mating success, it does not necessarily translate into a higher number of offspring in men (13). Similarly, neuroticism has repeatedly been linked to reproductive costs [i.e., reduced survival and female fertility (8)], yet no reproductive benefits have been identified. Thus there is an overall shortage of knowledge of whether personality relates to differential reproduction in humans and of how interindividual variation in personality might be maintained.

Recent work from behavioral ecologists suggests that interindividual differences in temperament might be maintained if personality affects trade-offs between life-history traits (e.g., survival vs. reproduction), leading to coevolution between personality and life-history strategies (13–17, but see refs. 18 and 19). Consistent with this idea, a recent study suggests that highly extraverted modern British men trade off increased access to mates with increased risk of hospitalization for accident or illness (6). Similar trade-offs may apply to other personality dimensions (reviewed in ref. 13) and to life-history traits critical to long-lived species where juveniles are highly dependent on parental care, e.g., the optimization of investment in quantity vs. quality of offspring (20, 21). Because the sexes differ in their level of obligatory parental investment in humans, men are thought to benefit more from risk taking and social dominance and women from cautious and nurturing behavior (22). Consequently, which personality traits are related to quantity/quality trade-offs, as well as the shape of any such relationships, is expected to be sex-specific. Considering the two most relevant personality traits for fertility in modern populations, i.e., extraversion and neuroticism, we can

Author contributions: A.A., M.J., and V.L. designed research; A.A. performed research; A.A. and M.J. analyzed data; and A.A. and V.L. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

¹To whom correspondence should be addressed. E-mail: a.alvergne@ucl.ac.uk.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1001752107/-DCSupplemental.

predict that the link between personality and quantity/quality trade-offs will be stronger for extraversion in men and for neuroticism in women. If personality variation is maintained by such quality–quantity trade-offs, we might further predict that the strength and direction of these associations may differ between the sexes and be more pronounced in polygynous mating systems with distinctively different reproductive trade-offs affecting male and female lifetime success (23).

This article describes our investigation of a polygynous, high-fertility human population to determine (i) whether personality traits are associated with reproductive success, as measured by both offspring quantity and quality (physical condition), in men and women; (ii) whether personality traits affect offspring quality and quantity in a similar manner or antagonistically, resulting in trade-offs that favor intermediate personality phenotypes; and (iii) whether there exist any sex differences in such effects. Our data have at least four strengths in addressing these questions. First, we use rich demographic, anthropomorphic, and questionnaire data from four traditional villages in rural Senegal where fertility and mortality rates remain high (characteristic of pre-industrial societies). Second, we apply powerful statistical techniques to control for confounding effects and investigate whether any detected relationships depend on socio-environmental circumstances. We additionally compare co-wives within polygynous marriages to provide a study design to control for partner characteristics. Third, we estimate personality traits using self-reports on the Big Five dimensions, the most widely accepted model of personality in humans (24), and showing significant heritability (25). Such self-reports correlate well with objective measures of behavior and are stable over time (13), a key prerequisite if we are to explain interindividual variation from an evolutionary perspective. Finally, we are able to investigate the effects of personality for both partners in a marriage not only on their overall reproductive success (age-specific number of offspring), but also on offspring physical condition. This latter measure is likely to correlate with their offspring's future health, survival, and reproductive success (26), helping provide a better insight into the evolutionary processes involved in shaping personality dimensions in both sexes than measures of offspring quantity alone.

Results

We found evidence that in a contemporary polygynous, high-fertility human population, personality dimensions predict reproductive success differently in men and women and, particularly in women, lead to a trade-off between offspring quantity and quality, with selection favoring intermediate phenotypes.

Women. First, we investigated how each personality dimension relates to the total number of living offspring among all women in the sample. We focus here on neuroticism and extraversion, the two main personality dimensions in women that are independent of each other in the studied sample and present in almost all psychological models of personality. The other traits were excluded as correlated (all $|r| > 0.20$), presumably due to a very low variability, biased toward the maximum (conscientiousness and agreeableness) or the minimum (openness). Individuals with high neuroticism tend to be anxious, depressive, and moody. Individuals with high extraversion are characterized as sociable, outgoing, and sensitive to positive emotions. We found that the number of living children of women increases with their level of neuroticism ($F_{1,65} = 5.60$, $\beta \pm SE = 0.25 \pm 0.11$, $r = 0.20$, $P < 0.05$), with women with above-median neuroticism having 12% more children after controlling for age and marital rank (unique wife of a monogamous husband or first or second wife of a polygynous husband) than those with below-median neuroticism (Table S1 and Fig. 1). When the interaction between neuroticism and social class is included in the model, the relationship between neuroticism and number of children is marginally stronger among

rich women ($F_{1,64} = 3.29$, $\beta \pm SE = 0.40 \pm 0.22$, $P = 0.07$). This argues against neuroticism being the consequence of social stress. Furthermore, the fact that neuroticism does not increase with age (*Materials and Methods*), whereas the number of children does also suggests that, in this population, neuroticism is more likely to be responsible for, rather than a consequence of, differential reproduction. Finally, extraversion does not predict a woman's number of children (Table S1).

Second, we confirmed the above link between neuroticism and number of children within polygynous families only using a balanced subsample (comparison of two co-wives with differing personality, both married to the same man). Similarly to the overall sample, the more neurotic wife of the two has more living children ($\beta \pm SE = 0.45 \pm 0.17$, $t = 2.57$, $df = 9$, $r = 0.27$, $P < 0.05$). These differences are unlikely to result from differences in women's age, which was controlled for. Note that, in both analyses, if maternal age is replaced by the total duration of marriage, the results remain unchanged.

Third, we investigated how personality dimensions are related to the quality (physical condition) of offspring. In both traditional and modern societies, individuals with high overall numbers of offspring often have reduced offspring quality (20, 21). However, the underlying mechanisms predisposing individuals toward either end of this trade-off are not well understood. We found support for a link between a quantity/quality trade-off in women and their personality differences in neuroticism. Increased neuroticism among women results in their offspring aged 0–5 y having both decreased BMI (body mass index) and MUAC (mid-upper arm circumference). However, these effects depend on the social class (social class \times BMI interaction: $F_{1,74} = 4.04$, $P = 0.05$; social class \times MUAC interaction: $F_{1,75} = 5.78$, $P < 0.05$). In women from low social class, both child BMI ($F_{1,31} = 4.88$, $\beta \pm SE = -0.39 \pm 0.18$, $r = 0.31$, $P < 0.05$; Fig. 2A) and child MUAC ($F_{1,31} = 5.96$, $P < 0.05$, $\beta \pm SE = -20 \pm 0.08$, $r = 0.43$; Fig. S1A) decrease with the mother's neuroticism, whereas the relationships are not significant in high social classes (BMI: $F_{1,34} = 0.32$, $P = 0.57$; Fig. 2B; MUAC: $F_{1,39} = 0.23$, $P = 0.63$; Fig. S1B and Table S2). In low social classes, children 0–5 y of age with mothers in the top quartile of the neuroticism scale have 18% reduced BMI and 20% reduced MUAC compared with offspring of mothers from the bottom quartile of the neuroticism scale, after controlling for age and sex. Extraversion does not predict offspring quality in women. These analyses control for significant associations with child age and sex, whereas mother's body mass index, rank, and ethnic group were not significant (*Materials and Methods*).

Finally, to predict the direction of current selection on women's neuroticism, we investigated the shape of the relationship between

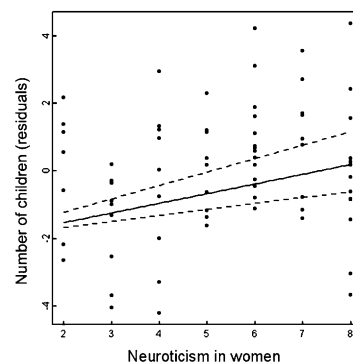


Fig. 1. Neuroticism is associated with an increased number of children in women. The figure shows the number of children controlled for age and rank (residuals) against scores of neuroticism ($n = 74$).

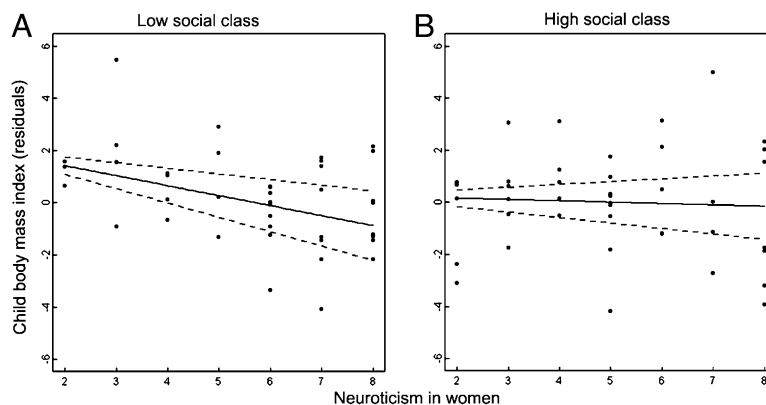


Fig. 2. Women's neuroticism is associated with a reduction in the child's physical condition at ages 0–5 y in low but not in high social classes. (A) Mean child BMI and low social class (n mothers = 41). (B) Mean child BMI and high social class (n mothers = 33). For similar relationship between women's neuroticism and mean child MUAC, see Fig. S1.

neuroticism and ultimate reproductive success in women accounting for both offspring quantity and quality (i.e., predicted survival given their body mass index; *SI Materials and Methods* and Fig. S2). We found that an intermediate level of neuroticism is associated with maximal ultimate reproductive success (Fig. 3). Ultimate reproductive success is higher for intermediate rather than for extreme levels of neuroticism (quadratic term: $\beta \pm \text{SE} = -0.10 \pm 0.05$, $F_{1,66} = 4.00$, $r = 0.22$, $P < 0.05$) when controlling for age ($F_{1,66} = 68.96$, $P < 0.001$).

Men. In men, personality is associated with a range of outcomes closely related to fitness. First, we investigated whether personality dimensions are associated with male social class, which is pivotal in providing reproductive opportunities for men in a range of human societies (27). We focus here on the four personality dimensions in men that are independent of one another (extraversion, neuroticism, agreeableness, and openness) in the studied sample. Because conscientiousness was significantly related to openness ($r = 0.34$, $P < 0.01$) and showed low intrinsic variation, probably as a result of enforced cultural standards, it was not retained. The probability of belonging to the highest social class (two classes; *Materials and Methods*) increases with extraversion ($\beta = 0.57$; 95% CI = 0.10, 0.91; $r = 0.34$, $P < 0.01$); men with above-median extraversion have a 31% higher chance of belonging to high social class than those with below-median extraversion (Fig. 4A). The probability of belonging to the highest class is also negatively associated with decreased neuroticism ($\beta = -0.36$; 95% CI = (-0.68, 0.01), $r =$

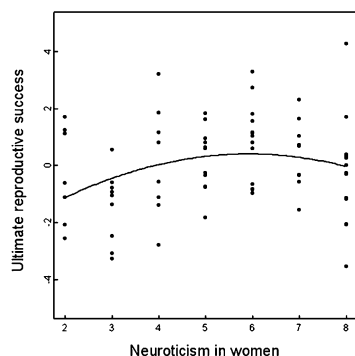


Fig. 3. The ultimate reproductive success in women is maximized for intermediate levels of neuroticism. For each woman, the ultimate reproductive success corresponds to her number of children times the mean chance of survival of her children to age 5 given their body mass index (n mothers = 74). See *SI Materials and Methods* and Fig. S2 for details.

26, $P = 0.05$), but is independent of other personality traits (all $P > 0.30$) when controlling for age and ethnic group (Table S1).

Second, as polygyny can have profound effects on male reproductive success (28), we investigated whether personality differences were related to the probability of simultaneously having more than one wife. We found that high extraversion in men leads to an increased probability of polygynous marriage ($\beta = 0.51$; 95% CI = 0.10, 0.91; $r = 0.28$, $P = 0.01$) controlling for age. Men with an above-median extraversion score are 40% more likely to have more than one wife than men with a below-median extraversion score (Fig. 4B). To further investigate whether such effects are mediated by social class we reran the model with this term (social status) included. The effect of extraversion was still significant ($\beta = 0.53$; 95% CI = 0.10, 0.91; $r = 0.28$, $P < 0.05$), suggesting that social class is not the only link between extraversion and marital status. None of the other personality traits are related to the chance of being polygynous (Table S1).

Third, we investigated whether personality differences among men give rise to differences in the total number of children under natural fertility conditions. We found that a man's total number of children significantly increases with extraversion ($\beta = 0.06$; 95% CI = -0.003, 0.11; $r = 0.27$, $P < 0.05$) when controlling for age. Men with above-median extraversion had 14% more children than men with below-median extraversion (Fig. 4C). Including marital status (one vs. multiple wives) or social class in the model renders the effect of extraversion nonsignificant ($P = 0.12$ and $P = 0.19$, respectively), suggesting that the link between extraversion and number of children in men is driven by the effects of extraversion on the probability of belonging to the high social class and gaining more than one wife. None of the other personality traits are related to the total number of children produced (Table S1).

Fourth, we investigated whether personality dimensions predisposing individuals to father high numbers of children are related to the quality (condition) of those offspring. The father's extraversion is not related to either of the two body-condition measures of offspring aged 0–5 y. These analyses controlled for child age, sex, and ethnic group (Table S2; note that mother's and father's body mass index, mother's rank, social class and ethnic group were nonsignificant). None of the other personality dimensions were related to offspring condition either ($P > 0.10$).

Discussion

Animal studies have established that persistent personality differences may underlie how individuals respond to environmental conditions and have profound consequences for evolutionary dynamics of reproductive traits (4, 15, 29). However, our understanding of how personality influences reproductive decisions

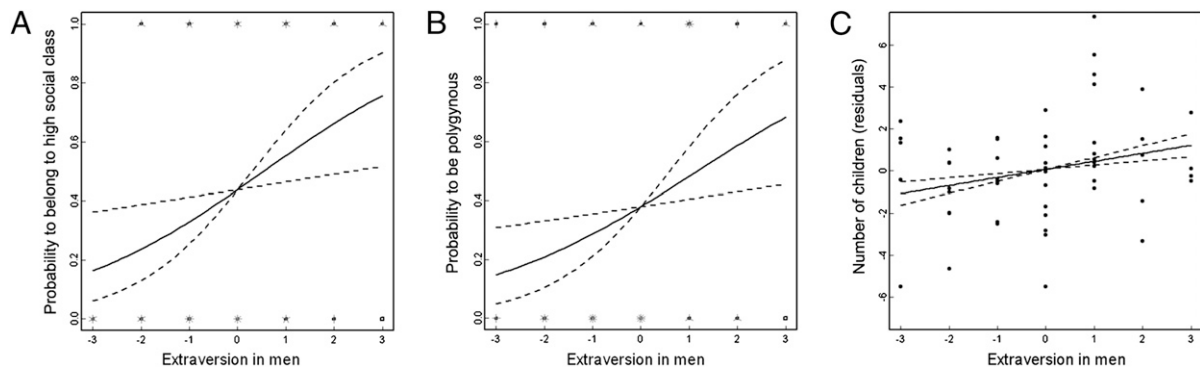


Fig. 4. Extraversion is positively related to fitness related traits in men. (A) Social class. (B) Marital status (C) Number of children controlled for age (residuals) ($n = 62$). Raw data are indicated by sunflower symbols in A and B, and by dots in C. Solid lines show predicted relationships between extraversion and reproductive success variables and dashed lines represent the 95% CI around the predicted slope.

in humans has been limited by few studies in this area and by a reliance on data from modern societies with low mortality–fertility schedules. Using data from a high-fertility polygynous human population, we provide evidence that personality traits are associated with reproductive success in both men and women in an alternative context, which is arguably more relevant to an evolutionary understanding of human life-history variation. In women, neuroticism (i.e., emotional instability) positively predicts the number of children both between and within families. Importantly, neuroticism is associated with a reproductive trade-off in women from low social classes: whereas women’s neuroticism positively predicts offspring quantity, it also negatively predicts offspring quality, leading to fitness payoffs maximized at an intermediate phenotypic level. In men, extraversion (i.e., sociality) is a strong predictor of high social class and polygyny, which leads extraverted men to produce a higher number of offspring compared with their introverted counterparts. These results carry important implications. First, from a biological and theoretical perspective, associations between personality traits and reproduction, as well as their sex differences, provide a basis for considering the role of the evolutionary processes that underlie the maintenance of variation in personality traits in current populations. Second, from a sociological and demographic point of view, these results provide an insight into the role of personality traits in influencing individual fertility in different socio-ecological contexts, which in turn is likely to prove enlightening when considering the role of individual factors in forming fertility patterns in contemporary humans.

Our finding that personality traits are related to reproductive success suggests that natural selection could shape personality patterns in humans. Two points must be acknowledged. First, the cross-sectional (vs. longitudinal) nature of our study design could be argued to hinder any inferences about the direction of causality between personality and reproduction. However, longitudinal studies conducted in modern environments find that personality (i.e., extraversion in men) predicts reproductive outcomes (i.e., male social class), rather than the other way around (7). We also found that personality traits in this population are not associated with age, whereas the number of children is, thus further reducing the likelihood that differential reproduction is the cause rather than the outcome of personality variation. Second, as with any empirical study, it is unknown whether current selection pressures reflect past selection in the ancestral human environment, and our study measures phenotypic correlations only. However, although the rates of evolution of complex polygenic traits are often thought to be slow, all of the main personality traits show significant additive genetic variance [10–50%, depending on the trait and the study (30)], indicating a potential to respond to prevailing current selection.

Investigating how personality variation is related to the number and health of children in current environments is thus of interest because, in both past and current environments, selection operates on differences in lifetime reproductive success (LRS) between individuals, with current populations showing both considerable variation in individual LRS (28) and rapid rates of adaptive evolution (31).

Behavioral ecologists are increasingly investigating the functional pathways by which interindividual variation in personality traits is generated and maintained (4, 29). One can first argue that such variation could result from the mutation-selection balance alone, the mutation load accounting for a substantial portion of genetic variance in many fitness-related traits (32). The extent to which this phenomenon introduces genetic variance, however, is proportional to the mutational target size (i.e., the number of loci involved). Because the polymorphism of personality traits in humans appears associated with a limited number of loci (e.g., DRD4 loci for extraversion), such polymorphism is unlikely to be explained by mutation-selection balance alone (25). An additional mechanism to account for variation in personality traits is fluctuating selection, i.e., different reproductive outcomes in different environments or times (33). According to this perspective, the link between women’s neuroticism and a quantity/quality trade-off in low but not in high social classes suggests that optimum phenotypic levels of neuroticism might differ among women as a result of a differential impact of family size on the quality of children in different social environments (i.e., higher in families from the low social class). Conversely, male extraversion is not associated with a quantity/quality trade-off. Nevertheless, the possibility that individual differences in male extraversion are maintained through life-history trade-offs is not ruled out if extraversion is associated with reproductive costs through reduced survival (13), although whether such effects are enough to counter-balance higher mating and reproductive opportunities is unknown. Other processes might be involved in maintaining variation in personality. That different personality traits are associated with reproductive success in men compared with women suggests that sexual selection is playing a role in maintaining variation in psychological dispositions. Why, however, mean extraversion does not differ between men and women (ANOVA: $F_{1,132} = 0.00$, $P = 0.9$) despite different sex-specific selection pressures on extraversion, is puzzling. It might first result from sexual reproduction and recombination, assuming that the trait is controlled by the same genes in both sexes (34). Alternatively, similar levels of extraversion in men and women might result from assortative mating for extraversion, as is observed in this study (Pearson’s correlation test $r = 0.39$, $t = 3.76$, $df = 74$, $P < 0.001$) and others. Overall, because individuals face several evolutionary challenges at a time, it appears critical to consider whether vari-

ation in selective pressures might explain observed patterns of personality traits.

Our results have further implications for our understanding of the role of individual personality traits in influencing fertility patterns in high- and low-fertility human populations. The comparison of the present results with those obtained by previous studies conducted in low-fertility populations reveals both similarities and differences in how personality traits are related to reproductive success in humans. First, extraversion is positively linked to the number of potential conceptions and the social class in men from low fertility populations (8, 13). Note that although the number of potential conceptions does not always predict fertility in such populations, social class does (27). Furthermore, leadership (a correlate of extraversion) during adolescence has been shown to predict men's probability to have children in adulthood (7), which, along with the present results, suggests that extraversion is a universal predictor of fertility. Assessing whether or not this is the case will however require data from other preindustrial populations. Concerning women's neuroticism, a different pattern is observed between natural and controlled fertility populations. Although in rural Senegal neuroticism is associated with a higher number of children, the relationship is either nonsignificant (9) or negative (8) in industrialized settings. How can this apparent contradictory pattern be explained? One possibility is that neurotic women seek more sexual intercourse than others, leading them to produce more children in social systems where the access to modern contraception remains limited. Indeed, previous research has linked neuroticism and its correlates of attachment anxiety to high sexual motivation (35) and increased short-term mating in the United States and Western Europe (36). Another possibility is that, in social environments where reproduction is highly valued, women want more babies (and behave accordingly) to outcompete their co-wives. As neuroticism is associated with competitiveness (13), this possibility could go some way toward explaining its positive association with fertility in a polygynous population. Understanding the proximate mechanisms by which neuroticism affects reproductive decisions is the key to deciphering the evolutionary significance of this trait and thus to cross-cultural variation and its relationship with fertility. In contrast with fertility, the relationship between women's neuroticism and child quality seems to be less context-specific: Neuroticism in women predicts poorer child condition both in the studied population and in modern settings where high neuroticism has been associated with inadequate parenting practices and the creation of a stressful family environment (37). Neuroticism also brings with it additional costs in terms of reduced survival and health-related problems (13). Generally, although the reproductive costs associated with neuroticism have been well identified, the potential benefits have not (13). Based on our study that investigates both the costs and benefits simultaneously in a single population, we propose that neuroticism may have allowed women to produce more children in high-fertility populations characterized by high-mortality risks.

Understanding individual-level determinants of reproductive decisions has gained considerable governmental as well as interdisciplinary academic attention during recent decades against the backdrop of decreasing birth rates in industrialized countries (i.e., the demographic transition) and repeated failures to predict corresponding shifts in many current developing countries (10). The association between increasing resources and decreasing family size in modern populations—instead of the opposite pattern observed in both preindustrial human societies (38) and all animal species (39)—has posed one of the biggest challenges for successfully applying an evolutionary approach to understanding human behavior (10). Recently, it was argued that a change in modern societies might be interpreted in terms of a shift toward investment in quality over quantity of offspring

resulting from the increased costs of child rearing (40). Here we show that some individual psychological dispositions influence this important trade-off, which is faced by all human populations. This suggests that the distribution of personality traits within a population, as well as the selective pressures acting on them, might be of significant importance to understanding the variation in fertility patterns across environments.

Materials and Methods

Study Population. The study was conducted in traditional villages in rural Senegal, located on the western coast of Africa (see ref. 41 for details on the population). The most common ethnic groups are the Sereer and Wolof. The main mode of subsistence is agriculture for cash crops such as peanuts and cashew nuts, but also crops such as millet, grown for subsistence. This society is generally patrilineal and patrilocal and characterized by a polygynous mating system. The protocols used to recruit families and to collect data were approved by both the ethical committee of the Senegalese National Research Council for Health and the French National Committee of Information and Liberty, and informed consent was obtained from all participants. We recruited 65 families from four villages, with the husband's age averaging 46.6 y (range: 30–66 y) and the wife's age 34.4 y (range: 21–48 y). Selection of both the villages and the families was random (although dependent on the willingness of families to participate), and for at least one village, all resident families were included, so our sample likely represents the larger community. Female fertility in our sample is 5.0 ± 2 children, consistent with the Senegalese national fertility rate (4.7 in 2007; see <http://www.who.int>).

Demographic and Anthropometric Data. To investigate the effects of personality variation on the quantity and quality of offspring, we recorded for each family the total number of children alive and their body condition. Anthropometric measurements taken were height, weight, and MUAC. BMI (weight/height squared) and MUAC were used as indices of nutritional status (42) (BMI \times MUAC Pearson's correlation, $r = 0.85$, $df = 71$, $P < 0.001$). Information on child age, sex, and birth order were also recorded to control for their influence on the outcomes measured ($n = 229$). We also recorded both mother's and father's age, body condition (BMI and MUAC), and birth order. Marital status was recorded for each man as either monogamous ($n = 38$) or polygynous ($n = 27$) and for each woman as either unique wife of a monogamous man or first or second wife of a polygynous man. Finally, social class was assessed on the basis of the type of house lived in: either modern (high social class $n = 28$) or traditional (low social class $n = 37$) (Table S3). This measure also reflects land possessions (mean number of hectares \pm SEM = 6.4 ± 1.0 and 10.1 ± 2.4 for men living in traditional vs. modern houses, respectively).

Assessment of the "Big Five" Personality Dimensions. Personality was assessed using an adapted version of the international Big Five minimarkers questionnaire (43). The original 40-item questionnaire was reduced to 27 adjectives after assessment of the functional and conceptual equivalence of the adjectives in the Senegalese culture and to keep the questionnaire short to maintain the attention of participants. Interviews were conducted in privacy, and the questionnaire was translated into the local language by a professional linguist and played using a voice recorder. The participants were told to describe how much each adjective described their personality on a scale ranging from 1 to 4 (1: not at all; 2: a little bit; 3: a lot; 4: perfectly). Only questions that maximized the internal reliability of each dimension assessed through the α Cronbach coefficient were used to build personality variables (Table S4). The reliability of the obtained personality traits did not differ from those usually found in Africa [extraversion: 0.55; agreeableness: 0.62; conscientiousness: 0.68; neuroticism: 0.63; openness: 0.58 (35)]. For both men and women, all personality dimensions were independent of age (all $|r| < 0.15$).

Statistical Analyses. Statistical analyses were carried out with R software (R.2.4.1 2006; The R Development Core Team). Mixed models were used to control for repeated measures within villages (lme4 package). *P* values were estimated using Markov Chain Monte Carlo methods for models with either binary or quasi-Poisson errors structure, and *F*-tests for models with normal error structure. To avoid over-parameterization of models, a first model including all potential confounding factors was built. Then, the variables that were significant were added to a second model investigating the effects of interest (personality dimensions). Interactions among personality dimensions and between personality dimensions and social class were included in

the final model if significant. For nonbinary response models, the normality of residuals was checked. For each significant result, the proportion of variation in the dependent variable accounted for by the independent variable is indicated [i.e., effect size (r)].

First, we investigated potential confounding factors associated with the number of children. For women, the number of children was modeled using a normal error structure (Shapiro test of normality: $P = 0.09$). To take into account nonindependence of data due to the inclusion of multiple individuals from the same households (co-wives), we used a weighting factor to ensure that each man contributed equally to the observed variability in number of children. In women, the number of children was associated with her age ($F_{1,60} = 12.02$, $\beta \pm SE = 0.15 \pm 0.04$, $P = 0.001$), but not with her rank (unique or first or second wife), ethnic group, birth order, or husband's social class ($P > 0.50$). Because of the absence of any factors that could act as plausible mediators between personality and reproductive success (compare with results for men, below), only the number of children was used as an indicator of women's reproductive success. To strengthen inferences from these models explicitly investigating between-women differences, we additionally compared differences between women within the same polygynous family (balanced design, one man with two wives). For men, the number of children was modeled using a quasi-Poisson error structure to account for overdispersion. A man's number of children increases with age ($\beta = 0.02$; 95% CI = 0.01, 0.03; $P < 0.001$) and social class ($\beta = 0.16$; 95% CI = -0.02, 0.36; $P < 0.05$) and is higher in men with multiple wives ($\beta = 0.28$; 95% CI = 0.09, 0.49; $P < 0.001$), but it was not affected by birth order or ethnic group (all $P > 0.20$). Because social and marital status significantly predict male reproductive success, we investigated whether these could act as mediators between personality and reproductive success in addition to measuring the relationships between personality and reproductive success directly. The effect of personality dimensions in affecting the probability of becoming polygynous and the probability of belonging to the high social

class were modeled using a binary error structure. We then investigated the link between personality dimensions and reproductive success (number of children).

Second, all personality dimensions related to reproductive success at the individual level were included in the same model to investigate links between personality and child BMI and MUAC for children 0–5 y of age. As the variables describing BMI were skewed, they were log-transformed. Repeated measures within families (siblings) were considered by including a weighting factor so that each family contributed equally to each model.

Third, we investigated the relationship between neuroticism and ultimate reproductive success in women. Ultimate reproductive success was defined as the product of the number of children times the mean survival of children to age 5, given their BMI. Under-5 y mortality is the leading indicator of the level of child health and overall development worldwide (in Senegal, under-5 y mortality was 114 deaths for 1,000 births in 2007; <http://www.who.int>). Child BMI is associated with child survival in Senegal: in the 1990s, 1 SD from standard BMI, given age and sex (based on a sample of French children), was associated with a 3.8 increase in the relative risk of death in Senegal (44, 45). *SI Materials and Methods* and *Fig. S2* give details of the estimation of the mean probability for each mother of having a child surviving to age 5, given the deviation of his/her BMI from standard BMI.

ACKNOWLEDGMENTS. We are very grateful to all families for their participation as well as to the ethical committees for useful comments. We also thank M. Cissé, C. Moysse-Faurie, C. Faurie, S. Faye, and S. Robert for their assistance in the translation of the questionnaire; D. Sarr for his work as a local guide; S. Sarr, T. Bakhroum, M. Kerinec, and P. Guevara-Fiore for their assistance in the field; I. Rickard for his help in editing the manuscript; and M. Raymond for continuing support. This study was funded by the Kone Foundation, the University of Helsinki, the Royal Society of London, and the European Research Council.

- Réale D, Reader SM, Sol D, McDougall PT, Dingemans NJ (2007) Integrating animal temperament within ecology and evolution. *Biol Rev Camb Philos Soc* 82:291–318.
- Bell AM (2007) Future directions in behavioural syndromes research. *Proc R Soc B-Biol Sci* 274:755–761.
- Dall SRX, Houston AI, McNamara JM (2004) The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecol Lett* 7:734–739.
- Smith BR, Blumstein DT (2008) Fitness consequences of personality: a meta-analysis. *Behav Ecol* 19:448–455.
- Chapple ED (1940) "Personality" differences as described by invariant properties of individuals in interaction. *Proc Natl Acad Sci USA* 26:10–16.
- Nettle D (2005) An evolutionary approach to the extraversion continuum: Evolution and human behaviour. *Evol Hum Behav* 26:363–373.
- Jokela M, Keltikangas-Järvinen L (2009) Adolescent leadership and adulthood fertility: revisiting the "central theoretical problem of human sociobiology." *J Pers* 77:213–229.
- Jokela M, Kivimäki M, Elovainio M, Keltikangas-Järvinen L (2009) Personality and having children: a two-way relationship. *J Pers Soc Psychol* 96:218–230.
- Eaves LJ, Martin NG, Heath AC, Hewitt JK, Neale MC (1990) Personality and reproductive fitness. *Behav Genet* 20:563–568.
- Mulder MB (1998) The demographic transition: Are we any closer to an evolutionary explanation? *Trends Ecol Evol* 13:266–270.
- King AJ, Johnson DDP, Van Vugt M (2009) The origins and evolution of leadership. *Curr Biol* 19:R911–R916.
- Figueredo AJ, et al. (2005) Evolutionary personality psychology. *Handbook of Evolutionary Psychology*, ed Buss DM (Wiley, Hoboken, NJ), pp 851–877.
- Nettle D (2006) The evolution of personality variation in humans and other animals. *Am Psychol* 61:622–631.
- Stamps JA (2007) Growth-mortality trade-offs and 'personality traits' in animals. *Ecol Lett* 10:355–363.
- Biro PA, Stamps JA (2008) Are animal personality traits linked to life-history productivity? *Trends Ecol Evol* 23:361–368.
- Wolf L, Ketterson ED, Nolan V (1988) Paternal influence on growth and survival of dark-eyed junco young: Do parental males benefit? *Anim Behav* 36:1601–1618.
- Réale D, Martin J, Coltan DW, Poissant J, Festa-Bianchet M (2009) Male personality, life-history strategies and reproductive success in a promiscuous mammal. *J Evol Biol* 22:1599–1607.
- McElreath R, Strimling P (2006) How noisy information and individual asymmetries can make 'personality' an adaptation: a simple model. *Anim Behav* 72:1135–1139.
- Massol F, Crochet PA (2008) Do animal personalities emerge? *Nature*, 451:E8–E9, discussion E9–E10.
- Gillespie DO, Russell AF, Lummaa V. When fecundity does not equal fitness: Evidence of an offspring quantity versus quality trade-off in pre-industrial humans. *Proc Biol Sci*. 2008 Mar 22;275:713–722.
- Lawson DW, Mace R (2010) Optimizing modern family size: Trade-offs between fertility and the economic costs of reproduction. *Human Nature* 21:39–61.
- Schmitt DP, Realo A, Voracek M, Aliik J (2008) Why can't a man be more like a woman? Sex differences in Big Five personality traits across 55 cultures. *J Pers Soc Psychol* 94:168–182.
- Gangestad (2000) The evolution of human mating: trade-offs and strategic pluralism. *Behav Brain Sci* 23:573–644.
- McCrae RR, John OP (1992) An introduction to the five-factor model and its applications. *J Pers* 60:175–215.
- Penke L, Denissen JJA, Miller GF (2007) The evolutionary genetics of personality. *Eur J Pers* 21:549–587.
- Lummaa V, Clutton-Brock T (2002) Early development, survival and reproduction in humans. *Trends Ecol Evol* 17:141–147.
- Nettle D, Pollet TV (2008) Natural selection on male wealth in humans. *Am Nat* 172:658–666.
- Brown GR, Laland KN, Mulder MB (2009) Bateman's principles and human sex roles. *Trends Ecol Evol* 24:297–304.
- Dingemans NJ, Réale D (2005) Natural selection and animal personality. *Behaviour* 142:1159–1184.
- Bouchard TJ, Jr (1994) Genes, environment, and personality. *Science* 264:1700–1701.
- Hawks J, Wang ET, Cochran GM, Harpending HC, Moyzis RK (2007) Recent acceleration of human adaptive evolution. *Proc Natl Acad Sci USA* 104:20753–20758.
- Zhang XS, Hill WG (2005) Genetic variability under mutation selection balance. *Trends Ecol Evol* 20:468–470.
- Dingemans NJ, Both C, Drent PJ, Tinbergen JM (2004) Fitness consequences of avian personalities in a fluctuating environment. *Proc R Soc Lond Ser B-Biol Sci* 271:847–852.
- Lande R (1980) Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution* 34:294–305.
- Eysenck HJ (1971) Personality and sexual adjustment. *Br J Psychiatry* 118:593–608.
- Schmitt DP (2008) Big five traits related to short-term mating: From personality to promiscuity across 46 nations. *Evol Psychol* 6:246–282.
- Ellenbogen MA, Hodgins S (2004) The impact of high neuroticism in parents on children's psychosocial functioning in a population at high risk for major affective disorder: A family-environmental pathway of intergenerational risk. *Dev Psychopathol* 16:113–136.
- Hopcroft RL (2006) Sex, status and reproductive success in the contemporary united states. *Evol Hum Behav* 27:104–120.
- Stearns SC (1992) *The Evolution of Life Histories* (Oxford University Press, Oxford).
- Mace R (2008) Reproducing in cities. *Science* 319:764–766.
- Alvergne A, Faurie C, Raymond M (2009) Father-offspring resemblance predicts paternal investment in humans. *Anim Behav* 78:61–69.
- Viswesvara R, Singh D (1970) An evaluation of the relationship between nutritional status and anthropometric measurements. *American Journal of Clinical Nutrition* 23:83–93.
- Thompson ER (2008) Development and validation of an international English big-five mini-markers. *Pers Individ Dif* 45:542–548.
- Rosetta L (1988) Seasonal changes and the physical development of young Serere children in Senegal. *Ann Hum Biol* 15:179–189.
- Rosetta L, O'Quigley J (1990) Mortality among Serere children in Senegal. *Am J Hum Biol* 2:719–726.