Original Article

The evolutionary fitness of personality traits in a small-scale subsistence society ☆

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ABSTRACT

The maintenance of personality variation remains an unexplained puzzle in evolutionary biology. Despite evidence among non-humans that personality variation affects fitness, few data exist to assess the personality–fitness relationship in humans. Among Tsimane forager–horticulturalists (n = 632), we test whether personality traits (assessed using a 43-item Big Five Inventory administered orally in native language) predict fertility, offspring survivorship, age of first reproduction, and other fitness correlates (extramarital affairs, conflicts, social visitation, food production, and several health measures). Among men, several personality factors associate with higher fertility, more time spent producing food and social visitation. Among women, the relationship between personality and fitness varies across regions of Tsimane territory. The only case of an intermediate personality level associated with highest fitness was found for Industriousness in men. We find that personality factors positively associated with fitness do not associate with greater health costs, although greater Extraversion and Openness may lead to more conflicts among men. Factor heritability ranges from 60% for Prosociality and Extraversion to 8% for Neuroticism. We interpret our results in light of evolutionary models that explain maintenance of personality variation, including incomplete directional selection, mutation–selection balance, condition-dependent reaction norms and fluctuating selection based on sex or spatial variability in selection pressures.

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1. Introduction

Personality or "behavioral syndromes" are relatively stable dispositional traits and behaviors that have now been identified in a myriad of social species (Gosling, 2001; Sih, Bell, Johnson, & Ziemba, 2004), and with clear consequences on fitness (Smith & Blumstein, 2008). The canalization of personality during development and relative stability thereafter, despite varying circumstances over the life course that might otherwise favor greater plasticity, is an important problem attracting much theoretical and empirical attention (Dall, Houston, & McNamara, 2004; Dingemanse, Kazem, Réale, & Wright, 2010). Further, personality is highly heritable, yet how heritable genetic variation in personality traits is maintained over generations remains another conundrum (Buss & Hawley, 2011). If selection effects on personality vary over space or time, or by organismal state or condition, then variation in personality could be adaptive. Frequency-dependence could also affect fitness if payoffs vary based on the frequency of personalities in the population. However, empirical evidence to support these adaptive explanations is sparse in humans. One approach to studying the adaptive value of personality variation considers costs

and benefits of specific dispositions, and how these may maintain multiple phenotypic equilibria along personality dimensions. Extraverted individuals may be bold, sociable and may obtain greater mating access, but may also incur greater risks of injury, morbidity and mortality (Nettle, 2006). Conscientious individuals may be goal-oriented, hard working, and cautious about health, but may also miss out on short-term mating and resource opportunities (Schmitt, 2004). Neurotic individuals may be prone to greater depression, anxiety and chronic stress, but may also be more risk-averse and vigilant concerning environmental dangers (Nettle, 2006).

A theory of personality that specifies its ontogeny, the contributions of life history strategy and social norms, and the ways by which selection pressures impact personality variation over space and time, remains lacking. Furthermore, existing models of decision-making in the social sciences rarely consider dispositional traits as critical components of behavioral strategies. The standard framework underlying decision-making in optimization models assumes that situational costs and benefits impact all individuals equally, except when individuals vary by condition or state (Almlund, Duckworth, Heckman, & Kautz, 2011). Across many species and taxa, however, individuals often act consistently across contexts and over time when the standard approach predicts more flexible "optimal" responses (Bell, Hankison, & Laskowski, 2009). What we can learn about personality variation in small-scale societies will aid our understanding of the

selection pressures responsible for shaping human personality traits. It is in small-scale societies that humans have lived for the majority of our existence. Variations within and across modern small-scale societies in access to contraception, health care, formal legal systems, or the market economy present unique opportunities to understand the origins of human personality variation and how personality responds to socioecological context.

Most human personality studies to date are descriptive, aimed at testing the existence of a specific personality structure (e.g. Big Five) based on inductive factor analysis of self- or third-party reports (e.g. McCrae & Terracciano, 2005; Schmitt, Allik, McCrae, & Benet-Martínez, 2007). Approaches in evolutionary psychology have traditionally focused on human universals, and with a few exceptions (e.g. Buss, 1991; MacDonald, 1995; Wilson, 1994), have only recently attempted to explain individual variability (Buss & Hawley, 2011). Almost all studies have been restricted to low-fertility, heterogeneous, modern populations. In these societies, personality variation in the "Big Five" is associated with a variety of outcomes affecting health, mortality, education and income (Ozer & Benet-Martinez, 2006). It also correlates with reproductive behavior among Australian and U.S. adults (Eaves, Martin, Heath, Hewitt, & Neale, 1990; Jokela, Alvergne, Pollet, & Lummaa, 2011). Only two studies have examined fitness correlates of personality variation in natural fertility populations. Among rural Senegalese farmers, extraverted men and women with intermediate levels of neuroticism have more children (Alvergne, Jokela, & Lummaa, 2010). Among Ache forager–farmers, extraverted men have more children (Bailey et al., 2013). Both studies, however, have small sample sizes, do not consider potential costs of specific dispositions, or whether dispositions co-vary with observed fitness-related behavior.

Here we investigate the relationship between personality and fitness among Tsimane forager–horticulturalists of Bolivia with four goals in mind. We first explore the relationship between reproductive success (RS) and two sets of personality dimensions: the traditional Big Five and a population-specific Big Two derived from exploratory factor analysis ("pro-sociality" and "industriousness") for both men and women. While among Tsimane the Big Five correlate with observed behavior and are replicable, their internal consistency is lower than commonly encountered; for this reason, we provide the Big Two as an alternative and more robust personality structure (Gurven, von Rueden, Massenkoff, Kaplan, & Lero Vie, 2013). Fitness is proxied as age-specific cumulative fertility, offspring survivorship, and age at first reproduction (AFR). In natural fertility populations without deliberate fertility control, these are reliable measures of future genetic representation. AFR is the most indirect fitness measure of the three, but has been linked to fitness among Tsimane and other subsistence populations (von Rueden, Gurven, & Kaplan, 2011).

Second, we consider potential costs of several personality traits by testing for longitudinal associations with health indicators and frequency of social conflicts among men in a society lacking modern healthcare and a formal legal system. Prospective study permits causal inference beyond simple correlation between personality and health. Third, we examine several behavioral correlates of personality that relate to fitness, such as time spent in productive tasks, direct care of offspring, social visitation and number of extramarital affairs. Fourth, we assess the heritability of personality by considering multigenerational pedigrees. Heritability describes the proportion of variance in an observable trait within a population that is due to inter-individual variance in genetic factors. Hence, the heritability of personality describes the extent to which selection can maintain variability in personality within a particular population (Falconer & Mackay, 1996). As our estimate is not based on an adoption or twin study, and so does not completely control for shared environment, we label our estimate "quasi"-heritability. We consider different modes of selection in the interpretation of personality–fitness associations: stabilizing, directional and fluctuating (in which the fittest phenotype within a population varies across time, space or by individual condition).

Highest fitness at intermediate levels of personality traits is consistent with stabilizing selection on personality, while linear effects are consistent with directional selection. Variation in personality and the personality–fitness relationship by geographic region is consistent with spatially fluctuating selection. Fluctuating selection is also consistent with personality–fitness relationships differing among men and women. Men and women may be expected to differ in personality because their reproductive, social and parental investment strategies may diverge (Schmitt, Realo, Voracek, & Allik, 2008).

2. Methods

2.1. Study population

Tsimane are semi-sedentary forager–horticulturalists of Amazonian Bolivia, inhabiting over 90 villages ranging from 50 to 500 individuals. They cultivate plantains, rice, corn, and sweet manioc in small swiddens, and regularly fish and hunt for meat. These foods together provide over 90% of the calories in the diet, with the remainder coming mainly from store-bought items or trade with itinerant merchants. Tsimane live in extended family clusters, where the majority of food- and labor-sharing occurs. Polygyny exists at low frequencies (~5%) and is concentrated in more remote communities. Approximately 20% of offspring never reach age 5 (Gurven, Kaplan, & Zelada Supa, 2007). The Tsimane rarely use modern contraceptives and total fertility rate is very high (~9 births per woman). The population growth rate is 3.6% per year. Mean ± SD age of first birth for men and women in this sample is 22.8 ± 4.2, and 18.6 ± 2.9 years, respectively.

Many villages now have schools, taught by bilingual Tsimane teachers, most of whom were trained by missionaries. Secondary schools now exist in several larger villages, and young Tsimane adults are starting to become high school graduates. However, overall adult literacy rate is low (25%). Fluency in Tsimane language is universal, and 40% of adults are moderately fluent in Spanish.

2.2. Personality instrument

The 43-item Tsimane Big Five Inventory (BFI) was administered to 632 adults from 28 villages from Jan 2009 to Dec 2010, as part of the Tsimane Health and Life History Project (THLHP) (see Gurven et al., 2013). Average age is 47 ± 14 years (range 20–88). The Tsimane BFI was conducted verbally in a private location by a male, bilingual Tsimane research assistant trained in the administration of anthropological and psychological interviews. As in the English version of the BFI, responses were given on a translated scale where 1 corresponds to "strongly disagree" and 5 corresponds to "strongly agree." Participants were first given a quick tutorial and comprehension test on the use of the scale, after which all participants showed clear evidence of understanding the scale, and the task. Additional details are given in (Gurven et al., 2013). The least internally consistent item was removed from each of the five personality dimensions (E, C, A, O, N), which were then scored according to standard protocol, and standardized as percentage of the maximum possible score (Benet-Martinez & John, 1998). The Tsimane-specific "Big Two" (Prosociality, Industriousness) were derived from exploratory factor analysis and validated against a separate sample of spouse-derived ratings, as described in (Gurven et al., 2013); the Big Two are presented as z-scores. See supplementary material for factor internal reliability and inter-factor correlations (Table S1 and S2, available on the journal's website at www.ehbonline.org).

2.3. Fitness, behavior and health

Data on fertility and offspring survivorship come from reproductive histories, updated censuses and medical histories from 2002 to

2010 (Gurven et al., 2007). Number of sex partners before and after marriage (men only) comes from a subset of the demographic interviews conducted by MG (n = 83). Tsimane adult men (n = 208) from four villages were asked to list and describe any conflicts they had with other individuals over the past six months. Conflict frequency was operationalized as the number of times ego was named as having been involved in a conflict by all interviewees in the village. Time spent working in productive tasks, parenting and visiting was measured for a subset of individuals (n = 90) using behavioral scans with 3-h household cluster sampling, as described in Gurven, Winking, Kaplan, von Rueden, and McAllister (2009). Work here is defined as food production and wage labor.

Prospective measures of health status include body mass index (BMI), C-reactive protein (CRP), erythrocyte sedimentation rate and leukocyte counts, determined from serum samples collected during subsequent THLHP clinic visits. The average time of follow-up from personality assessment was 2.1 years (SD = 0.8, range 1–3 years). Biomarker collection and analysis procedures are described in Gurven et al. (2009). Additional covariates, such as years of schooling, Spanish fluency (none, little, fluent) and village distance to town (in km), were measured during annual census updates.

Procedures for all methods described here have been approved by the UCSB Human Subjects Review Board, Tsimane government (*Gran Consejo Tsimane*), village leaders, and study participants.

2.4. Data analysis

Effects of personality on RS are analyzed using multilevel regression where geographic region is modeled with a random intercept. Models of fertility and number of surviving offspring were also analyzed using a Poisson error distribution, although no differences with the above regressions were found. For analysis of offspring survivorship, extramarital affairs and health outcomes, a control variable designating the temporal lag between personality inventory and demographic interview or medical checkup was added. Regional variation in the personality–fitness relationship was inves-

tigated treating region as a fixed effect and including interaction terms using OLS regression. Quasi-heritability was estimated using a variance components model with the software Sequential Oligonucleotide Linkage Analysis Routines (SOLAR) (Falconer & Mackay, 1996). The model takes as input pedigrees for the 632 individuals in our sample, and controls for age, age^2, sex, and village affiliation. We include the age^2 term due to the observed age effects shown in Figure S1, available on the journal's website at www.ehbonline.org.

3. Results

Descriptive statistics for personality measures and covariates by sex are provided in Table 1.

3.1. Does personality vary by age and sex?

Tsimane men are more extraverted (E), open (O), conscientious (C), agreeable (A), and less neurotic (N) than women (Table S1, Figure S1, available on the journal's website at www.ehbonline.org). Men also score substantially higher in prosociality (P) and industriousness (I) (Table S1, Figure S1, available on the journal's website at www. ehbonline.org). These sex differences are 9%–17% of the maximum scores for each factor, and remain after controlling for age. We further control for Spanish fluency, literacy and schooling due to men having higher levels of each (Table 1). After these additional controls, the sex difference reduces by a range of 4% (for I) to 56% (for P), and from 11% to 30% for the Big Five. Sex differences persist across adulthood, but diminish slightly with age. Only C, P and I vary systematically with age (Table S3, available on the journal's website at www.ehbonline.org).

3.2. Is personality associated with reproductive success?

3.2.1. Men
Men with higher E, O, and C, and lower N have greater fertility and more surviving offspring, but do not start reproduction earlier (Table 2, S4). While age at first reproduction (AFR) is largely unrelated

Table 1
Descriptive statistics for independent and dependent variables.

Variable	MALES				FEMALES			
	Mean ± SD	Min.	Max.	N	Mean ± SD	Min.	Max.	N
Socio-demographics								
Age (years)	46.9 ± 14.5	21.0	88.0	326	46.4 ± 14.4	20.0	88.0	305
Years of schooling	1.6 ± 2.7	0.0	12.0	307	0.8 ± 1.4	0.0	8.0	285
Spanish fluency[a]	1.0 ± 0.8	0.0	2.0	308	0.5 ± 0.7	0.0	2.0	287
Village size (n)	215.0 ± 163.1	9.0	524.0	314	237.9 ± 173.5	9.0	524.0	303
Distance to San Borja (km)	41.9 ± 24.3	5.9	82.2	326	43.2 ± 24.3	5.9	82.2	306
Fitness proxies								
Age at birth of 1st child	22.8 ± 4.2	16.0	39.0	200	18.6 ± 2.9	12.0	36.0	226
# lifetime sexual partners	3.4 ± 5.1	0.0	29.0	83	–	–	–	–
# surviving children	6.9 ± 4.2	0.0	21.0	229	7.4 ± 3.4	0.0	16.0	299
Health status								
BMI (kg/m²)	23.8 ± 2.6	15.6	36.4	316	24.1 ± 3.6	17.0	37.9	297
Hemoglobin (g/dL)	14.3 ± 7.3	5.9	143.0	322	12.7 ± 1.1	9.4	15.8	296
Sedimentation rate (mm/h)	29.6 ± 20.8	1.0	112.0	241	40.4 ± 20.0	3.0	105.0	226
White blood cell count (WBC) (cells/mm³)	10754 ± 2507	4200	20000	311	11031 ± 2822	4500	20700	293
Eosinophil count (cells/mm³)	2036 ± 1060	416	7760	235	1976 ± 1051	204	6072	224
C-Reactive Protein (mg/L)	3.1 ± 2.3	0.7	10.5	54	3.6 ± 4.8	0.6	31.1	50
Cortisol-creatinine ratio	264.3 ± 168.6	6.3	855.1	160	269.5 ± 172.8	9.1	1080.2	164
Personality factors (% of maximum score, or factor score)								
Agreeableness	78.9 ± 9.9	47.5	97.5	326	71.7 ± 10.6	42.5	97.5	306
Conscientiousness	74.8 ± 10.2	37.5	95	326	64.0 ± 11.2	35.0	92.5	306
Extraversion	70.9 ± 14.2	34.3	100.0	326	58.9 ± 13.0	31.4	100.0	306
Neuroticism	61.9 ± 10.3	37.1	88.6	326	69.5 ± 10.2	40.0	97.1	306
Openness	71.4 ± 10.8	40.0	95.0	326	61.0 ± 9.6	37.5	87.5	306
Industriousness	0.4 ± 0.8	−3.9	2.0	326	−0.4 ± 1.0	−3.5	1.9	306
Prosociality	0.2 ± 1.0	−2.3	2.2	326	−0.2 ± 0.9	−2.3	2.1	306

Note: San Borja is the largest town in the Tsimane area (population ~24,000).
   [a] None=0, little=1, fluent=2.

to personality using the Big Five, I is significantly associated with later reproduction (β = .86, p = 0.037). These results hold after controlling for age, schooling and Spanish fluency and using region as a random effect. One SD unit difference in E, N, C, and O is associated with a difference in 0.94, −0.70, 0.85, and 0.54 additional child, respectively (Table 2). One SD unit increase in I is associated with 0.53 additional child, respectively (same controls). All results for E, N and C, and for I on total surviving children (Table S4, available on the journal's website at www.ehbonline.org) withstand Bonferroni corrections for multiple tests (p < 0.01).

The effects of personality on RS are derived largely from fertility, as personality is not associated with the percentage of live births resulting in death before age 15 in multivariate regressions (Table 2).

Mean ± SD number of non-marital sex partners is 3.4 ± 5.1 (range: 0 to 29), 2.3 ± 2.9 (range: 0–15) before marriage and 1.0 ± 3.2 (range: 0–19) after marriage. Controlling for age and Spanish fluency, men with greater E, A and O have more sex partners. One SD unit increase in these personality factors is associated with 1.7 (p = 0.003), 1.7 (p = 0.024), and 1.2 (p = 0.037) additional partners, respectively. The relationship between P and non-marital partners trends toward significance, with one SD unit increase associated with 1.0 additional partner (p = 0.076).

3.2.2. Women

None of the Big Five or Big Two factors is significantly associated with fertility, number of surviving offspring, or AFR among women (Table 2, S4). Higher C is marginally associated with lower percentage of offspring dying before age 15 (Table 2).

3.3. Intermediate optima for personality?

We test for the presence of intermediate optima for personality for each fitness outcome by including a quadratic term for each personality factor in regression analyses from Tables 2 and S4 that control for age, Spanish fluency and education, and using region as a random effect. A quadratic effect is only marginally significant for I

and number of surviving offspring among both men (linear term, p = 0.018; quadratic term, p = 0.092) and women (linear term, p = 0.020, quadratic, p = 0.055). Among men, highest number of surviving children is 7.2 children when I = 1.1 (Figure S2a, available on the journal's website at www.ehbonline.org); mean ± SD I for men is 0.39 ± 0.84. Among women, there is no intermediate optimum; highest RS is associated with greatest level of I, whereas median I is much lower (I = −0.31) (Figure S2b, available on the journal's website at www.ehbonline.org). O and C could be confounded by education and Spanish fluency, but reduced models eliminating these two covariates did not change results.

3.4. Are there costs of high E, O, P, I, or low N?

3.4.1. Health

The relationship between personality and health was studied using seven measures collected during clinic visits: urinary cortisol, BMI, hemoglobin, CRP, leukocyte and eosinophil counts and erythrocyte sedimentation rate. We restrict analysis to E, N, O, P and I to limit the number of statistical tests, and because three of these factors have been previously linked to morbidity (Nettle, 2006). Most relationships in Table 3 are consistent with better health among those with greater E, O, P and I, and lower N. Only two cases are consistent with worse health: leukocyte count and eosinophils are higher among more industrious men (r = 0.19, p = 0.023, n = 145; r = 0.24, p = 0.003, n = 144, respectively) (Table 3). However, with Bonferroni corrections for multiple tests (5 factors*7 health measures), a conservative adjusted critical p-value is 0.05/35 = 0.0014. Both relationships showing greater health costs do not meet this criterion. In total, only 4 of the 13 significant relationships in Table 3 remain using this criterion, and all are consistent with higher E, O and I associated with better health. Controlling for measures of baseline health permits stronger causal inference, but reduces sample size; results from analyses controlling for baseline health are largely similar to those reported here (Table S5, available on the journal's website at www.ehbonline.org).

3.4.2. Conflicts

Mean ± SD number of conflicts for men in the past six months is 1.4 ± 2.1 (range 0–11, n = 62). Conflicts are primarily verbal disputes but occasionally escalate into physical violence. Over one-fourth of conflicts concern disputes over access to desired land for horticulture. Arguments over insufficient contributions to community

Table 2
Association between selected reproductive success measures and personality for men and women, using mixed effects regression models.

RS Measure	FERTILITY			% OFFSPRING	
Personality Factor	b	p	std. beta	DYING < AGE 15	
				b	p
MEN		(n = 215)		(n = 198)	
Extraversion	0.066	***	0.23	0.044	ns
Neuroticism	−0.068	**	−0.17	−0.136	ns
Agreeableness	0.024	ns	0.06	−0.049	ns
Conscientiousness	0.084	**	0.20	−0.117	ns
Openness	0.051	*	0.13	0.020	ns
Pro-sociality	0.392	ns	0.10	0.640	ns
Industriousness	0.632	^	0.13	−2.597	ns
WOMEN		(n = 274)		(n = 274)	
Extraversion	−0.009	ns	−0.04	−0.096	ns
Neuroticism	0.002	ns	0.01	0.019	ns
Agreeableness	0.014	ns	0.04	−0.050	ns
Conscientiousness	−0.003	ns	−0.01	−0.145	ns
Openness	−0.025	ns	−0.07	−0.090	ns
Pro-sociality	−0.325	ns	−0.09	−1.401	ns
Industriousness	0.166	ns	0.05	0.944	ns

All models control for age, education, Spanish fluency and time lag between demographic and personality interview, with region as random effect (see Table S2, available on the journal's website at www.ehbonline.org for additional tests and exact p-values).
^ p < .1.
* p < .05.
** p < .01.
*** p < .001.

Table 3
Health correlates of personality.

Variable	Men					(n)	Women					(n)
	E	N	O	P	I		E	N	O	P	I	
lnCortisol	−		−	−	−	78				−		155
BMI	+ +		+ +	+		168						184
Hb					+	149		−	+			204
lnCRP						139						157
WBC					+	145			−		−	163
Sed Rate				− −		148						207
Eosinophil	−				+ +	145			−			163

"+" indicates significant (p < 0.05) positive relationship between personality factor and health measure; "−" indicates significant (p < 0.05) negative relationship. Double "+ +" or "− −" symbol connotes statistical significance after Bonferroni correction (p < 0.002). Dark shading denotes effect size of 0.2 < partial r < 0.3, or 0.1 < partial r < 0.2 otherwise. Models control for age and time between personality assessment and subsequent clinic visit. CRP and cortisol are logged due to non-normal distribution of raw values.

lnCRP = log(C-reactive protein), Hb = hemoglobin, WBC = white blood cells.

Table 4

Regional differences in personality scores (n = 281). Analyses are multiple linear regressions controlling for age, sex, age*sex, age*age, schooling and Spanish fluency. Baseline is near town.

Personality Factor	Downriver		Forest		Upriver	
	b	p	b	p	b	p
Extraversion	−2.31	ns	−0.36	ns	−0.62	ns
Neuroticism	4.09	***	1.71	ns	0.76	ns
Agreeableness	−3.32	**	0.29	ns	2.34	*
Conscientiousness	−1.36	ns	−1.44	ns	−1.81	^
Openness	−3.18	**	2.66	*	1.13	ns
Prosociality	−0.26	*	−0.04	ns	0.37	***
Industriousness	0.04	ns	0.08	ns	0.21	*

Forest and Upriver are both remote regions; Downriver refers to villages closer to town located within the Beni Biological Reserve.

^ p < .1.
* p < .05.
** p < .01.
*** p < .001.

projects, disputes over reconciling debts in a timely fashion, conflicts over marital infidelity, and accusations of theft each account for 1/8 of all conflicts. Most conflicts are resolved by the parties directly involved or with arbitration from influential members of the community (e.g. village chief). Some, however, remain unresolved and/or provoke migration to other communities.

Controlling for age and region, E and O are marginally associated with greater number of conflicts. One SD unit increase in E and O is associated with 0.45 (p = 0.081) and 0.42 (p = 0.052) more conflicts, respectively. P is positively associated with conflicts (std. β =0.63, p = 0.006), while I is negatively associated with conflicts (std β = −0.75, p = 0.017). Prior research showed that larger men were judged by other Tsimane as more dominant and aggressive, and therefore more prone to conflicts (von Rueden, Gurven, & Kaplan, 2008). Adding BMI to these models eliminates the effects of E and O on conflicts, as BMI is positively related to both of these personality factors and to conflicts. The effects of P and I, however, remain significant after controlling for BMI (p = 0.027, p = 0.036, respectively).

3.5. Regional differences

Linear regressions that control for age, sex, education and schooling reveal substantial differences in personality factors across geographic regions (Table 4). Relative to those living near town, Tsimane living downriver within a protected forest reserve score higher in N, but lower in A, O and P. Those living in remote villages upriver from town score higher in A, P and I, but trend towards lower C (Table 4).

3.6. Does the relationship between reproductive success and personality vary by region?

If so, this would suggest that selection pressures could vary by region, consistent with models of fluctuating selection that help maintain genetic variation in personality traits. We test this by adding a region*personality factor interaction variable to each of the regression models in Table 2 and S4. For three fitness measures (fertility, percentage or total number of surviving children and AFR) and seven personality factors, there are 42 possible interaction terms to test. We find significant interaction terms in 6 of the 42 possible analyses. Fig. 1 illustrates three of these, and Figure S3, available on the journal's website at www.ehbonline.org shows the remaining three (see Table S6, available on the journal's website at www.ehbonline.org, for parameter estimates).

Despite no significant relationships between personality and fitness among women (Table 2), adding a personality*region interaction term produces four significant relationships among women. The greatest contrast is between women living near town and those in the forest. Among women near town, fertility increases with I and E, total number of surviving children increases with P, and AFR increases with N (Figs. 1 and S4; Table S6, available on the journal's website at www.ehbonline.org). Among women residing in the forest, each of these relationships is in the opposite direction: fertility is lower among women scoring higher in I and E; women scoring higher in P have fewer surviving offspring, and those scoring higher in N start reproducing earlier. Women living upstream along the Maniqui River largely show similar relationships between personality factors and fitness as women near town, whereas women living downstream in the protected reserve show a mix of the forest and near town patterns. However, the N–AFR relationship is the only regional difference that remains significant with a Bonferroni corrected p-value of 0.002.

Among men, the relationship between AFR and P and I varies by region. Near town and downriver, there is no relationship between personality and AFR. In the forest, men scoring higher in I and lower in P initiate reproduction earlier (Figs. 1 and S4; Table S6, available on the journal's website at www.ehbonline.org). Men living upriver show a mix of these two patterns.

3.7. Personality and activity budgets

To explore possible behavioral pathways by which personality may impact fitness, we examine the relationship between men's and women's personality traits and time spent in fitness-related activities. We test whether time spent working is positively associated with C and I, whether time spent in direct childcare is positively associated with C and negatively associated with E and O, and whether time
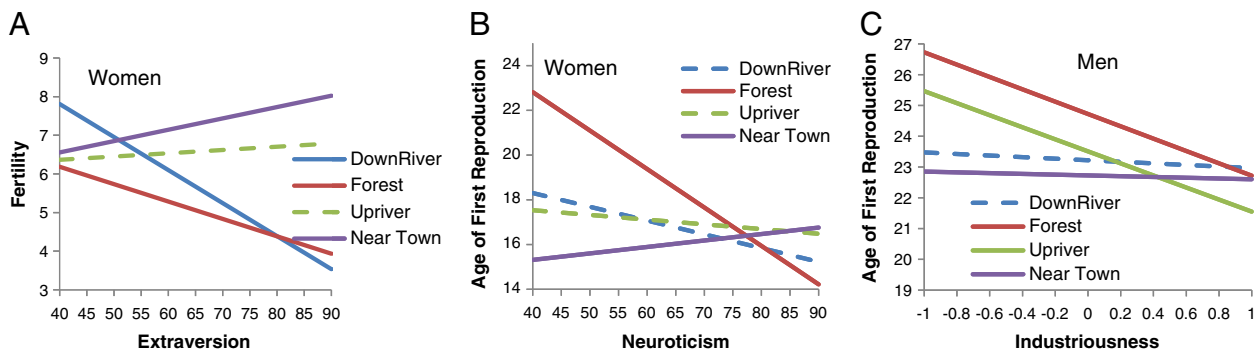
Fig. 1. The relationship between personality and fitness varies by region. (A) Extraversion and fertility among women; (B) Neuroticism and age at first reproduction among women; (C) Industriousness and age at first reproduction among men. All models control for age, Spanish fluency and schooling. Dashed lines refer to regions that were not significantly different from the baseline level (near town). Statistical models are given in Table S6, available on the journal's website at www.ehbonline.org, and additional relationships are graphed in Figure S3, available on the journal's website at www.ehbonline.org.

spent socializing is positively associated with E, A, O and P, and negatively with I.

We find partial support for these predictions, and most significant relationships are borne out only among men. Controlling for age, men with greater C and I spend significantly more time working (std. $\beta = 0.445$, $p = 0.002$; $\beta = 0.433$, $p = 0.008$; $n = 49$). Among women, only lower P is associated with work time ($\beta = -0.331$, $p = 0.037$) (same controls, $n = 41$). Controlling for age and number of surviving children, men with greater O spend less time in child care ($\beta = -0.301$, $p = 0.040$). Among women, greater A is associated with less time in childcare ($\beta = -0.267$, $p = 0.026$) (same controls). Controlling for age and village size, greater E, A, O and P are positively correlated with time spent socializing by men ($\beta = 0.247$, $p = 0.099$; $\beta = 0.335$, $p = 0.022$; $\beta = 0.273$, $p = 0.048$; $\beta = .317$, $p = .021$). Higher I is associated with less time socializing for men ($\beta = -0.342$. $p = 0.046$), but more time socializing for women ($\beta = 0.330$, $p = 0.048$).

3.8. Heritability of personality

Estimates of the additive genetic variance contributing to personality differences range from 0.08 for N to 0.60 for P, controlling for age, age^2, sex, age*sex, and village of residence ($n = 632$) (Table 5). These quasi-heritability estimates are only approximations of heritabilities since we do not control for any shared environmental effects.

4. Discussion

In a natural fertility context with rapid population growth, we find that greater E, C, O and I, and lower N, are associated with higher fertility and reproductive success among men. Fitness differences due to personality among men are realized through increased fertility rather than offspring survival. These differences persist when other potential confounds like age, schooling and Spanish fluency are controlled. Furthermore, only men lower in I had an earlier age at first birth, so earlier initiation of reproduction is not driving the relationship between men's personality and fitness.

Among men, personality traits were associated with more time spent working and socializing. Productivity is highly valued by potential mates and allies (Gurven, Kaplan, et al., 2009; Gurven, Winking et al., 2009), and greater access to resources should increase fertility and improve offspring survivorship. Socializing is an important venue for cementing allies and social partners, gaining valuable information, organizing collective labor, and obtaining potential mates. In a previous study, we found that Tsimane men who are visited more often, have more allies, and are more influential have more surviving offspring (von Rueden et al., 2011).

On the other hand, we find no global relationships between personality factors and fitness outcomes among women (cf. Alvergne

et al., 2010). The relationship between women's personality and fitness is only revealed when considering regional variation. The personality–fitness relationship for several personality factors differs among forest and near town regions. Living near town in close proximity to roads and schools can provide mating and market opportunities for individuals high in E, O and P. Few relationships between personality and time usage were found among women: lower P is associated with more time spent working, yet higher I is associated with time spent socializing. The latter result is unexpected, although women are commonly observed socializing while working, and exchange of social information may enhance productivity.

Our health measures were taken on average two years after personality assessment and so permit causal inference. While greater scores in multiple personality factors are positively associated with fitness in men, we find evidence of no substantial health cost subsequently. Instead, we only found that leukocyte and eosinophil counts were higher in men with greater I, and that men with greater E and O may be more prone to conflicts. Higher eosinophils suggest a higher level of parasitism, which in adults does not usually provoke serious morbidity or drastically inhibit work effort. While many conflicts are often verbal skirmishes, conflicts carry the possibility of escalating to physical fighting and injury, residential moves, or homicide in rare cases (often during drunken binges). Finally, intermediate levels of personality factors in men are not associated with optimal fitness outcomes. Our findings are based on a large sample using a valid and reliable survey instrument to assess the traditional Big Five and Tsimane-specific Big Two (Gurven et al., 2013).

4.1. Implications for evolutionary models of personality

The fitness effects documented here and elsewhere suggest that selective neutrality, or "mutation-drift equilibrium", is an unlikely candidate for explaining the maintenance of personality variation. Recent evolutionary approaches argue that stable differences in personality can be fitness maximizing if they operate as behavioral "reaction norms" (Denissen & Penke, 2008; Dingemanse et al., 2010). In this view, personality traits are motivational responses to specific stimuli that are programmed, over ontogeny, by individual variation in somatic condition, and socio-ecological experience (McElreath & Strimling, 2006; Wolf, Van Doorn, Leimar, & Weissing, 2007). Invoking such an approach, Denissen and Penke (2008) portray E as the reward value of social interactions, A as a disposition to react cooperatively or selfishly in resource conflicts, C as the tenacity to pursue goals despite potential distractions, O as the reward value of cognitive activity and N as sensitivity to signs of social exclusion. Similarly, our derived two-factor approach can be conceptualized as dispositions to be social and cooperative (Prosociality) and to obtain rewards from active pursuit of productive goals (Industriousness). Framed in this way, personality can be interpreted as alternative general strategies for handling a variety of recurrent adaptive problems, such as extracting resources from the physical and social environment, negotiating conflicts, forming alliances, obtaining and holding on to mates, and avoiding dangers.

While personality variation according to a reaction norm approach does not require genetic variation, we nonetheless find significant heritability in our personality measures. Quasi-heritability for E and P is high at 59% and 60%, respectively, while heritability for the other personality factors ranges from 8% to 27%. The heritability of personality traits in industrial populations is usually in the range of 40%–60% (Bouchard & Loehlin, 2001). While our quasi-heritability measures account for shared village residence, we do not control for aspects of home environment that may cause similarity among kin, such as shared experiences, social support, or material resources, thereby potentially altering our estimates of heritability if shared environment contributes to personality. Our quasi-heritability estimates should be interpreted with caution, although personality

Table 5
Quasi-heritability estimates (h^2) are result of quantitative genetic models conducted with Sequential Oligonucleotide Linkage Analysis Routines software (SOLAR). Models take as input pedigrees for individuals in our sample and include sex, age, age*age, age*sex, and village of residence as covariates.

Personality Factor	h^2	SE	p
Extraversion	0.594	0.100	***
Neuroticism	0.084	0.071	ns
Agreeableness	0.270	0.083	***
Conscientiousness	0.251	0.083	***
Openness	0.264	0.099	***
Prosociality	0.598	0.098	***
Industriousness	0.117	0.075	*

* $p < .05$.
*** $p < .001$.

studies based on adoption and twins design typically reveal small effects for shared environment (Bouchard & Loehlin, 2001).The comparatively low heritability estimates for A, C, N, O, and I suggest relatively greater effects of environment or gene–environment interactions. This is surprising given the political egalitarianism and limited range of social niches and productive opportunities in small-scale societies. However, the differential exposure of Tsimane individuals to schooling, healthcare, and the market economy, both within and across villages, presents a significant source of environmental variation. Prior to increased rates of market participation by the Tsimane in the twentieth century, we speculate that heritability estimates may have been higher.

Understanding the evolutionary basis of heritable personality variation remains one of the major outstanding questions in evolutionary biology (Mitchell-Olds, Willis, & Goldstein, 2007). One set of alternatives invokes balancing or fluctuating selection, where selection pressures can vary by sex, spatially, temporally or by condition. Selection pressures varied over time and space, and differently among male and female great tits, leading Dingemanse, Both, Drent, and Tinbergen (2004) to conclude that genetic variation in avian exploratory behavior was maintained through fluctuating selection. Some authors have argued that humans are adept at shaping their physical and social environments and that environmental heterogeneity is the most likely reason why fluctuating selection would maintain genetic variation in personality (Laland, Odling-Smee, & Feldman, 2001; Penke, Denissen, & Miller, 2007). Consistent with these views, we found that personality varied across Tsimane territory and that its relationship with fitness outcomes also differed by region, consistent with spatial heterogeneity in ongoing selection pressures. E, P, O and A were highest in larger villages close to town and lowest in small villages close to town (Fig. 1 and S3). A recent study by Jokela (2012) shows evidence of temporal variability in selection pressures, as higher C and O predicted lower fertility only among cohorts born after 1950. While we observe evidence of directional selection on men's personality, the effects of personality on women's reproductive success differ by region, with positive effects of E and I on fertility, and P on number of surviving children only among women living close to town; the opposite relationships were found among women living in more remote villages (Table S5; Figs. 1 and S3, available on the journal's website at www.ehbonline.org). One possibility for this pattern is greater female choice in sexual relationships in villages closer to town, whereas arranged marriages may be more common in more traditional villages (Gurven, Kaplan, et al., 2009; Gurven, Winking, et al., 2009). We have no longitudinal data on personality to test for temporal variability, but it is likely that the recent availability of novel types of wealth, schooling and wage labor (all largely restricted to men) has benefited more outgoing, adventurous, curious and risk-prone men with higher mating access (Stieglitz et al., 2012).

The sex differences in personality we identify may provide an additional source of fluctuating selection. Sex differences in personality have been identified almost everywhere they have been investigated. Sex differences in Tsimane personality, however, vary from those widely observed around the world. Across 55 nations and using the same BFI instrument to assess personality, women tend to score higher in E, A, C and N. While we also find that N is higher among women, we find that men score substantially higher in E, A, C, O, P and I (Table S4; Figure S1, available on the journal's website at www.ehbonline.org). While ethnographic evidence and observation of interview procedures suggest otherwise, it is possible that sex differences may be inflated due to differing self-reporting styles of men and women, especially when interviews are conducted by a male researcher. We do find that the sex differences reduce but remain robust to controls for literacy, Spanish fluency and years of schooling. Greater E and O are consistent with behavioral observations showing Tsimane men's greater travel to other villages and town, and overt

locution at village meetings. Greater P among men is consistent with higher pro-social behavior as revealed by economic games (Gurven, 2004). It has been argued that sex differences are amplified in developed societies where fewer constraints are believed to tether free expression of personality (Schmitt et al., 2008). However, we find that sex consistently has the largest effect in most models presented here. In populations with marked divisions of labor, and where entrepreneurial opportunities are limited to one sex, sex differences in personality might also be common. Consistent with our results, E, A and O are more likely to be higher among men than women in developing countries (Schmitt et al., 2008).

An alternative scenario to fluctuating selection focuses on the balance between accumulation of weakly deleterious mutations and selection against them, or mutation–selection balance; in this case, selection favors an optimal phenotype but does not weed out the accumulation of weak mutations (Penke et al., 2007). A recent study of Cloninger personality traits analyzed 250,000 SNPs on 8000 Australians and Finns, and found results consistent with mutation–selection balance (Verweij et al., 2012). Most of the genetic variation they encountered was due to rare variants and non-additive genetic effects. It is possible that several evolutionary processes can be operating simultaneously to produce the heritability in personality we find among the Tsimane: directional selection has yet to reach new phenotypic optima, the direction and strength of selection vary by geographic region and by sex, and mutation maintains variation around these local optima. A final possibility is that personality appears heritable because it is a facultative response (i.e. reaction norm) to genetic variation in condition-dependent traits (e.g. BMI) elsewhere in the phenotype. For example, genetic cues of future somatic condition trigger a reaction norm that optimally calibrates the level of extraversion (Lukaszewski & Roney, 2011).

4.2. Limitations

Our personality–fitness correlations were based on cross-sectional data or retrospective data (e.g. lifetime fertility), and so causal inference is difficult to assess without a longitudinal study design. However, the associations we find between E, N, O and fertility parallel previous findings in other populations (Alvergne et al., 2010; Jokela et al., 2011; Nettle, 2006). Personality is a relatively stable characteristic with most change established by adolescence (Caspi, Roberts, & Shiner, 2005; Roberts & DelVecchio, 2000). While life events can affect personality, and bidirectional effects may exist between child rearing and personality, having children seems to show minimal effects on personality (Specht, Egloff, & Schmukle, 2011), or instead appears only to strengthen existing dispositions rather than alter personality in a substantial way. Ongoing data collection on Tsimane marriage, fertility and child survivorship will permit longitudinal follow-up in several years to test whether causal inference is warranted.

Another limitation is that we were unable to examine effects of personality on adult survivorship, and so cost measures are confined to health and conflicts, and fitness measures are restricted to reproductive outcomes. Another limitation is that due to cultural feasibility, data on EPCs and conflicts were collected among men, but not among women. Nettle suggests that mortality might be higher among men with higher E and O (Nettle, 2006), and other studies have related lower C (Martin, Friedman, & Schwartz, 2007) and both lower and higher N to greater mortality (Friedman, Kern, & Reynolds, 2010). If there were strong relationships between E, O, C or N and mortality we would expect lower levels of these factors at later adult ages due to mortality selection. However, we did not observe late life declines in E, O or N (Figure S1; Table S3, available on the journal's website at www.ehbonline.org). In fact, the strongest age-related declines were found for C and I, while N and P saw slight increases in later adulthood. Although personality traits have been shown to

be relatively stable and consistent over the life course, they also show systematic shifts with age and life stage (Roberts, Walton, & Viechtbauer, 2006). Among Tsimane, I and C peak in middle age at the same time that caloric production also peaks, while I, C and caloric production decline thereafter (Gurven, Kaplan, et al., 2009; Gurven, Winking, et al., 2009). Prosociality is highest among young men, during the period when men are establishing reputations in their communities and extended networks. It also increases at late ages among post-reproductive aged women who may be actively helping their adult children and grandchildren. Such shifts might reflect general motivational changes due to the variable adaptive problems commonly faced by men and women during different life stages.

5. Conclusion

The evolutionary fitness consequences of human personality variation have been difficult to assess because of the main focus on modern societies with controlled fertility (Alvergne et al., 2010; Gurven et al., 2013). Yet even in modern societies, personality predicts income, occupation, reproduction, marital stability and other fitness-relevant outcomes in both sexes (Ozer & Benet-Martinez, 2006). Personality has equally strong effects as cognitive ability and socioeconomic status in predicting mortality, divorce and occupation (Roberts, Kuncel, Shiner, Caspi, & Goldberg, 2007). Here we showed that personality varies within and among sexes, that variation carries fitness consequences under natural fertility conditions, and that those consequences may vary locally and between men and women. We also showed evidence for how personality might impact fitness through several behavioral pathways. Ongoing changes in Tsimane socioeconomic environment will likely provide additional opportunities for personality variation to impact life trajectories and outcomes.

Supplementary Materials

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.evolhumbehav.2013.09.002.

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