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Is there a psychological proximate mechanism for inducing a Trivers-Willard effect in humans? Results of an internet experiment looking at the desired sex composition of children after mortality priming

Paul Mathews
Department of Social Policy, London School of Economics and Political Science
Email: p.s.mathews@lse.ac.uk

Abstract
Background: The Trivers-Willard hypothesis predicts that in species where competition for mates limits males’ reproductive success, it is adaptive for parents in relatively poor condition, and thus with limited parental investment capacity, to produce more female offspring. Conversely those in good condition, with greater capacity for parental investment, are predicted to have more male offspring. Most previous research has looked at physiological indicators of condition. This study tests whether psychologically priming human participants to make them think they are in relatively poor condition leads to the reporting of fertility preferences consistent with the Trivers-Willard hypothesis.

Methods: An internet experiment was used to randomly allocate childless participants to one of three groups. The first two groups were primed to think about a) their own mortality (to prime low parental investment - poor condition) or b) their dental health (to control for negative mood – though this would not effect parental investment). A second control group was not provided with any priming. Participants were then asked the number of sons / daughters they desired.

Results: No statistically significant associations were found between priming group and the desired sex composition of future children.

Conclusions: This study does not find any evidence for a psychological proximate mechanism, whereby the desired sex composition of offspring is consistent with predictions drawn from the Trivers-Willard hypothesis.

Key words: Trivers-Willard hypothesis, psychological proximate mechanism
Introduction

Robert Trivers and Dan Willard article in Science in 1973 is one of the most influential and highly cited papers of 20th century evolutionary biology. The article sets out what came to be known as the Trivers-Willard hypothesis. Their hypothesis is that many species adaptively undertake conditional sex-biased investment in offspring where parents invest in the most beneficial sex of offspring for the conditions in which the parents find themselves. The logic of this hypothesis stems from differences in the limits of male and female reproductive capacity. Consider mammals, where males have a greater potential reproductive capacity than females. Males’ ‘fixed costs’ of impregnation (sperm) are negligible. Females have much higher ‘fixed costs’ through gestation and lactation. Males can potentially (and do) produce a very large number of offspring, though, if some males have many offspring, this must mean that some males have relatively few or no offspring. Males in short have more variance than females in their reproductive success (Bateman, 1948). Males will compete for mating as the main limitation on male reproductive success is access to mates. Relative status and condition will also influence an individual’s reproductive strategy, and investment from parents will influence their offspring’s condition. Therefore Trivers and Willard hypothesised that because relatively high-status, good-condition parents are able to invest more in their offspring, in such circumstances it would normally be adaptive to invest in male offspring, who can successful compete for mates and thus ‘maximise’ their parents’ reproductive success in subsequent generations. On the other hand relatively low-status, poor-condition parents are less able to provide investment. This means that any male offspring will be at a disadvantage when competing for mates. Therefore such parents should invest relatively more in female offspring to ‘minimise’ the risk of having no grand-offspring.

Sex specific allocation of resources can occur during two stages of offspring development (Keller et al., 2001). First, the allocation can be biased before the birth of the offspring. This will lead to variance in the sex ratio at birth, and the Trivers-Willard hypothesis would predict that those in good condition will have more sons, whilst those in poor condition will have more daughters. Secondly, resources can be allocated through parental investment after birth. In their 1973 article Trivers and Willard explicitly stated that the hypothesis could also apply to humans. Most of the work testing the Trivers-Willard hypothesis in contemporary low-fertility resource-rich human populations has been focused on the latter stage (investment after birth e.g. (Smith et al., 1987; Gaulin and Robbins, 1991; Koziel and Ulijaszek, 2001; Hopcroft, 2005). Whether humans in
low-fertility resource-rich societies genuinely display behaviour in keeping with the hypothesis is still very much debated (Freese and Powell, 1999; Keller et al., 2001).

The literature that has looked at associations between parental condition and sex ratio at birth, have generally found a relationship in the direction predicted by Trivers-Willard. For example more male offspring than average are born in good-condition, high-status families e.g. billionaires (Cameron and Dalerum, 2009), US senior political executives (Betzig and Weber, 1995) and heavier Ethiopian women (Gibson & Mace 2003). On the other hand, poor-condition low-status groups such as Hungarian Gypsies give birth to more daughters (Bereczkei and Dunbar, 1997).

The Trivers-Willard hypothesis explains the logic at the ultimate level of varying the allocation of resources by sex of offspring. But as set out by Tinbergen (1963), it is also important to develop an explanation of the phenomenon at the proximate/mechanistic level. Where research has occurred on mechanisms for explaining Trivers-Willard sex ratios at birth the focus has predominately been on the physiological mechanism. For example Mathews et al. (2008) looked at maternal diet and James (2008) examined hormonal correlates linking condition and offspring sex-ratio.

Another less well studied, but potential important, mechanism is psychological. Human reproduction is partly the product of our decision-making. In virtually every human population where demographic data has been collected, average fertility is below our species’ theoretical physiological average maximum of 15 children, which is taken by many demographers as evidence of human populations constraining their fertility (Livi-Bacci, 2001). In contemporary low-fertility resource-rich societies the prevalence of contraceptives and safe abortion means that fertility is largely under the control of the individual, and so childbearing is even more the product of a series of decisions (even if the decisions are not always consciously expressed). The Trivers-Willard hypothesis could be of great utility in explaining sex composition of families in low-fertility resource-rich populations, if a psychological decision-making proximate mechanism can be found that induces adaptive responses to perceived condition. This is because couples can alter the sex composition of their family by stopping reproduction after births of children of a particular sex (Yamaguchi 1989).

There is limited empirical evidence to support this claim. However, the sex of preceding offspring is a significant factor in explaining differential parity progressions in many low fertility societies at the population level (Hank and Kohler, 2000; Pollard and Morgan, 2002; Kippen et al., 2005). At the individual
level Johns (2004) has highlighted the possibility of psychological factors influencing childbearing by showing that individuals who thought they had low life expectancy had a female biased sex ratio amongst their children. It is often adaptive for individuals to change their reproductive strategy to fit the conditions in which they find themselves (Stearns, 1992). In humans one of the major mechanisms for phenotypic plasticity is through our higher than average cognitive capacity; it is our capacity for decision-making that lets us adapt to diverse conditions. Therefore taking the underlying ultimate logic of Trivers-Willard, there could be a psychological adaptation whereby individuals who think they are in relatively poor condition will want more daughters, and vice versa, those who think they are in relatively good condition will want more sons.

The theoretical relationship is set out in Figure 1. Arrow A represents the majority of research that has been conducted on the physiological link between condition / status and sex-ratio of offspring. This article is setting out the possible relationship between shown in Arrow C. It is important to note that the relationships envisaged in Arrows B and D will not always be entirely straightforward. There will be inaccuracies as individuals are unable to fully measure their actual relative condition and the risks prevalence (Montgomery 1998; Montgomery 2000; Carvalho 2005). With Arrow D demographers have shown that fertility attitudes regularly predicted actualised fertility, so individuals who want to have a lot of children per se tend to have more children than those whose preference is for a smaller families (though it should be noted that the associations are not always particularly strong (Miller and Pasta 1995; Gipson and Hindin 2009; Ni Bhrolchain, Beaujouan et al. 2010).

Most of the work cited above looking at sex ratios at birth has been observational, which can weaken arguments of causality: the theoretical relationship between condition and sex ratio at birth is tested by looking at associations observed in particular populations. In such observational studies heterogeneity might be a problem as it is difficult to rule out the possibility that an unmeasured characteristic is influencing both the measurement of condition and the sex-ratio. For example a failure to control for ethnicity and migration might mask the relationship between poor condition and female preference in an observation study. In the UK relatively disadvantaged groups include recent migrants from regions such as South Asian where there is a cultural legacy for son preference. Trivers-Willard (page 90, 1973) make clear the effect will be seen only relative to the average condition, though for South Asian in the UK the appropriate ‘average’ may be that of fellow South Asian migrants, not the UK average.
Randomisation of participants produces two or more systematically identical groups, an experimental ‘treatment’ can then be provided to one of the groups. As the groups were identical to prior to the treatment, after the treatment has been administered differences between the groups can be attributed to the effect of the treatment. In this study I investigate two psychological components; i) perceived condition and ii) desired sex composition of offspring. As these components can be manipulated experimentally within ethical parameters (see methods section for details) this makes this study well suited to a randomised experiment.

Methods

I obtained data from students at several UK higher education institutions, who voluntarily took part in a series of online experiments. Students are a good group to study for experiments of this nature because they are generally in a relatively similar positions in terms of their individual socio-economic status and life course. As university students are normally young and childless the measurement of the desired sex composition of offspring will not be confounded by actualised childbearing. This article reports the results of one
component of these experiments. The experiment was described to participants as a ‘survey’ to conceal its experimental nature, though respondents were provided with introductory information sufficient to ensure informed consent, along with subsequent debriefing information. Participation was entirely voluntary and as is standard in experimental psychology the respondents are not considered to have been sampled from any wider population.

**Dependent variable - Desired sex composition of offspring**

The desired sex composition of participants’ offspring was measured using two questions. ‘Do you have any preferences on the minimum number of daughters that you have?’ and ‘Do you have any preferences on the minimum number of sons that you have?’ They had to choose a response from the following answer categories:

- I would not like any sons / daughters
- I would like at least one son / daughter
- I would like at least two sons / daughters
- I would like three or more sons / daughters
- I have no gender preferences
- Prefer not to say / Cannot say

From these responses a measure was calculated with three outcomes; the respondent wanted as a minimum a) more sons than daughters, b) more daughters than sons, c) the same number of sons and daughters (including those who did not want any children).

**Explanatory variable**

Participants were randomly allocated to one of three ‘treatment’ groups i) mortality primed ii) dental health primed and iii) unprimed. The first ‘mortality’ group were primed with a series of preceding questions regarding their own mortality and potentially fatal health problems. This prime should induce the respondents’ salient thoughts towards a condition where they are questioning their survival, and thus unavailable to invest heavily in their future offspring. If parental investment is limited then the Trivers-Willard hypothesis suggests female offspring represent a better ‘risk minimising’ evolutionary strategy. So priming questions on own mortality should induce a female biased composition of desired offspring, compared to the control groups. Mortality primes have been shown to influence the reporting of indicators of reproductive strategy (Matthews and Sear, 2008; Wisman and Goldenberg 2005; Fritsche, 2007; Zhou et al., 2008; Zhou et al., 2009). This is the first time, as far as I am aware, that the
effect of such primes on the sex composition of desired offspring has been measured.

The second ‘dental health’ group were asked a series of questions about visiting a dentist and poor dental health before answering the questions on desired sons and daughters. This group was included as a control for negative mood, as questions about dentistry would act as an unpleasant, but non-fatal, prime. This prime should therefore not induce individuals to consider their capacity for parental investment substantially compromised, and thus it should not influence the desired sex composition of their children. This prime also acted as secondary control for the effect of participants answering preceding questions per se. The final ‘unprimed’ group were not asked any questions prior to questions about the desired sex composition of their offspring. This group is somewhat larger because it acted as a control group for several other experiments not reported here.

First, I tested for significant bivariate associations between priming and the desired sex of offspring with a chi square test. I then fitted multivariate regression models and tested the significance of the priming using Wald tests on the regression coefficients. Whilst the participants were randomly allocated between each of the groups (i.e. the only systematic difference between the groups is in the primes they received before the questions on desired sex composition of offspring), I nevertheless asked participants about their family and socio-economic background to test whether any observed effects were caused by random concentrations of particular subgroups within any of the treatment groups. Specifically I collected information on the respondents’ age, expected future income, parental education, country of birth, ethnicity, religiosity, partnership status, sibship size, experiences of mortality and the deprivation and life expectancy of the participant’s local neighbourhood. This information is used as control variables in a multivariate analysis, and I also controlled for the total number of desired children. Due to the non-representative nature of the information the coefficients for these control variables are not reported.

Males and females were analysed separately, due to the underlying theoretical differences in their reproductive strategies: in previous work I have reported differential responses between the sexes to mortality priming (Mathews and Sear 2008). I fitted multinomial logistic regression models, separately for each sex. I used those respondents who did not indicate any sex preference for their children as a base group, the model coefficients therefore show the unexponentiated relative probability that the respondent reported wanting a) relatively more male children or b) relatively more female children. Coefficients
great than zero indicate that the variable increases the likelihood of the particular desired sex composition of offspring, compared to the base condition of having no bias in their preference for male or female offspring and having no priming.

Ethical clearance was obtained from the London School of Economics ethics committee, and from the ethics committees of those participating institutions who deemed it necessary. For experimentation to be ethically justifiable any risk to the human subjects should be minimised. The participants were primed towards thoughts salience with poor condition and mortality, which could be emotionally upsetting, so it was necessary to ensure that along with introductory and debriefing information, such priming was relatively mild and will only have a short term effect. Nevertheless if a short term artificial prime induce significant short term effects in the predicted direction it is then possible to argue that real stimuli that are stronger and more continuous will have greater long-term effects. The experiments took place between October 2008 and April 2009. Analysis is limited to respondents who were childless and under forty years of age.

Results

In total 1,222 female and 503 male students participated in the relevant sections of the experiment. The median age of participants was 21 years. The results for the bivariate analyses are given in Table 1, and the results for the multivariate analyses are given in Tables 2 and 3. Both the bivariate and multivariate results show that there is no relationship between priming and desired sex composition for either sex. It was expected that own mortality priming would i) increase the percentage of respondents desiring more daughters than sons, and ii) decrease the percentage reporting a desire for more sons than daughters. In Table 1 the bivariate analyses shows that it is actually the unprimed control group that has the highest percentage desiring daughters for male and female participants. This is in the opposite direction to the hypothesised relationship, though the overall association is not statistically significant.

The lack of the hypothesised relationship is also seen in the multivariate models. Mortality priming did not induce any statistically different effects compared to the control group who were unprimed. The only marginally statistically significant effect is from the female dental health primed group, who reported wanting more daughters than sons, though this effect is only barely within a 10% significance level.
Table 1. Bivariate analysis

<table>
<thead>
<tr>
<th>Priming</th>
<th>FEMALES</th>
<th>MALES</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>a) Desires more sons</td>
<td>b) Desires more daughters</td>
</tr>
<tr>
<td>Own mortality</td>
<td>7.4%</td>
<td>13.1%</td>
</tr>
<tr>
<td>Dental health</td>
<td>11.5%</td>
<td>9.3%</td>
</tr>
<tr>
<td>Control - No</td>
<td>10.3%</td>
<td>13.9%</td>
</tr>
<tr>
<td>priming</td>
<td>123</td>
<td>160</td>
</tr>
<tr>
<td>N</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chi square test p</td>
<td>0.347</td>
<td>0.440</td>
</tr>
</tbody>
</table>

Table 2. Multivariate analysis for females

a) Effect on likelihood of reporting desires more sons than daughters

<table>
<thead>
<tr>
<th>Priming</th>
<th>Coef</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Own mortality</td>
<td>-0.22</td>
<td>0.50</td>
</tr>
<tr>
<td>Dental health</td>
<td>0.11</td>
<td>0.69</td>
</tr>
</tbody>
</table>

b) Effect on likelihood of reporting desires more daughters than sons

<table>
<thead>
<tr>
<th>Priming</th>
<th>Coef</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Own mortality</td>
<td>-0.06</td>
<td>0.83</td>
</tr>
<tr>
<td>Dental health</td>
<td>-0.48</td>
<td>0.09</td>
</tr>
</tbody>
</table>

Table 3. Multivariate analysis for males

a) Effect on likelihood of reporting desires more sons than daughters

<table>
<thead>
<tr>
<th>Priming</th>
<th>Coef</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Own mortality</td>
<td>0.33</td>
<td>0.31</td>
</tr>
<tr>
<td>Dental health</td>
<td>0.23</td>
<td>0.54</td>
</tr>
</tbody>
</table>

b) Effect on likelihood of reporting desires more daughters than sons

<table>
<thead>
<tr>
<th>Priming</th>
<th>Coef</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Own mortality</td>
<td>0.11</td>
<td>0.81</td>
</tr>
<tr>
<td>Dental health</td>
<td>-1.04</td>
<td>0.19</td>
</tr>
</tbody>
</table>

Conclusion

The Trivers-Willard hypothesis has undoubtedly been highly influential in contemporary evolutionary biologists when measured in the number of citations the original 1973 article has received. But as Festa-Bianchet (1996) suggested, there may be a publication bias towards results that show support for the Trivers-Willard framework. As such the literature may represent a 'biased sample' of unusual sex-ratio studies. It is therefore important to present research that does not simply reinforce the potential for biased sex allocation. In this study I have outlined a new potential proximate mechanism for humans to bias the sex-
ratio of their offspring via psychological decision making. However, I have not found any evidence for such a mechanism’s existence in an experiment with a large number of participants.

The Trivers-Willard hypothesis has been regularly applied to help explain human behaviour. There are, however, many factors and trade-offs that will occur as individuals attempt to maximise their reproductive success. If psychological as well as physiological proximate mechanisms are found, it may increase the utility of the Trivers-Willard hypothesis for explaining the sex composition of families in low-fertility resource-rich populations. In such populations, almost all members are well nourished, and parents can choose (due to effective contraceptives) when to stop reproduction based on the sex composition of their existing children. This means that psychological decision-making is an important route for understanding variance in the sex composition of families in such populations, and the lack of a Trivers-Willard psychological proximate mechanism means that other factors (such as social norms) may be of greater utility in understanding differences in families’ sex composition.

This study has limitations; it uses a relatively small and non-representative group of childless individuals. The priming was, for obvious ethical reasons, relatively weak. Similarly whilst there was negative priming there was not compensatory positive condition priming, so that this side of the effect is still unknown. So it would be inappropriate to conclude that there are not any psychological routes through which Trivers-Willard effects could operate in fertility decision-making, but this study does not find any evidence for their existence.

Acknowledgements

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