

Natural Selection on Male Wealth in Humans

Daniel Nettle* and Thomas V. Pollet†

Centre for Behaviour and Evolution, Newcastle University, Henry Wellcome Building, Framlington Place, Newcastle NE2 4HH, United Kingdom

Submitted March 31, 2008; Accepted June 17, 2008;
Electronically published September 22, 2008

Online enhancement: appendix.

ABSTRACT: Although genomic studies suggest that natural selection in humans is ongoing, the strength of selection acting on particular characteristics in human populations has rarely been measured. Positive selection on male wealth appears to be a recurrent feature of human agrarian and pastoralist societies, and there is some evidence of it in industrial populations, too. Here we investigate the strength of selection on male wealth, first in contemporary Britain using data from the National Child Development Study and then across seven other varied human societies. The British data show positive selection on male income driven by increased childlessness among low-income men but a negative association between personal income and reproductive success for women. Across cultures, selection gradients for male wealth are weakest in industrial countries and strongest in subsistence societies with extensive polygyny. Even the weakest selection gradients observed for male wealth in humans are as strong as or stronger than selection gradients reported from field studies of other species. Thus, selection on male wealth in contemporary humans appears to be ubiquitous and substantial in strength.

Keywords: natural selection, natural populations, humans, selection gradients, sexual selection.

Biologists have long been interested in measuring ongoing natural selection in wild populations (Endler 1986; Grant and Grant 1989; Hoekstra et al. 2001; Kingsolver et al. 2001). However, natural selection within human groups is rarely quantified, despite clear molecular signatures of ongoing selection in the human genome—selection that appears to have accelerated in the past few thousand years

(Reed and Aquadro 2006; Voight et al. 2006; Wang et al. 2006; Hawks et al. 2007). One trait on which phenotypic selection is likely to be acting is wealth. A consistent finding from many societies is that wealthier individuals, particularly men, have higher reproductive success than less wealthy ones (Borgerhoff Mulder 1987; Voland 1990; Cronk 1991; see Hopcroft 2006 for a review). Both anthropologists (Irons 1979) and historians (Clark and Hamilton 2006) have thus concluded that a fundamental feature of human societies is that men strive for cultural goals such as wealth and status in order to convert these achievements into reproductive success.

Studies of contemporary developed economies have produced an unclear picture of whether selection on male wealth is still operative. Some studies have found a null or even a negative relationship between socioeconomic status and reproductive success in men (Vining 1986; van den Berghe and Whitmeyer 1990; Perusse 1993), leading to the general view that modern societies are paradoxical from a Darwinian perspective (Vining 1986; Borgerhoff Mulder 1998). However, there are methodological and conceptual problems with the studies that demonstrate null or negative associations. Some of these studies (Vining 1986; Kanazawa 2003) include individuals who are in the midst of their reproductive careers and thus potentially confound differences in the timing of reproduction with differences in final reproductive success. Also, the measures used in these studies often fail to distinguish the effects of wealth, on the one hand, from education, on the other (Hopcroft 2006). This is significant because prolonging parental education may reduce the amount of time that can be devoted to reproduction, and increasing offspring education increases the per-offspring investment cost. Thus, one might expect smaller families in social strata whose members either have prolonged education themselves or who expect it for their children. Many measures of socioeconomic status are based on the prestige of a person's occupation, and thus they confound educational and wealth effects that may be operating in opposite directions.

A small number of studies have overcome these limitations. Hopcroft (2006) uses a probability sample of the U.S. population and measures individual income and ed-

* E-mail: daniel.nettle@ncl.ac.uk.

† E-mail: t.v.pollet@ncl.ac.uk.

ucation separately. This study shows that education and income do indeed work in opposite directions, with more education reducing offspring number for both sexes but a larger income causing offspring number to increase for men. Fieder and Huber (2007) show, for a representative sample of the Swedish population, that both education and income increase reproductive success for men but that increasing income is associated with fewer children for women. Another study has shown that, when educationally homogenous subsets of populations are considered (and education is thus controlled for), significant positive associations between income and reproductive success appear for men but not for women (Weeden et al. 2006). Thus, the best studies suggest that selection on male income is still occurring in contemporary industrial societies and that women display an opposite pattern.

The association between male income and reproductive success could arise in three ways. First, among those men who have one family, those with higher incomes could have more children. Second, higher-income men could be more likely to form a family in the first place, and thus the association would be driven by a disproportionate level of childlessness among low-income men. Third, men with high incomes might have an increased probability of forming second or subsequent families. In Fieder and Huber's (2007) study, the association between male income and reproductive success is accounted for entirely by the second mechanism, disproportionate childlessness in low-income men. They argue that this is due to low-income men having difficulty attracting spouses, which is plausible given the well-documented female preference for male resources (Buss 1989; Borgerhoff Mulder 1990; Pollet and Nettle 2008). Hopcroft (2006) suggests that the third mechanism (multiple family formation) might be important for the association between male wealth and reproductive success in her U.S. sample, but she is unable to test the hypothesis directly.

This study has two parts. In the first part, we investigate whether there is phenotypic selection acting on wealth in the contemporary British population, how the pattern differs between the sexes, and what mechanisms are involved. We use data from the National Child Development Study (NCDS), which is an ongoing longitudinal investigation of all the individuals who were born in the United Kingdom in a single week in March 1958. This design has the advantage of guaranteeing social representativeness of the sample. Indeed, strictly speaking, the NCDS is not a sample at all but is the entire British population of a particular narrow age band. There has been considerable loss to follow-up over the years, and this loss is not completely random with respect to socioeconomic status (Nettle 2003). However, the data set remains sizable and broadly representative. The NCDS also has the advantage that all

cohort members are exactly the same age, removing any need to statistically control for age. We examine income, education, and number of children at age 46 years. Fieder and Huber (2007) estimate that, in their Swedish cohort, more than 99% of all female reproduction and more than 96% of all male reproduction occurs before this age, and so the number of children reported is close to final lifetime reproductive success.

The second part of the study is comparative, both within and across species. If there is phenotypic selection on male wealth in contemporary Britain, how strong is it compared with the selection on male wealth in other industrial and in preindustrial societies? Moreover, how strong is it compared with selection that is typically observed by biologists working with other species in the field? Directional phenotypic selection can be usefully compared across studies by considering β , the standardized linear selection gradient (Kingsolver et al. 2001). This is the standardized slope of the regression relationship of the fitness measure (e.g., number of offspring) on the trait under selection (e.g., wealth). It is an important measure in evolutionary terms because, together with the heritability, it determines the response to selection. We compare estimated values of β on male wealth across eight societies with significant accumulable wealth (two ethnographic agrarian or pastoralist societies, three historical agrarian societies, and three contemporary industrial societies) and set these alongside recent estimates of the selection acting on male hunting ability in hunter-gatherer populations (Kaplan and Hill 1985; Marlowe 1999; Smith 2004; Gurven and von Rueden 2006). We then compare the selection gradients for male wealth in humans against a large set of selection gradients from other taxa drawn from the literature (Kingsolver et al. 2001).

Methods

NCDS

The NCDS began with a sociological and perinatal medical investigation of all the babies born in Britain during the period March 3–9, 1958 ($n = 17,416$). The cohort formed by these babies has been restudied in seven major "sweeps" consisting of parental, medical, or teacher reports and, especially more recently, self-reports by the cohort members themselves. It is possible to combine information from different sweeps using a unique identifier for each cohort member. Data reported here are derived mainly from NCDS7 (2004; cohort age, 46 years; $n = 11,939$), with additional material from NCDS6 (2000; cohort age, 42 years; $n = 10,979$) and NCDS5 (1991; cohort age, 33 years; $n = 10,986$). Degrees of freedom vary from analysis

to analysis because of missing data points within a survey or the individual not having participated in all relevant sweeps. Descriptive statistics for key variables are given in table A1 in the appendix in the online edition of the *American Naturalist*.

Number of children is a composite variable derived from responses to questions about biological children born or fathered in 1991, 2000, and 2004. Income is from 2004 and is based on responses to questions about take-home pay from employment or self-employment. The vast majority of cohort members had some form of employment or self-employment (92% of men, 83% of women). Note that individuals who are homemakers, are unemployed, or are acquiring an education are absent from the reporting of the income variable rather than being entered as zero. Income has been annualized (median income, £15,236) and is logged to reduce skewness.

The education variable is based on responses to questions in 2004 about highest academic qualification obtained. Here, we distinguish three groups: those with only academic qualifications usually acquired at age 16 (i.e., General Certificate of Secondary Education; $n = 6,477$), those with academic qualifications usually acquired at the age of 18 (i.e., A-levels; $n = 1,277$), and those with a university degree or equivalent ($n = 1,780$). More fine-grained classifications produce essentially the same results (data not shown).

To investigate patterns of relationship formation, we derive two additional variables. Marital situation is based on marital status in 2004 and divides the cohort into three groups: never married ($n = 691$), married once (still with first spouse; $n = 5,394$), and multiple marriages (either remarried or now cohabiting with someone other than first spouse; $n = 1,852$). Although marriage was overwhelmingly the norm in this cohort, the marital situation variable does entirely not account for unmarried cohabitations, so we also derive a second variable, cohabitations, which is a sum over responses from 1991, 2000, and 2004 of all reported lifetime cohabitations with a partner that lasted more than 1 month. We use general linear models and least squares regression to examine the effects of $\ln(\text{income})$ and education on number of children, and we use logistic regression for secondary analyses where the outcome is categorical (e.g., childlessness or marital status).

Comparative Analysis

The comparative analysis presented here has two parts. First, we identified 10 other studies in the literature that contain data that would allow for the estimation of a linear

selection gradient for male wealth or a related measure. Two studies in addition to ours were from representative samples of contemporary industrial populations (Hopcroft 2006; Fieder and Huber 2007). Three more were from historical studies of European and European-descended agrarian populations before industrialization (Mealey 1985; Roskaft et al. 1992; Clark and Hamilton 2006). Two more were from ethnographic studies of African subsistence societies, one agrarian and one pastoralist (Borgerhoff Mulder 1987; Cronk 1991). The final three studies came from ethnographically studied hunter-gatherer populations, where there is little accumulated wealth. However, for hunter-gatherers, there is a large quantity of literature showing relationships between male hunting ability and reproductive success (Kaplan and Hill 1985; Marlowe 1999; Smith 2004; Gurven and von Rueden, 2006), so we include estimated selection gradients on hunting ability for comparison. Standardized linear selection gradients (β) were taken directly from the papers, obtained from the authors of the studies, or calculated ourselves from data presented. All the coefficients were either from individuals at the end of their reproductive careers or from mixed-age samples for which age was statistically controlled. Sample size varied from a few dozen men in the ethnographic studies to thousands in the contemporary cohorts. Wealth was assessed in different ways and with varying precision in the different studies as a result of the large cross-cultural differences in economic system (see table A1; note that large stochastic variation in hunting returns makes the hunting ability β values particularly prone to error; K. Hill and K. Kintig, unpublished manuscript). However, because these are unitless coefficients, they can reasonably be informatively compared, despite the variation in study design and statistical procedures.

In the second part of the comparative analysis, we used the database of selection gradients observed in field populations provided by Kingsolver et al. (2001). These researchers performed a search of the literature from 1984 to 1997 for all reported estimates of selection strength in diverse species. The resulting database contains more than 2,500 estimates, from 62 species in 51 genera. Of these, 995 were standardized linear selection gradients and were thus directly comparable to those reported here for human male income. For these purposes, only the strength and not the direction of the gradients is important, and so we consider the absolute β values, henceforth $|\beta|$. First, we calculated where in the overall distribution of $|\beta|$ values our observations for human male wealth were located. Subsequently, because typical selection strength is different for fecundity, survival, and mating success (Kingsolver et al. 2001), we restricted the comparison to gradients where the measured component of fitness is fecundity or mating success.

Results

NCDS

Full results of general linear models are presented in table A2 in the appendix. For the whole cohort, using number of children as the dependent variable, sex and education as factors, and $\ln(\text{income})$ as a covariate, there are significant effects of sex ($F = 104.29$, $df = 1, 5,575$, $P < .01$) and education ($F = 5.15$, $df = 2, 5,575$, $P < .01$) but not of $\ln(\text{income})$ ($F = 0.18$, $df = 1, 5,575$, P value not significant). However, there are significant interactions between sex and education ($F = 3.61$, $df = 2, 5,575$, $P < .05$) and between sex and income ($F = 104.40$, $df = 1, 5,575$, $P < .01$). The sex effect is the result of women on average having more children than men (marginal means: women, 1.83 children; men, 1.66 children), whereas the education effect is the result of the least educated group having more children than the other groups (marginal means: 16 years of education, 1.82 children; 18 years of education, 1.70 children; degree achieved, 1.71 children). The sex-education interaction can be appreciated by comparing mean number of children in the most and least educated groups for men and for women. The most educated men have 0.09 fewer children than the least educated men, whereas the most educated women have 0.22 fewer children than the least educated women (table A3 in the appendix). Thus, an increased level of education has a greater negative effect on women's fertility than on men's.

The sex-income interaction is illuminated by regressing the number of children on $\ln(\text{income})$ separately in the male and the female halves of the cohort. For men, the relationship is significant and positive ($F = 23.93$, $df = 1, 2,592$, $P < .01$; $\beta = 0.10$), whereas for women it is significant and negative ($F = 97.38$, $df = 1, 2,987$, $P < .01$; $\beta = -0.18$). Because previous literature suggests that the effects of income may be seen most clearly within educationally homogenous subsets, we also carried out regressions separately for each sex in each educational group (table A3). The β values of $\ln(\text{income})$ were significant and positive in all three male education groups and were significant and negative in all three female groups (see fig. 1). Within each sex, none of the slopes differs significantly from the others and none differs from the slope obtained in the sample not divided by education.

In order to investigate the roles of family size, childlessness, and multiple family formation, we first repeated general linear models for each sex with $\ln(\text{income})$ and education as predictors and number of children as the dependent variable, but we excluded childless individuals. For men, neither $\ln(\text{income})$ ($F = 2.43$, $df = 1, 2,073$, P value not significant) nor education ($F = 1.27$, $df = 2, 2,073$, P value not significant) has a significant effect.

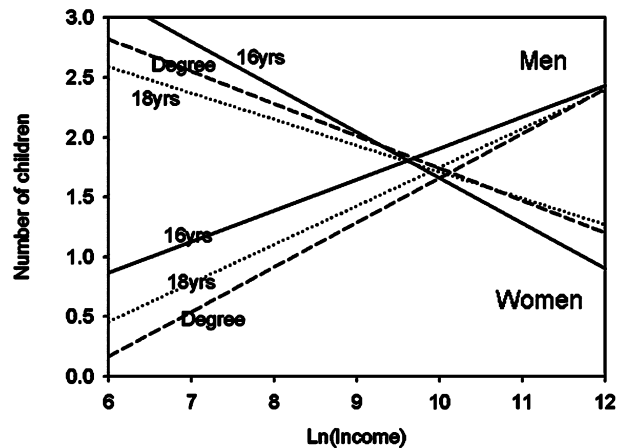


Figure 1: Plot of best-fit linear regression equations of number of children against natural log of income ($\ln[\text{income}]$), National Child Development Study data, for men and women of different education groups.

For women, $\ln(\text{income})$ does have a significant effect ($F = 6.73$, $df = 1, 2,505$, $P < .01$), but education does not ($F = 0.62$, $df = 1, 2,505$, P value not significant). This suggests that the effects of education on number of children in both sexes are driven by more education increasing the likelihood of childlessness.

We verified that this is the case using binomial logistic regression of childlessness on education and $\ln(\text{income})$ (table A4 in the appendix). More educated men were significantly more likely to be childless (odds ratio for childlessness in the most vs. the least educated group, 2.17; $P_{\text{Wald}} < .01$), and the same was true for women (odds ratio for childlessness in the most vs. the least educated group, 1.47; $P_{\text{Wald}} < .01$). The same regressions showed that increasing income significantly reduces the likelihood of childlessness for men (odds ratio for childlessness with each unit of $\ln[\text{income}]$, 0.43; $P_{\text{Wald}} < .01$). For women, it has the opposite effect, significantly increasing the likelihood of childlessness (odds ratio for childlessness with each unit of $\ln[\text{income}]$, 2.28; $P_{\text{Wald}} < .01$). Figure 2 illustrates the effects of income on childlessness for both sexes.

To examine whether income increases the probability of multiple family formation, we used multinomial logistic regression to test the effect of $\ln(\text{income})$ on marital situation (never married, first and only marriage, or multiple marriages; table A4). For men, the overall effect of $\ln(\text{income})$ is significant, which is accounted for by an increased $\ln(\text{income})$ sharply reducing the likelihood of never marrying compared with being in the first and only marriage category (odds ratio, 0.27; $P_{\text{Wald}} < .01$). Increasing $\ln(\text{income})$ does not significantly affect the odds of having multiple marriages versus having only one marriage (odds ratio, 0.85; P value not significant). For women, too, the

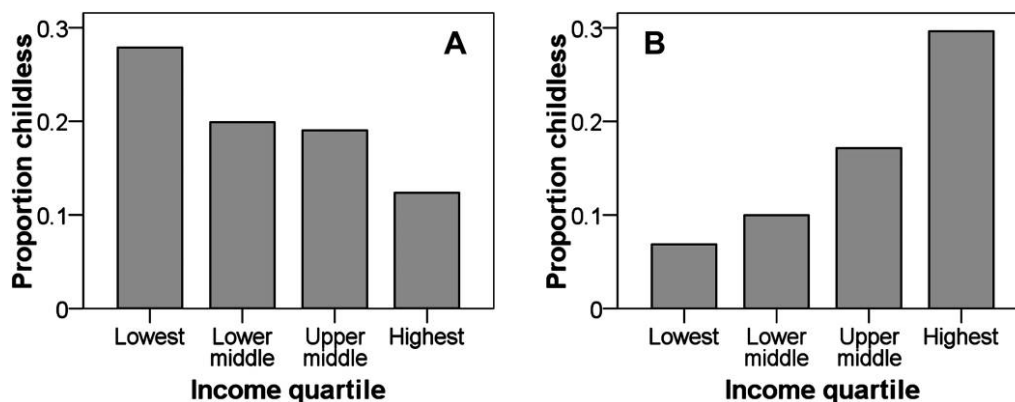


Figure 2: Proportion of (A) men and (B) women in the National Child Development Study who were childless in 2004, by for-sex quartile of income.

overall effect of $\ln(\text{income})$ is significant. This is due to $\ln(\text{income})$ increasing the likelihood of never marrying compared with having only one marriage (odds ratio, 1.85; $P_{\text{wald}} < .01$) and also increasing the likelihood of having multiple marriages compared with having only one marriage (odds ratio, 1.31; $P_{\text{wald}} < .01$). We performed the same analysis using reported cohabitations rather than marriages and achieved essentially identical results (data not shown).

Comparative Analysis

Table 1 shows the linear selection gradients (β) on male wealth calculated for eight agrarian and pastoralist societies plus the estimated β values on hunting ability for three hunter-gatherer groups. The β values from the three contemporary industrial societies are in the range 0.10–0.17, with a mean value of 0.13, which is lower than the historical and ethnographic societies. The historical European and European-descended agrarian societies have a mean gradient of 0.24 and the two remaining ethnographic societies, the Mukogodo pastoralists and the Kipsigis farmers of Kenya, produce the highest gradients, with a mean of 0.63 (see “Discussion”). The hunter-gatherer estimates for hunting ability are in the range 0.22–0.36, with a mean value of 0.30.

The β values for male wealth among individuals from contemporary industrial societies fall in the center of the cross-taxa $|\beta|$ distribution (forty-sixth percentile), whereas those from other societies are at the higher end (historical European, sixty-eighth percentile; polygynous African, ninety-fourth percentile; fig. 3A). The mean hunter-gatherer hunting ability gradient is at the seventy-sixth percentile of the cross-taxa distribution. Restricting the comparison to just the studies in Kingsolver et al.’s

(2001) database, which measured fecundity as the component of fitness, does not dramatically change these conclusions (contemporary industrial, forty-fifth percentile; historical European, sixty-eighth percentile; polygynous African, ninety-second percentile; fig. 3B). We additionally compared the $|\beta|$ values for male wealth in humans with those based on measurements of mating success in the cross-taxa database, because although our measure, strictly speaking, is one of fecundity, our interpretation is that variation in male fecundity is driven primarily by variation in mating success. This reduces the position of the contemporary industrial β values to the thirty-eighth percentile of the cross-taxa distribution and the historical European β values to the sixty-second percentile, with the polygynous African β values once again at the ninety-second percentile.

Discussion

NCDS

The results of the analysis of the NCDS show that increasing income has a significant positive effect on reproductive success in contemporary British men. This is partly offset by a negative effect on reproductive success of level of education achieved. However, the effect of income is significant even without partialing out educational differences. Thus, this study confirms comparable investigations demonstrating positive selection on male income in developed economies (Hopcroft 2006; Fieder and Huber 2007), contradicting earlier null or negative findings.

The pattern for women is very different from that for men. There is a strong negative relationship between education and reproductive success and also a negative relationship between income and reproductive success. It is

Table 1: Linear selection gradients on male wealth or male hunting ability across 11 different human societies

Characteristic, source	Population	Measurement	β	Comment
Male wealth:				
Borgerhoff Mulder 1987	Kipsigis agriculturalists	Land ownership	.68	Weighted mean for two oldest cohorts
Cronk 1991	Mukugodo pastoralists	Livestock	.58	Controlling for age
Røskaft et al. 1992	Norwegian farmers, 1700–1900	Agricultural resources	.32	From table 2
Clark and Hamilton 2006	English testators, 1540–1850	Assets in will	.18	Data (including some not in article) supplied by G. Clark; assets log transformed
Mealey 1985	Nineteenth-century Mormons	Wealth	.23	Middle value from three cohorts reported
Hopcroft 2006	Contemporary United States	Income	.12	Controlling for age
Fieder and Huber 2007	Contemporary Sweden	Income	.17	Number of children square-root transformed
NCDS data (this article)	Contemporary Britain	Income	.10	Income log transformed
Male hunting ability:				
Kaplan and Hill 1985	Aché	Hunting ability (weighed returns)	.31	From data in table 1 controlling for age
Marlowe 1999	Hadza	Hunting ability (ranked by peers)	.36	Controlling for age
Gurven and von Rueden 2006	Tsimane	Amount of meat acquired (kg)	.22	Controlling for age

Note: NCDS = National Child Development Study.

likely that the male and female patterns arise in different ways. The negative effects for women can mainly be interpreted as the results of trade-offs that women have to face if they desire children—for example, ceasing their education or working part-time to allow for motherhood (Marini 1984). For men, by contrast, a possible explanation of the income effect is female choice. A large portion of the literature that analyzes across many cultures has documented female preferences for men with resources (Buss 1989; Borgerhoff Mulder 1990; Pollet and Nettle 2008), and the increased probability of never being married or of having no cohabitations among men with low incomes in the NCDS is consistent with poorer men having difficulty attracting mates. Thus, the causal pathways to childlessness do indeed seem to be rather different for the two sexes (Keizer et al. 2007).

Note, however, that we cannot completely exclude the possibility of reverse causality from male reproductive success to income, with men with children seeking and gaining higher wages than those without. To do so would

require finer-grained longitudinal analyses than are possible using the data we have here. However, given earlier literature on wealth and marital transitions that point to an influence from income on marriage rather than the other way around, we feel this is an unlikely scenario (Nakosteen and Zimmer 1997; Burgess et al. 2003).

Although we found negative selection gradients on income for women, we note that this does not mean that women in households with lower incomes have higher reproductive success. Rather, women have to trade personal income generation for children. They may compensate for this by seeking mates with relatively high incomes; thus, the relationship between a woman’s reproductive success and her household’s income could be positive.

In the NCDS sample, the positive effects of male income on reproductive success were entirely due to a reduction in the probability of childlessness. This is similar to the findings for Sweden reported by Fieder and Huber (2007; cf. our fig. 2 with their fig. 1E). We did not find any evidence of high-income men increasing reproductive suc-

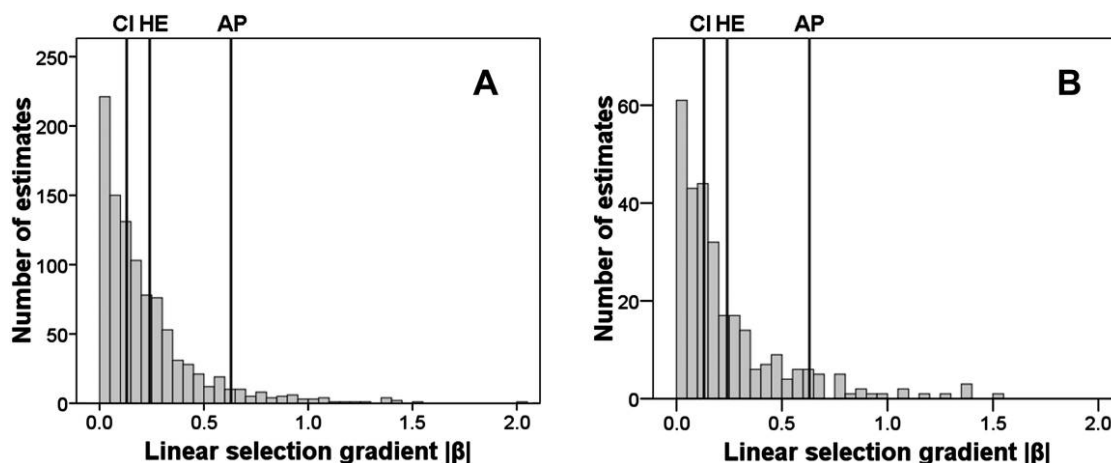


Figure 3: A, Position in the cross-taxa distribution of linear selection gradients ($|\beta|$) of selection on male wealth in contemporary industrial (CI), historical European (HE), and African polygynous (AP) human societies. B, Comparison restricted to $|\beta|$ values where the component of fitness measured is fecundity. Cross-taxa data are from Kingsolver et al. (2001).

cess with serial marriages. However, we note that there is still scope for additional male reproduction in this cohort, given that men generally have wives who are younger than they are. Indeed, the fact that the women in the cohort currently have more children than the men do suggests that this will occur. Thus, the data do not preclude the emergence of income-related multiple marriages in the next few years, which will strengthen the selection on male wealth.

Comparative Analysis

The intraspecific comparative analysis found that the strength of selection on male wealth for contemporary Britain is comparable to that of Sweden and the United States, but selection in all three industrial societies appears to be weaker than for preindustrial European populations and for two African societies. A potential confounding factor here is that, in the industrial societies, the measure is annual income, whereas in the other societies it is accumulated wealth. Although it is likely that there is a correlation between these two quantities, the former will be much noisier than the latter because of year-to-year income fluctuations. However, we assume that this difference is not entirely responsible for the lower coefficients in the industrial societies. Instead, it seems likely that the combination of effective monogamy and reduced variation in family size weakens selection on male wealth. Thus, there is some truth in the perception that the evolutionary dynamics of modern societies are different from preindustrial ones. However, the claim that modern societies represent a theoretical problem for Darwinian approaches to be-

havior (Vining 1986) is not realized. Men pursue status and resources in order to convert these into reproductive success, just as is the case in preindustrial contexts, and positive phenotypic selection on male wealth is still operative. Our results suggest that selection on male wealth is culturally and temporally ubiquitous in food-producing societies and is generally of comparable magnitude to selection on hunting ability found among hunter-gatherers.

Two selection gradients, from the Kipsigis and Mukogodo, were remarkably strong. These are both resource-based, polygynous African societies in which most of the large variance in male reproductive success is explained by variation in numbers of wives, which in turn is largely explained by men's holdings of land and cattle (Borgerhoff Mulder 1987; Cronk 1991). It is therefore not surprising that the effective selection on male wealth is so much higher in these groups than in the others, which are monogamous or more mildly polygynous.

The cross-species comparisons show that, even in contemporary industrial societies, the strength of selection on male wealth falls in the middle of the distribution of selection strengths ever measured by biologists, with the historical European societies above the middle of the distribution and the African polygynous societies in the top 10%. Thus, we conclude that ongoing phenotypic selection on male wealth is of substantial strength even in the most developed societies and has historically been rather strong in comparative terms.

General Implications

This study raises some general evolutionary issues. First, it shows that modern societies are only quantitatively, not

qualitatively, different from preindustrial ones. That is, the selective gradients on resources, at least for men, are attenuated but not abolished or reversed. This means that ultimate fitness-maximizing explanations of the kind espoused by behavioral ecologists may be more relevant to the dynamics of contemporary societies than is commonly assumed. The data also suggest considerable continuity between modern human societies and those of hunter-gatherers, where selection is on male hunting ability, and indeed between human societies and other species, where male rank is generally positively related to reproductive success (Ellis 1995).

The cross-cultural results reveal that phenotypic selection on human male wealth is pervasive wherever there are accumulable resources. The data presented here show this phenomenon for African herders and farmers, for 300 years of preindustrial English history, and for contemporary Britain, Sweden, and the United States. Of course, phenotypic selection produces evolutionary change only if the trait has some heritable basis. Information is lacking about whether genetic variation affects income-generating propensities across cultures, but estimates using twin and adoption studies suggest a moderate genetic heritability within industrial populations (Bowles and Gintis 2002; Bjorklund et al. 2006). This raises the interesting possibility that ongoing genetic evolution, as well as phenotypic selection, is related to male wealth in humans.

Acknowledgments

The NCDS is performed by the Centre for Longitudinal Studies, Institute of Education, London, which makes the data available to interested researchers. The cross-taxa database has kindly been made available by J. G. Kingsolver and colleagues. We are grateful to G. Clark, M. Fieder, and R. Hopcroft for their assistance in comparing our results with theirs and to K. Hill for sharing a prepublication manuscript with us.

Literature Cited

- Bjorklund, A., M. Lindahl, and E. Plug. 2006. The origins of inter-generational associations: lessons from Swedish adoption data. *Quarterly Journal of Economics* 121:999–1028.
- Borgerhoff Mulder, M. 1987. On cultural and reproductive success: Kipsigis evidence. *American Anthropologist* 89:617–634.
- . 1990. Kipsigis women's preferences for wealthy men: evidence for female choice in mammals. *Behavioral Ecology and Sociobiology* 27:255–264.
- . 1998. The demographic transition: are we any closer to an evolutionary explanation? *Trends in Ecology & Evolution* 13:266–270.
- Bowles, S., and H. Gintis. 2002. The inheritance of inequality. *Journal of Economic Perspectives* 16:3–30.
- Burgess, S., C. Propper, and A. Aassve. 2003. The role of income in marriage and divorce transitions among young Americans. *Journal of Population Economics* 16:455–475.
- Buss, D. M. 1989. Sex differences in human mate preferences: evolutionary hypotheses tested in 37 cultures. *Behavioral and Brain Sciences* 12:1–49.
- Clark, G., and G. Hamilton. 2006. Survival of the richest: the Malthusian method in pre-industrial England. *Journal of Economic History* 66:707–736.
- Cronk, L. 1991. Wealth, status and reproductive success among the Mukogodo of Kenya. *American Anthropologist* 93:345–360.
- Ellis, L. 1995. Dominance and reproductive success among non-human animals: a cross-species comparison. *Ethology and Sociobiology* 16:257–333.
- Endler, J. A. 1986. *Natural selection in the wild*. Princeton University Press, Princeton, NJ.
- Fieder, M., and S. Huber. 2007. The effects of sex and childlessness on the association between status and reproductive output in modern society. *Evolution and Human Behavior* 28:392–398.
- Grant, B. R., and P. R. Grant. 1989. Natural selection in a population of Darwin finches. *American Naturalist* 133:377–393.
- Gurven, M., and C. von Rueden. 2006. Hunting, social status and biological fitness. *Biodemography and Social Biology* 53:81–99.
- Hawks, J., E. T. Wang, G. M. Cochran, H. C. Harpending, and R. K. Moyzis. 2007. Recent acceleration of human adaptive evolution. *Proceedings of the National Academy of Sciences of the USA* 104:20753–20758.
- Hoekstra, H. E., J. M. Hoekstra, D. Berrigan, S. N. Vignieri, A. Hoang, C. E. Hill, P. Beerli, et al. 2001. Strength and tempo of directional selection in the wild. *Proceedings of the National Academy of Sciences of the USA* 98:9157–9160.
- Hopcroft, R. L. 2006. Sex, status and reproductive success in the contemporary United States. *Evolution and Human Behavior* 27:104–120.
- Irons, W. 1979. Cultural and biological success. Pages 257–272 in N. A. Chagnon and W. Irons, eds. *Evolutionary biology and human social behavior: an anthropological perspective*. Duxbury, North Scituate, MA.
- Kanazawa, S. 2003. Can evolutionary psychology explain reproductive behavior in the contemporary United States? *Sociological Quarterly* 44:291–302.
- Kaplan, H., and K. Hill. 1985. Hunting ability and reproductive success amongst male Aché foragers. *Current Anthropology* 26:131–133.
- Keizer, R., P. A. Dykstra, and M. D. Jansen. 2007. Pathways into childlessness: evidence of gendered life-course dynamics. *Journal of Biosocial Science* 35:213–226.
- Kingsolver, J. G., H. E. Hoekstra, J. M. Hoekstra, D. Berrigan, S. N. Vignieri, C. E. Hill, A. Hoang, et al. 2001. The strength of phenotypic selection in the natural populations. *American Naturalist* 157:245–261.
- Marini, M. M. 1984. Women's educational attainment and the timing of entry into parenthood. *American Sociological Review* 49:491–511.
- Marlowe, F. W. 1999. Showoffs or providers? the parenting effort of Hadza men. *Evolution and Human Behavior* 20:391–404.
- Mealey, L. 1985. The relationship between social and biological success: a case study of the Mormon religious hierarchy. *Ethology and Sociobiology* 6:249–257.
- Nakosteen, R. A., and M. A. Zimmer. 1997. Men, money and mar-

- riage: are high earners more prone than low earners to marry? *Social Science Quarterly* 78:66–82.
- Nettle, D. 2003. Intelligence and class mobility in the British population. *British Journal of Psychology* 94:551–561.
- Perusse, D. 1993. Cultural and reproductive success in industrial societies: testing the relationship at the proximate and ultimate levels. *Behavioral and Brain Sciences* 16:267–322.
- Pollet, T. V., and D. Nettle. 2008. Driving a hard bargain: sex ratio and male marriage success in a historical U.S. population. *Biology Letters* 4:31–33.
- Reed, F. A., and C. F. Aquadro. 2006. Mutation, selection and the future of human evolution. *Trends in Genetics* 22:479–484.
- Roskaft, E., A. Wara, and A. Viken. 1992. Human reproductive success in relation to resource access and parental age in a small Norwegian farming parish during the period 1700–1900. *Ethology and Sociobiology* 13:443–461.
- Smith, E. A. 2004. Why do good hunters have higher reproductive success? *Human Nature* 15:343–364.
- van den Berghe, P. L., and J. Whitmeyer. 1990. Social class and reproductive success. *International Journal of Contemporary Sociology* 27:29–48.
- Vining, D. R. 1986. Social versus reproductive success: the central theoretical problem of human sociobiology. *Behavioral and Brain Sciences* 9:167–187.
- Voight, B. F., S. Kudaravalli, X. Q. Wen, and J. K. Pritchard. 2006. A map of recent positive selection in the human genome. *PLoS Biology* 4:446–458.
- Voland, E. 1990. Differential reproductive success within the Krummhorn population (Germany, 18th and 19th century). *Behavioral Ecology and Sociobiology* 26:65–72.
- Wang, E. T., G. Kodama, P. Baidi, and R. K. Moyzis. 2006. Global landscape of recent inferred Darwinian selection for *Homo sapiens*. *Proceedings of the National Academy of Sciences of the USA* 103:135–140.
- Weeden, J., M. J. Abrams, M. C. Green, and J. Sabini. 2006. Do high-status people really have fewer children? education, income, and fertility in the contemporary U.S. *Human Nature* 17:377–392.

Associate Editor: Edmund D. Brodie III
Editor: Michael C. Whitlock