

Big and tall parents have more sons: Further generalizations of the Trivers–Willard hypothesis

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Abstract

This paper proposes the generalized Trivers–Willard hypothesis (gTWH), which suggests that parents who possess any heritable trait which increases male reproductive success at a greater rate than female reproductive success in a given environment will have a higher-than-expected offspring sex ratio, and parents who possess any heritable trait which increases female reproductive success at a greater rate than male reproductive success in a given environment will have a lower-than-expected offspring sex ratio. Since body size (height and weight) is a highly heritable trait which increases male (but not female) reproductive success, the paper hypothesizes that bigger and taller parents have more sons. The analysis of both surviving children and recent pregnancies among respondents of the National Child Development Survey and the British Cohort Survey largely supports the hypothesis.

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1. Introduction

In their classic paper, Trivers and Willard (1973) suggest that parents might under some circumstances be able to vary the sex ratio of their offspring in order to maximize their reproductive success. The Trivers–Willard hypothesis (TWH) proposes that, for all species for which male fitness variance exceeds female fitness variance, male offspring of parents in better material and nutritional condition are expected to have greater reproductive success than their female siblings, because their greater size allows them to outcompete their intrasexual rivals and monopolize available reproductive opportunities. The converse is true of offspring of parents in poorer material and nutritional condition, because the smaller males, who are not intrasexually competitive, are excluded from mating opportunities. Parental conditions affect the reproductive prospects of female offspring to a much lesser extent. Almost all

females get to reproduce some offspring, even though no female can produce a large number due to their greater obligatory parental investment into each offspring (Trivers, 1972).

It therefore pays parents in good condition to bet on male rather than female offspring. Since females have much lower variance in reproductive success, parents in poor material and nutritional condition should prefer to produce females as a safe bet. Trivers and Willard (1973) thus hypothesize that parents in better condition should produce more male offspring than female offspring. Their facultative parental investment into male and female offspring should be similarly biased. These predictions have been supported by data from a large number of experiments with a wide array of species (Venezuelan opossum: Austad and Sunquist, 1986; Red deer: Clutton-Brock et al., 1986; Spider monkey: Symington, 1987).

Evolutionary psychologists have since applied the original formulation of the TWH to modern humans and derived further hypotheses. Sons' expected reproductive success depends largely on the parents' wealth,

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so that sons from wealthy families are expected to attain much greater reproductive success than sons from poor families. This is because sons from wealthy families typically inherit the wealth from their fathers, and can in turn invest the resources into their offspring. Women prefer to mate with men with greater resources, and thus wealthy men throughout human evolutionary history have been able to attract a large number of high-quality mates (Betzig, 1986).

In contrast, daughters' expected reproductive success is largely orthogonal to parents' wealth, because it mostly depends on their youth and physical attractiveness. Men in general prefer younger and physically more attractive women, not wealthy women, for their mates (Buss, 1989; Kanazawa, 2003). The TWH in both of its specifications (offspring sex ratio and biased parental investment) has been supported with data from a wide variety of human societies, including the contemporary United States (Betzig and Weber, 1995; Gaulin and Robbins, 1991; Kanazawa, 2001; Mueller, 1993). Cronk (1991) provides a comprehensive review of the empirical evidence in support of the hypothesis, and Trivers (2002, pp. 120–122) adds a brief update on the status of the TWH.

While the TWH is one of the most celebrated principles in evolutionary biology and the preponderance of empirical evidence supports it, it has nonetheless received some criticisms. Myers (1978) and Leimar (1996) provide analytical critiques of the TWH's predictions. A comprehensive review (Brown, 2001) and a meta-analysis (Brown and Silk, 2002) find no consistent evidence for the TWH in the non-human primate literature. For the human populations, Koziel and Ulijaszek (2001) provide only qualified support, and Freese and Powell (1999) and Keller et al. (2001) find no support for the TWH for the contemporary United States.

While the TWH in its original formulation has specifically to do with material and economic conditions of parents and their ability to vary the sex ratio of their offspring in response to such conditions, the basic insight behind it may be more general. The fundamental assumption underlying the TWH is that, if males are expected to attain greater reproductive success than females, *for whatever reason*, then parents may have more sons than daughters. If, in contrast, females are expected to attain greater reproductive success than males, *for whatever reason*, then parents may have more daughters than sons.

For example Kanazawa and Vandermassen (2005) synthesize the TWH with Baron-Cohen's extreme male brain theory of autism. Baron-Cohen (1999, 2002, 2003; Baron-Cohen and Hammer, 1997; Baron-Cohen et al., 2004) proposes that there are "male (or Type S) brains," which are good at systemizing (dealing with physical objects and entities in non-social manners) and were

adaptive for our ancestral men, and "female (or Type E) brains," which are good at empathizing (relating to people in social situations) and were adaptive for our ancestral women. Baron-Cohen further suggests that brain types are substantially heritable. Kanazawa and Vandermassen then derive logical implications of the convergence of Baron-Cohen's theory and the TWH, and predict that, if Type S brain increases male reproductive success in the ancestral environment and Type E brain increases female reproductive success in the ancestral environment, then individuals with strong Type S brains (such as engineers and mathematicians) should have more sons than daughters, and individuals with strong Type E brains (such as nurses and school teachers) should have more daughters than sons. Their analysis of the 1994 US General Social Surveys supports their predictions.

In an entirely different paper, Kanazawa (2004) ponders why so many battered women choose to remain in their abusive relationships. He first points out that violence and aggression were adaptive for men (but not for women) in the ancestral environment, where much of male intrasexual competition for status and thus reproductive access to women was physical; violent and aggressive men may therefore have often had greater reproductive success in the ancestral environment than less violent and aggressive men. Kanazawa then notes that men's tendency toward violence and aggression, particularly, their tendency toward domestic violence, is a function of their baseline levels of testosterone (Booth and Osgood, 1993; Dabbs and Morris, 1990; Soler et al., 2000), and that testosterone levels are highly heritable ($h^2 = 0.60$) (Harris et al. 1998). These two sets of observations lead Kanazawa to predict that battered women have more sons than daughters. His analysis of both American and British samples confirms his prediction.

At the same time, there is some evidence for the logical converse of the TWH. Tallal et al. (1989) show that mothers (but not fathers) with a developmental language impairment have an exceedingly high sex ratio (0.7143: 25 boys vs. 10 girls). Women normally have greater language and communication skills than men, and thus language impairment is relatively more problematic and maladaptive for girls than for boys. It is an example of a heritable trait that would decrease the female reproductive success to a much greater extent than it decreases male reproductive success, and thus the logical converse of the TWH would predict that language-impaired parents should have more sons than daughters.

The conditions that trigger biased sex ratio may therefore not be limited to the parents' material and economic conditions, but may extend to all factors that affect sex-specific reproductive success in a given environment, so long as such factors are heritable.

I therefore propose *the generalized Trivers–Willard hypothesis* (gTWH):

gTWH: Parents who possess any heritable trait which increases the male reproductive success at a greater rate (or decreases the male reproductive success at a smaller rate) than female reproductive success in a given environment will have a higher-than-expected offspring sex ratio (more males). Parents who possess any heritable trait which increases the female reproductive success at a greater rate (or decreases the female reproductive success at a smaller rate) than male reproductive success in a given environment will have a lower-than-expected offspring sex ratio (more females).

Since parental wealth and status are two heritable (at least culturally, if not genetically) traits of parents which increase the sons' reproductive success to a much greater degree than they increase the daughters', the original formulation of the TWH (Trivers and Willard, 1973) is indeed a special case of the gTWH as stated above. Burley's (1986) experiment has previously demonstrated a similar effect of parental attractiveness on the offspring sex ratio among zebra finches.

One highly heritable phenotype which influences sex-specific reproductive success is the body size. In the ancestral environment, where male intrasexual competition was both fierce (in the absence of socially imposed monogamy) and largely if not entirely physical, big and tall men had particular advantages over smaller and shorter men. In contrast, large body size was not particularly adaptive for ancestral women. Probably for this reason, taller men to this day have greater reproductive success than shorter men (Nettle, 2002a; Pawlowski et al., 2000), but shorter women have greater reproductive success than taller women (Nettle, 2002b). And body size (height and weight) is substantially heritable (Chambers, et al., 2001; Silventoinen et al., 2001). The gTWH therefore suggests novel predictions about the effect of body size on the offspring sex ratio.

H₁. Parents who are taller have a higher-than-expected number of sons. Conversely, parents who are shorter have a lower-than-expected number of sons (or a higher-than-expected number of daughters).

H₂. Parents who are heavier have a higher-than-expected number of sons. Parents who are lighter have a lower-than-expected number of sons (or a higher-than-expected number of daughters).

Among human populations, the expected (mean) sex ratio at birth is 105:100 (0.5122), 105 boys for every 100 girls (Grant, 1998).

No one to my knowledge has proposed or empirically tested these hypotheses regarding the effect of body-height and body-weight on the offspring sex ratio *among*

humans, which is very curious, given that body size was the key variable of interest in the original formulation of the TWH among non-human species (Trivers and Willard, 1973). Material and nutritional conditions of the mother were important in determining the offspring sex ratio among non-human species because these factors were (correctly) assumed to influence the offspring body size significantly; well-fed and well-cared-for offspring among non-human species grow larger than their poorly fed and less-well-cared-for counterparts. When modern evolutionary psychologists began applying the TWH to human populations, however, the attention quickly shifted to parental wealth and social class, away from body size. I will therefore test these curiously novel predictions with empirical data. While the original formulation of the TWH focuses on the environmental determinants of body size (material and nutritional conditions), the current hypotheses focus instead on their genetic (heritable) determinants and thus individual differences in body size.

2. Empirical analysis

2.1. Data

I use the 1999–2000 combined follow-up sample of the National Child Development Study (NCDS) and the 1970 British Cohort Study (BCS70). The NCDS originates in the “Perinatal Mortality Survey,” which examines social and obstetric factors associated with stillbirth and infant mortality. All babies born in Great Britain (England, Wales, and Scotland) during the week of March 03–09, 1958, were contacted for inclusion into the study. The initial sample in 1958 consists of more than 17,000 babies. All surviving children, who remained in the United Kingdom, have subsequently been followed in order to examine their health, education, social and economic circumstances, in 1965 (age 7), 1969 (age 11), 1974 (age 16), 1981 (age 23), and 1991 (age 33).

The BCS70, originally developed as the British Birth Survey in line with the NCDS, includes all babies born in Great Britain during the week of April 05–11, 1970. The initial sample contains over 17,000 babies. All surviving members of the cohort, who still reside in the United Kingdom, have since been followed in 1975 (age 5), 1980 (age 10), 1986 (age 16), and 1996 (age 26).

In 1985, the administration of the NCDS was transferred from the National Children's Bureau to the Centre for Longitudinal Studies (CLS) at the Institute of Education, University of London. In 1991, the administration of the BCS70 was similarly transferred from the University of Bristol to the CLS. Professor John Bynner, Director of the CLS, has sought to integrate the timing, design, and analysis of future waves of the

NCDS and BCS70. The 1999–2000 follow-up is the first integrated survey of the NCDS and BCS70. It contains 22,680 respondents (11,419 respondents from the NCDS, who are 41–42 years old, and 11,261 respondents from the BCS70, who are 29–30 years old).

2.2. Dependent variables

The following analyses use two separate dependent variables: All surviving children (as of 1999–2000), and all pregnancies between 1991 and 2000 (for the NCDS) or between 1996 and 2000 (for the BCS70), regardless of the outcome.

The NCDS/BCS70 asks its respondents to list all members of their household, their precise relationships to the respondents (if respondents' children, then if they are biological, adopted, step, or foster children), and their sex (among other characteristics). From these questions, I can count the number of biological sons and daughters of the respondents who still reside with them in 1999/2000. The respondents may list up to nine household members, any number of which may be their biological children.

The NCDS/BCS70 then asks its respondents about all their other biological children who do not live with them, and their sex (among other characteristics). From these questions, I can enumerate all of respondents' non-coresident biological children. The respondents may list up to eight non-coresident biological children. The sum of these figures (0–17) measures the total number of all biological children of both sexes that the respondents have had, who are still alive in 1999/2000.

One problem with constructing offspring sex ratio from the surviving children is the higher mortality rate of male offspring throughout the life course. Male children die at higher rates at all stages of life, so the sex ratio of surviving children will systematically underestimate the sex ratio at birth. In order to get around this problem, the following analyses use a second measure of sex ratio, constructed from the total number of pregnancies that the respondents have had (if female) or caused (if male) since the last survey, regardless of whether or not these resulted in a live birth. In 1999/2000, the NCDS/BCS70 asks its respondents to list all pregnancies that they have had or caused since the last survey (1991 for the NCDS respondents and 1996 for the BCS70 respondents). The respondents may list up to eight pregnancies in these years, and, for each pregnancy, up to five children (allowing for multiple fetuses per pregnancy); they can therefore list up to 40 fetuses that they have created since the last survey.

I use count measures (the number of sons and daughters or the number of male fetuses and female fetuses), rather than ratio measures (such as (Number of sons/Number of daughters)) because ratio measures have a couple of undesirable features at the

individual level. First, when the denominator is zero (for instance, if the individual has no daughters), the ratio is mathematically undefined. However, one can get around this problem by adding an epsilon to the denominator (so that the dependent measure becomes, e.g. Number of sons/Number of daughters + 0.0001). More importantly, however, ratio measures cannot distinguish between two sonless individuals with different numbers of daughters. If someone has no sons and one daughter (0/1), and someone else has no sons and five daughters (0/5), both of them would have zero as a dependent measure, even though the latter individual is much more prone to producing daughters than the former individual. Because of these problems, I use the number of sons or daughters as the dependent variable, while controlling for the number of children of the opposite sex (see below).

2.3. Independent variables

The primary independent variables of interest are the respondents' height and weight. The NCDS/BCS70 asks its respondent to report their height and weight. Some respondents report their height in meters and centimeters, others report it in feet and inches. All height measures are standardized in centimeters. Some respondents report their weight in kilograms, others report it in (the curiously British unit of) stones and pounds. All weight measures are standardized in kilograms.

2.4. Control variables

2.4.1. Social class

Because the TWH in its original formulation, applied to human populations, explains the offspring sex ratio in terms of the material wealth of the parents, it is important to control for parental social status, in order to estimate the *partial* effects of parents' height and weight on the offspring sex ratio. I therefore control for respondents' years of education (measured as the age at which the respondent first left full-time continuous education) and their net (take-home) income (in GBP).

2.4.2. Risk factors

There are several risk factors which affect the number of children or pregnancies one might have. First, sex is an important confound, because it is correlated with both the dependent variables (number of children and pregnancies) and the key independent variables (height and weight). On the one hand, men in general are taller and heavier than women. On the other hand, while each child or fetus must have a biological father and a biological mother, men may not be always aware of all of their biological children or pregnancies that they have caused, while women are always aware of all of their biological children (and most of their pregnancies).

Table 1
Analyses of surviving children

	Number of boys		Number of girls	
Height	0.0000 (0.0001) <i>0.0021</i>		−0.0002* (0.0001) <i>−0.0152</i>	
Weight		0.0004** (0.0001) <i>0.0183</i>		0.0000 (0.0001) <i>0.0021</i>
<i>Social class</i>				
Years of education	−0.0165**** (0.0014) <i>−0.0722</i>	−0.0163**** (0.0015) <i>−0.0711</i>	−0.0154**** (0.0014) <i>−0.0695</i>	−0.0155**** (0.0014) <i>−0.0700</i>
Respondent's income	−0.0000* (0.0000) <i>−0.0160</i>	−0.0000* (0.0000) <i>−0.0160</i>	−0.0000* (0.0000) <i>−0.0153</i>	−0.0000* (0.0000) <i>−0.0154</i>
<i>Risk factors</i>				
Sex (1 = male)	−0.1544**** (0.0107) <i>−0.0929</i>	−0.1572**** (0.0108) <i>−0.0947</i>	−0.1543**** (0.0104) <i>−0.0957</i>	−0.1574**** (0.0105) <i>−0.0977</i>
Currently married (1 = yes)	0.5168**** (0.0111) <i>0.3079</i>	0.5167**** (0.0112) <i>0.3079</i>	0.4889**** (0.0108) <i>0.3004</i>	0.4913**** (0.0109) <i>0.3019</i>
Number of girls/boys	−0.0167* (0.0069) <i>−0.0162</i>	−0.0195** (0.0069) <i>−0.0189</i>	−0.0158* (0.0065) <i>−0.0163</i>	−0.0184** (0.0065) <i>−0.0189</i>
Constant	0.7003 (0.0323)	0.6771 (0.0294)	0.7176 (0.0313)	0.6786 (0.0285)
R ²	0.1080	0.1078	0.1046	0.1045
n	22,529	22,130	22,529	22,130

Note: Main entries are unstandardized regression coefficients. (Numbers in parentheses are standard errors). Numbers in italics are standardized regression coefficients (beta weights).

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; and **** $p < 0.0001$.

Thus, men are expected to have significantly fewer reported numbers of biological children and pregnancies than women.¹ I therefore control for the respondent's sex (1 if male, 0 if female).

Second, while one does not necessarily have to be married to have children or get pregnant in a liberal western society like the UK, marriage is nonetheless a significant risk factor for childbirth and pregnancy; married people are far more likely to have children than unmarried people. I therefore control the respondent's current marital status (1 if currently married, 0 if otherwise). Controlling for whether the respondents have ever been (rather than currently) married does not alter the substantive findings.

Finally, because individuals can have more sons or daughters, not necessarily because they are more likely

to have children of one sex or the other but because they have more children (both sons and daughters), I control for the number of biological children or fetuses of the opposite sex, to estimate whether the respondent's body size has an effect on the number of biological children or fetuses of one sex net of the number of biological children or fetuses of the opposite sex. Naturally, the bivariate correlation between the number of boys and the number of girls is significantly (albeit very weakly) positive ($r = 0.0923$, $n = 22,680$, $p < 0.0001$), as is the bivariate correlation between the number of male fetuses and the number of female fetuses ($r = 0.1530$, $n = 22,680$, $r < 0.0001$). (But see below for their partial correlations.)

Controlling for religion as a potential risk factor, by including a set of five dummy variables (Anglican, Roman Catholic, mainstream Christian, other Christian, and non-Christian, with atheist/no religion as the reference category) does not alter the substantive findings; in fact, it increases the significance of many coefficients. Note that, unlike cross-sectional samples, the respondent's age is not a variable in the

¹In any cohort data (such as the NCDS/BCS70) where all respondents are the same age, men are also expected to have fewer actual (not only reported) numbers of children than women because men typically begin and complete their reproductive careers at later ages than do women. I thank one anonymous reviewer for making this point.

NCDS/BCS70. Because they are cohort members, all born during a single week, everyone in the NCDS is 41 or 42, and everyone in the BCS70 is 29 or 30.

2.5. Results

2.5.1. Analysis of surviving children

Table 1 presents the results of the OLS regression of the number of boys or girls on body size (height or weight), along with a set of control variables discussed above. While respondents' height does have a positive effect on the number of boys (controlling for the number of girls), the effect is not statistically significant. However, the respondents' weight does have a statistically significantly ($p < 0.01$) positive effect on the number of boys, as predicted. So while tall parents do not seem to have more sons, big parents do have more sons than expected.

The analysis of the number of girls the respondents have had produces complementary results. Here, the respondents' height has a statistically significantly ($p < 0.05$) negative effect on the number of girls, controlling for the number of boys, while their weight

does not seem to have an effect on the number of girls. Taken together, the results presented in Table 1 show that taller parents have significantly fewer daughters than shorter parents, while bigger parents have significantly more sons than smaller parents. Both of these patterns are consistent with Hypotheses 1 and 2.

2.5.2. Analysis of recent pregnancies

Table 2 presents the results of the OLS regression of the number of male or female fetuses that the respondents have recently had on their body size, along with the same set of control variables as in Table 1. The analysis of the number of male fetuses strongly supports the hypotheses. The respondents' height has a statistically significantly ($p < 0.01$) positive effect on the number of male fetuses that they have recently produced, controlling for the number of female fetuses, supporting Hypothesis 1. And the respondents' weight has a statistically significantly ($p < 0.05$) positive effect on the number of male fetuses, supporting Hypothesis 2.

The analysis of the number of female fetuses does not produce significant results. While the coefficients for height and weight both have the right sign, their effects

Table 2
Analyses of recent pregnancies

	Number of male fetuses		Number of female fetuses	
Height	0.0002** (0.0001) <i>0.0182</i>		-0.0001 (0.0001) <i>-0.0082</i>	
Weight		0.0002* (0.0001) <i>0.0154</i>		-0.0001 (0.0001) <i>-0.0082</i>
<i>Social class</i>				
Years of education	-0.0057**** (0.0011) <i>-0.0347</i>	-0.0056**** (0.0011) <i>-0.0342</i>	-0.0042**** (0.0010) <i>-0.0262</i>	-0.0041*** (0.0011) <i>-0.0256</i>
Respondent's income	-0.0000*** (0.0000) <i>-0.0226</i>	-0.0000*** (0.0000) <i>-0.0231</i>	-0.0000** (0.0000) <i>-0.0204</i>	-0.0000** (0.0000) <i>-0.0210</i>
<i>Risk factors</i>				
Sex (1 = male)	-0.0317**** (0.0080) <i>0.0264</i>	-0.0293*** (0.0081) <i>-0.0244</i>	-0.0374**** (0.0077) <i>-0.0323</i>	-0.0359**** (0.0078) <i>-0.0311</i>
Currently married (1 = yes)	0.1412**** (0.0080) <i>0.1162</i>	0.1401**** (0.0081) <i>0.1157</i>	0.1181**** (0.0077) <i>0.1011</i>	0.1209**** (0.0078) <i>0.1037</i>
Number of female fetuses/male fetuses	0.1418**** (0.0069) <i>0.1363</i>	0.1368**** (0.0069) <i>0.1317</i>	0.1315**** (0.0064) <i>0.1368</i>	0.1271**** (0.0064) <i>0.1321</i>
Constant	0.2664 (0.0241)	0.2842 (0.0219)	0.2925 (0.0232)	0.2829 (0.0211)
R ²	0.0394	0.0378	0.036	0.035
n	22,529	22,130	22,529	22,130

Note: Main entries are unstandardized regression coefficients. Numbers in parentheses are standard errors. Numbers in italics are standardized regression coefficients (beta weights).

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; and **** $p < 0.0001$.

do not reach statistical significance. Thus the results presented in Table 2 show that taller and bigger parents have more sons than shorter and smaller parents, but they do not seem to have fewer daughters.

3. Discussion

The results presented in Tables 1 and 2 largely support the hypotheses, derived from the gTWH, that taller and bigger parents have higher-than-expected numbers of male offspring, while shorter and smaller parents have lower-than-expected numbers of female offspring. All coefficients, except for one, have the right sign, and half of them are statistically significant. Any supportive evidence for the hypotheses in modern society is remarkable, given that male intrasexual competition no longer takes the physical form in the current environment and thus the body size does not confer particular advantages to men today, even though taller men still have higher social statuses than shorter men (Kanazawa and Kovar, 2004, pp. 231–232). The empirical analysis tentatively confirms the hypotheses regarding the effect of parental body size on the offspring sex ratio, and thus, together with earlier studies (Kanazawa, 2004; Kanazawa and Vandermassen, 2005), the gTWH. However, both the specific hypotheses about the body size and the gTWH require further empirical tests and confirmation.

While the empirical analysis presented above largely supports the gTWH, it presents us with one curious puzzle. Results in Table 1 show that, while the bivariate correlation between the number of boys and the number of girls is significantly positive, their partial correlations in every equation are significantly ($p < 0.05$ or 0.01) negative. In other words, when all the other variables are controlled, parents who have more sons have fewer daughters, and vice versa. Parents appear to specialize in producing either sons or daughters. This finding with the British sample is consistent with Kanazawa and Vandermassen's (2005) finding with the American sample.

This is not the puzzle, however. The puzzle is that the results in Table 2 show that the partial correlations between the number of male fetuses and the number of female fetuses remain significantly ($p < 0.0001$) positive even after controlling for all the other variables. In other words, parents who conceive more male fetuses also conceive more female fetuses. Apart from widespread use of sex selection with the aid of abortion, it seems very difficult to reconcile these two findings: Parents who conceive more male fetuses conceive more female fetuses, yet parents who have more surviving sons have fewer surviving daughters. I will leave the solution of this puzzle to future research.

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