

NO EVIDENCE FOR THE GENERALIZED TRIVERS-WILLARD HYPOTHESIS FROM BRITISH AND RURAL GUATEMALAN DATA

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Abstract. In a series of recent papers, Kanazawa has extended the Trivers-Willard hypothesis by suggesting that possession of any heritable trait that improves male reproductive success to a greater extent than it does female reproductive success will lead to a male-biased offspring sex ratio (at the individual level). He produces supporting evidence that big and tall parents have more sons than daughters. Here we test this hypothesis using two large datasets from very different populations, one British and one from rural Guatemala. There was no support for Kanazawa's extension of the Trivers-Willard hypothesis in either sample. Maternal marital status was the only predictor of offspring sex ratio but this effect was very small and limited to the British sample. Results are discussed with reference to recent studies of sex-ratio variation in humans.

Keywords: anthropometry, generalized Trivers-Willard hypothesis, sex ratio, height, weight

INTRODUCTION

Over three decades ago, TRIVERS and WILLARD (1973) argued that natural selection could favour the ability to adjust the sex ratio of offspring as a function of parental phenotypic state. In addition, they argued that natural selection could favour the evolution of mechanisms for biasing post-birth investment in one sex or other, again contingent upon parental condition. We can therefore distinguish between Trivers-Willard effects in sex ratio at birth, and those in post-birth resource allocation (KELLER et al. 2001). There are three essential assumptions to the Trivers-Willard hypothesis (TWH; BROWN 2001; FRANK 1990; KOZIEL and ULJASZEK 2001; LAZARUS 2002; TRIVERS and WILLARD 1973). Firstly, the condition of the off-

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spring at the end of parental investment should be a reflection of the condition of the parents during the period of their investment. Secondly, the effect of parental investment should endure until parenthood. Finally, an advantage in condition should have a greater effect on male reproductive success than on female reproductive success.

TRIVERS and WILLARD (1973: 91) suggested that their hypothesis applied to humans: parents in good condition should have relatively more sons than daughters and invest more in sons than daughters. While some studies on resource allocation biasing have found effects in line with the Trivers-Willard hypothesis (for example: GAULIN and ROBBINS 1991; HOPCROFT 2005), others have failed to find any support for it (for example: FREESE and POWELL 1999, 2001; KELLER, NESSE and HOFFERTH 2001; MACE 1996). The evidence for biasing of offspring sex ratio is also equivocal. For example, a recent large study covering 48 million births showed that mothers in 'better condition', namely married and educated, were more inclined to bear sons rather than daughters and to have sons surviving until age one (ALMOND and EDLUND 2007). Other studies have also found support for sex ratio biasing in line with TWH, though mostly in non-Western societies. BERECZKEI and DUNBAR (1997) found that Hungarian gypsies, a relatively worse off group than the general Hungarian population, were more likely to bear daughters than sons. GIBSON and MACE (2003) found that mothers in better condition, as measured by upper arm muscle mass, were more likely to have sons rather than daughters. However, some studies have failed to find a link between parental status and offspring sex ratio (for example: ZALDIVAR, LIZARRALDE and BECKERMAN 1991) or have found only a negligible effect size (CHACON-PUIGNAU and JAFFE 1996). For non-human species, there is also ongoing debate on whether or not the Trivers-Willard hypothesis is supported (BROWN and SILK 2002; CAMERON 2004; LEIMAR 1996).

Recently, Kanazawa extended the Trivers-Willard hypothesis, by showing that big and tall parents have more sons than daughters (KANAZAWA 2005). He relates this to a generalised form of the TWH (henceforth gTWH), namely that if parents possess *any* heritable trait which increases male reproductive success to a greater extent than it does female reproductive success, they should be inclined to have relatively more sons than daughters (KANAZAWA 2005, 2006, 2007). For example, KANAZAWA (2006) showed that violent men typically have more sons than daughters. Doubt has been cast on the evidence KANAZAWA presented in support of the gTWH. While KANAZAWA (2005) found support for the prediction that big and tall cohort members had significantly more sons than daughters using the National Child Development Study, DENNY (2008) failed to find any evidence that male cohort members had bigger or taller parents than female cohort members using the same set. The validity of the statistics presented by KANAZAWA has also been debated (GELMAN 2007; GELMAN and WEAKLIEM 2007). In addition, there are various theoretical problems with the gTWH. For example, RICKARD (2008) highlighted that for gTWH to hold, offspring sex ratio has to be a heritable trait and this is at odds with population sex ratio theory.

The gTWH is, however, supported by MANNING and colleagues (1996) who found a relationship between maternal BMI and offspring sex ratio in a sample of 102 English women. The relationship between maternal waist-to-hip ratio and offspring sex was stronger than the relationship between maternal BMI and offspring sex ratio, however. In addition, a quadratic term of maternal BMI appears to predict offspring sex equally as well. GIBSON and MACE's (2003) Ethiopian data also supported Kanazawa's hypothesis: they found that heavier mothers were more likely to bear sons rather than daughters. STEIN and colleagues (2004), however, did not find conclusive evidence for a relationship between maternal BMI and offspring sex, using data covering entire Ethiopia. A recent study by HELLE (2008) using a sample of 324 Finnish women also corroborates Kanazawa's study, at least to a certain extent. HELLE (2009) found an interaction effect of maternal BMI and birth order as well as an interaction effect between maternal BMI and maternal age on offspring sex. If the mother was older and had a relatively high BMI, then the offspring was relatively more likely to be male. On the other hand, if there were previous births and the mother was relatively older, the offspring was relatively more likely to be female. However, HELLE (2009) did not find support for a main effect of weight on offspring sex.

In an epidemiological study covering 244 American women by TAMIMI and colleagues (2003) a significant relationship between maternal energy intake and offspring sex was found. Their data do not suggest a mediation of this relationship by maternal weight, however. They did find a marginally significant effect of maternal height on caloric intake, which in turn influences offspring sex. CAGNACCI and colleagues (2004) also found a positive relationship between weight gain during pregnancy and secondary sex ratio in a sample of over 10,000 Italian women. Women in the highest weight gain quartile were significantly more likely to bear sons than women in the lower weight gain quartiles. They also found that mothers with low pre-pregnancy weight were more inclined to bear daughters than sons. This relationship between weight gain during pregnancy and bearing a son was also supported by a recent study by MATHEWS and colleagues (2008). They did, however, not find any support for a relationship between maternal BMI and offspring sex. While there thus might be a positive relationship between maternal caloric intake and offspring sex, there is no conclusive evidence, however, for a positive relationship between maternal nutritional status, as measured by weight or BMI, and offspring sex (see review in LAZARUS 2002). In other mammals, there is also little evidence for a relationship between maternal weight and offspring sex ratio (CAMERON 2004; SHELDON and WEST 2004).

In this paper, we further test whether big and tall mothers tend to have relatively more sons than daughters. Tests of Kanazawa's hypothesis have been mostly limited to Western societies (DENNY 2008; HELLE 2009; KANAZAWA 2005). Here we test the hypothesis in two very different samples: one from Britain and one from rural Guatemala.

METHODOLOGY

We will present data relating to maternal but not paternal condition, as the data set from Guatemala only has information on mothers. Following KANAZAWA (2005), we will control for maternal age (here: at time of the survey), maternal marital status, educational attainment as well as ethnicity. We will test whether maternal height, weight or BMI predict offspring sex. As general health follows a curvilinear relationship with BMI (for example: ZHU et al. 2003), we will also explore whether a quadratic function of maternal BMI predicts offspring sex. The Trivers-Willard hypothesis leads us to predict a relationship between a quadratic function of BMI, reflecting good condition, and offspring sex. The generalized Trivers-Willard hypothesis, by contrast, predicts a linear relationship between BMI and the likelihood of bearing a son. We now describe the assumptions and the two samples in more detail.

Assumptions for the Generalized Trivers-Willard Hypothesis

We argue that the necessary assumptions for the Generalized Trivers-Willard hypothesis are met in both samples. Firstly, it is important to note that while the original Trivers-Willard hypothesis assumes that the parental condition is related to the offspring's condition (at the end of development), for the generalized Trivers-Willard hypothesis this is *not* the case. The trait under study does not need to relate parental condition: all that is required is that the trait influences male reproductive success to a greater extent than it does female reproductive success (KANAZAWA 2005). As KANAZAWA (2005) has argued before, it is reasonable to assume that height and weight influence male reproductive success to a greater extent than they do female reproductive success. This assumption certainly holds true for height in Britain. Male height is positively and linearly related to reproductive success, whereas female height is not linearly related to reproductive success (NETTLE 2002a–b). For Britain, the data suggest that while the relationship is curvilinear, the optimum lies below the mean: women who are shorter than the mean tend to have higher reproductive success than women of mean height. Thus, for Britain we can conclude that 'growing tall' is indeed more beneficial for male reproductive success than for female reproductive success. Unfortunately, no comparable data exist for Guatemala on the relationship between male height and reproductive success are available. However, data from Namibia, a population with demographic patterns close to the rural Guatemalan population, suggest that, in general, taller men tend to have higher reproductive success [KIRCHENGAST 2000; but see SEAR (2006) who did not find conclusive evidence for a linear relationship in a Gambian population]. For women this is not necessarily the case, studies have found positive linear, negative linear and curvilinear or even no relationships between maternal height and reproductive success in natural fertility populations (for example: *positive linear*: ALLAL et al. 2004; SEAR, ALLAL and MACE 2004; *negative linear*: DEVI, KUMARI and SRIKU-

MARI 1985; *curvilinear*: BRUSH, BOYCE and HARRISON 1983; MUELLER 1979; VETTA 1975; *no relationship*: LASKER and THOMAS 1976; KIRCHENGAST 2000). Studies covering (rural) Guatemala have either found a positive linear relationship between maternal height and reproductive success (MARTORELL et al. 1981) or have found curvilinear relationships between maternal height and reproductive success, with reproductive success maximization above the mean height (POLLET and NETTLE 2008). Across studies covering different populations, it is clear however, that while for males the relationship reproductive success tends to be positive and linear, for women this is not the case. This thus suggests that a linear increase in height would have stronger effect on male reproductive success than on female reproductive success. In addition, vignette studies and analyses of lonely heart advertisements show that women generally prefer a taller man over a shorter man as mate (GILLIS and AVIS 1980; HENSLEY 1994; SHEPPERD and STRATHMAN 1989). By contrast, tall women are not preferred over shorter women as a mate by men (HENSLEY 1994; SHEPPERD and STRATHMAN 1989; PAWLOWSKI and KOZIEL 2002). In summary, ‘growing tall’ appears to be more important for male reproductive success than for female reproductive success.

Little is known about whether male weight influences male reproductive success to a greater extent than it does female reproductive success. Studies by KIRCHENGAST and colleagues indicate that weight affects male reproductive success to a greater extent than it does female reproductive success in natural fertility populations (!Kung: KIRCHENGAST 2000; !Kung and Kavango: KIRCHENGAST and WINKLER 1996; WINKLER and KIRCHENGAST 1994). However, no comparable data exist for Guatemala and Britain.

Data from clinical studies do suggest, however, that even moderate obesity might have deleterious effects on female fecundity, pregnancy and pregnancy outcomes (for example: BAETEN, BUKUSI and LAMBE 2001; LINNÉ 2004; WANG, DAVIES and NORMAN 2002). These data also suggest that being overweight influences female fecundity to a greater extent than does being underweight. For men, by contrast, being underweight appears to affect semen quality to a greater extent than obesity does (JENSEN et al. 2004; QIN et al. 2007). Thus, while there is no data available on weight differentially affects male versus female reproductive success in Britain or Guatemala, clinical data as well as data from natural fertility populations suggest this assumption is reasonable. We thus concur with KANAZAWA that it is reasonable to assume, that *in general* males benefit to a greater extent from being ‘bigger and taller’ than women do in terms of reproductive success (KANAZAWA 2005).

British Dataset: The Millennium Cohort Study (MCS)

The Millennium Cohort Study is an ongoing, nationally representative study of pregnancy and child development (PLEWIS and KETENDE 2006; CLS, 2003). It contains data on 18,819 children born between 2000 and 2002 (HANSEN 2006). The response rate was 68% (% of individuals who agreed after being contacted). The data

we present below are from the first survey wave. The sample is disproportionately stratified, and ethnic minorities as well as respondents from deprived areas were oversampled (HANSEN 2006; PLEWIS 2004). We excluded twins from the analysis and coded maternal characteristics. The respondent was not measured but gave her own height and weight measures at the time of the interview. Previous studies have shown that in general self-reports of height by women tend to be reliable (CIZMECIOGLU et al. 2005; SPENCER et al. 2002). While there is very possibly a considerable error margin on these self-reported measures, there is no reason to assume that the dependent variable of interest (sex of offspring) is systematically related to these errors. Height and weight were converted to metric units and the maternal body mass index (BMI) was subsequently calculated. Ethnicity was recoded into five categories [White (English), Asian, Black, Mixed or Other]. Missing data points were treated listwise. Additional information about the sample can be found in the codebook of this study (HANSEN 2006).

In this set, we will test whether taller and bigger mothers are more likely to have given birth to a son than a daughter ($n = 10,354$ mothers). In addition, we will test whether taller and bigger mothers are more inclined to have more sons than daughters. From the dataset we derived the sex of the most recent born child and also of all ever born children based on which we calculated a son ratio statistic, which is the number of everborn sons divided by the number of everborn children ($n = 10,313$ mothers). Son ratio measures have been used before to study sex ratio biasing (e.g. POLLET et al. 2009).

Guatemalan Dataset: The Encuesta Guatemala de Salud Familiar (EGSF)

Our second sample is the Encuesta Guatemalteca de Salud Familiar of 1995 (EGSF; PEBLEY and GOLDMAN 1995). This is a cross-sectional study that collected data from 2,872 women between 18- and 35-year-old in rural Guatemala on a wide variety of economic, anthropometric, and sociodemographic variables. Data were collected in 1995 and participation rate in this survey was 89% (PETERSON, GOLDMAN and PEBLEY 1997). The Guatemalan population is strongly socially divided into two ethnic groups of more or less equal size (GLEI, GOLDMAN and RODRIGUEZ 2003; GOLDMAN and GLEI 2003). Only a fraction of the population, about 2% of the sample, does not identify themselves as being part of either group. The indigenous population consists of descendants of the Mayan and other pre-conquest populations, of which some only speak Mayan. The Ladina group is Spanish speaking and are of both pre-conquest population and European descent. The indigenous group is more socially excluded and poorer than the Ladina group. While the Ladina group can be found in all social strata of society, the indigenous group predominantly occupies the lowest social stratum. Guatemala was among the poorest countries in Latin America and the world at the time of the survey and this still remains the case (EDWARDS 2002; GRAGNOLATI and MARINI 2006; STEELE 1994). The majority of the population did not have appropriate access to affordable public health, sanitation,

potable water, and electricity at the time of the survey (GOLDMAN and GLEI 2003; PETERSON, GOLDMAN and PEBLEY 1997). The average household income was around 29 US\$ a month at the time of the survey. Compared to other countries in Latin America, infant and maternal mortality in Guatemala is high (49 per 1,000 and 190 per 1,000, respectively; WORLD BANK 1999 in GOLDMAN and GLEI 2003; for 2004: infant mortality is 45 per 1,000; WORLD HEALTH ORGANIZATION 2006).

Guatemala, especially the rural areas, is only just beginning the demographic and epidemiological transition (GOLDMAN, PEBLEY and BECKETT 2001; GRAGNOLATI and MARINI 2006). The total fertility rate has dropped from 5.8 in 1990 to 3.82 in 2006 (CIA 2006; UNPD 2005). The demographics of this rural population are thus useful to study reproductive patterns of a natural fertility population in a vastly different environment from the first sample. This sample has been widely used for the study of provision health care (GLEI, GOLDMAN and RODRIGUEZ 2003; GOLDMAN and GLEI 2003), beliefs about illness (GOLDMAN, PEBLEY and BECKETT 2001; HEUVELINE and GOLDMAN 2000) and female reproductive success (POLLET and NETTLE 2008). Additional information on the sample can be found in the codebook or in these previously published articles. We tested whether maternal height, weight or BMI predicted the sex of the firstborn child. Height and weight were measured at the time of the interview (PETERSON, GOLDMAN and PEBLEY 1997) and BMI was calculated. In this set we also tested whether height, weight and maternal BMI predicted the respondent's son ratio (number of ever born sons / number of ever born children) as we did for the MCS. In the analyses we will control for number of years in education, marital status and ethnicity (Ladina or indigenous). Missing data points were treated listwise. The final sample consisted of 1,888 women.

Statistical Analyses

For both datasets, we used binomial logistic regression to analyze the likelihood of having given birth to a son instead of having given birth to a daughter. Binomial logistic regression as a statistical technique is relatively free of assumptions and statistically robust (HOSMER and LEMESHOW 1989; MENARD 1995; PAMPEL 2000). Unlike ordinary least square regression (OLS), parameters are estimated by maximum likelihood. As a parameter selection procedure we used backward stepwise. Model outcomes were not different in terms of model fit and Nagelkerke R^2 (NAGELKERKE 1991) when forward stepwise was used instead. Here we will report the likelihood ratio tests for variables (p_{LIR}) in the model and the parameter estimates for the models (see PENG et al. 2002). Given that these are dichotomous data, binomial logistic regression is a preferred technique over Generalized Linear Mixed Models (GLMM's) which requires the dependent to be interval.

Generalized Linear Mixed Modelling was used to examine the ratio of (ever-born) sons to total number of (everborn) children in the EGFS. The models had absolute parameter and loglikelihood convergence and parameters were estimated by Restricted Maximum Likelihood (SPSS, 2005; see VERBEKE and MOLENBERGHS

2000). We first examined baseline models with no random effects, then constructed models with a random intercept and subsequently models with random intercepts and random slopes. We used an unstructured covariance matrix for the random effects (LITELL, PENDERGAST and NATARAJAN 2000). We selected the final model based on Schwarz's Bayesian Information Criterion (BIC) (smaller-is-better; we also examined AIC: see, KUHA 2004). This model could be a baseline model without random effects, have a random intercept or have a random intercept and random slope(s). Only significant parameters were retained for the final model (based on F-test).

As height, weight and BMI covary substantially, we could not simultaneously enter them into a model. Instead, for each data set, we test three models in sequence, the first with maternal height plus the control variables, the second with maternal weight plus the control variables, and the third with maternal BMI plus the control variables.

RESULTS

MCS

The descriptive statistics for the British sample are summarized in *Table 1*.

Table 1. Descriptive statistics (frequencies or means and standard deviations) for the British MCS sample

Millennium cohort study		
Educational attainment	Higher degree	355
	First degree	1316
	Diplomas in higher education	906
	A / AS / S levels	875
	O level / GCSE grades A–C	3463
	GCSE grades D–G	1205
	Other academic qualifications (incl. overseas)	336
	None of these qualifications	1878
	Missing	20
Marital status	Legally separated	278
	Married, 1st and only marriage	5897
	Remarried, 2nd or later marriage	444
	Single never married	3290
	Divorced	428
	Widowed	17
Ethnicity	Other	439
	Mixed	129
	Asian	1409
	Black	495
	White	7883
Age	(years)	29.83 (+/- 5.88)
BMI	(kg/m ²)	24.74 (+/- 4.86)
Weight	(kg)	66.22 (+/- 13.66)
Height	(m)	1.64 (+/- 0.07)
Cohort member	Daughter	5080
	Son	5275
Son Ratio		0.51 (+/- 0.41)

1. Maternal Height

Using binomial logistic regression to examine the relationship between maternal height, the control variables and sex of cohort child, none of the proposed variables predicted the sex of the cohort member (p_{llr} ; all $p > 0.2$), with the exception of marital status, which was marginally significant ($\chi^2 = 10.72$; p_{llr} : 0.057). Legally separated, remarried and single mothers were more inclined to have a son than a daughter as compared to married mothers (respectively: OR(legally separated): 1.245; $\chi^2 = 3.15$; $p = 0.076$; OR(remarried): 1.2; $\chi^2 = 3.43$; $p = 0.064$; OR(single): 1.09; $\chi^2 = 4.04$; $p = 0.044$). However, the variance explained by marital status was minimal (Nagelkerke $R^2 = 0.001$). Maternal height did not predict the cohort member's sex at all ($\chi^2 = 0.001$; $df = 1$; $p_{llr} = 0.99$; *Figure 1*).

In the linear mixed model, none of the variables predicted son ratio (all F-tests; $p > 0.6$), with the exception of maternal marital status ($F_{(5,10327)} = 1.92$; $p = 0.087$). Similar to the binomial regression, we found that remarried women tended to have relatively more sons than daughters in comparison to married women ($\beta = 0.03$; $t_{(10327)} = 1.86$; $p = 0.06$). Single women also tended to have relatively more sons than daughters in comparison to married women ($\beta = 0.03$; $t_{(10327)} = 2.25$; $p = 0.02$). The other comparisons were not significant (t -tests; all $p > 0.3$). Maternal height did not predict son ratio at all ($F_{(1,10326)} = 0.18$; $p = 0.67$). A quadratic function of height also did not predict son ratio ($F_{(1,10326)} = 0.15$; $p = 0.69$).

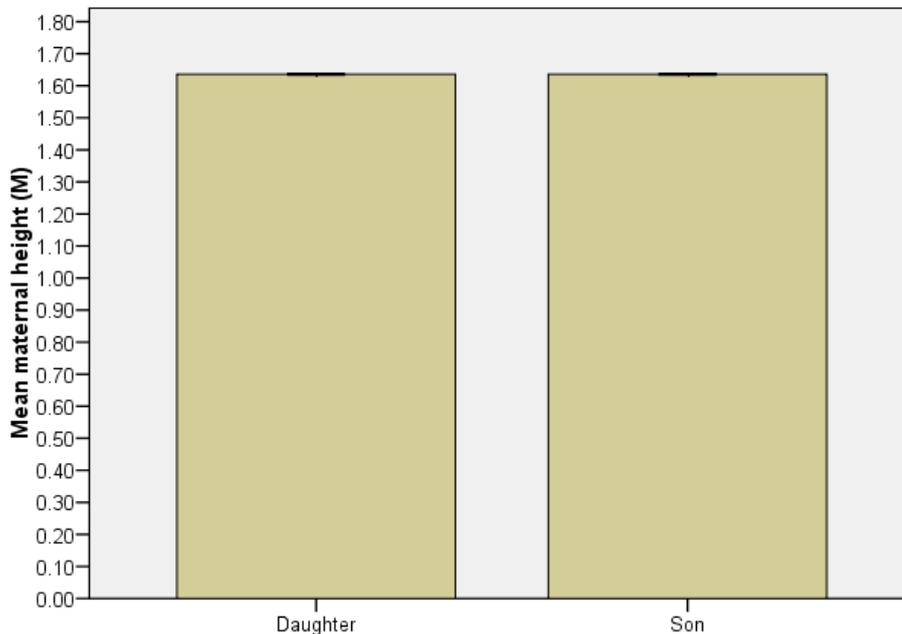


Figure 1. Relationship between maternal height and offspring sex in the Millennium Cohort Study (bars represent 95% confidence interval)

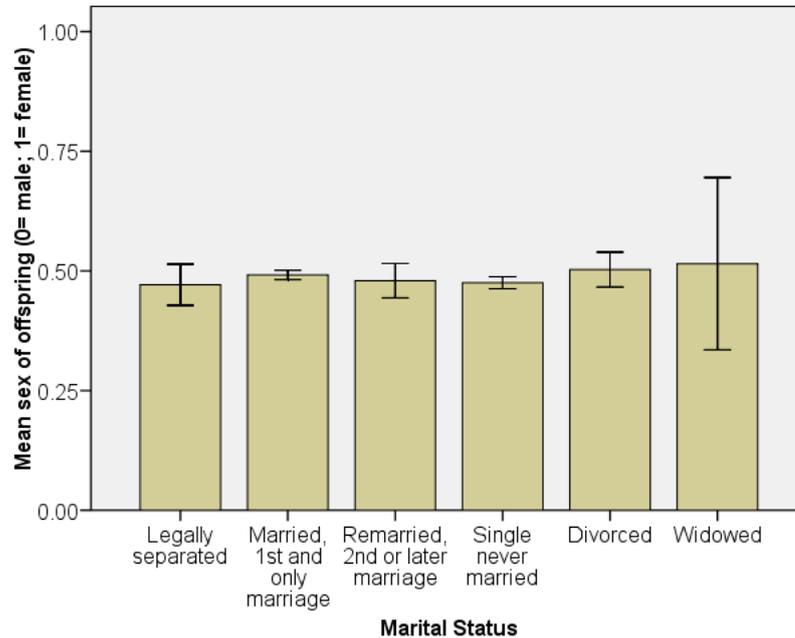


Figure 2. Relationship between maternal marital status and sex of child (0 = male; 1 = female) in the Millennium Cohort Study (bars represent 95% confidence interval)

2. Maternal Weight

Maternal weight did not predict the cohort member's sex in the binomial logistic regression model ($\chi^2 = 0.23$; $df = 1$; $p = 0.63$). As with the analyses for height, none of the variables predicted the sex of the cohort member (χ^2 tests; all $p > 0.2$), except for marital status for which the effect is described above. In the linear mixed model, none of the variables predicted son ratio (all F-tests; $p > 0.6$), with the exception of maternal marital status for which the effect is described above. Maternal weight did not predict son ratio at all ($F_{(1,10326)} = 0.09$; $p = 0.76$).

3. Maternal BMI

As with the analyses for height, none of the variables predicted the sex of the cohort member (χ^2 tests; all $p > 0.2$), except for marital status, for which the effect is described above. BMI did not predict the cohort member's sex at all ($\chi^2 = 0.37$; $df = 1$; $p = 0.55$). In the linear mixed model, none of the variables predicted son ratio (all F-tests; $p > 0.6$), with the exception of maternal marital status for which the effect is described above. Maternal BMI did not predict son ratio at all ($F_{(1,10326)} = 0.11$;

$p = 0.73$). A quadratic term of BMI also failed to predict son ratio ($F_{(1,10326)} = 0.14$; $p = 0.71$).

EGSF

The descriptive statistics for the Guatemalan sample are summarized in *Table 2*.

Table 2. Descriptive statistics (frequencies or means and standard deviations) for the Guatemalan EGSF sample

Encuesta General de Salud Familiar		
Educational attainment	(years)	1.98 (+/-2.08)
Marital status	Married	1248
	In a union	477
	Widowed	20
	Divorced	2
	Separated	80
	Single	61
Ethnicity	Ladina	689
	Indigenous	1199
Age	(years)	26.93 (+/-4.89)
BMI	(kg/m ²)	23.19 (+/-3.51)
Weight	(kg)	50.27 (+/-8.83)
Height	(m)	1.47 (+/-0.06)
Sex of firstborn child	Male	980
	Female	908
Son ratio		0.5 (+/-0.33)

1. Maternal Height

None of the proposed variables predicted the sex of the firstborn child (χ^2 tests; all $p_{lr} > 0.2$), except for age ($\chi^2 = 2.75$; $df = 1$; $p = 0.097$) in the binomial logistic regression. Elder women were more inclined to have a daughter, instead of a son (OR(increase by a year) = 1.02; $\chi^2 = 2.75$; $p = 0.097$). Height did not predict sex of the firstborn child ($\chi^2 = 1.59$; $df = 1$; $p = 0.21$).

None of the proposed variables predicted son ratio in the Generalized Linear Mixed Model containing maternal height and the control variables (F-tests; all $p > 0.15$). Height did not predict son ratio at all ($F_{(1,1886)} = 0.09$; $p > 0.75$; *Figure 3*).

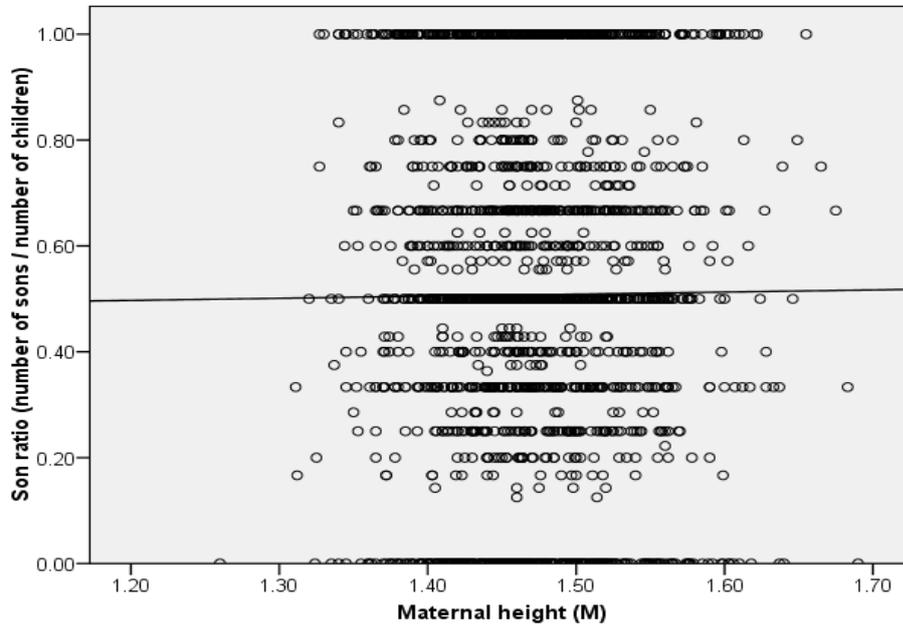


Figure 3. Relationship between maternal height and offspring sex ratio in the Encuesta Guatemala de Salud Familiar. Line represents ordinary least squares regression fit line

2. Maternal Weight

As in the previous model, maternal age predicted sex of the firstborn child. Weight also tended to predict sex of the first child ($\chi^2 = 3.74$; $df = 1$; $p = 0.053$). The effect was, however in the opposite direction than predicted. Heavier women were more inclined to have a daughter rather than a son (OR(increase by one kg): 1.002; $\chi^2 = 3.42$; $df = 1$; $p = 0.064$). None of the proposed variables predicted son ratio (F-test; all $p > 0.15$). Weight did not predict son ratio at all ($F_{(1,1886)} = 0.136$; $p > 0.7$).

3. Maternal BMI

As described above, maternal age predicted sex of the firstborn child. Maternal BMI did not predict sex of the firstborn child at all ($\chi^2 = 0.23$; $df = 1$; $p = 0.63$). A squared term of BMI also did not predict sex of the firstborn child ($\chi^2 = 0.44$; $df = 1$; $p = 0.5$). None of the proposed variables predicted son ratio (F-tests; all $p > 0.15$). BMI did not predict son ratio at all ($F_{(1,1886)} = 0.253$; $p > 0.6$). A quadratic term of BMI did not predict son ratio at all ($F_{(1,1886)} = 0.46$; $p > 0.49$).

DISCUSSION

There was no support for the generalized Trivers-Willard hypothesis in two very different samples. Maternal height, weight and BMI did not predict bearing relatively more sons than daughters at all in either sample. There was also no evidence that a quadratic term of BMI predicted offspring sex. Unlike GIBSON and MACE (2003) we thus did not find any support that heavier women are more likely to have sons rather than daughters. The effect found by GIBSON and MACE (2003) of maternal BMI on offspring sex ratio was quite sizeable but there appears to be no evidence for any effect whatsoever in this larger dataset from rural Guatemala. The conditions in rural Ethiopia at the time of their survey were far more adverse than in rural Guatemala, however (see STEIN, BARNETT and SELLEN 2004). CAGNACCI and colleagues (2004) also found evidence that heavier mothers were more inclined to have sons than daughters in an Italian sample. However, their study showed only a very small effect size of maternal weight on offspring sex (see GELMAN and WEAKLIEM 2007). It appears that, if we can expect any effect of maternal condition as measured by height, weight or body mass index on offspring sex ratio in populations under conditions of adequate subsistence, it will likely be very small in magnitude. The effects previously found by KANAZAWA (2005) are possibly due to chance and/or selection bias (GELMAN 2007).

This study, along with DENNY (2008), thus fails to find any support for the gTWH. Further testing with different sets from populations across various human ecologies are necessary, but for now we can conclude that there is very little evidence for KANAZAWA's (2005) claim that bigger and taller mothers would be more inclined to have sons rather than daughters. In addition, it is necessary to point out that other theories apart from KANAZAWA's (2005) generalized Trivers-Willard hypothesis might lead to similar predictions about offspring sex ratio variation, for example, the Maternal Dominance hypothesis (e.g. Grant, 1994).

Contrary to other studies on Trivers-Willard effects of parental status (for example: CHACON-PUIGNAU and JAFFE 1996), we find no evidence that educational attainment predicts offspring sex ratio. The lack of evidence for an effect of maternal educational attainment on the sex of offspring at birth appears to be in line with recent evidence from a large study (ALMOND and EDLUND 2007). This study, covering 48 million births, shows that while maternal educational attainment strongly influenced sex specific mortality rates, the effect of educational attainment on sex ratio at birth was significant but considerably smaller than the effect on mortality rates (ALMOND and EDLUND 2007). This study found a trend for maternal marital status on sex ratio in the British sample, but it is in the opposite direction compared to ALMOND and EDLUND'S (2007) findings: that is, we find more sons amongst unmarried as opposed to married women. It is possible however, that this effect is an artefact of the disproportionate sampling of relatively worse-off groups in the MCS. Further studies are necessary to establish whether or not this finding holds true.

In conclusion, we have presented evidence that there is no relationship between maternal weight, height and BMI on sex ratios at birth in two large samples. Together with another study (DENNY 2008) as well as the statistical critiques on KANAZAWA's work (GELMAN 2007; GELMAN and WEAKLIEM 2007), there thus appears to be relatively little empirical support for the Generalized Trivers-Willard Hypothesis. Further research, covering more populations from different ecologies, is however necessary to dismiss the Generalized Trivers-Willard Hypothesis.

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REFERENCES

- ALLAL, N., SEAR, R., PRENTICE, A. & MACE, R. (2004): An evolutionary analysis of stature, age at first birth and reproductive success in Gambian women. *Proceedings Royal Society London B: Biological sciences*, 271, 465–470.
- ALMOND, D. & EDLUND, L. (2007): Trivers–Willard at birth and one year: evidence from US natality data 1983–2001. *Proceedings Royal Society London B: Biological Sciences*, 274, 2491–2496.
- BAETEN, J. M., BUKUSI, E. A. & LAMBE, M. (2001): Pregnancy complications and outcomes among overweight and obese nulliparous women. *American Journal of Public Health*, 91, 436–440.
- BERECZKEI, T. & DUNBAR, R. I. M. (1997): Female-biased reproductive strategies in a Hungarian Gypsy population. *Proceedings Royal Society London B: Biological Sciences*, 264, 17–22.
- BROWN, G. R. (2001): Sex-biased investment in nonhuman primates: Can Trivers & Willard's theory be tested. *Animal Behaviour*, 61, 683–694.
- BROWN, G. R., SILK, J. B. (2002): Reconsidering the null hypothesis: Is maternal rank associated with sex ratios in primate groups? *Proceedings of the National Academy of Sciences (USA)*, 99, 11252–11255.
- BRUSH, G., BOYCE, A. J. & HARRISON, G. A. (1983): Associations between anthropometric variables and reproductive performance in a Papua New Guinea highland population. *Annals of Human Biology*, 10, 223–234.

- CAGNACCI, A., RENZI, A., ARANGINO, S., ALLESANDRINI, C. VOLPE, A. (2004): Influences of maternal weight on the secondary sex ratio of human offspring. *Human Reproduction*, 19, 442–444.
- CAMERON, E. Z. (2004): Facultative adjustment of mammalian sex ratios in support of the Trivers-Willard hypothesis: evidence for a mechanism. *Proceedings Royal Society London B: Biological Sciences*, 271, 1723–1728.
- CHACON-PUIGNAU, G. C. & JAFFE, K. (1996): Sex ratio at birth deviations in modern Venezuela: The Trivers-Willard effect. *Social Biology*, 43, 257–270.
- CIZMECIOGLU, F., DOHERTY, A., PATERSON, W. F., YOUNG, D., DONALDSON, M. D. C. (2005): Measured versus reported parental height. *Archives of Diseases in Childhood*, 90, 941–942.
- CIA (2006): *CIA World Fact Book*. Washington: CIA.
- CENTRE FOR LONGITUDINAL STUDIES (CLS) (2003): *Millennium Cohort Study, First Survey: CAPI Questionnaire Documentation*. London: Institute of Education (University of London).
- DENNY, K. (2008): Big and tall parents do not have more sons. *Journal of Theoretical Biology*, 250, 752–753.
- DEVI, M. R., KUMARI, J. R., SRIKUMARI, C. R. (1985): Fertility and mortality differences in relation to maternal body size. *Annals of Human Biology*, 12, 479–484.
- EDWARDS, J. (2002): *Education and Poverty in Guatemala. Technical Paper No. 3*. Washington, D.C.: The World Bank.
- FRANK, S. A. (1990): Sex allocation theory for birds and mammals. *Annual Review of Ecology and Systematics*, 21, 13–55.
- FREESE, J. & POWELL, B. (1999): Sociobiology, status, and parental investment in sons and daughters: Testing the Trivers-Willard Hypothesis. *American Journal of Sociology*, 104, 1704–1743.
- FREESE, J. & POWELL, B. (2001): Making love out of nothing at all: Null findings and the Trivers-Willard Hypothesis. *American Journal of Sociology*, 106, 1776–1788.
- GAULIN, S. J. C. & ROBBINS, C. J. (1991): Trivers-Willard effect in contemporary North-American society. *American Journal Physical Anthropology*, 85, 61–69.
- GELMAN, A. (2007): Letter to the editors regarding some papers of Dr. Satoshi Kanazawa. *Journal of Theoretical Biology*, 245, 597–599.
- GELMAN, A. & WEAKLIEM, D. (2007). Of beauty, sex, and power: Statistical challenges in estimating small effects, [http://www.stat.columbia.edu/~gelman/research/unpublished/ power.pdf](http://www.stat.columbia.edu/~gelman/research/unpublished/power.pdf) consulted online (8–3–2008).
- GIBSON, M. A. & MACE, R. (2003): Strong mothers bear more sons in rural Ethiopia. *Proceedings Royal Society London B: Biological Sciences*, 270, S108–S109.
- GILLIS, J. S. & AVIS, W. E. (1980): The male-taller norm in mate selection. *Personality and Social Psychology Bulletin*, 6, 396–401.
- GLEI, D. A., GOLDMAN, N. & RODRIGUEZ, G. (2003): Utilization of care during pregnancy in rural Guatemala. *Social Science and Medicine*, 57, 2447–2463.
- GOLDMAN, N. & GLEI, D. A. (2003): Evaluation of midwifery care: results from a survey in rural Guatemala. *Social Science and Medicine*, 56, 685–700.
- GOLDMAN, N., PEBLEY, A. R. & BECKETT, M. (2001): Diffusion of ideas about personal hygiene and contamination in poor countries: evidence from Guatemala. *Social Science and Medicine*, 52, 53–69.
- GRAGNOLATI, M. & MARINI, A. (2006): Health and poverty in Guatemala technical paper no. 5. *World Bank working paper (36206)*.
- GRANT, V. J. (1994): Maternal dominance and the conception of sons. *British Journal of Medical Psychology*, 67, 343–351.
- HELLE, S. (2008): Height, weight, body mass index and offspring sex at birth in contemporary Finnish women. *Journal of Theoretical Biology*, 252, 273–275.

- HENSLEY, W. E. (1994): Height as a basis for interpersonal attraction. *Adolescence*, 29, 469–474.
- HEUVELINE, P. & GOLDMAN, N. (2000): A description of child illness and treatment behavior in Guatemala. *Social Science and Medicine*, 50, 345–364.
- HOPCROFT, R. L. (2005): Parental status and differential investment in sons and daughters: Trivers-Willard revisited. *Social Forces*, 83, 1111–1136.
- HANSEN, K. (ed.) (2006): *Millennium Cohort Study: First and Second Surveys. A Guide to the Datasets*. Institute of Education (University of London), London.
- HOSMER, D. & LEMESHOW, S. (1989): *Applied Logistic Regression*. New York, Wiley & Sons.
- JENSEN, T. K., ANDERSSON, A.-M., JØRGENSEN, N., ANDERSEN, A.-G., CARLSEN, E. & PETERSEN, J. H. et al. (2004): Body mass index in relation to semen quality and reproductive hormones among 1,558 Danish men. *Fertility and Sterility*, 82, 863–870.
- KANAZAWA, S. (2005): Big and tall parents have more sons: further generalizations of the Trivers-Willard Hypothesis. *Journal of Theoretical Biology*, 235, 583–590.
- KANAZAWA, S. (2006): Violent men have more sons: Further evidence for the generalized Trivers-Willard Hypothesis (gtwh). *Journal of Theoretical Biology*, 239, 450–459.
- KANAZAWA, S. (2007): Beautiful parents have more daughters: A further implication of the generalized Trivers-Willard Hypothesis (gTWH). *Journal of Theoretical Biology*, 244, 133–140.
- KELLER, M. C., NESSE, R. M. & HOFFERTH, S. (2001): The Trivers-Willard hypothesis of parental investment: No effect in the contemporary United States. *Evolution and Human Behavior*, 22, 343–360.
- KIRCHENGAST, S. (2000): Differential reproductive success and body size in !Kung San people from northern Namibia. *Collegium Anthropologicum*, 24, 121–132.
- KIRCHENGAST, S. & WINKLER, E. M. (1995): Differential reproductive success and body dimensions in Kavango males from urban and rural areas in Northern Namibia. *Human Biology*, 67, 291–309.
- KIRCHENGAST, S. & WINKLER, E.M. (1996): Differential fertility and body build in !Kung San and Kavango females from northern Namibia. *Journal of Biosocial Science*, 28, 193–210.
- KOZIEL S. & ULJASZEK, S. J. (2001): Waiting for Trivers and Willard: Do the rich really favor sons? *American Journal of Physical Anthropology*, 115, 71–79.
- KUHA, J. (2004): AIC and BIC: comparisons of assumptions and performance. *Sociological Methods and Research*, 33, 188–229.
- LASKER, G.W. & THOMAS, R. (1976): Relationship between reproductive fitness and anthropometric dimensions in a Mexican Population. *Human Biology*, 48, 775–791.
- LAZARUS, J. (2002): Human sex ratios: adaptations and mechanisms, problems and prospects. In: Hardy, I. C. W.: *Sex Ratios: Concepts and Research Methods*. Cambridge, Cambridge University Press, pp. 287–311.
- LEIMAR, O. (1996): Life history analysis of the Trivers-Willard sex-ratio problem. *Behavioral Ecology*, 7, 316–325.
- LINNÉ, W. (2004): Effects of obesity on women's reproduction and complications during pregnancy. *Obesity Reviews*, 5, 137–143.
- LITTELL, S. C., PENDERGAST, J. & NATARAJAN, R. (2000): Modelling covariance structure in the analysis of repeated measures data. *Statistics in Medicine*, 19, 1793–1819.
- MACE, R. (1996): Biased parental investment and reproductive success in Gabbra pastoralists. *Behavioral Ecology and Sociobiology*, 38, 75–81.
- MANNING, J. T., ANDERTON, R. & WASHINGTON, S. M. (1996): Women's waists and the sex ratio: evolutionary aspects of the ideal female body shape. *Journal of Human Evolution*, 31, 41–47.
- MARTORELL, R., DELGADO, H. L., VALVERDE, V., KLEIN, R. E. (1981): Maternal stature, fertility and infant mortality. *Human Biology*, 53, 303–312.

- MATHEWS, F., JOHNSON, P. J. & NEIL, A. (2008): You are what you eat: Evidence for maternal pre-conception diet influencing foetal sex in humans. *Proceedings Royal Society London B: Biological Sciences*, 275, 1661–1668.
- MENARD, S. (1995): *Applied Logistic Analysis, Quantitative Applications in the Social Sciences Series #106*. Thousand Oaks, Sage Publications.
- MUELLER, W. H. (1979): Fertility and physique in a malnourished population. *Human Biology*, 51, 53–166.
- NAGELKERKE, N. J. D. (1991): A note on a general definition of the coefficient of determination. *Biometrika*, 78, 691–692.
- NETTLE, D. (2002a): Height and reproductive success in a cohort of British men. *Human Nature*, 13, 473–491.
- NETTLE, D. (2002b): Women's height, reproductive success and the evolution of sexual dimorphism in modern humans. *Proceedings Royal Society London B: Biological Sciences*, 269, 1919–1923.
- PAMPEL, F. C. (2000): *Logistic Regression: A Primer, Quantitative Applications in the Social Sciences Series #132*. Thousand Oaks, Sage Publications.
- PAWLOWSKI, B., DUNBAR, R. I. M. & LIPOWICZ, A. (2000): Evolutionary fitness: Tall men have more reproductive success. *Nature*, 403, 156.
- PAWLOWSKI, B. & KOZIEL, S. (2002): The impact of traits offered in personal advertisements on response rates. *Evolution and Human Behavior*, 23, 139–149.
- PEBLEY, A. R. & GOLDMAN, N. (1995): *Guatemalan Survey of Family Health (EGSF)*, [Computer file]. ICPSR version. Santa Monica, CA: RAND [producer], Ann Arbor, MI: Interuniversity Consortium for Political and Social Research [distributor], 1998.
- PETERSON, C., GOLDMAN, N. & PEBLEY, A. R. (1997): *The 1995 Guatemalan Survey of Family Health (EGSF): Overview and Codebook*. Santa Monica, CA: RAND.
- PLEWIS, I. (ed.) (2004): *Millennium Cohort Study: Technical Report on Sampling*. London: Institute of Education (University of London).
- PLEWIS, I. & KETENDE, S. (eds) (2006): *Technical Report on Response: First Edition*. London: Institute of Education (University of London).
- POLLET, T. V. & NETTLE, D. (2008): Taller women do better in a stressed environment: Height and reproductive success in rural Guatemalan women. *American Journal of Human Biology*, 20, 264–269.
- POLLET, T. V., FAWCETT, T. W., BUUNK, A. P. & NETTLE, D. (2009): Sex-ratio biasing towards daughters among lower ranking co-wives in Rwanda. *Biology Letters*, 5, 765–768.
- QIN, D.-D., YUAN, W., ZHOU, W.-J., CUI, J.-Q., WU, J.-Q. & GAO, E.-S. (2007): Do reproductive hormones explain the association between body mass index and semen quality? *Asian Journal of Andrology*, 9, 827–834.
- RICKARD, I. J. (2008): Kanazawa's 'Generalized Trivers-Willard Hypothesis' and the heritability of offspring sex-ratio. *Journal of Evolutionary Psychology*, 6, 255–260.
- SEAR, R. (2006): Height and reproductive success: How a Gambian population compares to the West. *Human Nature*, 17, 405–418.
- SEAR R., ALLAL N., MACE R. (2004): Height, marriage and reproductive success in Gambian women. *Research in Economic Anthropology*, 23, 203–224.
- SHELDON, B. C. & WEST, S. A. (2004): Sex ratio variation in ungulate mammals. *American Naturalist*, 163, 40–45.
- SHEPPERD, J. A. & STRATHMAN, A. J. (1989): Attractiveness and height: The role of stature in dating preference, frequency of dating, and perceptions of attractiveness. *Personality and Social Psychology Bulletin*, 15, 617–627.

- SPENCER, E. A., APPLEBY, P. N., DAVEY, G. K. & KEY, T. J. (2002): Validity of self-reported height and weight in 4808 EPIC-Oxford participants. *Public Health and Nutrition*, 5, 561–565.
- SPSS (2005): *Linear Mixed-Effects Modeling in SPSS: An Introduction to the MIXED Procedure*. Chicago: SPSS Inc.
- STEELE, D. (1994): Guatemala. In: Psacharopoulos G., Patrinos H.A., (eds): *Indigenous People and Poverty in Latin America: An Empirical Analysis*. Washington, DC: World Bank, pp 105–140.
- STEIN, A., BARNETT, P. G. & SELLEN, D. W. (2004): Maternal undernutrition and the sex ratio at birth in Ethiopia: Evidence from a national sample. *Proceedings Royal Society London B: Biological sciences*, 270, S37–S39.
- TAMIMI, R. L., LAGIOU, P., MUCCI, L. A., HSIEH, C.-C., ADAMI, H.-O. & TRICHOPOULOS, D. (2003): Average energy intake among pregnant women carrying a boy compared with a girl. *British Medical Journal*, 326, 1245–1246.
- TRIVERS, R. L. & WILLARD, D. E. (1973): Natural selection of parental ability to vary the sex ratio of offspring. *Science*, 191, 249–263.
- UNPD (2005): *World Population Prospects: The 2004 Revision*. New York: UN.
- VERBEKE, G. & MOLENBERGHS, G. (2001): *Linear Mixed Models for Longitudinal Data*. New York: Springer.
- VETTA, A. (1975): Fertility, physique and intensity of selection. *Human Biology*, 47, 283–293.
- WANG J. X., DAVIES, M. J., NORMAN, R. J. (2002): Obesity increases the risk of spontaneous abortion during infertility treatment. *Obesity Research*, 10, 551–554.
- WINKLER E. M. KIRCHENGAST S. (1994): Differential fertility and body dimensions in Namibian !Kung San males. *American Journal of Human Biology*, 6, 203–213.
- WORLD HEALTH ORGANIZATION. (2006): Working together for health: The world health report. Available at http://www.who.int/whr/2006/whr06_en.pdf. (Retrieved on 8–3–2009).
- ZALDIVAR, M. E., LIZARRALDE, R. & BECKERMAN, S. (1991): Unbiased sex ratios among the Bari: an evolutionary interpretation. *Human Ecology*, 19, 469–498.
- ZHU, S., HEO M., PLANKEY, M., FAITH, M. S. & ALLISON, M.B. (2003): Associations of body mass index and anthropometric indicators of fat mass and fat free mass with all-cause mortality among women in the first and second National Health and Nutrition Examination Surveys follow-up studies. *Annals of Epidemiology*, 13, 286–293.