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Original Article

Adaptive personality calibration in a human society: effects of embodied capital on prosocial traits

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Evolutionary theories of personality origins have stimulated much empirical research in recent years, but pertinent data from small-scale human societies have been in short supply. We investigate adaptively patterned personality variation among Tsimane' forager-horticulturalists. Based on a consideration of cost-benefit tradeoffs that likely maintain variation in human prosociality, we hypothesize that individual differences in prosocial personality traits are facultatively calibrated to variation in "embodied capital"—that is, knowledge, skills, or somatic traits that increase expected future fitness. In support of this hypothesis, 2 components of embodied capital—physical strength and formal education—associated positively with Tsimane' prosocial leadership orientation (PLO), a broad personality dimension representing gregarious cooperation, interpersonal warmth, and pursuit of leadership. Moreover, using pedigrees to compute heritability estimates, strength and education had additive effects on the heritable variance in PLO, which suggests that prosocial traits may be "reactively heritable" by virtue of their calibration to condition-dependent components of embodied capital. Although alternative explanations must be falsified in future research, our findings 1) provide one of the first demonstrations of adaptively patterned personality variation in a small-scale society and 2) illustrate the potential power of an adaptationist approach to elucidate the causal underpinnings of heritable personality variation.

Key words: **cooperation; embodied capital; leadership; personality; prosociality; reactive heritability.**

INTRODUCTION

Personality variation refers to individual differences in behavioral phenotypes that are relatively stable over time and across situations (Sih et al. 2004; Penke et al. 2007; John et al. 2008). Such individual differences—also referred to as behavioral syndromes (Sih et al. 2004)—are ubiquitous within social species and predictive of fitness-related outcomes (Nettle 2005; Roberts et al. 2007; Gurven et al. 2014), including reproductive success (Smith and Blumstein 2008; Alvergne et al. 2010; Jokela 2012; Bailey et al. 2013; Berg et al. 2014; Gurven et al. 2014). Recent years have seen a surge of interest among evolutionary behavioral scientists in explaining the ultimate and proximate origins of personality variation in multiple species (Sih et al. 2004; Wolf et al. 2007; Smith and Blumstein 2008; Dingemanse et al. 2010), including humans (Nettle 2006; Alvergne et al. 2010; Buss and Hawley 2011; Del Giudice et al. 2011; Lukaszewski and Roney 2011; Jokela 2012; Verweij et al. 2012; Bailey et al. 2013; Lukaszewski 2013; Berg et al. 2014; Gurven et al. 2014).

Evolutionary theories of adaptive personality variation, although heterogeneous in emphasis, tend to argue that natural selection will maintain personality differences within or between populations when a behavioral phenotype is subject to fluctuating or frequency-dependent selection regimes—wherein the costs and benefits of different trait levels vary depending on individual circumstance (Sih et al. 2004; Nettle 2006; Penke et al. 2007; Dingemanse et al. 2010). For example, different levels along a personality continuum may be optimal for individuals in different socioecologies (Sih et al. 2004; Dingemanse et al. 2010; Penke 2011) or who differ in somatic condition or "state" (Luttbeg and Sih 2010; Lukaszewski 2013). A first-order prediction from this theoretical perspective is that individuals' personality traits will often be coupled to the circumstances under which their personality trait levels were ancestrally most adaptive.

To date, most empirical research that has applied this perspective to elucidate adaptively patterned personality variation in humans has done so using subjects from Western, postindustrial societies

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with low fertility and formal legal institutions (e.g., Simpson et al. 1999; Pound et al. 2007; Sell et al. 2009; Jonason et al. 2010; Campiero Ciani 2011; Holtzman et al. 2011; Lukaszewski and Roney 2011; Lukaszewski 2013). Although such research can inform evolutionary theories of personality, it is limited in that modern societies differ in important respects from the small-scale, natural fertility societies in which humans have spent most of our existence (Henrich et al. 2010; Gurven et al. 2013a). In moving forward, therefore, it is important to test functional theories of personality origins using human subjects whose behaviors are evoked within the socioecological contexts of small-scale societies (Alvergne et al. 2010; Bailey et al. 2013; Gurven et al. 2014).

The current research investigates adaptively patterned personality variation among the Tsimane', a group of forager-horticulturalists indigenous to the Bolivian Amazon. Based on a consideration of cost-benefit tradeoffs that have likely maintained variation in aspects of prosociality over human evolution, we advance the hypothesis that individual differences in prosocial traits are facultatively calibrated (i.e., conditionally adjusted over ontogeny) to variation in "embodied capital"—that is, skills, abilities, or somatic traits that enhance an individual's expected future fitness (Kaplan 1996). This hypothesis is similar to state-dependent personality models, which consider how body size (McElreath and Strimling 2006), reproductive value (Wolf et al. 2007), productivity (Biro and Stamps 2008) and other aspects of phenotype can regulate personality. To evaluate our hypothesis empirically, we test whether prosocial traits (related to leadership and gregarious cooperation) are positively associated with 2 important components of embodied capital among the Tsimane': physical strength and locally valued knowledge.

Facultative calibration of prosocial traits to variation in embodied capital

Much research on human cooperation—behaviors that incur personal costs to deliver fitness benefits to others—has focused on characterizing the mechanisms that sustain dyadic exchange, collective action, and leader-follower dynamics. Theory and evidence suggest that these mechanisms evolved because of gains in trade that accrue over time via cooperative behavior. In dyadic exchange, Person A's delivery of benefits (e.g., food items) to Person B occurs within an implicit social contract that specifies a reciprocal obligation—which 1) produces gains in trade, and 2) serves for both individuals as a form of social insurance against occasional bouts of injury, illness, or bad luck in foraging (Sugiyama and Scalise-Sugiyama 2003; Gurven 2006; Cosmides et al. 2011). In collective action, multiple individuals pay the cost of contributing to a group project and share in the resulting benefit (Price et al. 2002; Delton et al. 2012). Leadership (and followership) occurs when some individuals pay more of the costs of implementing collectively generated goals and policies within a social group and receive in return respect, deference, or a greater share of the spoils (Hooper et al. 2010; Price and Van Vugt 2014; von Rueden et al. 2014). Humans show a degree of cooperation in these domains that is unique among primates, including a tendency to seek and act on opportunities for mutual benefit (Tomasello et al. 2005; Jaeggi and Gurven 2013).

These considerations suggest that different levels of cooperativeness across individual humans are a function of circumstances that modulate the costs and benefits of cooperation (Denissen and Penke 2008; Nettle et al. 2014)—which in turn helps explain the evolutionary maintenance of individual differences in cooperativeness within (Kurzban and Houser 2005) and between human populations (Henrich et al. 2001; Schmitt et al. 2007). For example, over human evolution, there may have been regularities in the phenotypic characteristics possessed by individuals who were likely to cost-efficiently obtain the potential benefits of *n*-person cooperation and to actively pursue leadership positions (von Rueden et al. 2008; Lukaszewski 2013; von Rueden 2014; von Rueden et al. 2014). As a result, natural selection would have favored facultative adaptations that calibrate levels of cooperativeness to variations in such characteristics over ontogeny (Lukaszewski and Roney 2011; Lukaszewski 2013). The stability of cooperation may itself depend on consistent individual variation in degree and kind of cooperative behavior (Bergmuller et al. 2010; McNamara and Leimar 2010). For example, leader-follower relationships can be critical to cooperation in groups (Hooper et al. 2010; Price and Van Vugt 2014; von Rueden et al. 2014).

Based on this logic, we propose that personality traits related to gregarious cooperation and the pursuit of leadership are facultatively calibrated to individuals' levels of "embodied capital" relative to others in their local community. In Embodied Capital Theory (Kaplan 1996; Kaplan et al. 2009), the allocation of effort toward the growth and maintenance of phenotypic traits is conceptualized as investment in future reproduction, undertaken at a cost to current reproduction (Kaplan et al. 2009). The cumulative result of such future-oriented investments over time is the cultivation of capital that is embodied in the soma—skills, abilities, or other traits that increase expected fitness through greater resource accrual, mate value, fertility, or survivorship (Kaplan et al. 2009). Embodied capital is the evolutionary analogue of human capital in economics, replacing income generation with fitness maximization.

Investment in future reproduction often occurs through components of embodied capital that increase an individual's ability to generate benefits for others as a social exchange partner, coalition member, or leader (von Rueden et al. 2008; Kaplan et al. 2009; von Rueden et al. 2014). For example, individuals who have invested in the development of greater physical strength will be better able to extract resources from the physical and social world (Hess et al. 2010; Sell et al. 2012), provide protection against predators or hostile conspecifics (Coy et al. 2014), or cost-effectively administer punishment of others who violate norms (von Rueden and Gurven 2012; Price and Van Vugt 2014; von Rueden et al. 2014). Similarly, individuals who have invested in the acquisition of locally valuable knowledge (e.g., languages or customs of neighboring trading partners) or skill sets (e.g., hunting) can generate a variety of benefits for others that correspond to the abilities they possess (Sugiyama and Scalise-Sugiyama 2003; Gurven and von Rueden 2006; Kaplan et al. 2009).

Supporting the hypothesis that these components of embodied capital enhance one's social value to others, research indicates that physically stronger individuals are preferred as friends, mates, and allies (von Rueden et al. 2008; Lukaszewski 2013; Coy et al. 2014), have larger social support networks (von Rueden et al. 2008; Lukaszewski 2013), have reputations as superlative hunters (Apicella 2014), and attain greater community-wide status and influence (von Rueden et al. 2008; Re et al. 2013; von Rueden et al. 2014). Possession of useful knowledge and skill is likewise an influential determinant of social partner value (Sugiyama and Scalise-Sugiyama 2003; Cottrell et al. 2007; von Rueden et al. 2008; Apicella 2014), and is seen as an indispensable characteristic of high-quality leaders (Anderson and Kilduff 2009; Price and Van Vugt 2014; von Rueden et al. 2014). In sum, others see individuals

who are physically strong or knowledgeable as valuable social partners, and as good candidates for positions of leadership.

Individuals with more embodied capital are also more capable of inflicting costs on others, and they are more likely to respond with anger when things do not go their way (Hess et al. 2010; Sell et al. 2012). However, benefit conferral and cost infliction are tactics that may be used in parallel, within, and across contexts. Furthermore, individuals whose embodied capital principally motivates antisocial behavior risk loss of social support that can be critical to reproductive success (von Rueden et al. 2011; Gurven et al. 2012). In small-scale societies, domineering leaders are punished, ostracized, or even executed (Boehm 2001), whereas generosity is typically requisite for acquiring and maintaining social status (von Rueden 2014; von Rueden et al. 2014).

Our hypothesis is that people with greater embodied capital will be relatively likely to capture net benefits through prosocial behavioral strategies—especially when such strategies involve maintaining large social networks and pursuing leadership positions. This is because physically stronger or knowledgeable individuals will more readily succeed in attracting new social partners, in generating resources in the service of existing relationships, and in attaining high status (Cottrell et al. 2007; von Rueden et al. 2008; Anderson and Kilduff 2009; Lukaszewski and Roney 2011; Re et al. 2013; Apicella 2014; von Rueden et al. 2014). Moreover, such individuals may be less likely to experience the potential costs of prosocial strategies, such as exploitation by self-interested exchange partners (Sell et al. 2012), opportunity costs of unsuccessful status pursuit (Anderson and Kilduff 2009), or conflict arising as blowback in response to leadership decisions (von Rueden and Gurven 2012). If so, it follows that natural selection would have favored facultative adaptations that calibrate levels of prosocial personality traits to manifest levels of embodied capital.

The current study: embodied capital and prosocial traits among the Tsimane'

The Tsimane' are semisedentary forager-horticulturalists indigenous to the Bolivian Amazon. They are dispersed among approximately 95 villages, which range in size from 30 to 700 individuals. The Tsimane' cultivate plantains, rice, corn, and sweet manioc in small swiddens, and regularly fish and hunt for meat. Only in the late twentieth century where Tsimane' villages given formal geographic boundaries; the extended family, not the community, remains the central unit of social organization. Food sharing and productive activities are mostly confined to extended families. On the other hand, unrelated community members will regularly visit each other to socialize and drink *shocdye*' (chicha), an alcoholic beverage fermented from manioc. Villagers hold occasional meetings, which are used to plan collective activities, such as clearing of community trails or responding to incursion by illegal loggers. Village meetings are also used to mediate conflicts that were unresolved by the parties directly involved. Although certain men tend to wield more informal influence during meetings, no individual or group within a village maintains coercive authority over others. This includes the village *corregidor* (literally, "corrector"). In the late twentieth century, missionaries helped establish the election of *corregidores*, to represent community interests to outside political bodies and to facilitate community meetings.

Gurven et al. (2013) investigated the structure of personality variation in this small-scale society, and found that Tsimane' personality is best described by 2 broad dimensions. Notably, these dimensions—the "Tsimane' Big Two"—contain a mixture of behavioral content from each of the factor scales from the Big Five Inventory (BFI), which was designed to measure the 5 nearly orthogonal trait dimensions often found in post-industrial societies (Benet-Martinez and John 1998; John et al. 2008): Extraversion (E), Agreeableness (A), Conscientiousness (C), Neuroticism (N), and Openness to Experience (O).

The first Tsimane'-specific personality dimension, labeled Prosocial Leadership Orientation (PLO), represents a combination of high E (example BFI items: "Assertive," "Outgoing"), high A ("Cooperative," "Trusting"), high O ("Ingenious," "Original"), and low N ("Depressed," "Blue"). In terms of behavioral content, this means that individuals high in PLO tend to seek social attention and status, socialize gregariously, exhibit interpersonal warmth, offer innovative solutions to problems, and maintain an emotionally stable orientation when facing social threats (Gurven et al. 2013a). The second Tsimane' dimension, labeled Industriousness (I), primarily represents high C ("Reliable worker," "Thorough"), as well as limited aspects of high E ("Energetic"), O ("Inventive"), and A ("Helpful, unselfish"). Individuals high in I tend to work diligently (alone or with others), meet goals, and honor local norms (Gurven et al. 2013a).

Predictions regarding associations of embodied capital with Tsimane' personality

The arguments advanced above predict that components of embodied capital—physical strength and possession of locally valued knowledge—will exhibit positive associations with levels of PLO.

We further predict that physical strength will correlate with levels of PLO only among men. Physical contests have ancestrally been, and continue to be, more important regulators of reproductive competition among men than women (Puts 2010; Plavcan 2012; Sell et al. 2012; Benenson 2013; Campbell 2013). Men are more likely to use physical aggression against rivals (Archer 2004; Hess et al. 2010; Benenson 2013; Campbell 2013), and physically stronger men are more likely than weaker men to experience success in social conflict and to be desired as a coalition partner (von Rueden et al. 2008; Sell et al. 2009). Greater strength may also enhance one's desirability as a social partner due to a greater ability to generate resources via physical work. Within traditional societies, men tend to specialize in aspects of food production that reward substantial strength, such as bow hunting (Gurven and von Rueden 2006; Apicella 2014). However, it seems likely that certain subsistence tasks in which women participate (e.g., horticultural production) would also be facilitated by greater physical strength. Evidence from college students indicates that strength positively predicts aspects of prosociality (e.g., extraversion) among men but not women (Lukaszewski and Roney 2011; Lukaszewski 2013), but this pattern may not hold in societies like the Tsimane' where women participate significantly in manual labor (Hess et al. 2010; Gurven et al. 2013b). Nonetheless, we tentatively predict that PLO will associate with strength among Tsimane' men more than among Tsimane' women. To test this prediction, we obtained direct measurements of physical strength from a large sample of men and women for whom we also had personality measurements.

Prediction 1: men's physical strength will associate positively with levels of PLO. There will be a significantly weaker association among women

To assess subjects' possession of locally valued knowledge, we used previously collected data regarding their attainment of formal

education. Elementary public education has been sporadically available to the Tsimane' since the 1970s, and focuses on helping students obtain basic literacy and other skills that can help Tsimane' obtain wages—primarily through engagement in commerce within the Spanish-speaking cities and towns nearby (Reyes-Garcia et al. 2007). Several secondary schools now exist in larger villages, and young Tsimane' adults are starting to become high school graduates. Approximately 45% of adults have had at least 1 year of education. However, the overall adult literacy rate remains low, at 25%. Because individuals with formal education have the ability to generate monetary wealth and interface with the market economy, the attainment of formal education is seen as a valuable characteristic and is associated with a variety of positive social outcomes including income and political influence (Reyes-Garcia et al. 2007; von Rueden et al. 2008). Because of this, within the current Tsimane' social context, the attainment of formal education provides locally valued knowledge that should lower the cost-benefit ratio of a highly prosocial behavioral strategy among members of both sexes. Additionally, because formal schooling is a social activity, it is conceivable that Tsimane' higher in prosocial traits are therefore more likely to seek out or remain in school. These lines of reasoning are not mutually exclusive, and they converge on the same empirical prediction.

Prediction 2: attainment of formal education will associate positively with levels of PLO

We also predict that levels of I will be positively associated with attainment of formal education. As described above, the Tsimane' I dimension overlaps substantially with the Big Five's C dimension—both of which capture the tendency to work diligently and meet goals. Given this phenotypic description, it is perhaps unsurprising that C has often been found to positively predict academic success in modern industrialized populations (Noftle and Robins 2007). Accordingly, Tsimane' individuals who are high in I would presumably be more likely to attend school, work hard, receive positive feedback from teachers, and therefore stay longer in formal schooling than individuals lower in I.

Prediction 3: levels of I will associate positively with attainment of formal education

Predictions regarding contributions of embodied capital to the heritability of Tsimane' personality

The hypothesis that levels of PLO are facultatively calibrated to embodied capital also has implications for explaining the substantial heritability of personality variation (Turkheimer 2000). The specific causal basis of heritable variation in personality and behavior in general has gone largely unaccounted for in the genomic era (Johnson et al. 2011; Verweij et al. 2012). Because physical strength is itself a heritable characteristic (Silventoinen et al. 2008), any personality trait that is facultatively calibrated to strength will also exhibit heritability—even if 1) there are no genetic polymorphisms with reliable effects on the neural substrates of personality, and 2) the facultative mechanisms that calibrate personality to strength have a species-typical, universal genomic basis (Lukaszewski 2013). Although this phenomenon—referred to as "reactive heritability"—has long been recognized by theorists as a viable partial explanation for the heritability of personality (Tooby and Cosmides 1990; Buss 2009; Lukaszewski and Roney 2011), it has not yet been empirically tested. We used Tsimane' pedigree data (Gurven et al. 2014) to estimate heritability for physical strength as well as the focal personality traits. This allowed us to test a core prediction generated by the reactive heritability hypothesis as applied to physical strength.

Prediction 4: the estimated heritability of men's PLO will be reduced when controlling for physical strength

The reactive heritability hypothesis could also apply to the attainment of formal education. This is because intelligence, like strength, is highly heritable (Turkheimer 2000). Individuals with greater intelligence may be more likely than less intelligent individuals to seek out and be selected for specific educational opportunities (Johnson et al. 2011; Plomin et al. 2012). If a similar pattern holds among the Tsimane', then individuals with greater heritable intelligence may thereby seek out, or be encouraged by adults to obtain, more education. Under this scenario, the calibration of prosocial traits to the attainment of formal education could ultimately reflect, at least in part, heritable aspects of intelligence and ability.

Prediction 5: the estimated heritability of PLO will be reduced when controlling for attainment of formal education

Additionally, if high I is a determinant of persistence and success in school, as suggested by Prediction 3, then heritable individual differences in I would also lead to heritable variance in educational attainment.

Prediction 6: the estimated heritability of educational attainment will be reduced when controlling for I

For all predictions, we expected that the same patterns would obtain when controlling for potentially relevant confounding variables (age, village of origin, and, when applicable, sex). In addition, although our predictions apply to the Tsimane' Big Two dimensions, we also present all results in relation to the standard Big Five trait dimensions in order to facilitate comparisons with data from modern societies for whom the Five Factor Model is descriptively accurate.

METHODS

Personality instrument

The 43-item Tsimane' BFI was administered to 632 adults from 28 villages from January 2009 to December 2010, as part of the Tsimane' Health and Life History Project (THLHP: http://www.unm.edu/~tsimane). Average age of participants is 47 ± 14 year (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. (2013a). The least internally consistent item was removed from each of the 5 personality dimensions (E, C, A, O, N), which were then scored according to standard protocol (Benet-Martinez and John 1998). The Tsimane'-specific "Big Two" (PLO, I) was derived from exploratory factor analysis and validated against a separate sample

of spouse-derived ratings, as described in Gurven et al. (2013a). For factor, internal reliability and interfactor correlations see Tables S1 and S2 in Gurven et al. (2013a).

Other measures

The age, village of residence, and years of formal education of all participants were ascertained from demographic interviews initially conducted in 2002 and updated annually thereafter (Gurven et al. 2007). A pedigree file that specifies subjects' parents and grandparents was generated based on reproductive histories and kinship interviews. Contemporaneous with the personality interviews, clinicians employed by the THLHP measured shoulder and chest strength with a Lafayette Manual Muscle Tester, and grip strength was measured with a Smedley III dynamometer; we sum these values to create a composite upper-body strength measure. Missing education and strength observations reduced our sample size from 632 to 622.

Data analysis

Using linear regression, we model the effects of upper-body strength and education on personality, for the sexes combined and for men and women separately. Due to zero-inflated skew, we dichotomized the education variable into no education (0) and any education (1) prior to analysis. We assess the contribution of strength and education to the heritability of personality using a variance components model with the software Sequential Oligonucleotide Linkage Analysis Routines (SOLAR) (Almasy and Blangero 1998). The model takes as input pedigrees for the 622 individuals in our sample. During heritability (h^2) estimation, insignificant ($P \geq 0.1$) covariates were screened out to minimize convergence errors. Although we control for village, our heritability estimates are not based on an adoption or twin study, and so do not completely control for shared environment. We therefore label our estimates "quasi"-heritability. Also, relationships in the pedigree file were not evaluated based on molecular markers, so the quasi-heritability estimates will be affected by any nonpaternity. We do not expect this to be a significant problem, given the validity checks within our demography interview protocol and the relative stability of Tsimane pair-bonds. All models control for age, sex, and village affiliation. Models also include an age^2 term due to the curvilinear effects of age on personality among the Tsimane' (Gurven et al. 2014).

RESULTS

In support of Prediction 1, physical strength was positively correlated with PLO, both in bivariate relationship ($r = 0.306$, $P < 0.001$) and after controlling for age, age^2, sex, education, and village of residence (Table 1, column 1). In the multivariate model, neither of the age terms significantly predicted PLO, and the effect of sex was small ($\beta = 0.097$, $P = 0.045$). Standardized effect sizes for village of residence dummy variables ranged from −0.139 ($P < 0.000$) to 0.094 ($P = 0.010$). In relation to the Big Five traits, which overlap with PLO and I, strength was positively associated with E, C, and O. (Table 1, column 1). Counter to Prediction 1, the effect of strength on PLO was similar in magnitude for women and men (Table 1, columns 2 and 3). Sex by strength interactions was insignificant for all personality dimensions (β's < 0.045, P's > 0.250), indicating that the associations of strength with personality traits were not significantly different across the sexes (Figure 1).

In support of Prediction 2, attainment of formal education positively associated with PLO, both in bivariate relationship ($r = 0.303$, $P < 0.001$) and after controlling for age, age^2, sex, strength, and

Table 1

Standardized effects of physical strength on personality, for (1) full sample, (2) women only, and (3) men only

Personality dimension	(1) Full sample	(2) Women	(3) Men
PLO	0.217***	0.160*	0.186**
Industriousness (I)	0.029	−0.002	0.036
Extraversion (E)	0.184**	0.142	0.163*
Agreeableness (A)	0.110	0.099	0.072
Conscientiousness (C)	0.180**	0.127	0.157*
Neuroticism (N)	−0.030	0.002	−0.055
Openness (O)	0.164**	0.051	0.218**
N	622	301	321

*$P < 0.05$ **$P < 0.01$ ***$P < 0.001$.
All models control for age, age^2, education, and village of residence, and (1) also controls for sex.

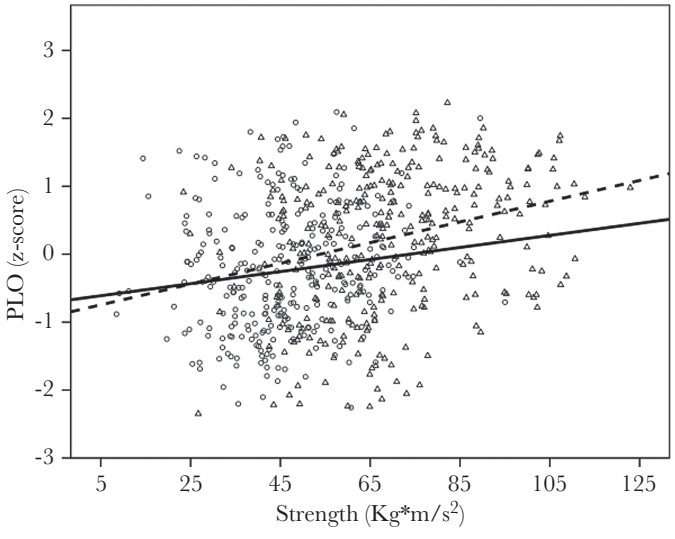

Figure 1
Linear regression of PLO on strength, for women ($n = 301$, solid line) and men ($n = 321$, dashed line).

village of residence (Table 2, column 1). Tsimane' with any education have greater PLO than average and those lacking education have lower PLO than average (Figure 2). In relation to the Big Five traits, education was positively associated with E, A, C, and O. Sex by education interactions was insignificant when added to the models (β's < 0.055, P's > 0.145), indicating that the associations of education with personality traits were not significantly different in magnitude between the sexes (Table 2, columns 2 and 3). Although the effects of education on personality were independent of strength, education, and strength are positively correlated, controlling for age and age^2 (r = 0.207, P < 0.001).

Prediction 3 was not supported. There was no evidence that I associated with educational attainment, whether in men or in women (Table 2).

As previously established (Gurven et al. 2014), heritability estimates indicated that additive genetic effects accounted for approximately 60% of the variance in PLO and 12% of the variance in I (Table 3, column 1). The quasi-heritabilities for strength and education were 0.364 (SE = 0.083) and 0.636 (SE = 0.130), respectively, controlling for age, age^2, and sex, and village of residence. Dummy variables for village of residence were insignificant in the quantitative genetic models of PLO and strength and explained none of the estimated heritability of these traits. Effects of village of residence on the estimated heritability of I and education were not calculable. Model convergence failure prevented inclusion of village dummy variables in the quantitative genetic models of I, and a quantitative genetic model of education that lacked village dummy variables yielded a quasi-heritability of 0.911 (SE = 0.099), indicative of estimation problems. In general, SOLAR software is more susceptible to erroneously inflated heritability estimates with discrete models (Blangero et al. 2014).

In support of Prediction 4, physical strength explained 15% of the heritable variance in PLO (Table 3, column 2). In support of Prediction 5, education explained 22% of the heritable variance in PLO (Table 3, column 3). Furthermore, despite the correlation between strength and education reported above, their combined effect on heritable variation in PLO was mostly additive. When included in the same model, each of these components of embodied capital was significant (P < 0.001) and together explained 31% of the heritable variance in PLO. Controlling for strength and education lowered the h^2 estimate for PLO from 0.60 to 0.41, which is at the lower extreme of the 95% confidence interval (CI) for the original 0.60 estimate (95% CI: 0.41–0.79).

Given that education was not associated with I, it is unsurprising that Prediction 6 was not supported: Education did not explain any of the additive genetic variance associated with I (Table 3, column 3).

Table 2

Standardized effects of education on personality, for (1) full sample, (2) women only, and (3) men only

Personality dimension	(1) Full sample	(2) Women	(3) Men
PLO	0.222***	0.174*	0.259***
Industriousness (I)	−0.039	−0.008	−0.071
Extraversion (E)	0.248***	0.223**	0.303***
Agreeableness (A)	0.154**	0.164*	0.153*
Conscientiousness (C)	0.094*	0.129	0.086
Neuroticism (N)	−0.074	−0.067	−0.089
Openness (O)	0.245***	0.278***	0.269***
N	622	301	321

*P < 0.05 **P < 0.01 ***P < 0.001.

All models control for age, age^2, strength, and village of residence. Models in column (1) also control for sex.

DISCUSSION

Results supported 4 of 6 predictions regarding adaptively patterned phenotypic and quasi-genetic correlations of embodied capital with personality traits among the Tsimane'. Consistent with the hypothesis that prosocial traits are facultatively calibrated to components of embodied capital, physical strength, and attainment of formal education exhibited independent positive associations with levels of PLO—a broad personality dimension that captures individual differences in cooperativeness, sociability, emotional stability, and the pursuit of leadership (Gurven et al. 2013a). However, counter to our expectation that the correlation between strength and PLO would be significantly stronger for men, this effect was

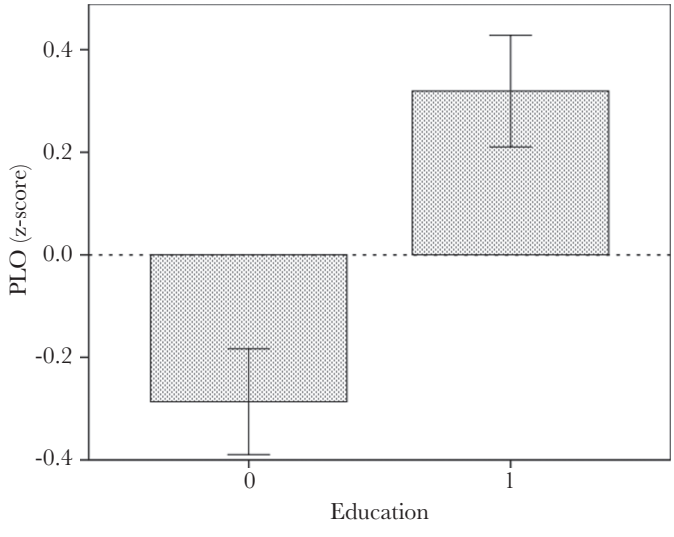

Figure 2

PLO of Tsimane' without (0; n = 334) and with education (1; n = 288). Error bars are 95% CIs.

Table 3

Quasi-heritability (H^2) estimates for personality dimensions

Personality dimension	(1)	(2) w/strength control	(3) w/education control	(4) w/strength and education controls
PLO	0.597 (0.097)	0.506 (0.099)	0.463 (0.104)	0.414 (0.101)
Industriousness (I)	0.119 (0.076)	0.124 (0.077)	0.119 (0.076)	0.124 (0.077)
Extraversion (E)	0.626 (0.103)	0.584 (0.105)	0.496 (0.110)	0.483 (0.107)
Agreeableness (A)	0.270 (0.083)	0.254 (0.081)	0.188 (0.079)	0.193 (0.079)
Conscientiousness (C)	0.249 (0.084)	0.228 (0.083)	0.187 (0.082)	0.185 (0.081)
Neuroticism (N)	0.084 (0.072)	0.084 (0.072)	0.058 (0.071)	0.054 (0.071)
Openness (O)	0.303 (0.100)	0.253 (0.095)	0.224 (0.091)	0.213 (0.087)
N	622	622	622	622

Standard errors are in parentheses. Models control for age, age^2, sex, and village of residence (except for models of Industriousness, which omit village dummy variables due to convergence failure with their inclusion). Models in column (2) also control for strength, models in column (3) also control for education, and models in column (4) also control for strength and education.

very similar in magnitude between the sexes. Additionally, in support of the hypothesis that PLO is reactively heritable in relation to embodied capital, strength and education together explained 31% of the quasi-heritable variance in PLO. Finally, inconsistent with the notion that hard-working, industrious Tsimane' might be more likely to seek or achieve education, there was neither a phenotypic nor a genetic correlation between levels of educational attainment and I.

We also presented parallel analyses in relation to the "Big Five" personality dimensions often found within complex postindustrial societies (Schmitt et al. 2007; John et al. 2008). Given that the item content of the Big Five traits overlaps heavily with the Tsimane' Big Two, it is unsurprising that results were broadly consistent with the findings summarized in relation to PLO and I. Physical strength positively associated with E, C, and O; and attainment of formal education positively associated with E, A, C, and O. Neither strength nor education was correlated with N. Because some N items load (negatively) onto the PLO dimension, this suggests that some but not all components of N are associated with embodied capital among the Tsimane'. Similarly, although certain items from A are part of PLO, physical strength was not associated with the A dimension.

It is noteworthy that both components of embodied capital were positively correlated with C, despite the fact that I (which contains many C items) did not, as expected, associate with education. C is typically correlated with educational attainment in modern environments (Noftle and Robins 2007), so it is not clear why Tsimane' I did not exhibit the same pattern. One likely possibility is that the I dimension may capture the tendency to engage diligently and persistently in traditional subsistence work (Gurven et al. 2013a), rather than to seek out and excel in formal schooling (which could be better captured by aspects of C not represented in I). Future research investigating the determinants of enrollment and success in formal schooling among the Tsimane' will be critical in interpreting these discrepancies.

In sum, although there were a few discrepancies between the findings in relation to the Tsimane'-specific Big Two and standard Big Five dimensions, respectively, both sets of results converge on the conclusion that components of embodied capital associate positively with prosocial aspects of personality. As noted above, results were presented in relation to the Big Five traits primarily to facilitate comparison with data from industrialized societies for whom the 5 factor model is descriptively accurate. Because the Big Two factor structure is a better descriptor of Tsimane' personality than the Big Five (Gurven et al. 2013a), we focus on interpreting the theoretical significance of our findings in relation to these dimensions, PLO and I.

Physical strength as a calibrator of prosocial traits

Our main hypothesis posited that levels of PLO are facultatively calibrated in response to components of embodied capital. Of course, the correlational data presented here do not conclusively establish this causality. However, when it comes to the observed association of physical strength and PLO, it is unlikely that the causality runs in the other direction (such that a higher level of PLO leads to greater strength). This is because the Tsimane' do not engage in any purposeful strength-building activities (i.e., weightlifting or other recreational exercise). One could speculate that individuals who are dispositionally inclined to engage in more intensive horticultural activities, etc., would thereby gain physical strength. But this hypothesis would most straightforwardly predict a positive association between levels of I and physical strength—an association that we neither predicted nor observed. In favor of our proposed model, on the other hand, extant research among the Tsimane' indicates that physically formidable individuals are more attractive as mates and social allies, more effective as leaders, and also seen by others as more politically influential (von Rueden et al. 2008, 2014)—all of which would directly lower the cost-benefit ratio of a prosocial behavioral strategy. For these reasons, we prefer an explanation wherein the possession of greater relative strength adaptively calibrates individuals toward higher levels of PLO.

The positive association of physical strength with PLO was similar in magnitude among men and women, respectively. This ran counter to our prediction that this effect would be stronger among men. In previous studies using undergraduates from postindustrial societies as subjects, the effect of physical strength on levels of prosocial traits (e.g., extraversion) has been observed only among men (Lukaszewski and Roney 2011; Lukaszewski 2013). Notably, a parallel divergence between large-scale and small-scale societies has been documented in relation to the effect of physical strength on levels of anger and aggression. Among college students, physical strength positively predicts levels of anger proneness and aggressiveness in men but not women (Sell et al. 2009; Price et al. 2012); whereas, among the Aka foragers of Central Africa, strength predicts anger and aggression in both sexes (Hess et al. 2010). One plausible explanation for this discrepancy between modern and traditional societies is that, within subsistence groups such as the

Tsimane' and Aka, greater physical strength enhances the ability to generate resources for others via physical work (Gurven et al. 2013b)—which would increase one's social value regardless of sex (Hess et al. 2010). Another possibility is that physical contests are more important regulators of social conflict among women in traditional societies than in modern societies (Hess et al. 2010). Either way, the current findings considered together with those of Hess et al. (2010) strongly suggest that physical strength calibrates prosocial and aggressive personality traits among members of both sexes within small-scale subsistence societies.

Possession of locally valued knowledge and prosocial traits

Attainment of formal education was also positively correlated with PLO among the Tsimane'. According to our hypothesis, 1) though schools have only existed in most villages for the past 2–4 decades, knowledge and skills derived from formal education has become a socially valued form of embodied capital that increases one's ability to generate access to novel resources, and therefore 2) attainment of formal education, like greater physical strength, calibrates individuals toward higher levels of PLO. However, given that schooling is a social activity that is noncompulsory among the Tsimane', it is also possible that individuals with prosocial personalities are more likely to seek out or remain in school than others. Our data cannot discriminate between these nonmutually exclusive causal hypotheses, but it will be important for future research to test between them.

The current results are bolstered by other recent findings among the Tsimane' (Reyes-Garcia et al. 2007), which indicate that the attainment of formal education was associated with lower temporal discounting rates—that is, the tendency to choose smaller immediate rewards over larger rewards in the future (Kirby et al. 2002). As with the association between education and PLO, however, it is unclear which way(s) the causality flows: Future-oriented individuals could be more likely to invest in education, or the acquisition of resource-linked knowledge might calibrate people toward a slower, more future-oriented life history strategy (Kirby et al. 2002). Given this latter possibility, it would be of interest to determine whether Tsimane' with greater levels of PLO and physical strength also exhibit lower temporal discounting rates. If so, this would suggest that investment in physical strength, acquisition of locally valued knowledge, high PLO, and low temporal discounting rates are all components of an embodied capital-oriented life history strategy.

Our argument implies that individuals who lack embodied capital calibrate toward low PLO because keeping a low profile within the community maximizes net fitness benefits relative to gregarious cooperation and pursuit of leadership. In the Tsimane' context, low PLO individuals may restrict their cooperation largely to close kin due to coordination costs and risk of conflict from cooperating with other community members. Conflict frequency associates positively with embodied capital, number of allies, and political influence, and high PLO individuals are more likely to get their way in the event of conflict (von Rueden 2011). When individuals low in PLO experience conflict, they may opt to migrate with their immediate family to another community rather than seek assistance in conflict resolution (von Rueden and Gurven 2012).

Implications for explaining the heritability of prosocial traits

Physical strength and formal education each contributed additively to the quasi-heritable variance in PLO. These results provide preliminary support for the reactive heritability hypothesis (Tooby and Cosmides 1990)—which, in the current application, posits that levels of PLO exhibit heritability in part because they are facultatively calibrated over ontogeny to heritable components of embodied capital. In this regard, the finding that controlling for physical strength reduced the estimated heritability of PLO provides the strongest evidence in support of reactive heritability. This is because, as argued above, we believe it is much more likely that strength calibrates levels of PLO than vice versa.

If PLO is indeed reactively heritable in relation to physical strength, this in turn raises the question of what explains the heritability of strength itself. Here, it becomes relevant that physical strength is widely considered to be an indicator of overall phenotypic condition in humans (Bribiescas 2001; Frederick and Haselton 2007; Penke et al. 2007; Lukaszewski and Roney 2011; Lukaszewski 2013). Broadly speaking, phenotypic condition refers to an individual's ability to efficiently convert energy into fitness-enhancing traits and outcomes (Rowe and Houle 1996; Tomkins et al. 2004; Gangestad 2011). Although low physical strength is not necessarily an indicator of being in poor overall condition (because energy is finite and can be allocated in multiple ways), high physical strength indicates that one is in good enough condition to invest in the growth and maintenance of energetically expensive muscle tissue (Bribiescas 2001).

Because phenotypic condition will always be under positive directional selection (as physical strength appears to be among the Tsimane': von Rueden et al. 2011), genetic variance in condition may be a consequence of mutation-selection balance or pathogen-host coevolution (Rowe and Houle 1996; Tomkins et al. 2004; Penke et al. 2007; Gangestad 2011; Lukaszewski and Roney 2011). In effect, then, adaptations for condition-dependent personality calibration provide a solution to the adaptive problem created by the perpetual maintenance of heritable variance in condition: The ability to accrue fitness benefits via prosociality is constrained by one's condition, which is constrained in turn by mutation load and one's possession of pathogen-resistant genotypes. If so, condition-dependent features such as physical strength will have a noisy genetic basis that varies dramatically across individuals and consists mostly of low-frequency genotypes. Under this scenario, one should not necessarily expect to find consistent associations of specific genotypes with 1) condition-dependent physical features (such as strength), or 2) personality traits that are reactively heritable in relation to condition-dependent features. The current state of the behavioral genetics literature is consistent with these predictions: Gene association studies have uncovered few specific genotypes that reliably explain even a tiny fraction of the variance in any human personality trait or condition-dependent morphological trait (Johnson et al. 2011; de Moor et al. 2012; Verweij et al. 2012). Moreover, genetic markers of mutational load are directionally predictive of both condition-dependent physical features and personality traits, such that individuals with fewer expressed mutations have greater physical strength (Verweij et al. 2014) and score higher on prosocial traits such as extraversion (Verweij et al. 2012). Thus, reactive heritability of prosocial traits to levels of physical strength provides a coherent causal model to explain the current findings that is consistent with multiple phenotypic and genetic sources of evidence.

The same basic arguments for reactive heritability might apply to the finding that education also contributed to the estimated heritability of PLO. Specifically, this finding is consistent with the idea that PLO is reactively heritable in relation to skill-related aspects

of intelligence—which, like strength, is a heritable, condition-dependent characteristic (Penke et al. 2007; Plomin et al. 2012). In postindustrial societies, individuals with greater intelligence often either seek out, or are encouraged to obtain, more education (Plomin et al. 2012). If the same is true among the Tsimane', then the heritability of educational attainment, and therefore of PLO, could ultimately reflect heritable levels of intelligence. However, direct assessment of intelligence would be necessary to test this possibility.

In sum, our findings are consistent with the hypothesis that PLO is reactively heritable in relation to condition-dependent components of embodied capital (physical strength and educational attainment). However, limitations of the current study's design warrant caution in drawing firm conclusions, and suggest directions for future research. The Tsimane' are experiencing rapid social change due to market integration and encroachment on their territory by ranchers, loggers, and other colonists. They are not at evolutionary equilibrium, and the components of embodied capital that motivate a prosocial disposition and facilitate status acquisition may be undergoing change. Also, our quasi-heritability estimates do not control for possible effects of shared environment at the household level—which could in principle explain why genetic relatedness predicted phenotypic similarity in strength, education, or personality. Concerns regarding this limitation might be assuaged given that effects of shared environment on personality tend to be near zero across various human populations, whereas substantial genetic variance in personality is ubiquitous (Turkheimer 2000; Bouchard and Loehlin 2001). Consistent with this, in the current study, effects of shared environment at the village level explained no quasi-heritable variance in PLO and strength. Thus, under the reasonable assumption that shared environment has a minimal influence on personality among the Tsimane', the current quasi-heritability estimates are not likely to be misleading (Gurven et al. 2014). In any case, our findings suggest that similarity among family members in physical strength (and possibly intelligence) partially explains why kinship predicts personality resemblance in PLO—which is theoretically important regardless of whether individual differences in strength and intelligence reflect genetic or environmental variance.

Toward an integrative model of the causes and consequences of prosocial traits

In Figure 3, we depict an integrative causal model to explain associations among phenotypic condition, embodied capital, prosocial traits, social status, and reproductive success. As we argue above, the extent to which it will be adaptive for an individual to invest in the cultivation of greater embodied capital over ontogeny will partly depend on one's phenotypic condition, which is itself a joint function of noisy genetic factors (e.g., mutational load) and environmental quality (e.g., access to high quality nutrition and parental care, and the embodied capital and social status of parents) (Figure 3). Variance in embodied capital could also theoretically depend on genotype-environment covariance, such as with spatially structured selection or assortative migration. Independent of phenotypic condition, investment in embodied capital, as part of a slow life history strategy, is expected to vary in response to environmental cues indicating the degree of mortality risk (Kaplan et al. 2009). To reiterate the primary hypothesis that motivated the current study, individuals who have successfully cultivated greater embodied capital will be 1) seen by others as high-quality mates and allies and good candidates for positions of high status and leadership, and therefore 2) relatively likely to accrue net benefits through highly prosocial strategies. These effects of embodied capital on prosocial traits and status are expected to be mutually reinforcing. Embodied capital and prosocial behavior promote high status (von Rueden et al. 2008; Anderson and Kilduff 2009) and, symmetrically, positions of high status bring deference and alliances that increase embodied capital and buffer risk (Sugiyama and Scalise-Sugiyama 2003; Gurven 2006; Cosmides et al. 2011; von Rueden et al. 2011; Price and Van Vugt 2014; von Rueden 2014). Furthermore, positions of status or leadership, particularly in small-scale societies, may carry an implicit obligation to act prosocially toward others (Fiddick et al. 2013; Price and Van Vugt 2014; von Rueden 2014; von Rueden et al. 2014). In general, feedback between state and behavior can amplify even minor initial differences between individuals (Luttbeg and Sih 2010; Wolf and Weissing 2010).

In sum, the proposed model can potentially predict prosocial personality traits in individuals, based on their phenotypic condition, perceived extrinsic mortality risk, embodied capital, and

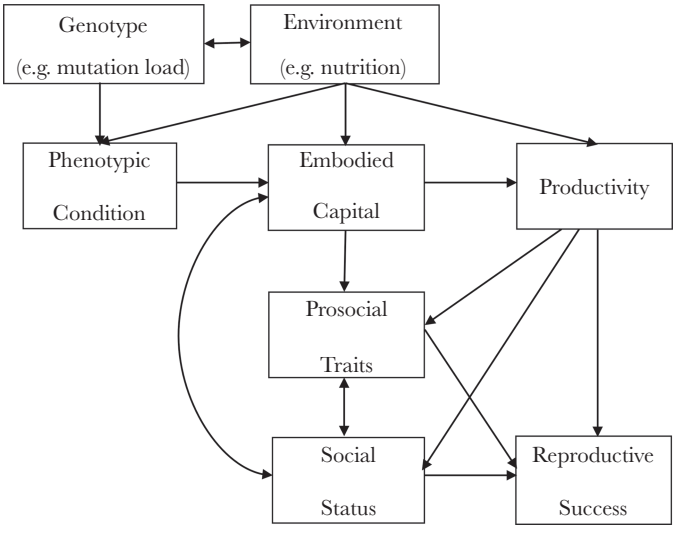

Figure 3
Causal pathways that determine variance in prosocial traits, social status, and reproductive success.

social status. The adaptationist logic uniting the model is supported by evidence, in small-scale societies, that levels of prosocial traits and social status have positive effects on reproductive success (von Rueden et al. 2011; Gurven et al. 2014; von Rueden 2014), and prosociality and achieved status mediate effects of condition-dependent components of embodied capital on reproductive success (Gurven and von Rueden 2006; von Rueden et al. 2011; Apicella 2014). Embodied capital may also affect reproductive success independent of prosociality and social status, as a direct result of increased food or income production (von Rueden et al. 2011). Data that permit all the proposed links in Figure 3 to be estimated simultaneously will ultimately be necessary to provide compelling tests of these hypotheses.

CONCLUSIONS

The current study is among the first to investigate the determinants of adaptively patterned personality variation within a small-scale human society. In demonstrating that physical strength and formal education independently associated with individual differences in PLO among the Tsimane', the findings preliminarily support the hypothesis that levels of prosocial traits are facultatively calibrated to phenotypic components of embodied capital. These results are broadly consistent with state-dependent models of adaptive personality variation from animal behavioral ecology (Luttbeg and Sih 2010; Wolf and Weissing 2010). We do not claim that facultative calibration to embodied capital explains all of interindividual variation in prosocial personality traits. Results from the Tsimane' are modest in size and restricted to aspects of prosociality involving gregarious cooperation and pursuit of leadership.

Quasi-heritable variation in strength and education contributed additively to quasi-heritable variation in PLO, which is consistent with a model wherein prosocial traits are "reactively heritable" in relation to these components of embodied capital. If valid, this model would 1) account for a substantial portion of the genetic variance in prosocial traits without appeal to specific polymorphic genotypes, and thereby 2) illustrate how universal adaptations for personality calibration can systematically produce heritable individual differences. Because our model has the potential to account for the "missing heritability" (de Moor et al. 2012; Vinkhuyzen et al. 2012) of prosocial and other personality traits, future research should attempt to conceptually replicate and extend the current findings using superior methods of heritability estimation.

Whereas a large body of research has focused on explaining the evolution of human prosociality, the current study is among the first, in general, to investigate the ontogenetic calibrators of individual differences in prosocial traits. According to similar adaptationist logic, a recent study by Nettle et al. (2014) provided evidence that variation in human prosocial behavior is calibrated to levels of apparent trust within the local community. Likewise, emerging evidence supports the hypothesis that prosocial traits are calibrated in response to the local prevalence of disease-causing pathogens (Schaller and Murray 2008; Mortensen et al. 2010). Thus, in attempting to explain the substantial variation in prosociality within and between human populations (Henrich et al. 2001; Kurzban and Houser 2005), future research might profitably examine integrative models wherein prosocial traits are jointly calibrated in response to multiple cues present in the individual's phenotype and external socioecology.

Although the current findings remain subject to potential alternative explanations, they nonetheless demonstrate patterns that any complete theory regarding the origins of individual differences in prosociality must be able to explain. At the very least, the results suggest that physical strength, locally valued knowledge, and prosocial personality traits are inter-correlated components of an embodied capital-oriented life history strategy. The data therefore carry importance for basic debates within personality psychology, behavioral genetics, and evolutionary behavioral science. We hope this research motivates scientists to investigate the causes and consequences of variation in embodied capital and personality across a wide range of human societies.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

CONFLICT OF INTEREST

None declared. Use of human subjects was approved by the University of California, Santa Barbara and the University of New Mexico. Informed consent was received prior to subjects' participation.

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