

Original Article

The maternal dominance hypothesis: questioning Trivers and Willard

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Abstract: Thirty years ago, Trivers and Willard (1973) hypothesized that parental “condition” could be central in influencing the sex ratio of offspring, “good condition” being associated with the conception of males. However, I argue that “condition” is a distraction in this otherwise useful hypothesis, because it is merely a frequent indicator of dominance (a characteristic which often leads to priority access to resources); and that it is dominance, a biologically-based characteristic underpinned by testosterone, which is of interest. Shifting the focus from good condition to the dominance-testosterone link could help explain otherwise anomalous findings in the literature on the sex ratio. In addition, in female mammals, testosterone is hypothesized to have a role in reproductive processes such that the mother could influence or even control the sex of her offspring, conceiving whichever sex she is, at that time, and in that place, best suited to raise. Such a mechanism would confer an evolutionary advantage on those females able to make use of it.

Keywords: evolutionary psychology; Trivers-Willard hypothesis; maternal dominance; sex ratio; testosterone.

Introduction

Thirty years ago *Science* published Trivers and Willard’s paper “Natural selection of parental ability to vary the sex ratio of offspring” (1973). In it they argued that reproductive success should be enhanced in parents who could manipulate the sex of their offspring according to their condition. Noting that a male’s reproductive success may potentially vary far more widely than a female’s,

Trivers and Willard argued that it would therefore pay females in “good condition” to produce male offspring and conversely, females in “poor condition”, female offspring. Providing that good condition was transferred to the offspring, and providing that such good condition was sustained into adulthood, a female who could bias the sex ratio would be more reproductively successful than a female who could not. The condition of females thus became a key factor in attempts to explain variations in the sex ratio of the offspring they produced.

Doubts were expressed about the plausibility of this hypothesis shortly after publication. For example Myers (1978) showed through computerized mathematical modeling that the hypothesis did not, and could not, hold for all circumstances. Nevertheless the Trivers and Willard hypothesis has provided the theoretical framework for almost all studies of the sex ratio in the last thirty years. It is only recently that sustained criticisms of it have been published.

For example, Leimar (1996), examining lifetime reproductive success, showed that in some circumstances, “high quality” females can have higher reproductive value than high quality males, in direct contrast to the Trivers and Willard prediction. Five years later, in a thorough investigation of the primate literature on sex ratios Brown (2001) found “a lack of correlation between maternal condition, birth sex ratios and maternal care”. Then Brown and Silk (2002) reported on a meta-analysis of all primate studies of the sex ratio which, largely because of conflicting results, found no overall difference in the sex ratio of offspring of high and low status mothers.

In studies of humans, it could be suggested that one reason for inconsistent results is that there is little consensus on what constitutes “parental investment”. For example, Keller et al (2001) found no support for the suggestion that higher status parents would invest more in their sons, and lower status parents more in their daughters. But their measure of parental investment consisted of “time diaries” and “self-report data”, whereas, in contrast, Koziel and Ulijaszek (2001) found limited support for the Trivers and Willard hypothesis using “first birth interval and extent of breastfeeding” as their measures of parental investment.

In an attempt to resolve the problems, Bercovitch (2002) described three possible models in which parental investment might be related to sex-biases in primate offspring, but came to the conclusion that testing the models would be very difficult, and that, in any event, no single model would be likely to apply to all primates. West and Sheldon (2002) however argued that parents “should” adjust the sex of their offspring according to conditions in the environment and further that “parental ability to predict their offsprings’ environment influences the evolution of sex ratio patterns across taxa”. Thus on the one hand, there has been an increase in the number of authors describing difficulties in sustaining the Trivers and Willard hypothesis; yet on the other, further evidence from a large variety of species, that manipulation of the sex ratio by parents seems to be a fundamental part of successful reproductive strategies.

The problem

In illustrating their original hypothesis Trivers and Willard used a population of caribou as an example. A male caribou in good condition would “tend to exclude other males from breeding, thereby inseminating many more females themselves, while females in good condition, through their greater ability to invest in their young, [would] show only a moderate increase in reproductive success” (Trivers and Willard, 1973). Even a small advantage in a male’s condition could make a very large difference to his reproductive success. Thus, “females in better condition tend to invest in males. Adverse environmental conditions for the mother during pregnancy are correlated with a reduced sex ratio at birth in deer and humans” (Trivers and Willard, 1973).

The prediction that “adverse environmental conditions” would give rise to more female offspring “in deer and in humans” ran directly counter to the accepted tradition in sex ratio studies in both species. In humans it ran up against the now fully supported, uncontroversial finding of raised sex ratios during and immediately following war (McMahon and Pugh, 1954). In deer it ran into conflict both with reports from nineteenth century breeding trials, and contemporary wildlife experiments. In one, a longitudinal, controlled cross-over field trial, deer had more male offspring if they were in poor condition (Verme, 1969).

However, more recent reports appeared to confirm the Trivers and Willard hypothesis. In one, a naturalistic longitudinal study conducted on the Island of Rhum, deer had more male offspring if they were in good condition (Clutton-Brock et al, 1984). In another, it was shown that high status humans, presumed to be in good condition, had an excess of sons (Teitelbaum and Mantel, 1971). Both studies appeared to confirm the Trivers and Willard hypothesis. All the studies were methodologically sound, and their conflicting results invited closer inspection. In fact, two papers (Verme, 1983; McGinley, 1984) were published suggesting an adaptive advantage in male-biased sex ratios in adverse environments, but neither of these precipitated a discussion of the anomalies.

The maternal dominance hypothesis suggests a resolution for the apparently conflicting results, namely that the association between dominance and good condition, although clearly legitimate in many circumstances, is likely to be a spurious one from the point of view of sex ratio adjustment. Although dominance may lead to good condition in most settings, its key attribute *vis-à-vis* sex ratio adjustment is that it is underpinned by testosterone, and it is this which effects the sex ratio, not condition, good or otherwise. Therefore, although both hypotheses predict the same (dominant animals have male-biased sex ratios) in normal (i.e. non-stressful) conditions, they do not predict the same for adverse conditions.

As West et al (2002) have pointed out, the problem of sex determination in vertebrates (and certainly in mammals) is more likely to be solved by further

investigation of the way in which “individuals facultatively adjust their offspring sex ratios in response to environmental conditions (rather than population sex ratios)”. As they note, “birds consistently adjust their offspring sex ratios in the direction predicted by theory”, providing “strong evidence that even in vertebrates, CSD (chromosomal sex determination) is not an all-powerful constraint that prevents adaptive sex ratio manipulation” (West et al, 2002). Having shown that sex ratio adjustment appears very strongly in some organisms (for example ants, bees and wasps) and quite strongly in others (for example birds) these authors are primarily concerned with the question why there appear to be such wide differences across the taxa in the overall amount of sex ratio adjustment. This puzzle particularly applies to those species with chromosomal sex determination, where any form of adaptive sex ratio variation has proved hard to demonstrate. The results of studies on variations in the secondary sex ratio in mammals (many of which have cited the Trivers and Willard hypothesis as the theoretical context) have been inconsistent to the point that some authors have said that reports of statistically significant findings were nothing but the result of sampling error (Small and Smith, 1985). However the maternal dominance hypothesis provides a way of reconciling these alleged inconsistencies, mainly by postulating a hypothetical mechanism by which the mammalian mother could either predetermine, or at least partially control the sex of her offspring.

In the absence of knowledge of a proximate mechanism of sex determination (other than chance) a test of the competing hypotheses (Trivers and Willard versus the maternal dominance hypothesis) occurs in the context of adverse environmental conditions. In the presence of such adverse conditions, the Trivers and Willard hypothesis predicts female-biased sex ratios, and the maternal dominance hypothesis predicts male-biased sex ratios.

The maternal dominance hypothesis

The maternal dominance hypothesis arose from research in human females which showed that women more dominant in personality than other women are more likely to conceive male infants (Grant, 1994). Later, following evidence which showed that serum testosterone is correlated with dominance behaviours in male animals (Rose et al, 1971) and humans (Mazur and Booth, 1998) it was shown that serum testosterone in human females is significantly correlated with scores on a psychometric instrument designed to measure dominance (Grant and France, 2001). Thus, the presence of above average serum testosterone in a human female suggests both above average dominant behaviour and an increased likelihood of conceiving a male infant.

Based on observations beginning in the mid 1960s, and formally proposed in 1990 (Grant, 1990), this hypothesis appeared to run counter to the accepted truth that the sex of the infant in humans is determined by mere chance, depending on

whether an X- or a Y-chromosome-bearing spermatozoon happens to fertilize the ovum. The maternal dominance hypothesis, while recognizing the basic, indispensable function of X- and Y-chromosome -bearing spermatozoa, introduced the possibility of an additional component into the process of fertilization, namely some kind of discriminatory role for the mammalian mother, such that she could give an advantage to either an X- or a Y-chromosome-bearing spermatozoon, depending on which sex offspring she is, at that time, and in that place, more suited to raise.

The phrase “more suited to raise” refers to a multi-layered environmental, physiological and psychological suitability. Since mammalian testosterone levels have been shown to be responsive to environmental influences (Mazur and Booth, 1998; Rose et al, 1971; Gray, 1992; Kemper, 1990), environmental contingencies may contribute to an adaptive response about which sex offspring to conceive. Maternal psychoneuroendocrinology must play a role in interpreting the conditions, and varying the level of testosterone in accordance with these factors. Thus conditions in the environment could influence the individual female’s level of serum testosterone in each breeding season, or estrus or menstrual cycle. These differing levels could, in turn, differentially influence various mechanisms or pathways within the reproductive tract of the female. Several possible mechanisms have already been described (Eberhard, 1996). They include selection and development of the ovum within the follicle (Haning et al, 1993), timing of ovulation in relation to the length of the follicular phase (Weinberg et al, 1995), timing of conception within the menstrual or estrus cycle (Guerrero, 1974), and /or sex-specific embryonic mortality (Krackow, 1995). All of these are influenced by maternal hormone levels.

Thus female testosterone, already shown in some settings to be attuned and responsive to environmental influences, is hypothesized to be working in synchrony with maternal reproductive physiology to ensure that the sex of the offspring conceived is optimal to both maternal characteristics and environmental conditions. Physiologically, maternal testosterone levels are likely to be differentially suited to the development and growth of a male or a female embryo and fetus. Behaviourally, at least in humans and rats, it seems likely that maternal testosterone underpins small, but important qualitative differences in maternal-neonate interactions according to the sex of the infant/offspring. Such interactions tend to set the overall direction of development. In humans, mothers of female infants are more responsive to their babies than mothers of male infants (Grant, 1994). They respond to their infants’ vocalizations and movements by repeating them, thus providing very early experience of the synchronization of interpersonal interaction. Mothers of male infants appear to stimulate their babies more than the mothers of female infants. Mothers of male babies have been shown to hold their infants upright by the trunk, to arouse them and to initiate or provoke behaviours in them. Mothers of rats have been shown to stimulate male

neonates significantly more frequently than their female littermates (Beyer and Feder, 1987). Adaptively speaking, both the physiological and the psychological maternal differences appear to work in tandem to ensure the optimal development of the particular sex of offspring conceived.

Under normal conditions, dominance and serum testosterone (both normally distributed) are likely to be highly correlated. Females that have more of both will be likely to conceive male offspring and to raise them successfully. Females that have less of both will be more likely to conceive and raise reproductively successful female offspring. Testosterone fluctuates over time, according to environmental conditions both physical and psychological (Gray, 1992). Suppose individual females are born with genetically imposed limits in their ability to manufacture testosterone. Each female's testosterone levels will fluctuate over a given range. Those with genetically low testosterone will fluctuate within a lower range and produce mainly female offspring; those with genetically high testosterone will fluctuate within a higher range and conceive mostly male offspring. Most will fluctuate within the medium range, tipping either side of an hypothesized critical threshold and produce offspring of both sexes.

Responsiveness to the environment

What sorts of conditions cause fluctuations in serum testosterone? In the female, anything that causes chronic stress will tend to raise an individual's serum testosterone levels (Gray, 1992). Female medical students, in the months building up to examinations, had higher testosterone levels than normal (Grant and France, 2001). Chronic hardship or stress, (as in food shortages, war or epidemic) appears to increase testosterone levels in many females, thus temporarily raising the number of females suited to conceiving male offspring. (This is in contrast to acute stress, as in earthquake, flood, or sudden bereavement, which appears to have the opposite effect, resulting in a lowered sex ratio nine months later, see for example Hansen et al, 1999.)

The relationship between chronic stress and raised testosterone levels in the mammalian female could be doubly adaptive. First the individual female (mother) enduring chronic stress would be slightly toughened to help withstand the stress; and secondly, there would be fewer females in the next generation, thus possibly protecting the habitat from excess population growth. Verme (1983) reviewed all studies on deer sex ratios and concluded that "an increase in the proportion of male fawns as range conditions deteriorated would serve as a population self-regulating mechanism". He came in for severe criticism for this, because his suggestion implied support for the controversial group selection theory. But the facts could equally well be explained by postulating the individual's reactions to reduced food, which had the effect of raising that individual's testosterone levels.

Adaptive manipulation of sex ratios by individuals could result in collateral benefit to a group, in just the same way as say, lack of water could cause kidney damage in some individuals, who then died, leaving more water for those that remained. This too might look like group selection, but it is not; those individuals with more efficient kidneys survived and the others did not. The problem of misattribution of group selection charges could be solved by reference to shared physiological mechanisms adapted in each individual to a greater or lesser extent, to solve the same problems.

In times of plenty and low stress, individual female serum testosterone levels would tend to drop allowing for more females to conceive female offspring. This too may be advantageous in that it would provide the vehicle for population expansion in times of plenty, and good conditions in which to produce and rear healthy females who may continue to be successful breeders and enhance their species, thus taking optimum advantage of the good conditions.

For a female mammal to adjust the sex ratio of her offspring in accordance with her perception of the environment there would need to be two related mechanisms in place. First, there would need to be a physiological mechanism by which a female was able to react sensitively to stress-inducing changes in the environment. Secondly, there would need to be a relationship between this mechanism and the mechanism by which the sex of her offspring was determined (or pre-determined). Both these mechanisms would need to react within the time scale of her estrus or menstrual cycle.

The maternal dominance hypothesis offers serum testosterone as a primary candidate. It is known that serum testosterone in males, both animal and human, can vary dramatically over time, according to the male's perception of changes in his social and physical environments (Kemper, 1990). There is also evidence to show that, unlike the male, female testosterone rises in response to (perceived) chronic stress. Female testosterone is also related to self-reported dominance (Grant and France, 2001).

Resolving existing problems

Postulating such a mechanism would help reconcile the studies (cited at the beginning of this article) of sex ratio variation in humans and in deer. It would solve many problems, from the rise in the number of human male births following war (MacMahon and Pugh, 1954), hardship (Martin, 1994) or disease (Lloyd et al, 1984) to distorted sex ratios in other primates (Meikle et al, 1984), ungulates (Cameron et al, 1999) and other mammals (Meikle et al 1993; Wiley and Clapham, 1993). There is already persuasive evidence to suggest a connection between maternal testosterone and offspring sex ratio in birds (Sheldon, 1999).

Consistent findings on mammalian sex ratios may emerge when "good condition" is seen for what it is - a frequently occurring, but nevertheless

spurious correlate of dominance and high status. Although all three descriptors – good condition, dominance and high status occur frequently in conjunction with one another, and look intuitively as though they should be connected, their co-occurrences are not logically necessary. An animal may be in good condition without being dominant and/or without having high status. In a group of animals in poor condition, some will still be dominant.

And in some settings high status animals are not necessarily the most dominant, for example when factors such as age, health and time of joining the group are major contributors to status. Although of signal importance in itself, even the characteristic dominance must be seen as a by-product of serum testosterone. For primatologists, who scarcely ever concern themselves with proximate mechanisms, this may seem limiting; however it has the advantage of being potentially falsifiable, and it minimizes the need for ingenious, but nevertheless speculative explanations of sex ratio variation.

Assuming similar physiological mechanisms for reproduction in female humans and other primates, it may also be possible to reconcile otherwise seemingly incompatible results in methodologically good research. For example, if female testosterone (not dominance or good condition) is the key, two different studies of rhesus monkeys which seemed to show contradictory results, may instead, demonstrate the workings of the hypothesized maternal dominance-testosterone link. In the first study, dominant, high status rhesus monkey mothers living in captivity gave birth to a significant number of female offspring (Simpson and Simpson, 1982). For these females living conditions were almost stress-free. Many, if not most, were born in captivity, and thus did not have a stressful adjustment to make to living in cages. There was always plenty of food and their sustained high status meant they had priority access to whatever was desirable. This comfortable lifestyle required little or no effort, and certainly no stress. Therefore testosterone levels were likely to be low and these high status females gave birth to daughters. For lower status females, life was (comparatively) more difficult. At best, they had to await their turn at the food hoppers and not get in the way of their superiors. At worst they were severely harassed. These females conceived more male offspring, which may have been a consequence of having higher stress-induced serum testosterone levels.

In the second study (Meikle et al, 1984), the quality of the environment was extremely harsh and the birth sex ratios the opposite of those born to the caged mothers. Here the high status, dominant females had more male offspring, and the low status mothers, more female offspring. These rhesus monkeys lived on an island on which there was intense competition for life-sustaining food supplies and water. Those adult females that were born with (genetically) higher levels of serum testosterone (than the other females) were able to fight that bit harder for access to supplies. Although all were in poor condition, the higher testosterone females were slightly better off in both condition and status. Those females had

more male offspring, whereas the low testosterone females, who had less success in the fights over food, were in poorer condition and had lower status, conceived female offspring, and fewer of them. As the harsh conditions continued, even those female infants that survived birth did not necessarily reach adulthood. Adaptively, such sequences result in falling populations and allow time for the habitat to be restored. When it is, there is less competition for food, lower stress-induced testosterone in the females and more likelihood of normal, or even below normal sex ratios in the offspring.

In this way natural selection could be shown to favour maternal ability to adjust the sex ratio of her offspring according to her circumstances, her “circumstances” being those environmental as well as genetic factors which give rise to both her physiological and her psychological condition at the time of conception. Such a re-conceptualization could provide the “single unifying framework ... required to explain variation in the extent to which different species adjust their offspring sex ratio” (West and Sheldon, 2002).

For a maternal sex-determining mechanism to have benefits greater than its costs, it would need to operate early and efficiently in the reproductive pathway. The most parsimonious point, the one with least waste and most efficiency, would be immediately prior to conception. The most efficient and timely mechanism for sex determination at this point in the reproductive pathway would perhaps be by selection and development of an ovum already adapted to receive an X- or a Y-chromosome-bearing spermatozoon. This would give the opportunity for the female to take a perfectly timed reading of both her internal and external environments and select and develop the ovum accordingly. Given that, in mammals, the female’s contribution to reproduction is overwhelmingly greater than the male’s, it may make sense for her to be the one to determine whether the offspring should be male or female.

Awesomely adaptive systems for ensuring appropriate sex ratios appear to be in place right across the taxa, from the haplodiploid species to those species with chromosomal sex determination (West et al, 2002). It may be that a very finely tuned or titrated system resting on both genetic potential and reactivity to environmental conditions of the female’s serum testosterone forms the basis of a proximate mechanism of sex pre-determination that keeps even mammalian sex ratios perfectly in balance with environmental contingencies.

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