

KANAZAWA'S 'GENERALIZED TRIVERS-WILLARD HYPOTHESIS' AND THE HERITABILITY OF OFFSPRING SEX-RATIO*

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Abstract. The 'generalized Trivers-Willard hypothesis' (gTWH) proposes that heritable traits associated with reproductive success of one sex will be positively associated with a genetic tendency to produce offspring of that sex. However, unlike the original Trivers-Willard hypothesis, the predictions of gTWH are proposed to be borne out regardless of environmental conditions. This is a problem because it ignores the influence of the hypothetical genetic variance in offspring sex-ratio on population operational sex-ratio and thus offspring's likely success in finding a mate. Accordingly, there is a notable lack of evidence to support the existence of such heritable variation in offspring sex-ratio in humans or other mammals. The genetic tendency for all individuals within populations of birds and mammals to produce a male offspring with the same probability as one another is well-established. In fact it is a cornerstone of population sex-ratio theory, upon which is built hypotheses of facultative (environmental) sex-ratio adjustment, including the original Trivers-Willard hypothesis. I therefore suggest that any phenotypic correlations between offspring sex-ratio and traits that may be associated with the reproductive success of offspring of one sex are most likely to be environmental in origin.

Keywords: generalized Trivers-Willard hypothesis, Trivers-Willard hypothesis, sex-ratio

THE HYPOTHESIS

In a recent issue of this journal, KANAZAWA (2008) presented some data to support the 'generalized Trivers-Willard hypothesis' (gTWH). This hypothesis is based upon observations that (1) male and female reproductive success respectively depend on different traits, and (2) some of these traits have heritable components.

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From these, gTWH proposes that both males and females with heritable trait values associated with high male reproductive success will have been selected to produce on average more sons than daughters, and vice versa (KANAZAWA 2005; KANAZAWA and VANDERMASSEN 2005; KANAZAWA 2006; KANAZAWA 2007a; KANAZAWA 2007b; KANAZAWA 2008). To date it has been suggested that such heritable associations are responsible for reports that sons are more likely to be born to parents who are relatively big and tall (KANAZAWA 2005; KANAZAWA 2007b; but see GELMAN 2007; DENNY 2008), that engineers are more likely have sons while nurses more likely to have daughters (KANAZAWA and VANDERMASSEN 2005; but see GELMAN 2007), that parents who are considered beautiful are more likely to have daughters (KANAZAWA 2007a; but see GELMAN 2007) and, most recently, that violent or aggressive men are more likely to have sons (KANAZAWA 2006; KANAZAWA 2008). The most fundamental assumption of gTWH is that there is *heritable variation of traits that directly determine offspring sex-ratio*. Whilst tests of gTWH have so far been criticised on statistical grounds (GELMAN 2007; DENNY 2008), what follows concerns problems with the theoretical basis of the hypothesis, in particular the conflict of the above assumption with established population sex-ratio theory.

THE INSPIRATION

The chosen namesake of gTWH is the original Trivers-Willard (1973) hypothesis (TWH), but the two hypotheses have otherwise little in common. TWH is perhaps the best-known of several hypotheses concerning facultative (conditional) sex-ratio variation that may apply to humans (TRIVERS and WILLARD 1973; LAZARUS 2002; JAMES 2006). Like all proposed facultative sex-ratio adjustment strategies, it predicts that it will sometimes be more beneficial for a parent to produce offspring of one sex than another, and that selection may therefore favour mechanisms to manipulate offspring sex in accordance with these benefits. In the case of TWH, it is predicted that provided three assumptions are satisfied mothers who are in relatively good physiological condition will produce more male offsprings compared to mothers who are in relatively poor condition. The three assumptions required for this strategy to evolve are: (1) maternal condition correlates with offspring condition; (2) offspring condition endures into adulthood; (3) a given unit of parental investment will have a greater effect on the reproductive success of sons than it will have on that of daughters (TRIVERS and WILLARD 1973). It follows that where these assumptions are met, variance in reproductive success will generally be higher in males than in females. Consequently sons will be more successful than daughters when produced by a mother with potential to invest a high level of parental care and less successful when produced by a mother with low potential to invest. Where these assumptions hold true, and there is no constraint on mechanism, selection could favour a positive association between a mother's condition, and the probability of her producing a son (TRIVERS and WILLARD 1973).

PLASTICITY VERSUS RIGIDITY

The crucial element common to all facultative sex-ratio strategies is that parents are able to actively respond to changing environmental or demographic circumstances. A parent must be able to accurately assess the ultimate fitness benefits of producing a male or a female. If a son is likely to eventually provide his mother with more grandoffspring than a daughter is, it will on average pay the mother to produce a son rather than a daughter. For the original TWH to work, mothers need information on the resources they are likely to be able to impart to a potential son, and therefore how well that son might eventually perform relative to its competitors in the population. This information may be provided by maternal condition (energy reserves) at the time of conception (CAMERON et al. 2008). However, gTWH is quite different to TWH and indeed all other hypotheses of facultative strategies, because it must operate *regardless of conditions*. The specific problem with this is that it ignores one of the most crucial determinants of offspring reproductive success: the probability of actually finding a mate.

IT TAKES TWO

Integral to facultative strategies is established sex-ratio theory, as developed by FISHER (1930, chapter 6) and others before him (see EDWARDS 1998). Sex-ratio theory explains the reproductive value of the two sexes as being irrevocably intertwined with their respective frequencies in the population, which are of course entirely co-dependent. In dioecious species (those with two sexes) with obligate sexual reproduction, an individual's reproductive value will be largely *equivalent to the rarity of its sex in the population*. This can be illustrated by a simple thought experiment. Let us consider the probability of producing a reproductively viable son as a heritable trait, in a population in which this trait is normally distributed, with a range of zero to one, and a mean value of 0.75. In a discrete generation model, the population will begin to produce more males than females in each successive generation. Given monogamy, all females will mate, whereas most of the males will not. Therefore parents who tend to produce females will produce more successful offspring, so trait values of <0.75 will be selected for and spread throughout the population over time. Eventually, equilibrium is reached where there is no selective benefit for any heritable tendency to produce more or less offspring of each sex than other members of the population (BODMER and EDWARDS 1960). This explanation can be modified to extend to all mating systems, and so does not rely upon any assumptions concerning the predominant pattern in ancestral humans. The hypothetical nature of the inheritance pattern suggested here is irrelevant. Any number of genes coding for offspring sex-ratio would respond in the same way to this 'rare sex advantage'. The tendency to produce male and female offspring with the same probability as other members of the population is an example of an 'Evolutionarily

Stable Strategy' (ESS), deviations from which will be selected against (MAYNARD SMITH and PRICE 1973; MAYNARD SMITH 1982).

THE PROBLEM

Any hypothesis concerning sex-ratio variation must take the demographic rule of the rare sex advantage to its heart, and gTWH does not. Heritability of offspring sex-ratio, on which gTWH relies, is not compatible with an evolutionarily stable strategy. Any gene(s) within a population that were predisposed towards producing offspring of one sex would in the long run be at a disadvantage when competing with genes that tended to produce the stable ratio (BODMER and EDWARDS 1960). This is because the probable sex-ratio produced by an individual will inevitably be correlated to the sex-ratio of the population of which it is a part. Any tendency to produce offspring of one sex will be matched by an over-abundance of this sex in the population, which will decrease that sex's reproductive value to parents and therefore their evolutionary success. By comparison, the under-represented sex will thrive. KANAZAWA (2006, 2008) suggests that men who are violent or aggressive should produce more sons because aggression may be positively associated with male, but not female reproductive success. However, even taking the link between aggression and male reproductive success for granted, this line of reasoning does not work. Any lineage of aggressive male-producers will become a victim of its own initial success, as progeny with the same inherited tendency to produce sons must compete with one another for access to rare females. Potentially an equal number of 'female-producers' in the same population could compensate, but a stable bimodal distribution of offspring sex-ratio would depend on a smooth distribution of male- and female-producers across the population. This is unlikely to be maintained because e.g. 'male-producers' would tend to be spatially clustered with other male-producers from the same genetic stock. gTWH depends on overcoming this seemingly intractable problem.

WHAT IS THE EVIDENCE?

In addition to the fundamental conflict with sex-ratio theory described above, evidence in support of gTWH appears scant. As mentioned previously, of the six studies published showing support for gTWH, four have so far drawn criticism for methodological problems (GELMAN 2007; DENNY 2008), and an attempted replication of one on the same dataset has failed to find the support for gTWH that Kanazawa did (KANAZAWA 2005; DENNY 2008). However, by themselves these objections do not conclusively show gTWH to be incorrect. An appropriate starting point for testing gTWH would be to *demonstrate heritable variation of offspring sex-ratio* in humans or other species. This crucial assumption of gTWH is unsupported,

but must be called for, particularly because it is in such fundamental conflict with the logic of sex-ratio theory. Sources of accurate pedigree data over several generations for humans are rare but available. EDWARDS (1962) reviewed studies of such data and concluded that “if genetic variability exists, it is of a very low order of magnitude”. Regarding animal studies, there is again little or no supporting evidence of genetic variation of offspring sex-ratio in wild animal populations (CLUTTON-BROCK and IASON 1986). Furthermore, it might be considered telling that despite evidence for the existence of genes that have opposing effects on male and female fitness (FOERSTER et al. 2007), breeders of domesticated mammals who have attempted to select for sex-ratio for commercial gain have generally been very unsuccessful in doing so (CHARNOV 1982, p.115).

CONCLUSION

Facultative sex-ratio variation of one form or another may well occur in humans. While the supporting data are equivocal (KOZIEL & ULJASZEK 2001), the hypotheses are built on sound theoretical ground and a solid empirical base from studies in other species (CAMERON 2004; SHELDON and WEST 2004). Thus, if associations between offspring sex-ratio and aspects of parental phenotype can convincingly be demonstrated in humans, they may be most parsimoniously interpreted as correlations between the environmental components of both these traits (HELLE 2008). By contrast, any hypothesis invoking stable heritable variation in offspring sex-ratio is in *fundamental* conflict with established sex-ratio theory. It should be emphasised that ‘theory’ encompasses not just the idea itself, but a vast body of congruent evidence. As such, any initial empirical foundation for gTWH would need to be evidence of heritable variation in offspring sex-ratio. There is very little to suggest that this will be forthcoming.

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