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Original Article

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

Michael Gurven [a,c,*], Christopher von Rueden [a,c], Jonathan Stieglitz [b,c], Hillard Kaplan [b,c], Daniel Eid Rodriguez [c]

[a] Integrative Anthropological Sciences Unit, Department of Anthropology, University of California, Santa Barbara, CA 93106
[b] Department of Anthropology, University of New Mexico, Albuquerque, NM 87311
[c] Tsimane Health and Life History Project, San Borja, Beni, Bolivia

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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.



## 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

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* Corresponding author.
*E-mail address:* gurven@anth.ucsb.edu (M. Gurven).

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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