

# Why do men seek status? Fitness payoffs to dominance and prestige

Christopher von Rueden<sup>1,\*</sup>, Michael Gurven<sup>1</sup> and Hillard Kaplan<sup>2</sup>

<sup>1</sup>*Department of Anthropology, University of California, Santa Barbara, CA 93106, USA*

<sup>2</sup>*Department of Anthropology, University of New Mexico, Albuquerque, NM 87131, USA*

In many human societies, high male social status associates with higher fertility, but the means by which status increases lifetime fitness have not been systematically investigated. We analyse the pathways by which male status begets reproductive success in a small-scale, Amerindian society. Men who are more likely to win a dyadic physical confrontation, i.e. dominant men, have higher intra-marital fertility for their age, and men with more community-wide influence, i.e. prestigious men, exhibit both higher intra-marital fertility and lower offspring mortality. Both forms of status elicit support from allies and deference from competitors, but high status men are not provisioned more than their peers. Prestigious but not dominant men marry wives who first give birth at earlier ages, which multivariate analysis suggests is the strongest pathway between status and fitness in this population. Furthermore, men are motivated to pursue status because of fitness gains both within and outside of marital unions: dominant and prestigious men have more in-pair surviving offspring as well as more extra-marital affairs.

**Keywords:** social status; fertility; behavioural ecology

## 1. INTRODUCTION

High status men frequently achieve higher fertility. A positive relationship between men's status and fertility is not restricted to pre-modern empires, kingdoms and sultanates, where high social status granted sexual access to a large number of women [1]. One of the first quantitative investigations of the status–fertility relationship in a small-scale society, among the pastoralist Yomut Turkmen of Iran, revealed that wealthier men have more offspring for their age [2]. Subsequent studies in other small-scale societies replicated the status–fertility relationship across different correlates of male social status: wealth [3], hunting skill [4–6], and warriorship [7]. High-income men in modern industrial societies also exhibit higher fertility [8] but often only after controlling for their level of education [9,10] and/or inclusion of childless men in the sample [11,12].

Comparisons of male status and fertility in small-scale societies can provide insight into how natural selection may have acted on status-seeking behaviour in ancestral human environments. If aspects of human behaviour and psychology have remained in long-term stasis due to stabilizing selection [13], then measures of fitness in modern populations will have relevance to our understanding of human evolution. While cross-cultural evidence, particularly from small-scale societies, suggests that male status-seeking has experienced positive selection, the means by which status generates fitness gains remain under-investigated. Past studies are selective in their analysis of the factors responsible for increases in fertility or offspring survivorship among high status men. Rarely are extra-marital affairs evaluated (but see [4]). Whether the fitness gains to status are concentrated

within the nuclear family or within the context of extra-marital affairs bear significance for debates about the evolution of human pair-bonding and male parental investment [14–16]. Identifying the proximate pathways by which status generates current fitness sheds light on the kinds of social relationships evolution has motivated men to maintain.

With ethnographic data from the Tsimane forager–horticulturalists of Bolivia, we analyse the relationship between male social status and in-pair fertility, in-pair offspring mortality and frequency of extra-marital affairs, and we test four proximate pathways by which status impacts fitness: (i) better access to mates, (ii) higher mate quality, (iii) more trading partners and allies, and (iv) greater deference from competitors. We employ two measures of social status, the ability to win a dyadic physical confrontation and community-wide influence, in order to capture the distinct types of status known as dominance and prestige [17]. We test whether dominant or prestigious men reap greater reproductive benefits, and whether they achieve their reproductive goals via different means.

## 2. WHAT IS SOCIAL STATUS?

Social status can be defined as relative access to contested resources within a social group [18,19]. Among most animals, social status largely results from a superior ability to inflict costs on others (i.e. dominance), including the withholding of benefits critical to others' fitness. Chimpanzees relinquish food and mating opportunities to individuals who threaten to injure them with greater physical strength and/or coalitional support [20,21]. Social status may also result from an individual's relative ability to confer benefits on others (i.e. prestige), such as coordinative leadership, knowledge, material goods and mate value. In human societies, social status is only sometimes based on dominance and is often based on

\* Author for correspondence ([vonrueden@umail.ucsb.edu](mailto:vonrueden@umail.ucsb.edu)).

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2010.2145> or via <http://rspb.royalsocietypublishing.org>.

prestige, due in part to the commodities made available by extensive cooperation, social learning and ratchet-like cultural evolution [17]. Importantly, social status is dependent not only on an ability to inflict costs or confer benefits but also on one's advertisement of those abilities [18]. Social status may be viewed less as the trait of an individual than as the behaviour produced by others' *perceptions* of that individual. Group members concede to higher-status individuals because they believe they will avoid harm or gain some benefit from their deference. Status hierarchies represent agreements, maintained by deference signals, to facilitate exchange or to avoid costs of repeated contest competition [22].

Winning dyadic physical confrontations and community-wide influence are distinct forms of social status that operate at different social scales, and they differ in the degree to which they reflect dominance versus prestige. Previous work among the Tsimane found that winning a dyadic physical confrontation is principally determined by physical characteristics such as muscle size while community-wide influence is tied to income, generosity, and support from allies [19]. Our measure of influence should not be considered tantamount to prestige, however; men who can recruit more allies during a conflict are capable of inflicting costs via 'derived dominance' [23].

### 3. HOW DOES HIGHER SOCIAL STATUS LEAD TO MORE SURVIVING OFFSPRING?

For high status men to produce more surviving offspring, their social status must increase fertility, reduce child mortality, or accomplish both. Status increases fertility, in part, by granting men access to more (fecund) wives, more durable marital unions, and more numerous extra-pair mates, either because status signals phenotypic quality [24] or represents a priority of resource access valuable to potential mates [25].

**Prediction 1:** *Higher status men have higher fertility.*

The offspring of high status men may experience lower childhood mortality because they have inherited their parents' genetic quality, they are better provisioned, they are protected from disease, or they receive better medical care.

**Prediction 2:** *Offspring of higher status men experience lower childhood mortality.*

While women should prefer husbands who exhibit resource accruing power and commitment, they may place more weight on indicators of 'good genes' when considering extra-marital affairs. Masculinized traits such as muscle mass may be costly signals of genetic quality in the face of testosterone-linked immune-suppression [26] and other tradeoffs due to increased mating effort [27]. Women may prefer dominant, physically robust men as short-term mates due to the developmental stability and 'good genes' these traits signal.

**Prediction 3:** *Higher status men have more extra-marital affairs, especially for dominant men.*

Women may not prefer dominant men as marital partners if dominant men are more likely to commit partner-directed aggression or provide unreliable paternal investment. U.S. undergraduate women prefer prestigious men over dominant men as romantic partners, particularly in the context of long-term relationships [28].

**Prediction 4:** *Higher status men marry at earlier ages and have more wives, especially for prestigious men.*

Either by coercion or mutual choice, high status men may be more likely to mate with physically attractive women. Cues of youth, such as smooth skin, are highly valued because female fecundity is strongly age dependent [29]. High status men may reproduce well into old age as a result of serial monogamy or polygynous matings with younger women [30]. Body mass index (BMI) is also a predictor of female attractiveness [31]. BMI may signal general energy reserves for pregnancy and lactation; better nutrition in mothers and earlier weaning of offspring can increase fertility by decreasing birth intervals [32]. Furthermore, mother's BMI predicts neonate weight [33], which is one of the most important predictors of infant mortality and morbidity [34].

**Prediction 5:** *Higher status men marry women who are younger, have higher BMIs, start reproducing early, and who are rated as more attractive by community-members.*

Studies among tribal societies show that while men value physical attractiveness more than women, both partners are concerned that long-term mates are hard-working, generous and high producers [35,36].

**Prediction 6:** *Higher status men marry women who are more hard-working and who spend relatively more time in productive and parenting activities.*

In times of food scarcity and sickness, the families of prestigious Ache men, particularly those known for their generosity, preferentially receive aid from others [37]. High status men also benefit in times of political conflict from a greater pool of allies [38], though the spoils of victory may not necessarily benefit men's families. In the face of risk and uncertainty, social status acts as a form of social insurance important for improving survival and capitalizing on resource consumption opportunities. This is less true of dominant than prestigious men, whose skills and prosociality provide direct benefits to long-term cooperative partners.

**Prediction 7:** *Higher status men, especially those who are prestigious, recruit more cooperative partners with respect to political alliances, food production and food sharing.*

In behavioural experiments, signals of high status elicit more helping behaviour [39,40]. It is not clear, however, whether these experiments reflect high status individuals' ability to garner cooperative partners or to instill deference in their competitors. Deference may accrue more to physically dominant men, whose competitors anticipate the indirect benefits to avoiding costly contest competition. Prestigious men, however, will also receive deference from competitors if the strength of their alliances grants them greater formidability in conflicts.

**Prediction 8:** *Higher status men, especially those who are dominant, are accorded more deference from community members.*

The pathways by which male status affects fertility and offspring mortality can be summarized as the following: (i) the length of a man's reproductive career and his number of mates, (ii) the age, fecundity, health and productivity of his mates, (iii) alliances and exchange partnerships, and (iv) resources gained as a result of others' deference or acquiescence. While this paper analyses extra-marital affair frequency, we do not report number of children produced from these affairs, due to the risks of over-speculation on the part of informants.

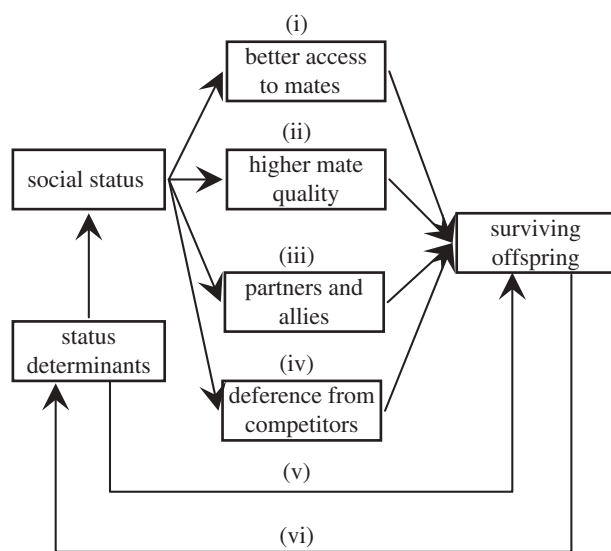


Figure 1. The pathways from status to lifetime fitness.

As a result, our comparisons of the status–fertility pathways are restricted to intra-marital fertility. Figure 1 illustrates these pathways, which may interact in more complex ways than depicted. For example, the quality of a wife with respect to offspring survival may depend on the allies (including affinal kin) a man expects to gain through the marriage. Alliances also facilitate mate acquisition. Humans use kin and allies to create, manipulate or circumvent marriage rules [41], to coercively acquire women from neighbouring groups [42], and to acquire women via trade or tribute [1]. While we model cooperative partnerships and deference from competitors as outcomes of social status, the relationships among these variables are in reality more reciprocal than unidirectional.

Pathways (v) and (vi) in figure 1 represent alternative explanations for the status–fitness relationship. Status may play a minimal role in a man's number of surviving offspring if they result more from his individual productivity than from his ability to procure quality mates, engender others' deference or recruit cooperative partners. Furthermore, status may result from having more offspring, rather than the reverse, due to incentives to increase one's productivity and social support with increasing child dependency.

#### 4. THE STUDY POPULATION: TSIMANE FORAGER–HORTICULTURALISTS OF BOLIVIA

The Tsimane inhabit areas of lowland Bolivia along the Maniqui River and in adjacent forests. While families may spend weeks or months on field cultivation trips away from settled villages, the Tsimane are semisedentary and live in communities ranging from 30 to 500 individuals. Kin-related families live in close proximity, forming well-defined household clusters. Polygyny is rare and occurs at low frequencies (5–10%) in more remote communities. Most food the Tsimane consume comes from swidden horticulture of plantains, rice, corn and manioc, supplemented with fishing, hunting and gathering activities. Incipient cattle ownership, wage labour with loggers and farmers, and produce sales to local markets are on the rise, especially for those villages located near the town of San Borja (population approx. 19 000). Land

close to village centres is de facto privately owned, and disputes among families over land access for horticulture are common. Men occasionally engage in dyadic physical confrontations, often the result of sexual jealousy, theft or stinginess. Dispute resolution is typically left to the parties directly involved or, on rarer occasions, adjudicated by an informal gathering of adult men. The Tsimane have no recent history of inter-community violence.

For much of Tsimane history, older adult males and shamans (cocojsi) wielded the most community-wide influence as a result of their ability to commune with forest spirits and ancestors. Shamans have all but disappeared among the Tsimane, due in part to the influence of missionaries. In the late twentieth century, regional political pressure led to the establishment of elected village leaders. These leaders are principally representatives to outside political bodies, and they generally have short tenure and little coercive authority within their villages. Community-wide meetings are common in Tsimane villages; they often concern disputes over land, the sale of community lumber, or participation in government or NGO-sponsored development projects.

#### (a) Data collection

The sample is the entire adult male population from two, more acculturated Tsimane villages: Ton'tumsi ( $n = 57$  men aged 18+ years, sampled in 2005) and Jinac ( $n = 31$  men aged 18+ years, sampled in 2009).

Using a block design (see electronic supplementary material), we asked adult men to photo-rank other males in their community on the following traits: ability to win a dyadic physical confrontation, community-wide influence, number of allies who would provide assistance during a conflict, ability to get one's way in the context of a conflict within a group, respect, hunting skill, meat-sharing generosity, money-lending generosity, whether a man is frequently visited by others, and wife's attractiveness. For all photo-ranked measures, each rater evaluated his peers with no one else present but C.V.R. Photos were Polaroids of the top-half of each man's body, set against as neutral a background as possible.

Time allocation data allow estimation of the time each man and his wife dedicated to direct childcare, food production (includes hunting, fishing, farming and collecting), and socializing with other adults. These data are based on spot observations in Ton'tumsi of all household residential clusters between February and December 2005 (average 81 time points per man; see [35] for methods).

Each man was interviewed concerning his food production, food sharing and income. These interviews allow calculation of each man's average weekly wage labour income and horticultural commerce income and the number of other men that regularly share food and labour with him. Labour assistance includes cooperation during hunting, fishing and horticultural work. In Ton'tumsi, we also calculate the calories each man and his wife produced per week as well as the average calories they received per week via inter-family food transfers.

All demographic data used to age individuals, describe kinship relations, determine within-marriage paternity and identify offspring who have died come from extensive reproductive history interviews. Men and their wives were interviewed separately, and their responses were

cross-validated with other community members' responses [43]. At the time of data collection, 15 of the 88 men were unmarried and two men had more than one wife. Each Ton'tumsi man's involvement in extra-marital affairs during the period 2000–2005 was ascertained from three well-trusted informants, who differ in age and family background.

Height was measured using a Seca 214 Portable Stadiometer and weight was measured using a portable digital weigh scale. BMI was calculated as weight/height<sup>2</sup>.

### (b) Data analysis

To test our eight predictions and compare the strengths of the pathways in figure 1, we first perform partial correlations among the two status variables, in-pair live births, in-pair offspring who died prior to age 15 (as a per cent of total offspring born), in-pair surviving offspring (who were alive at the time of data collection or who died subsequent to age 15), frequency of extra-marital affairs, and 19 other variables associated with the status–fitness pathways (table 1). All correlations control for the log of men's age. We preferred a logarithmic age control because quadratic models of the age-specific reproductive data tended to depict decreases in fertility and surviving offspring at the oldest ages. Some of the oldest men in Ton'tumsi had relatively low fertility for their age.

We next test five OLS regression models of in-pair surviving offspring (table 2). Models 1 and 2 serve two goals: they directly compare the strengths of the status–fitness pathways, and they determine whether these pathways mediate the effects of the status variables on reproductive outcomes. The independent variables in each model are log age, one of the two social status measures, and each variable from table 1 that produced significant ( $p < 0.05$ ) bivariate correlations with both surviving offspring and that status measure. Model 3 directly compares dominance and prestige as predictors of surviving offspring. Models 4 and 5 identify whether status has effects on offspring survivorship beyond a man's productivity and inherited social network (pathway v in figure 1). Independent variables in these models include log age, hunting skill, horticultural income, man's consanguineal kin and one of the two social status measures.

The potential for men to achieve higher status due to greater child dependency (pathway vi in figure 1) was evaluated by controlling for the producer–consumer ratio of each man's household when correlating his fertility with his social status. If status is a recent response to current child dependency, then the status variables may not predict fertility independent of the ratio of producers to consumers within his household. A producer was defined as anyone within the man's household older than 15 years.

## 5. RESULTS

Higher status Ton'tumsi and Jinac men produce more surviving offspring, at least within their marital unions. Winning dyadic physical confrontations significantly predicts number of in-pair surviving offspring (partial  $r = 0.362$ ,  $p = 0.001$ ). Men in the top quartile of winning dyadic fights have on average 2.07 more surviving offspring for their age than men in the bottom quartile (figure 2a). Community-wide influence is an even stronger predictor of in-pair offspring survivorship

(partial  $r = 0.424$ ,  $p < 0.001$ ). Men in the top quartile of influence have on average 2.62 more surviving offspring for their age than men in the bottom quartile (figure 2b). Despite their different determinants [19], the likelihood of winning a dyadic physical confrontation and community-wide influence are highly correlated (partial  $r = 0.651$ ,  $p < 0.001$ ).

### (a) Dominant and prestigious men have higher fertility, and the offspring of prestigious but not dominant men experience lower childhood mortality

We found more support for prediction 1 than for prediction 2: the effect of social status on in-pair offspring survivorship is due more to its effect on in-pair fertility than on offspring mortality. Winning dyadic physical confrontations predicts in-pair live births (partial  $r = 0.328$ ,  $p = 0.002$ ) but not in-pair offspring mortality rate ( $r = -0.055$ ,  $p = 0.650$ ). Men in the top quartile of winning dyadic fights have on average 2 more births and a 3.18 per cent lower offspring mortality rate for their age than men in the bottom quartile. Community-wide influence predicts in-pair live births ( $r = 0.358$ ,  $p = 0.001$ ) and in-pair offspring mortality rate ( $r = -0.252$ ,  $p = 0.034$ ). Men in the top quartile of influence have on average 2.57 more births and a 10.96 per cent lower offspring mortality rate for their age than men in the bottom quartile.

### (b) Dominant and prestigious men have more extra-marital affairs

Men of higher social status had more extra-marital affairs within the previous 5 years. Contrary to prediction 3, however, frequency of extra-marital affairs is predicted less by winning a dyadic physical confrontation (partial  $r = 0.312$ ,  $p = 0.019$ ) than by community-wide influence (partial  $r = 0.420$ ,  $p = 0.001$ ). Men in the top quartiles of winning dyadic fights and influence have on average 0.85 and 1.19 more extra-marital affairs for their age, respectively, than men in the bottom quartiles. Nineteen of the 57 men in Ton'tumsi were reported to have engaged in extramarital sex between 2000 and 2005. The majority of these affairs took place outside of the community: only eight of the 33 total reported affairs involved women married to other Ton'tumsi men in 2005.

### (c) Dominant and prestigious men are more likely to remarry, and prestigious but not dominant men marry at earlier ages

A man's number of serial marriages is predicted by winning physical confrontations and by community-wide influence (table 1). Of the 76 ever-married men, five remarried following the death of their spouse and six remarried after a divorce. Number of serial wives does not significantly affect fertility (partial  $r = 0.146$ ,  $p = 0.185$ ), but men who remarry following divorce or death of their spouse may increase their fertility relative to those who do not remarry. Men who win dyadic fights do not marry earlier (partial  $r = -0.050$ ,  $p = 0.685$ ), but in support of prediction 4, men with more influence do marry at earlier ages (partial  $r = -0.304$ ,  $p = 0.012$ ). Men in the top quartile of influence marry at age 18.5 on average, which is 1.7 years earlier than the average age of marriage for men in the bottom quartile.

Table 1. Coefficients from partial correlations of status and fitness measures, controlling for the log of men's age.

	social status			(i) mate access			(iii) trading partners and allies					
	wins dyadic fights (n = 88)	community-wide influence (n = 88)	1	marriage age (n = 68)	no. serial wives (n = 88)	extra-marital affairs (n = 57)	visited often <sup>a</sup> (n = 88)	allies <sup>a</sup> (n = 88)	labour partners <sup>a</sup> (n = 76)	food sharing partners <sup>a</sup> (n = 76)	times received food <sup>a</sup> (n = 52)	daily calories received <sup>a</sup> (n = 47)
social status												
wins dyadic fights	0.651***	0.651***	1	-0.050	0.292***	0.312**	0.284***	0.583***	0.239**	0.054	-0.113	-0.298**
community-wide influence				-0.304**	0.229**	0.420***	0.508***	0.818***	0.258**	0.094	0.008	-0.158
fitness measure												
in-pair fertility	0.328**	0.358***		-0.332**	0.146	0.092	0.162	0.311***	0.166	0.155	0.001	-0.105
offspring mortality rate	-0.055	-0.252**		-0.172	0.076	-0.107	-0.208*	-0.110	-0.099	0.149	0.403***	0.124
in-pair surviving offspring	0.362***	0.424***		-0.213*	0.120	0.131	0.228**	0.319***	0.157	0.104	-0.174	-0.187
	(iv) deference											
(ii) mate quality												
husband - wife age difference (n = 75)				wife average IBI (n = 62)	wife BMI (n = 69)	wife attractive (n = 72)	wife parent time <sup>b</sup> (n = 47)	wife production time <sup>b</sup> (n = 47)	wife calories produced <sup>b</sup> (n = 46)	affinal kin (n = 72)	gets way (n = 88)	respect (n = 88)
wins dyadic fights	0.229**	-0.035		0.189	0.237*	0.300**	0.289*	-0.185	-0.123	0.142	0.633***	0.405***
community-wide influence	0.192	-0.349***		0.098	0.208*	0.334***	0.106	0.062	-0.212	0.154	0.547***	0.601***
fitness measure												
In-pair fertility	-0.010	-0.441***		-0.470***	-0.251**	-0.148	-0.179	0.281**	0.166	-0.058	0.366***	0.105
offspring mortality rate	-0.242**	0.126		-0.113	0.034	-0.143	-0.184	-0.178	0.043	-0.243**	-0.042	-0.160
in-pair surviving offspring	0.117	-0.459***		-0.408***	-0.179	-0.023	0.014	0.291**	0.131	0.056	0.368***	0.148

\* $p < 0.10$ .\*\* $p < 0.05$ .\*\*\* $p < 0.01$ .<sup>a</sup>Also controls for man's number of consanguineal and affinal adult male kin living in the community.<sup>b</sup>Also controls for household producer-consumer ratio.

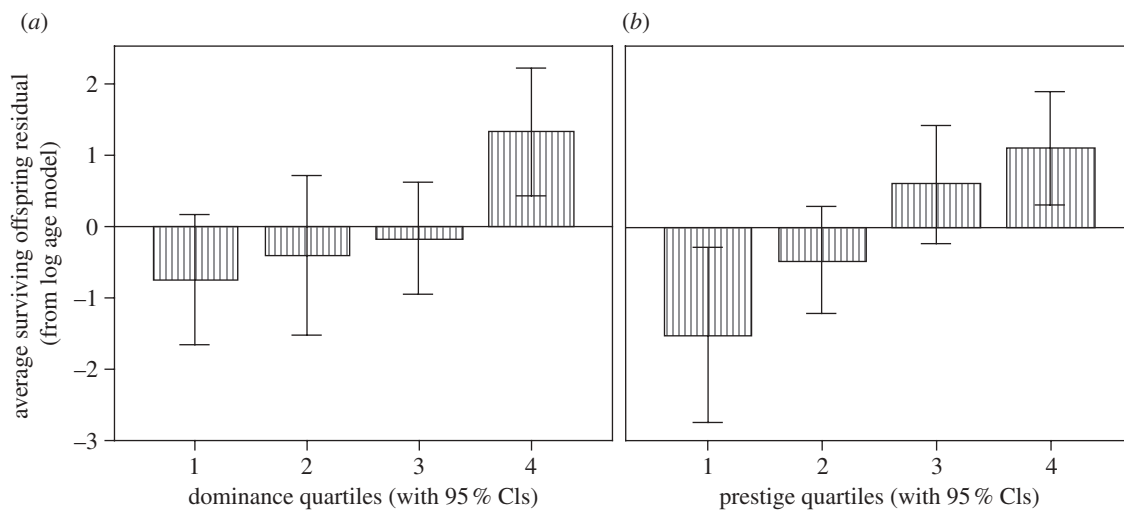


Figure 2. Offspring survivorship by (a) dominance and (b) prestige quartiles.

**(d) Wives of dominant and prestigious men are rated as more attractive, dominant men marry younger women, and wives of prestigious men have an earlier age at first birth**

In support of prediction 5, the wives of influential men first give birth at earlier ages (partial  $r = -0.349$ ,  $p = 0.003$ ). Women married to men in the top quartile of influence first give birth at 16.8 years on average, 2 years earlier than women married to men in the lowest quartile of influence. Men who win physical confrontations marry women significantly younger than themselves (partial  $r = 0.229$ ,  $p = 0.049$ ). Men in the top half of dominance are on average 0.8 years older than their wives while men in the bottom half of dominance are on average 1.1 years younger. High status men tend to have wives with marginally larger BMIs and who are rated as more attractive. However, wife's BMI is negatively associated with age-controlled fertility, and wife's attractiveness predicts neither fertility nor offspring mortality (table 1). Neither winning a dyadic confrontation (partial  $r = 0.189$ ,  $p = 0.144$ ) nor community-wide influence (partial  $r = 0.098$ ,  $p = 0.451$ ) predict wife's average inter-birth interval.

**(e) Wives of dominant and prestigious men do not produce more food than other men's wives; wives of dominant but not prestigious men spend more time caring for offspring**

To assess wives' parental investment and productivity, we control not only for log age but also for the household producer-consumer ratio, which is indicative of the amount of within-household alloparenting available. Prediction 6 is partially supported: wives' time spent interacting with offspring is greater the more probable her husband is to win physical confrontations (partial  $r = 0.289$ ,  $p = 0.054$ ) but not if her husband is more influential (partial  $r = 0.106$ ,  $p = 0.490$ ). Wives do not spend more time in direct food production the more her husband is physically dominant (partial  $r = -0.185$ ,  $p = 0.184$ ) or influential (partial  $r = 0.062$ ,  $p = 0.658$ ). Although the results are not significant, wives tend to produce fewer calories per day the more her husband is

physically dominant (partial  $r = -0.123$ ,  $p = 0.425$ ) or influential (partial  $r = -0.212$ ,  $p = 0.167$ ).

**(f) Dominant and prestigious men have more intra-village kin, labour partners, and allies but not more food-sharing partners**

A man's number of co-resident, consanguineal close kin predicts his likelihood of winning a physical confrontation and his community-wide influence (table 1). We defined close kin as adult male relatives with a coefficient of relatedness to ego of 0.5 or higher (i.e. sibling, parent or child). High status men do not tend to be married to well-connected women (table 1), even though number of affinal close kin predicts a lower offspring mortality rate (partial  $r = -0.243$ ,  $p = 0.041$ ).

In support of prediction 7, men with more influence are visited more often (partial  $r = 0.508$ ,  $p < 0.001$ ), have more labour partners (partial  $r = 0.258$ ,  $p = 0.026$ ), and have more allies who would aid them in a conflict (partial  $r = 0.818$ ,  $p < 0.001$ ), controlling for log age and number of co-resident consanguineal and affinal close kin. Men who win physical confrontations are also visited more often (partial  $r = 0.284$ ,  $p = 0.008$ ) and have more labour partners (partial  $r = 0.239$ ,  $p = 0.040$ ) and allies (partial  $r = 0.583$ ,  $p < 0.001$ ). Neither men who win physical confrontations nor influential men have more food sharing partners (table 1).

**(g) Prestigious but not dominant men are more generous; families of dominant and prestigious men do not receive more food from other households**

Generous meat-sharing is attributed to influential men (partial  $r = 0.211$ ,  $p = 0.051$ ) but not to men who win physical confrontations (partial  $r = 0.025$ ,  $p = 0.821$ ), controlling for log age and hunting ability. Money lending is attributed to influential men (partial  $r = 0.341$ ,  $p = 0.002$ ) but not to men who win physical confrontations (partial  $r = 0.181$ ,  $p = 0.110$ ), controlling for log age and average weekly income. Influential men spend more time socializing with other community members (partial  $r = 0.332$ ,  $p = 0.014$ ), and men who win physical confrontations do not (partial  $r = 0.171$ ,  $p = 0.215$ ).

Table 2. Standardized beta coefficients from regression of *surviving offspring* on (models 1 and 2) the status-fitness pathways, (model 3) dominance and prestige alone, and (models 4 and 5) determinants of status.

	model 1	model 2	model 3	model 4	model 5
log age	0.732***	0.773***	0.748***	0.732***	0.701***
wins dyadic fights	0.091	—	0.103	0.182**	—
community-wide influence	—	0.165*	0.208**	—	0.249***
wife age at first birth	—	-0.247***	—	—	—
visited often	0.057	-0.030	—	—	—
allies	0.083	—	—	—	—
gets way	0.121	0.115	—	—	—
hunting ability	—	—	—	0.062	0.021
consanguineal kin	—	—	—	0.125*	0.098
horticultural income	—	—	—	0.199***	0.225***
Adj. $R^2$	0.650	0.644	0.662	0.676	0.696
$F$ statistic	32.228***	26.354***	55.949***	33.929***	37.247***
total d.f.	84	70	84	79	79

\* $p < 0.10$ .\*\* $p < 0.05$ .\*\*\* $p < 0.01$ .

The generosity of influential men is not repaid in kind, at least not in the short-term. Families of higher status Ton'tumsi men are not given food more frequently than other households nor do they receive more calories per day (table 1). In fact, physically dominant men's households received *fewer* calories per day from other households (partial  $r = -0.330$ ,  $p = 0.025$ ) while households with higher offspring mortality rates received *more* frequent gifts of food (table 1). In Ton'tumsi, husbands and wives jointly produce on average 8320 kcals of food per day, their households give away 813 kcals and their households receive 720 kcals from other households.

#### (h) Dominant and prestigious men are accorded more deference

In support of prediction 8, dominant and prestigious men are more likely to get their way during a group dispute and they are accorded more respect (table 1). However, in a multiple regression model explaining 43.1 per cent of the variance in respect ( $F = 22.954$ ,  $p < 0.001$ ), community-wide influence (std.  $\beta = 0.550$ ,  $p < 0.001$ ) but not ability to win a dyadic fight (std.  $\beta = 0.021$ ,  $p = 0.841$ ) predicts respect.

#### (i) In-pair fitness gains are the result of multiple pathways

Bivariate correlations suggest that pathways i–iv in figure 1 all contribute to the in-pair fitness gains of Ton'tumsi and Jinac men. More surviving offspring is associated with a wife with an earlier age at first birth, being visited more often, more allies, greater likelihood of getting one's way, a wife with shorter inter-birth intervals and a wife who spends more time in food production (table 1). However, the latter two variables do not correlate with social status.

In regression model 1, which compares the pathways between physical dominance and lifetime fitness, no variable apart from the age term significantly predicted surviving offspring (table 2). Collinearity statistics do not indicate problems with model interpretation, but the strong inter-relationships among winning dyadic confrontations, allies and getting one's way probably reduced

their individual predictive power in the multivariate analysis. Getting one's way has the largest linear coefficient among these variables, which suggests that it is mediating the effect of dominance on fitness outcomes. In model 2, which compares the pathways between community-wide influence and lifetime reproductive success, wife's age at first birth is the strongest predictor. However, influence remains a marginally significant predictor of surviving offspring (table 2). Although number of allies met the criteria for inclusion in model 2, the allies variable was dropped because of its relatively high collinearity with influence ( $VIF = 3.731$ ).

In model 3, community-wide influence mediates the effect of winning dyadic fights on surviving offspring (table 2).

#### (j) Social status generates fitness gains independent of men's skill, income and inherited social network

Number of offspring surviving to age 15 is positively predicted by hunting ability (partial  $r = 0.231$ ,  $p = 0.035$ ), horticultural income (partial  $r = 0.344$ ,  $p = 0.002$ ), and within-village consanguineal kin (partial  $r = 0.266$ ,  $p = 0.014$ ). Wage income does not predict surviving offspring (partial  $r = 0.075$ ,  $p = 0.510$ ). Models 4 and 5, however, suggest that the status–fitness relationship is not driven by wealthier, more skilled men acquiring fitness independent of their status gains. In model 4, a man's likelihood of winning a dyadic physical confrontation but not hunting ability or consanguineal kin significantly predict number of offspring surviving to age 15 (table 2). Horticultural commerce income remains a strong independent predictor in model 4 and does not correlate with winning fights (partial  $r = 0.023$ ,  $p = 0.841$ ). In model 5, a man's community-wide influence but not hunting ability or within-village consanguineal kin predicts offspring survivorship (table 2). Influence correlates with both hunting ability (partial  $r = 0.348$ ,  $p < .001$ ) and consanguineal kin (partial  $r = 0.245$ ,  $p = 0.022$ ). Horticultural commerce income remains a strong independent predictor in model 5 and does not correlate with influence (partial  $r = -0.041$ ,  $p = 0.717$ ).

**(k) Social status differentials are not the result of current child dependency**

We find little evidence for reverse causality: having a larger family or greater number of dependents does not seem to motivate status seeking. After controlling for both log of age and household producer–consumer ratio, winning a dyadic confrontation (partial  $r = 0.232$ ,  $p = 0.037$ ) and influence (partial  $r = 0.259$ ,  $p = 0.019$ ) still predict in-pair fertility.

**6. DISCUSSION**

Dominance (measured as winning dyadic physical confrontations) and prestige (measured as community-wide influence) are related pathways to fitness gains for Ton'tumsi and Jinac men. Both forms of status produce higher in-pair fertility and more in-pair surviving offspring, but the effects are stronger for prestigious men. Furthermore, the offspring of prestigious but not physically dominant men experience lower pre-adult mortality. In general, total fertility is a better predictor of number of surviving offspring in Ton'tumsi and Jinac than is child mortality.

Prestigious Tsimane men have more surviving offspring in large part because they marry women with earlier ages at first birth. Among the historical Sami of Finland, marital fitness was maximized by men marrying women at least 10–15 years younger [44]. Older Sami men possessed greater wealth and food production skill, and they presumably invested more in their offspring. Physically dominant Tsimane men tend to be significantly older than their wives, but spousal age difference is not related to more surviving offspring. Prestigious Tsimane men are not significantly older than their wives. Prestigious men marry at earlier ages to wives who first give birth at earlier ages. Even though physical dominance peaks a decade or more earlier than community-wide influence [19], it may be that young men's future gains in community-wide influence are highly predictable based on their skills, prosociality and social support as adolescents.

Dominant Tsimane men have more surviving offspring in large part because they are also prestigious. The shared effects of dominance and prestige on surviving offspring are due more to the deference of peers than to wife's quality. Phenotypic correlations (e.g. better nutrition, health and intelligence among the higher status men) may underlie the strong association between dominance and prestige. Furthermore, it is to the advantage of high status men to diversify their bases of status, thereby increasing the scope of their power and precluding others from gaining ascendancy in a new status niche.

The fitness gains of high status Tsimane men do not result from wives' attractiveness or greater productivity. The wives of high status men have higher BMIs, are rated as more attractive, and spend more time in direct parenting, but these characteristics do not positively predict in-pair fertility. Controlling for the numbers of consumers and producers within families, wives of high status men neither spend more time in food production nor produce more calories per day than other men's wives. These results contrast with data from the Hadza [15], where the effects of male productivity and status on in-pair fertility were mediated by wife's productivity. In general, Tsimane women who spend more time in

food production have more surviving offspring, controlling for the number of consumers and producers within families. The wives of high status men may not have to increase their productivity to reap higher reproductive gains because their husbands are better hunters and receive more social support from kin and allies. Wives might have better support networks themselves, though high status Tsimane men do not have more intra-village affinal kin.

Community-wide influence, largely isomorphic with number of allies, is a marginally significant predictor of surviving offspring, independent of wife's age at first birth. During Tsimane community meetings, vocal support from allies is a principal means by which influential men swing opinion in their favour. When disputes over land access for horticulture are aired during community meetings, the collectively agreed terms of their resolution often favour high status men's families. Generous sharing of food builds social partnerships among the Tsimane, but subordinates may also cooperate with higher status men because of skills they hope to learn, the benefits from higher status men's coordinative leadership or physical labour in collective actions, or the indirect benefits of signalling membership in a powerful coalition. Men with community-wide influence are more generous and garner more social support than physically dominant men, but both forms of status associate with frequent visitation by peers, greater number of allies and more labour partners.

Sharing decisions which optimize resource consumption via in-kind reciprocal altruism might trade off with sharing decisions which optimize status acquisition. Prestigious Tsimane men share meat more widely, but they do not have more food-sharing partners nor do their families receive more calories per day from other households. Likewise, in the Meriam [24], Achuar [38], forest Ache [45] and Lamalera [46], generous food sharing or greater contribution to collective food production by higher status men is not reciprocated in-kind. Over the short-term, inter-household food exchange in Ton'tumsi may track need more than reciprocity. Physically dominant men receive fewer calories per day from other households while some of the oldest, lowest producing men receive the most calories per day. Households where infants experience higher mortality rates receive food more frequently than other households. Investments in social status via generosity might only payoff to men and their families over the long term [18], as with generous Ache hunters who are provisioned when sick [37]. The recruitment of labour partners, social visitors and allies by high status Tsimane men may be motivated primarily as insurance against losses from infrequent conflicts or shortfalls in production.

Exchange between higher and lower status men may not always involve a bidirectional flow of benefits. Among the Tsimane, both physically dominant men and prestigious men receive more deference from competitors, who may be ceding to their higher status peers simply to avoid the costs of contest competition. This is probably captured by our measure of getting one's way in the context of a conflict within a group. Our measure of respect may be capturing a different sort of deference. Respect is accorded to men who excel in traditional skills like hunting ability rather than to physically strong men [19]. Lower status men who defer to their higher status



peers out of respect may do so because the community legitimates the right of these prestigious men to more resources. While deference does not increase the fitness of prestigious men independent of the other status–fitness pathways, getting one’s way appears to be the strongest pathway to fitness gains for dominant men.

High status Tsimane men tend to be more productive and draw on a larger consanguineal kin network, but these variables alone do not produce the fitness gains of high status men. Better hunting ability and more numerous consanguineal kin increase a man’s total surviving offspring in part because of their effects on his social status. Wealth and skill attract mates and others’ allegiance and deference, important determinants of men’s reproductive success. Furthermore, potential mates and allies may use social status as a heuristic for ascertaining men’s skill and wealth. Hunting ability, for example, is not easily identified by co-residents based on return rates [47]. Some forms of production important to fitness may not lend themselves to social status gains, perhaps because they are less skill-intensive or are subject to less variance over time. Income from sales of horticultural goods predicted the number of Tsimane offspring surviving to maturity independent of social status. With the Tsimane, we were also able to discredit current offspring dependency as a principal motivator of status acquisition. Better tests of the causal relationships among productivity, status, and fertility among the Tsimane, and in other small-scale societies, must await the availability of longitudinal data.

Male status-seeking is associated with fitness gains within pair-bonds. Physically dominant and prestigious Ton’tumsi men have more extra-marital affairs, but these are in addition to the fitness gains they realize within their marital unions. Also, higher status men’s in-pair fitness gains were not driven by serial marriages. Tsimane men in Ton’tumsi and Jinac tend to invest in a single wife their entire reproductive careers.

#### (a) *Natural selection on male status-seeking behaviour*

Since humans have lived in small-scale societies without significant material wealth for the majority of their existence, reproductive data in these societies can help elucidate the selective forces that have shaped male status-seeking behaviour. One limitation of the present study is that our measures of fitness are restricted to a single generation. The reproductive success of fathers and sons are marginally correlated among the Tsimane [48]; this relationship may be stronger for higher status men and their offspring, who either obtain higher status themselves or continue to capitalize on their father’s status during their own reproductive years. Among the Martu of Australia, co-resident fathers enable their adolescent sons to achieve earlier initiation, which results in higher lifetime reproductive success [49].

Evidence for long-term, positive selection on heritable male traits is mixed, according to studies of Y chromosome haplotype variation. Among Indonesian foragers, horticulturalists and agriculturalists, high fertility along patriline rarely persists for more than a few generations [50]. On the other hand, 8 per cent of Asian men living between the Pacific Ocean and the Caspian Sea can

trace their Y chromosome to Genghis Khan and his relatives [51]. Most heritable genetic variation particular to status achievement will be associated with autosomal genes and not the few non-recombining genes on the Y chromosome. Even among autosomal genes we may not expect to see a clear signature of positive selection on heritable male traits: the genotypes of high status men may represent a fitness peak, which sexual recombination will break down in successive generations; balancing selection may prevent the traits of high status men from sweeping across a population; or status achievement may arise from conditional behavioural responses to uncorrelated genetic variation [52], such as extraversion increasing in response to muscle development [13]. Even if selection is inconsistent along particular lineages, heritable traits particular to high status will probably show positive selection whenever they arise. As the Tsimane and other small-scale societies demonstrate, male social status has strong fitness consequences, due to reproductive gains both within and outside of marital unions.

Thanks to the residents of Ton’tumsi and Jinac, Bolivia for their patience and participation. Jonathan Stieglitz, Helena von Rueden, and two anonymous reviewers provided helpful comments. Funding was provided by grants from the National Science Foundation (nos. BCS-0136274, BCS-0422690, and DDIG-0921429) and National Institutes of Health/National Institute on Ageing (no. 1R01AG024119-01).

#### REFERENCES

- 1 Betzig, L. 1986 *Despotism and differential reproduction: a Darwinian view of history*. New York, NY: Aldine.
- 2 Irons, W. 1979 Cultural and biological success. In *Evolutionary biology and human social behavior: an anthropological perspective* (eds N. A. Chagnon & W. Irons), pp. 257–272. North Scituate, MA: Duxbury Press.
- 3 Borgerhoff Mulder, M. 1987 On cultural and reproductive success: Kipsigis evidence. *Am. Anthropol.* **89**, 617–634. (doi:10.1525/aa.1987.89.3.02a00050)
- 4 Kaplan, H. & Hill, K. 1985 Hunting ability and reproductive success among Ache foragers: preliminary results. *Curr. Anthropol.* **26**, 131–133. (doi:10.1086/203235)
- 5 Smith, E. A. 2004 Why do good hunters have higher reproductive success. *Hum. Nat.* **15**, 343–364. (doi:10.1007/s12110-004-1013-9)
- 6 Gurven, M. & von Rueden, C. 2006 Hunting, social status, and biological fitness. *Soc. Biol.* **53**, 81–99.
- 7 Chagnon, N. 1988 Life histories, blood revenge, and warfare in a tribal population. *Science* **239**, 985–992. (doi:10.1126/science.239.4843.985)
- 8 Hopcroft, R. 2006 Sex, status, and reproductive success in the contemporary United States. *Evol. Hum. Behav.* **27**, 104–120. (doi:10.1016/j.evolhumbehav.2005.07.004)
- 9 Kaplan, H. & Lancaster, J. 2000 The evolutionary economics and psychology of the demographic transition to low fertility. In *Evolutionary biology and human social behavior: 20 years later* (eds L. Cronk, N. Chagnon & W. Irons), pp. 283–322. Hawthorne, NY: Aldine de Gruyter.
- 10 Weeden, J., Abrams, M. J., Green, M. C. & Sabini, J. 2006 Do high status people really have fewer children? Education, income, and fertility in the contemporary U.S. *Hum. Nat.* **17**, 377–392. (doi:10.1007/s12110-006-1001-3)
- 11 Fieder, M. & Huber, S. 2007 The effects of sex and childlessness on the association between status and reproductive output in modern society. *Evol. Hum.*

- Behav.* **28**, 392–398. (doi:10.1016/j.evolhumbehav.2007.05.004)
- 12 Nettle, D. & Pollet, T. V. 2008 Natural selection on male wealth in humans. *Am. Nat.* **172**, 658–666. (doi:10.1086/591690)
- 13 Tooby, J. & Cosmides, L. 1990 On the universality of human nature and the uniqueness of the individual: the role of genetics and adaptation. *J. Pers.* **58**, 17–67. (doi:10.1111/j.1467-6494.1990.tb00907.x)
- 14 Gurven, M. & Hill, K. 2009 Why do men hunt? A re-evaluation of ‘Man the Hunter’ and the sexual division of labor. *Curr. Anthropol.* **50**, 51–74. (doi:10.1086/595620)
- 15 Hawkes, K., O’Connell, J. & Blurton Jones, N. 2001 Hunting and nuclear families: some lessons from the Hadza about men’s work. *Curr. Anthropol.* **42**, 681–709. (doi:10.1086/322559)
- 16 Hawkes, K., O’Connell, J. & Coxworth, J. 2010 Family provisioning is not the only reason men hunt. *Curr. Anthropol.* **51**, 259–264. (doi:10.1086/651074)
- 17 Henrich, J. & Gil-White, F. 2001 The evolution of prestige: freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evol. Hum. Behav.* **22**, 165–196. (doi:10.1016/S1090-5138(00)00071-4)
- 18 Boone, J. 1998 The evolution of magnanimity: when is it better to give than to receive? *Hum. Nat.* **9**, 1–21. (doi:10.1007/s12110-998-1009-y)
- 19 von Rueden, C., Gurven, M. & Kaplan, H. 2008 The multiple dimensions of male social status in an Amazonian society. *Evol. Hum. Behav.* **29**, 402–415. (doi:10.1016/j.evolhumbehav.2008.05.001)
- 20 Cowlshaw, G. & Dunbar, R. I. M. 1991 Dominance rank and mating success in male primates. *Anim. Behav.* **41**, 1045–1056. (doi:10.1016/S0003-3472(05)80642-6)
- 21 de Waal, F. 2000 In *Chimpanzee Politics: Power and Sex Among Apes* Baltimore: Johns Hopkins University Press.
- 22 Maynard Smith, J. & Price, G. R. 1973 The logic of animal conflict. *Nature* **246**, 15–18. (doi:10.1038/246015a0)
- 23 Hand, J. L. 1986 Resolution of social conflicts: dominance, egalitarianism, spheres of dominance, and game theory. *Q. Rev. Biol.* **61**, 201–220. (doi:10.1086/414899)
- 24 Smith, E. A., Bliege Bird, R. & Bird, D. 2003 The benefits of costly signaling: Meriam turtle hunters. *Behav. Ecol.* **14**, 116–126. (doi:10.1093/beheco/14.1.116)
- 25 Pawlowski, B. & Dunbar, R. I. M. 1999 Impact of market value on human mate choice decisions. *Proc. R. Soc. Lond. B* **266**, 281–285. (doi:10.1098/rspb.1999.0634)
- 26 Folstad, I. & Karter, A. 1992 Parasites, bright males, and the immunocompetence handicap. *Am. Nat.* **139**, 603–622. (doi:10.1086/285346)
- 27 Gangestad, S. & Simpson, J. 2000 On the evolutionary psychology of human mating: Trade-offs and strategic pluralism. *Behav. Brain Sci.* **23**, 573–587. (doi:10.1017/S0140525X0000337X)
- 28 Snyder, J., Kirkpatrick, L. & Barrett, C. 2008 The dominance dilemma: do women really prefer dominant men as mates? *Pers. Relat.* **15**, 425–444. (doi:10.1111/j.1475-6811.2008.00208.x)
- 29 Williams, G. 1975 In *Sex and Evolution* Princeton, NJ: Princeton University Press.
- 30 Marlowe, F. 2000 The patriarch hypothesis: an alternative explanation of menopause. *Hum. Nat.* **11**, 27–42. (doi:10.1007/s12110-000-1001-7)
- 31 Tovee, M. J., Maisey, D. S., Emery, J. L. & Cornelissen, J. L. 1999 Visual cues to female physical attractiveness. *Proc. R. Soc. Lond. B* **266**, 211–218. (doi:10.1098/rspb.1999.0624)
- 32 Howell, N. 1979 In *Demography of the Dobe !Kung* New York: Aldine.
- 33 Pawlowski, B. & Dunbar, R. I. M. 2005 WHR versus BMI as predictors of fitness in women. *Hum. Nat.* **16**, 164–177. (doi:10.1007/s12110-005-1002-7)
- 34 Fields, S. J. & Frisncho, A. R. 1993 Selection on maternal and neonatal size at birth. *Hum. Biol.* **65**, 579–591.
- 35 Gurven, M., Winking, J., Kaplan, H., von Rueden, C. & McAllister, L. 2009 A bioeconomic approach to marriage and the sexual division of labor. *Hum. Nat.* **20**, 151–183. (doi:10.1007/s12110-009-9062-8)
- 36 Marlowe, F. 2005 Mate preferences among Hadza hunter-gatherers. *Hum. Nat.* **15**, 364–375.
- 37 Gurven, M., Allen-Arave, W., Hill, K. & Hurtado, M. 2000 It’s a wonderful life: signaling generosity among the Ache of Paraguay. *Evol. Hum. Behav.* **21**, 263–282. (doi:10.1016/S1090-5138(00)00032-5)
- 38 Patton, J. Q. 2005 Meat sharing for coalitional support. *Evol. Hum. Behav.* **26**, 137–157. (doi:10.1016/j.evolhumbehav.2004.08.008)
- 39 Bickman, L. 1971 The effect of social status on the honesty of others. *J. Soc. Psychol.* **84**, 87–92. (doi:10.1080/00224545.1971.9918547)
- 40 Ball, S. & Eckel, C. 1998 The economic value of status. *The J. Soc. Econ.* **24**, 495–514. (doi:10.1016/S1053-5357(98)80004-8)
- 41 Chagnon, N. 1988 Male Yanomamo manipulations of kinship classifications of female kin for reproductive advantage. In *Human Reproductive Behavior: A Darwinian Perspective* (eds L. Betzig, M. B. Mulder & P. Turke), pp. 23–48. Cambridge: Cambridge University Press.
- 42 Chagnon, N. 1983 In *Yanomamo: The Fierce People* New York: CBS College Publishing.
- 43 Gurven, M., Kaplan, H. & Zelada Supa, A. 2007 Mortality experience of Tsimane Amerindians: regional variation and temporal trends. *Am. J. Hum. Biol.* **19**, 376–398. (doi:10.1002/ajhb.20600)
- 44 Helle, S., Lummaa, V. & Jokela, J. 2008 Marrying women 15 years younger maximized men’s evolutionary fitness in historical Sami. *Biol. Lett.* **4**, 75–78. (doi:10.1098/rsbl.2007.0538)
- 45 Kaplan, H. & Hill, K. 1985 Food sharing among Ache foragers: tests of explanatory hypotheses. *Curr. Anthropol.* **26**, 223–246. (doi:10.1086/203251)
- 46 Alvard, M. & Gillespie, A. 2004 Good Lamalera whale hunters accrue reproductive benefits. *Res. Econ. Anthropol.* **23**, 225–247. (doi:10.1016/S0190-1281(04)23009-8)
- 47 Hill, K. & Kintigh, K. 2009 Can anthropologists distinguish good and poor hunters? Implications for hunting hypotheses, sharing conventions, and cultural transmission. *Curr. Anthropol.* **50**, 369–377. (doi:10.1086/597981)
- 48 Gurven, M. *et al.* 2010 Domestication alone does not lead to inequality: intergenerational wealth transmission among horticulturalists. *Curr. Anthropol.* **51**, 49–64. (doi:10.1086/648587)
- 49 Scelza, B. 2010 Father’s presence speeds the social and reproductive careers of sons. *Curr. Anthropol.* **51**, 295–303. (doi:10.1086/651051)
- 50 Lansing, J., Watkins, J. C., Hallmark, B., Cox, M. P., Karafet, T. M., Sudoyo, H. & Hammer, M. F. 2008 Male dominance rarely skews the frequency distribution of Y chromosome haplotypes in human populations. *Proc. Natl Acad. Sci. USA* **105**, 11 645–11 650. (doi:10.1073/pnas.0710158105)
- 51 Zerjal, T. *et al.* 2003 The genetic legacy of the Mongols. *Am. J. Hum. Genet.* **72**, 717–721. (doi:10.1086/367774)
- 52 Smith, E. A. In press. Comment on Lansing, J. S. & Cox, M. The domain of replicators: selection, neutrality, and cultural evolution. *Curr. Anthropol.*