

Article

Boy or girl: gender preferences from a Darwinian point of view



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Abstract

This article reviews evolutionary biological studies of sex-biased post-natal parental investment that may be relevant to the issue of preconception gender selection. The focus is on tests of the Trivers–Willard hypothesis, which predicts that natural selection has favoured parents that bias investment in favour of the sex with the best reproductive prospects. Because resource abundance and scarcity often have greater effects on male than on female reproductive success, the Trivers–Willard model predicts that natural selection will most often favour parents who favour males when conditions are good and females when conditions are poor. Empirical tests of this hypothesis are mixed in terms of the appropriateness of their methods and their relevance to the model. Tests with more appropriate measures of such key variables as parental investment tend more often to provide support for the hypothesis. The implications of these findings for the issue of preconception gender selection are briefly discussed.

Keywords: *parental investment, sex ratio, Trivers–Willard hypothesis*

Introduction

Ever since the development of anisogamy, natural selection has had the potential to shape the way that parents allocate resources to different sexes of offspring. This article explores the relevance of that evolutionary history to the contemporary issue of preconception gender selection, focusing on the question of whether evolutionary theory predicts the existence of a more specialized psychological mechanism or module that might have an impact on preconception gender selection. The empirical focus of this article is sex biases in human parental behaviour after birth rather than on biases in the primary and secondary sex ratios or other prenatal biases in parental investment. Unlike physiological mechanisms that affect the allocation of resources to sons and daughters before birth, psychological mechanisms that produce biases in parental behaviour after birth may also have an impact on parental decisions about preconception gender selection. The theoretical focus of this article is a model of sex-biased parental investment developed by Robert Trivers and Dan Willard (1973; see also Trivers,

1972, 2002). While other evolutionary models also predict sex biases in parental investment in certain circumstances, their focus on the economic costs and benefits of sons and daughters makes them more appropriate for an article on the economics of gender preselection.

The potential relevance of the Trivers–Willard model to the issue of preconception gender selection is demonstrated by Lena Edlund's exploration of some possible social costs of the new technologies (Edlund, 1999). Edlund points out that the Trivers–Willard model is appropriate in hypergynous mating systems, i.e. mating systems in which females marry up the socioeconomic hierarchy. In such circumstances, poor, low-status females have better marriage and reproductive prospects than their brothers. Pursuing the logic of Trivers–Willard, Edlund worries that preconception gender selection (or, more broadly, prenatal gender selection) will result in the creation of a permanent female underclass as poor families decide to have

more daughters than sons. I will revisit Edlund's argument after reviewing the evidence for and against the Trivers–Willard model among humans.

Evolutionary models of sex-biased parental investment

Offspring sex ratios have been an important topic in evolutionary biological theory ever since RA Fisher proposed that natural selection would favour equal investment in the sexes (Fisher, 1934). Fisher pointed out that if one sex is less abundant than the other, natural selection will favour greater production of that sex because it will, on average, out-reproduce the more abundant sex. If the sex ratio then becomes skewed the other way, the newly rare sex will have a reproductive advantage and natural selection will favour its production. The equilibrium is in the middle, when the reproductive payoff for investment in a son equals the reproductive payoff for the same amount invested in a daughter. If sons and daughters cost different amounts to rear, the actual sex ratio may be biased in favour of the cheaper sex, but overall investment in the sexes is predicted to be equal.

Evolutionary theorists have identified several circumstances in which parents may bias their investment in favour of sons or daughters while still adhering to Fisher's broader principle of equal investment in the sexes. Local mate competition (Hamilton, 1967) refers to a situation in which one sex is more costly than the other to rear because it competes with its parent or siblings for access to mates. Parents are predicted to adjust their investment towards the less costly sex to compensate for the cost imposed by the competitive sex. Hamilton (1967) identified a large number of insect and mite species in which brothers and sisters routinely mate. This results in competition between brothers for access to mates, and offspring sex ratios in such species are typically strongly biased in favour of females. Local resource competition (Clark, 1978) is the same idea but with one sex being more costly because it competes for resources other than mates. Local resource competition was first identified among galagos. While male galagos range widely, female galagos remain near their mothers and compete with them for food. Galago secondary sex ratios are biased in favour of the less competitive sex, i.e. males. The logical opposites of local mate and resource competition – local mate and resource enhancement – have also been postulated (Gowaty and Lennartz, 1985; Sieff, 1990; see also Trivers and Willard, 1973, footnote 21; Toro, 1982). If one sex makes itself less costly by enhancing its parents' or its siblings' abilities to gain additional matings or resources, then natural selection would favour greater investment in that sex. In all of these circumstances, only forms of investment over which parents have some control or discretion is postulated to be biased. Overall investment is still predicted to adhere to Fisher's principle of equal investment (Hoogland, 1981; Cronk, 1993). Lazarus (2002 p. 294) helpfully groups all of these models under the label 'local factors.'

Local-factor models of sex-biased parental investment have been supported by several studies among humans. Margulis *et al.* (1993) found that North American Hutterites nurse their daughters longer than their sons and that interbirth intervals following daughters are longer than those following sons. They attribute this to the fact that Hutterite daughters are cheaper

to rear than Hutterite sons because of the household help they provide. Similarly, Bereczkei and Dunbar (1997, 2002) found that Hungarian Gypsy daughters provide more household help and are nursed longer than their brothers. Evidence of local resource competition was found in data from the German community of Krummhörn in the 18th and 19th centuries. Individuals in farmers' families with more same-sexed siblings were less likely to survive, less likely to marry, and more likely to emigrate unmarried than those with fewer same-sexed siblings. Because no such effect of same-sexed siblings was found among landless labourers, it appears that competition among siblings over scarce farmland may be the driving force in this case (Volland and Dunbar, 1995; see also Borgerhoff Mulder, 1998, Mace, 1996).

Although local-factor models have shed light on some instances of post-natal sex-biased parental investment, their relevance to this discussion is dubious for two reasons. First, such models are generally cast in terms of currencies, such as scarce resources, that are better discussed in an article on the economics of gender selection. Second, local-factor models do not posit the existence of any special psychological mechanisms that would affect post-natal parental investment in the sexes other than a generalized ability to calculate costs and benefits. The question for this article is whether evolutionary theory predicts the existence of a more specialized psychological mechanism or module that might have an impact on preconception gender selection by affecting decisions about post-natal parental investment in the sexes.

Trivers–Willard: hypothesis, model, effect, mechanism and module

The Trivers–Willard model differs from local-factor models in several ways. First, it is not simply a modification of Fisher's principle that focuses on discretionary parental investment. Second, it is cast in terms of a currency that is unique to evolutionary biological theory and not usually considered by economists: grand-offspring. Third, it predicts the existence of psychological mechanisms affecting sex biases in post-natal parental investment that are distinct from a general ability to calculate costs and benefits. Thus, via the Trivers–Willard model, evolutionary theory has the ability to make unique and valuable contributions to discussions of issues such as preconception gender selection.

In its broadest formulation, the Trivers–Willard hypothesis is that natural selection should favour parents who bias their investment in favour of the sex of offspring with the best reproductive prospects. In order for natural selection to do this, parents would need to have some sort of cue regarding the relative reproductive prospects of sons versus daughters. Trivers and Willard noted that in many species, reproductive success is much more variable among males than among females. This is dramatically evident in many polygynous mammal species, where males may be extremely successful because they obtain a large number of matings or extremely unsuccessful because they obtain few or none, while females tend to have more moderate variations in their reproductive success. In such circumstances, the condition of the mother during the period of parental investment might be a reliable cue to her offspring's prospects. The offspring of a mother in poor condition may be expected

to do worse than the offspring of a mother in good condition. But because variance in reproductive success is greater among males than among females, the impact of maternal condition is expected to be greater on sons' than on daughters' reproductive success. Sons of mothers in good condition, for example, may be great reproductive success stories. Their sisters, on the other hand, may be successful compared with other females but not compared with their brothers. At the other end of the maternal condition spectrum, sons might be reproductive disappointments while their sisters, though having lower reproductive success than other females, would be successful compared with their brothers. The bottom line is that natural selection is predicted to favour mothers who bias investment towards sons when in good condition and towards daughters when in poor condition.

Since it was proposed more than three decades ago, the Trivers–Willard model has had a very fruitful and interesting history. Unfortunately, considerable confusion and misunderstanding about Trivers–Willard have also accumulated. To help clarify matters, I propose a distinction between several different things that have been labelled 'Trivers–Willard': hypothesis, model, effect, mechanism, and module. The Trivers–Willard hypothesis and model are closely related and both can be phrased in both broad and narrow ways, as I have done in the preceding paragraphs. The Trivers–Willard effect refers, at least here, only to the existence of data that fit the model and not to the mechanism(s) responsible for it. This leaves open the possibility that one might find a Trivers–Willard effect in a body of data without any Trivers–Willard mechanism or module being responsible for it. Trivers–Willard mechanisms are the factors that are proximately responsible for Trivers–Willard effects and that correspond with predictions derived from the Trivers–Willard hypothesis. Such mechanisms might take a variety of forms, including physiological processes before conception or during gestation and psychological processes after birth. A Trivers–Willard module is a specific sort of mechanism: an aspect of the mind that is a specific outcome of natural selection that produces Trivers–Willard effects. This use of the term 'module' is derived from its usage in psychology and philosophy of mind (Fodor, 1983). These distinctions will inform the review of empirical studies on Trivers–Willard presented in the next section.

A large literature has developed around the Trivers–Willard model, but only a portion of it is relevant to the issue of preconception gender selection in humans. Specifically, this review will focus on studies of sex biases in post-natal parental investment among humans. Studies of Trivers–Willard effects among non-humans and in prenatal parental investment among humans will be discussed only briefly. Fortunately, both of those topics have been the subjects of recent and thorough reviews. Cameron (2004) reviewed 422 tests for Trivers–Willard effects on birth sex ratios among non-human mammals. Although only 34% of those tests found Trivers–Willard effects, Cameron noted that studies were much more likely to find Trivers–Willard effects on birth sex ratios if they used good measures of maternal condition at or close to the time of conception. Studies measuring maternal body condition, body weight, or food availability at or near conception found a Trivers–Willard effect on birth sex ratios 74% of the time, while those using measures during gestation and at birth found such effects only 41% and 5% of the time, respectively. Cameron suggests that mammals may have a physiological mechanism that ties

birth sex ratio to maternal condition at conception through an association between maternal fat intake, glucose levels, and the development of male blastocysts. Although Cameron's study does not include the literature on Trivers–Willard among humans, it is important to note her finding that appropriate measures of maternal condition are crucial.

Lazarus (2002) reviewed 54 studies of status and birth sex ratio among humans. The Trivers–Willard hypothesis is supported by 26 of those studies (48%). Some of these studies also included measures of post-natal parental investment and so will be discussed below. Measures of maternal condition in these studies were, for the most part, actually measures of male status, such as political and religious ranks, social class, education, and wealth. This reflects a suggestion made by Trivers and Willard in their original article that, among humans, maternal condition could operationalize as socioeconomic status. It would be worth exploring the possibility that, as among non-human mammals (Cameron, 2004), more precise measures of actual maternal condition, especially at or near the time of conception, would show stronger Trivers–Willard effects on birth sex ratios. A few studies of Trivers–Willard effects on human prenatal parental investment have been published since Lazarus' review, mostly concerning birth sex ratios. Gibson and Mace (2003) found that women in rural Ethiopia with better nutrition were more likely to give birth to males. Ellis and Bonin (2002) found no association between parental social status and offspring sex ratio among a large sample of US and Canadian college students' families. Stein *et al.* (2004) found no increase in female births during the Dutch Hunger Winter of 1944–1945. In light of Cameron's (2004) findings among non-human mammals, it is worth noting that the one of these three studies with the best data on the conditions of individual mothers near the time of conception is the one that found a Trivers–Willard effect. Another recent study (Braza, 2004) finds a possible Trivers–Willard effect on birth weights, with women aged 25–29 years giving birth to heavier sons than younger women.

My examination of studies exploring Trivers–Willard effects on post-natal sex biases in parental investment among humans will be guided by two important questions. First, how is 'maternal condition' operationalized and assessed? Trivers and Willard suggested that socioeconomic status might play this role in studies of humans because of the impact it has on resources available for parental investment and on male mating success, particularly in polygynous societies with female hypergamy. Many studies have followed this suggestion by focusing on such characteristics as income, wealth, class or caste membership, ethnic status, educational attainment, husband–wife age differences, and occupational status. Typically, these are used as indicators of maternal condition even if they actually refer solely or additionally to paternal condition. Some studies refer entirely to paternal condition, e.g. use of paternal physical robustness (Winkler and Kirchengast, 1994), and make no connection at all, either implicit or explicit, between it and maternal condition. Others have used more direct measures of maternal condition such as age, nutritional status, mother's marital status, and receipt or non-receipt of public assistance.

Not all of these are equally appropriate ways to operationalize this aspect of the Trivers–Willard model. Given that conditions that would have favoured the evolution of Trivers–Willard mechanisms have existed far longer than humans, natural

selection is most likely to have resulted in a mechanism that uses aspects of the environment that are not specific to humans as its cues. For example, the availability of resources for parental investment is a cue that would be significant to mothers of all species that engage in post-conception parental investment, while educational attainment is evolutionarily novel and specific to humans. Those measures of maternal condition that have some demonstrable correlation with the reproductive prospects of male and female offspring are also superior to those without such a correlation, though evidence of such correlations is only rarely presented (see below). The use of less appropriate measures of maternal condition can lead to problematic claims and reduce a study's value as a test of the Trivers–Willard hypothesis. For example, Freese and Powell (1999, p. 1728) claim that 'The Trivers–Willard hypothesis predicts that increases in education and income should yield greater returns in investment for sons than for daughters.' However, it is not clear that the hypothesis actually makes any such claim given the evolutionary novelty of formal education and the lack of any demonstration of a correlation between these measures of maternal condition and differences in the reproductive prospects of sons and daughters.

Second, how is parental investment operationalized and assessed? Researchers have used a variety of indicators of parental investment levels while applying the Trivers–Willard model. These include the length of the interval following the birth of a boy or girl; observations of holding, nursing, and other types of direct care; time of weaning; infanticide; neglect; provision of health care; outcome measures, including offspring health, quality (e.g. their symmetry), and survivorship; investments in education; allocation of resources in experimental settings; inheritance patterns; and parents' diaries and self-reports regarding their investment in offspring.

Measures of parental investment vary in terms of their timing (e.g. infant holding versus investments in education), the extent to which they involve conscious thought (e.g. neglect versus infanticide), their distance from the actual phenomenon being measured, parental investment (e.g. nursing versus outcome measures), and the extent to which they are dependent upon parents' awareness of their own behaviour (e.g. diaries and self-reports versus observations of behaviour). Some of these measures are independent of one another (e.g. nursing and inheritance), while some are logically related (e.g. nursing and holding, direct care and neglect), and others may be causally related (e.g. weaning and birth spacing, healthcare provisioning and survivorship). Although parents' stated offspring sex preferences are often used by demographers as indicators of sex-biased parental investment, tests of the Trivers–Willard hypothesis rarely make use of such statements because of their well-documented lack of fit with actual investment patterns (e.g. Cronk, 1990, 1991a,b, 2000, 2004). Ideally, measures of investment should focus not simply on overall levels but rather the marginal return to investment in terms of its impact on the reproductive value of sons and daughters (Lazarus, 2002 pp. 304, 305; see also Krist, 2006). Although it is usually quite difficult to assess marginal returns to parental investment, careful consideration of the likely relationship between specific kinds of investment at specific points in time and their impact on offspring reproductive success might result in measures of parental investment that are more appropriate to testing the hypothesis.

Not all of these indicators of parental investment are equally likely to reflect mechanisms that have been naturally selected to produce a Trivers–Willard effect. The ones least likely to be manifestations of a Trivers–Willard mechanism are those that involve conscious calculations, particularly when they are made relatively late in the period of parental investment, and those that involve evolutionarily novel forms of parental investment. For example, while inheritance patterns may sometimes fit the Trivers–Willard model, they are so likely to involve conscious thought and come so late in the period of parental investment that it is unlikely that natural selection would have produced a mechanism that is specifically designed to produce such effects. The same might be said of investments in children's education, which also have the shortcoming of being evolutionarily novel (see Kanazawa, 2001 p. 1767, on Freese and Powell, 1999). Other measures of parental investment may come early in the child's life but, again, involve conscious thought to such an extent that they are unlikely to be the products of a Trivers–Willard module even when they produce Trivers–Willard effects. Infanticide may be a case in point. The implication for assessments of the Trivers–Willard hypothesis is that we may be more likely to find evidence of a Trivers–Willard module if we focus on types of investment that do not necessarily involve conscious thought in either the generation of the behaviour or its recall and that occur early in the period of parental investment (e.g. holding, nursing, and neglect of infants) and outcome measures that may be strongly influenced by such investment (e.g. infant health and survivorship) because natural selection is most likely to have resulted in a module that acts on these characteristics. This point, and particularly its implications for preconception gender selection, will be revisited after specific studies are reviewed.

A third question is also important, but so few studies address it that it is difficult to use it to organize a review: How are the relative reproductive prospects of sons and daughters assessed? Among the very few studies that include measures of reproductive outcomes are my own work among the Mukogodo (Cronk, 1989), Borgerhoff Mulder's work among the Kipsigis (1998), and Boone's study of early modern Portugal (1986). I can think of at least two reasons why this is so rarely included in studies attempting to test the Trivers–Willard hypothesis. First, it can be difficult to get demographic data complete enough to document any difference between male and female reproductive rates. Second, there is confusion in the literature about how exactly the reproductive prospects of sons and daughters should be assessed. Sieff (1990) argues that a shortcoming of my own study of sex-biased parental investment among the Mukogodo is that my indicators of offspring reproductive prospects are the relative reproductive rates of males and females in the parents' generation, not the children's. As I have argued elsewhere (Cronk, 2000, 2004), this apparent weakness of my study is actually a strength. The Trivers–Willard hypothesis is that natural selection will favour parents who use cues in their current environment— not in future ones — to inform their decisions about investment in sons and daughters. It is impossible for natural selection to have favoured a tendency to invest in particular ways in the present based on information available only in the future.

Review of empirical studies

Historical studies

Empirical work on Trivers–Willard effects in humans began in earnest with Mildred Dickemann's studies using historical data from medieval Europe, imperial China, and feudal north India (1979). High-status males in all three societies tended to have better reproductive prospects than their sisters, and their parents appear to have biased investment in favour of them in various ways. The most dramatic of Dickemann's findings was that during the late 17th and early 18th centuries, members of the ruling Jhareja subcaste in north India killed almost all female infants. Boone (1986) followed Dickemann's lead by testing the Trivers–Willard hypothesis with data from early modern Portugal. He found that males outreproduced females among the high nobility while females outreproduced males among the low nobility and that some indicators of parental investment patterns, such as dowries to daughters from the low nobility, were biased in favour of the sex with the best reproductive prospects. Because Dickemann's and Boone's findings fit the predictions of the Trivers–Willard model, they are certainly examples of the Trivers–Willard effect. However, because the indicators of parental investment in the two studies reflect deliberate and conscious acts, it is not necessarily the case that they are manifestations of a Trivers–Willard mechanism or module. It may be that, in some circumstances, conditions favouring one sex of offspring over the other are so extreme that parents are made consciously aware of them and act accordingly.

In contrast, Voland *et al.* (1997) provide an example of a study using historical data that may provide evidence not only of a Trivers–Willard effect but also of a Trivers–Willard mechanism. Using data from six different farming parishes in 18th and 19th century Germany and operationalizing maternal condition as wealth and occupation and investment as infant mortality, they found that lower-class families tended more to favour daughters than did upper-class families. Although it is unclear how the infant mortality differences were produced, the possibility exists that they are the result of the sort of evolved mechanism that the Trivers–Willard model predicts.

Large-scale studies in contemporary societies

An advantage of working in economically developed contemporary societies is that large data sets often already exist about them, so researchers do not need to engage in expensive and time-consuming data collection. This blessing, however, can also be a curse, because it is often the case that existing data sets do not provide good gauges of key elements of the Trivers–Willard model. This may explain why some of the most problematic applications of the Trivers–Willard model to data about post-natal parental investment come from large-scale studies conducted in contemporary societies. Almost all of the studies in this group suffer from problematic measures of either maternal condition or parental investment, though, in keeping with Cameron's (2004) finding, the studies with the fewest and least severe shortcomings seem to be the most likely ones to find a Trivers–Willard effect.

Problems with measures of parental investment begin with the earliest study in this group, an analysis of US couples' stated offspring sex preferences (Coombs, 1977). Although this study was not designed to test the Trivers–Willard model, and although the author herself seems to have been unaware of that model, it is worth mentioning because it has been cited as evidence against Trivers–Willard (e.g. Freese and Powell, 2001 p. 1714). Coombs reported that a son preference was common across most parts of US society, with poorer and less educated women stating a stronger preference for sons than wealthier and more educated women. Given that this study relies upon stated sex preferences as its only measure of parental investment, its usefulness as a test of the Trivers–Willard hypothesis is quite dubious.

A reliance on self-reports is also one of several weaknesses of Freese and Powell's (1999) attempt to test the Trivers–Willard hypothesis with data from surveys of US adolescents and their parents. Not only are such reports vulnerable to problems with recall, they are also often influenced by audience effects and may be products of self-deception (Trivers, 2000). Other problems with their study, which did not find a Trivers–Willard effect, include, as discussed above, the use of an evolutionary novelty (educational investment) as a measure of parental investment. Educational investment is also problematic in that it reflects conscious deliberations by the parents and mostly occurs late in the period of parental investment. In response to Freese and Powell, Kanazawa (2001) conducted his own study using another large body of survey responses. Although Kanazawa's study suffers from some of the same weaknesses as Freese and Powell's, such as a reliance on self-reports, it is interesting that it uses a measure of parental investment – interaction patterns with offspring – that is less likely to be evolutionarily novel than educational investment, and it does find a Trivers–Willard effect (cf. Freese and Powell, 2001). Keller *et al.* (2001), also using data from a large survey that also relies heavily on self-reports, find no support for the Trivers–Willard hypothesis in the USA. An awareness of the problems associated with self-report data led Hopcroft (2005) to look not at parents' reports regarding their investments in their children's education but rather at sons' and daughters' educational attainment, and she found a Trivers–Willard effect: among Americans of high status, sons attain more education than daughters, while daughters attain more education than sons among Americans of low status.

Malkin and Lamb (1994) present what is meant to be a test of the Trivers–Willard hypothesis that also suffers from very problematic measures of parental investment. Operationalizing maternal condition as receipt or non-receipt of public assistance (with receipt interpreted as an indication of low status) and parental investment as extreme physical and fatal child abuse, they found that 'the Trivers–Willard model does not predict patterns of parental maltreatment in the United States' (p. 130). One could point out that the Trivers–Willard model also does not predict earthquakes with any accuracy. It is not a good test of a hypothesis to use data that the hypothesis was never meant to explain. While Trivers–Willard is relevant to child neglect and, possibly, mild forms of abuse, it was never meant to explain the extreme forms of child abuse considered in this study. A strength of this study is that its authors do acknowledge these and other problems, including the evolutionary novelty of the environment in which the study was conducted, the fact that everyone in this study, regardless of their receipt or non-receipt

of public assistance, is likely to have been at the low end of the socioeconomic spectrum, and (citing Hrdy, 1987) the fact that non-lethal under-investment (neglect) of children may be both more common and more relevant as a test of the hypothesis than extreme abuse.

Problematic measures of parental investment are not limited to studies that claim to find evidence against Trivers–Willard. Gaulin and Robbins (1991) argue that longer intervals before births of daughters than of sons among US women who are poor and who are not coresiding with males support the hypothesis, but it is unclear how an ability to adaptively adjust birth intervals before rather than after a child of a particular sex could be produced by natural selection. Lazarus (2002) suggests that this result may be the result not of a Trivers–Willard module but of a relationship between male coresidence, coital frequency, and offspring gender. Better support for Trivers–Willard is provided by Gaulin and Robbins' data on nursing. They found that low-income women and women without coresiding males breastfed daughters more often and longer than sons.

Three studies that suffer from fewer problems also lend at least limited support to the hypothesis. Abernethy and Yip (1990), using a large sample of Americans of European descent from Tennessee between 1976 and 1983, report that, although human female infant survivorship is better than male over all, as mothers' and parents' education rises and as mothers age, the post-neonatal mortality rates converge, perhaps reflecting improved treatment of males at the higher end of the scale of indicators of maternal condition. A recent study in Poland (Koziel and Ulijaszek, 2001) combines relatively good measures of parental investment (birth interval and breastfeeding) with reasonable indicators of maternal condition (economic status and level of parental education) and finds weak support for the hypothesis. A recent study in Mexico (González-Cossio *et al.*, 2003) using a very large data set finds that higher socioeconomic status is associated with an increasing likelihood that boys will receive supplemental foods while still being nursed. The authors point out that, if the introduction of supplemental foods is indeed an indicator of higher levels of parental investment, it is ironic because early introduction of foods is actually associated with increased morbidity.

Finally, two studies are worth noting for the interesting ways in which they have operationalized variables and extended the original hypothesis. Manning and Anderton (1998) operationalized maternal condition as age difference between husband and wife, reasoning that men marrying women younger than themselves may be more desirable than men marrying women older than themselves. They operationalized parental investment as the symmetry of daughters, predicting that daughters of women married to low-status men will be more symmetrical than daughters of women married to high-status men. Although they find support for the hypothesis, the distance between the variables they were able to measure and the variables of interest to the hypothesis makes it difficult to interpret this as strong support. Euler and Weitzel (1996) extended the hypothesis to grandparental solicitude. They found no support for it, but they themselves pointed out that 'the method we employed is not a good test of this thorny hypothesis'.

Small-scale studies in contemporary societies

The main weakness of fieldwork-based studies is the relatively small sample size used. Their main strength is that they can be designed and carried out in ways that provide data that are as relevant as possible to the hypothesis at hand and that suffer from fewer of the problems, such as a reliance on self-reports and a focus on evolutionarily novel forms of parental investment, identified above. It is interesting that these studies almost uniformly find evidence in favour of the hypothesis.

My own study of the Mukogodo (Cronk, 1989, 1990, 1991a,b, 1993, 2000, 2004) operationalized maternal condition as status within a local hierarchy of wealth, status, and male marital success and parental investment as healthcare provisioning, survivorship, observed association patterns, and nursing. Mukogodo, who are at the bottom of the local hierarchy and among whom daughters have better reproductive prospects than sons, are more likely to take daughters than sons to local clinics, nurse daughters more frequently and longer than sons, hold daughters more than sons, and remain closer to daughters than to sons. Perhaps as a result, Mukogodo daughters are more likely to survive than Mukogodo sons. These same patterns do not appear among higher-status neighbouring groups with whom the Mukogodo share language and many other cultural traits. This study also demonstrates the potential for problems if parental investment is measured through stated offspring sex preferences (and, by implication, other parental self-reports): Mukogodo parents tend to express a desire for more boys than girls and are apparently unaware of the bias in their actual behaviour in favour of daughters. Similar discrepancies between stated sex preferences and other measures of parental investment have been found elsewhere (see Cronk, 1991b). Mukogodo parents' lack of awareness of their own behaviour strongly suggests that a specialized Trivers–Willard module has been triggered by the circumstances in which they find themselves.

Mukogodo wealth is primarily in the form of livestock, a characteristic shared by the Yomut Turkmen of Iran. But while the Mukogodo are at the bottom of their regional hierarchy, the Yomut are at the top of theirs, and Irons (2001) presents a variety of types of data, including qualitative assessments, survivorship rates, and sex ratios, that suggest that Yomut parents fit the Trivers–Willard model by investing more in sons (Irons, 2001). Maternal condition can sometimes be operationalized in terms of political hierarchies. Betzig and Turke (1986), working on the Micronesian island of Ifaluk, operationalized maternal condition as husband's political status and parental investment as observed association rates between parents and offspring. They found that high-status men were more likely than low-status men to spend time with sons. Groups that have political and economic hierarchies make it easier for researchers to operationalize maternal condition as status. Groups that do not have those features force researchers to come up with other ways to operationalize maternal condition. In a study of the hunter-gatherer !Kung of Namibia, who do not accumulate wealth or form political hierarchies, Winkler and Kirchengast (1994) operationalized maternal condition in terms of the robustness of men's physiques, finding that more robust men have more male children and that their children are more likely to survive than those of less robust men.

It is possible that studies conducted in non-Western non-industrialized, settings are more likely to uncover Trivers–Willard effects than those described above conducted in more economically developed settings because the former more closely resemble the environments in which humans evolved. Bereczkei and Dunbar (1997), however, working in a developed industrialized setting, found some of the strongest evidence yet in favour of the Trivers–Willard model. Comparing Hungarians of the dominant Magyar ethnic group with low-status Hungarian Gypsies, they found that Gypsies had a female-biased sex ratio at birth, were more likely to abort a fetus after having had one or more daughters, nursed their daughters longer, and sent their daughters to school for longer.

The situations of the Mukogodo and Gypsies are similar in a way that may be crucial for triggering the postulated Trivers–Willard module: both groups are at the bottom of long-standing, relatively rigid hierarchies, and both Mukogodo and Gypsy females are more likely than their brothers to marry hypergamously. Because such hierarchies and the hypergamy that often accompanies them have a persistence that may make them particularly relevant as cues of offspring reproductive prospects regardless of whether they occur in economically developed or undeveloped settings, they may be more likely than other environmental factors to trigger Trivers–Willard mechanisms. This study suggests that the environmental novelty of industrialized societies does not preclude the existence of Trivers–Willard effects, but perhaps it takes extreme situations and particular methods for them to be detected.

Studies of inheritance patterns

Because inheritance is evolutionarily novel, involves conscious deliberation, and occurs late in life, it is an unlikely candidate for adjustment by an evolved Trivers–Willard module. Even in situations that might select for daughter favouritism generally, it may also behave parents to pass property on to their sons because it has a greater impact on male than on female reproductive success. For example, despite the fact that Mukogodo parents tend to favour daughters as young children, they reckon descent patrilineally and pass their wealth, mostly in the form of livestock, on to sons. Livestock are useful to males not only for subsistence but also for bride-wealth payments, and males can have multiple wives. For the same reasons, although poor Gabbra women outreproduce poor Gabbra men, Gabbra parents pass livestock on to their sons (Holden *et al.*, 2003).

In light of inheritance's shortcomings as a way to operationalize parental investment in tests of Trivers–Willard, it is ironic that some of the oldest evidence of a Trivers–Willard effect comes from analyses of wills. Josiah Wedgwood, a British economist and relative of Darwin, found that the wealthiest British tended to give more to sons than to daughters, while people with smaller estates tended to divide them equally (Wedgwood, 1928, 1929). This 'Wedgwood effect' (Hrdy and Judge, 1993 p. 24) may also be a Trivers–Willard effect, but it is not necessarily the result of the operation of a Trivers–Willard mechanism or module. Other studies of inheritance patterns have had mixed results. Betzig and Weber (1995) show that, until the 1880s, US presidents had more sons and favoured them over daughters in their wills. Smith *et al.* (1987) found a Trivers–Willard effect in British Columbia, with wealthier decedents favouring male kin and poorer ones favouring females. Judge and Hrdy (1992),

in contrast, found no Trivers–Willard effect in a sample of inheritances from California in 1890–1984. Webster (2003) simulated inheritance in a laboratory setting by giving people money and the opportunity to allocate it to relatives. He found a marginally significant pattern consistent with Trivers–Willard among males.

Trivers–Willard as bandwagon and target

The Trivers–Willard hypothesis, particularly as it applies to humans, has attracted a great deal of attention since it was first put forward more than 30 years ago. This may be due to the fact that, unlike many other ideas that have emerged from the application of evolutionary biological theory to human behaviour, the Trivers–Willard hypothesis makes novel and unexpected predictions that cannot be easily derived from folk biology or folk psychology. And, as Kanazawa (2001) points out, Trivers–Willard may be particularly attractive to social scientists because it is a rare case of an evolutionary biological prediction that is linked to socioeconomic stratification.

This amount of attention has been both a blessing and a curse for the hypothesis and for the scientific quest for an understanding of the circumstances in which it is relevant and the mechanisms that produce it. The blessing has been that the many studies claiming to test Trivers–Willard have indeed shed light on these things. The curse is that both advocates and critics of the evolutionary biological study of human behaviour have muddied the scientific waters by sometimes claiming to have tested the hypothesis when their tests are either poorly designed (e.g. Malkin and Lamb, 1994; Freese and Powell, 1999; and other studies discussed above) or not really about Trivers–Willard in the first place. Ashorn *et al.* (2002) provide an example of the latter. They find that in rural Malawi, boys survive at a lower rate than girls and suggest that this is a result of the fact that girls stay near their parents and provide old age security, while boys tend to move away. This is an interesting finding, but, contrary to the authors' claim, it is not a demonstration of a Trivers–Willard effect. Rather, it is an example of the local resource enhancement model of sex-biased parental investment described earlier in this article.

The error by Ashorn *et al.* was simply to have misunderstood the Trivers–Willard model. Others understand it but want to stretch it in ways that do a disservice both to the model and to their own work. For example, Mackey (1993) examined birth intervals before and after sons in what he claimed was a test of Trivers–Willard. The difficulty lies in the fact that his study was related in no way to maternal condition and instead focused on the idea, derived not from Trivers–Willard but rather from Trivers' broader theoretical work on parental investment generally (Trivers, 1972), that if some type of parental investment provides more benefits to one sex of offspring than the other, then parents should give more of it to that sex. This is related to the discussion in the preceding section of this article about inheritance patterns. The fact that his results supported his hypothesis is interesting but not relevant to Trivers–Willard. Similarly, Kanazawa has suggested that the basic idea behind Trivers–Willard be generalized to include the idea that if parents have anything to offer offspring that would help one sex more than the other, they should favour the benefitting sex.

Kanazawa has presented evidence that people with 'strong male brains' produce more sons and those with 'strong female brains' produce more daughters (Kanazawa and Vandermassen, 2005), that big and tall parents have more sons (Kanazawa, 2005), that violent men have more sons (Kanazawa, 2006), and that attractive women give birth to more daughters (Kanazawa, 2007). As interesting as these findings may be, forcing them under the Trivers–Willard umbrella clarifies neither the Trivers–Willard hypothesis nor parental investment theory more generally (see also Gelman, 2007, for a methodological critique of Kanazawa's work on this topic).

A more thoughtful, balanced, and ultimately productive approach is demonstrated by other recent studies. Bereczkei and Dunbar (2002) supplemented their work on Trivers–Willard among urban Hungarian Gypsies with another study in a rural setting that supports not Trivers–Willard but another model of sex-biased parental investment, local resource enhancement. A female bias is present in both settings but, in the rural setting, it appears not to be due to opportunities for hypergamy, which are few, but rather to the role of daughters as helpers-at-the-nest. Similarly, Margulis *et al.* (1993) considered both Trivers–Willard and local resource enhancement in their study of daughter-biased investment among Hutterites. They found support for the local resource enhancement model but did not claim that this finding was evidence against Trivers–Willard. Rather, they thoughtfully considered local circumstances and concluded that Trivers–Willard was not the appropriate model to use because males and females have similar variances in reproductive success. Quinlan *et al.*'s (2003, 2005) work on the Caribbean island of Dominica provides another example of the thoughtful testing of different models of sex-biased parental investment. Operationalizing maternal condition as wealth, father presence or absence, and the presence or absence of alloparents, they found no support for a Trivers–Willard effect on weaning in a Dominican population (Quinlan *et al.*, 2003). More recently, they have presented evidence that local-factor models may be more relevant on Dominica than Trivers–Willard (Quinlan *et al.*, 2005; see also Quinlan, 2006).

Trivers–Willard and preconception gender selection

The studies described above provide some support for the idea that, in certain circumstances, post-natal parental investment may be biased in the way predicted by Trivers and Willard. In some of those circumstances, the bias may be produced by a mechanism naturally selected for this purpose, while in others it may involve nothing more special than a general ability to calculate costs and benefits. Edlund (1999) worries that the circumstances described by Trivers and Willard – socioeconomic hierarchies with female hypergamy – may combine with prenatal (including preconception) gender selection to foster the development of a permanent underclass with a female-biased sex ratio.

Parents empowered to make choices about the genders of their offspring would presumably make those decisions consciously and deliberately. However, if selection pressures like those identified by Trivers and Willard did indeed shape physiological and psychological mechanisms for adaptive sex biases in parental investment, those pressures and the mechanisms they produced

are likely to be quite ancient, predating not only humans as a species but, more generally, conscious deliberations by parents about the allocation of parental investment. The relevance of such mechanisms to conscious decision-making about things like offspring gender is unclear. Even after the evolution of consciousness, selection may favour retaining Trivers–Willard and other psychological mechanisms at an unconscious level in order to avoid the influence of external factors such as culturally transmitted offspring sex preferences. For example, I am certain that if Mukogodo parents were given the ability to select the gender of their offspring before conception, most would follow their patriarchal culture, not the logic of Trivers–Willard, and choose to have more sons.

Conclusion

While it is possible that some Trivers–Willard mechanism(s) have some impact on conscious decisions about the allocation of parental investment, the literature reviewed above provides, at best, only mixed support for that idea. Cases in which a Trivers–Willard effect has been produced by actions that must be preceded by some conscious thought (e.g. infanticide and preparation of a will) may reflect circumstances that are so extremely biased in favour of males or females in terms of marital or economic prospects that parents have little trouble concluding that a sex bias in parental investment, perhaps including a sex bias in preconception gender selection, is a sensible course of action. In such circumstances, no Trivers–Willard mechanism may be necessary. When social hierarchies are extreme enough and rigid enough to produce such effects, perhaps social planners would do better to focus on the problem of inequality itself rather than on specific effects such as sex-biased preconception gender selection.

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