

ARE WITHIN-SEX MATING STRATEGY PHENOTYPES AN EVOLUTIONARY STABLE STRATEGY?

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ABSTRACT

Humans have been found to display considerable variety in their pursuit of mating strategies, varying in their preference for short-term mating encounters versus established long-term relationships. While we know that differences in mating strategy exist between the two sexes (as predicted by parental investment theory), it has recently been shown that each sex may further exhibit two mating phenotypes. Here we explore the possibility that the presence of two phenotypes may be frequency dependent, thus comprising an Evolutionary Stable Strategy (ESS). We suggest that the presence of these phenotypes reflects a compromise between male preference for promiscuity and a female preference in favour of long-term mating by males.

Keywords: *mating strategies, sociosexuality, evolutionary stable strategies, 2D:4D*

HUMAN MATING STRATEGIES

Parental investment theory suggests that the sex undertaking the greater level of investment in offspring will be more discerning when it comes to selecting a mate (Andersson, 1994; Trivers, 1972). Furthermore, in pair-bonding species females are also more likely to pursue long-term mating strategies as compared to males, who stand to benefit differentially from promiscuous mating (Buss, 1989; Schmitt, 2003; Symons, 1979). In humans, as in all

mammals, the higher metabolic cost of parenting is paid by the female, and cross-cultural research confirms that males favour more promiscuous mating strategies compared to females, although the extent of these differences can vary across cultures (Buss, 1989; Schmitt, 2005). The preferential pursuit of either a short-term mating strategy or a long-term strategy is referred to as 'sociosexual orientation', and can be quantified using the Sociosexual Orientation Inventory (SOI, Penke & Asendorpf, 2008; Simpson et al., 1991).

Interestingly, the propensity to engage in casual sexual encounters also shows considerable variation within the sexes as well as considerable overlap between the sexes (Simpson et al., 1991). It has been suggested that the effect of sex on sociosexual orientation may account for only 10%-20% of the population variance, with intra-sexual variation accounting for a large part of the remaining variance (Gangestad & Simpson, 2000; Simpson et al., 1991).

VARIATION IN MATING STRATEGIES

Among males, the wide distribution of sociosexual orientations suggests that different males may be pursuing different strategies (Buss & Schmitt, 1993; Gangestad & Simpson, 2000). Long-term mating strategies among males are likely to involve increased parental investments which, although increasing the chances of offspring survival (Geary, 2000), must be made at the expense of other mating opportunities (Trivers, 1972). Male mating strategies have been found to vary with environmental conditions (Andersson, 1994) and individual male 'mate value' (Clark, 2006; Gangestad & Simpson, 2000).

Similar variation exists in female sociosexual orientation, varying across cultures with environmental stress (Gangestad & Buss, 1993; Schmitt, 2005), sex ratios (Stone, Shackelford, & Buss, 2007) and individual 'mate value' (Buss & Shackelford, 2008; Clark, 2006). Ultimately, the extent to which any one mating strategy is pursued, either within or between the sexes, will depend on the fitness benefits that the strategy confers on the individual, and this strategy will vary as those benefits change (Allen & Clarke, 1984).

WITHIN-SEX MATING STRATEGY PHENOTYPES

The wide variance in intra-sex sociosexuality, and the implication that both short- and long-term mating strategies may offer different fitness payoffs, raises the interesting possibility that within each sex individuals prefer to pursue one strategy rather than the other. Early studies hypothesized that sociosexuality, and its genetic drivers, might be bimodally distributed, and thus represent two alternative mating strategies maintained through frequency-dependent selection (Gangestad & Simpson, 1990).

We recently examined the possibility that within-sex mating strategies, and their purported biological drivers, may actually comprise two underlying phenotypes (Wlodarski,

Manning, & Dunbar, 2015). Here, the distributions of sociosexuality scores within two populations were examined using finite mixture modelling techniques to determine the likely underlying distribution patterns. It was found that a mixture of two underlying normal distributions best described the within-sex sociosexuality data of both British and U.S. populations – with relative proportions of short-term (unrestricted sociosexuality) vs. long-term (restricted sociosexuality) strategies found to be 43:57 and 47:53 for British and U.S. males respectively, and 57:43 and 52:48 for British and U.S. females respectively (see Figure 1).

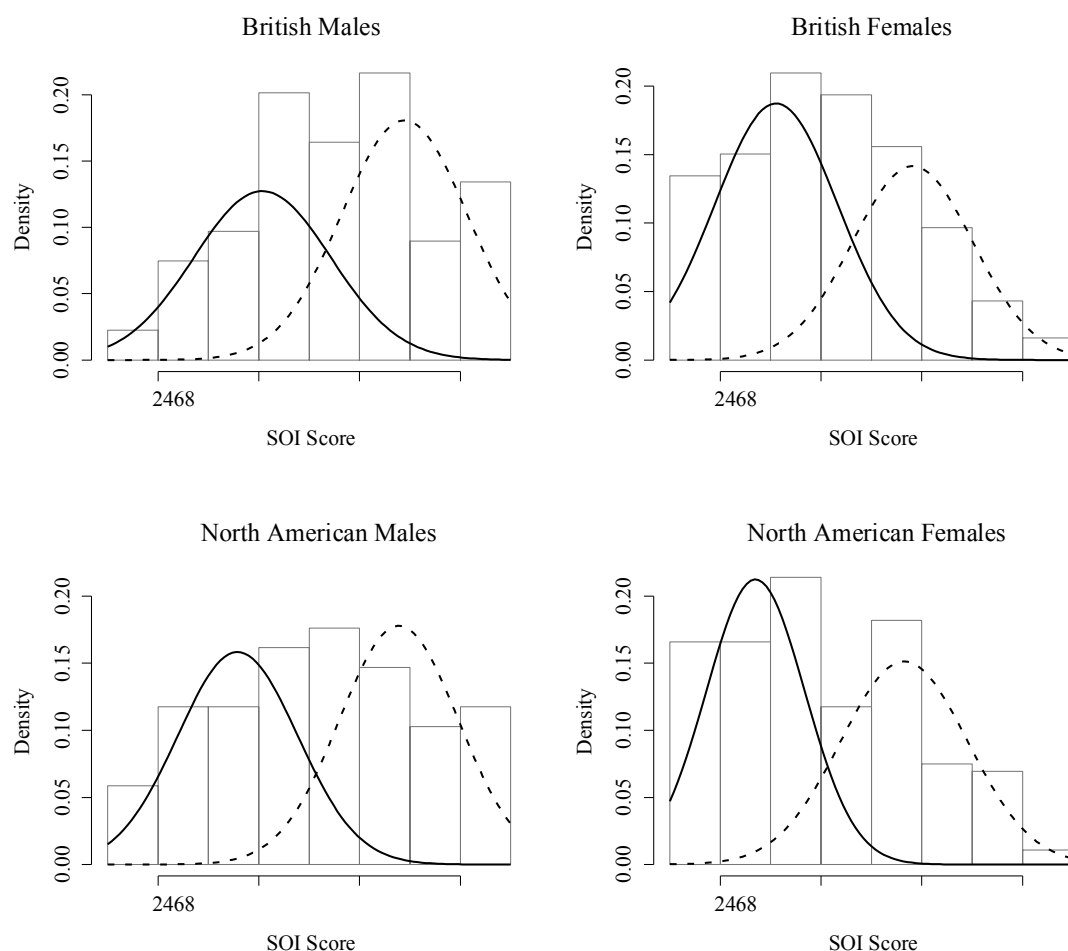


Figure 1. Modelled and actual distributions of sociosexuality in British and North American samples.

Modelled within-sex distribution mixtures of sociosexuality in British & North American samples, plotted against a histogram of the data. Sample sizes are 320 for the British sample and 255 for the American sample. Curves display best-fit models estimating underlying mixture distributions: solid lines represent low-sociosexuality (restricted) phenotype, dashed line high-sociosexuality (unrestricted) phenotype (reproduced from Wlodarski et al (2015) with permission from the Royal Society).

When the distributions of a purported genetic driver of mating strategy were examined (prenatal testosterone exposure as indexed by 2D:4D digit ratios¹), it was similarly found that the within-sex distribution in a British population comprises two distributions - with a low-vs high-2D:4D proportional split of 37:62 for males and 50:50 for females (see Figure 2). Overall, more males favoured a relatively unrestricted strategy as compared to females (average proportional splits of 57:43 versus 47:53 across the three datasets). 2D:4D digit ratios have been previously associated with male and female sociosexuality (Hönekopp, Voracek, & Manning, 2006), although such findings are not always replicated (e.g. Puts, Gaulin, Sporter, & McBurney, 2004), possibly because 2D:4D is associated with the desire and attitude sub-components of sociosexuality rather than the behavioural sub-component (Edelstein, Chopik, & Kean, 2011).

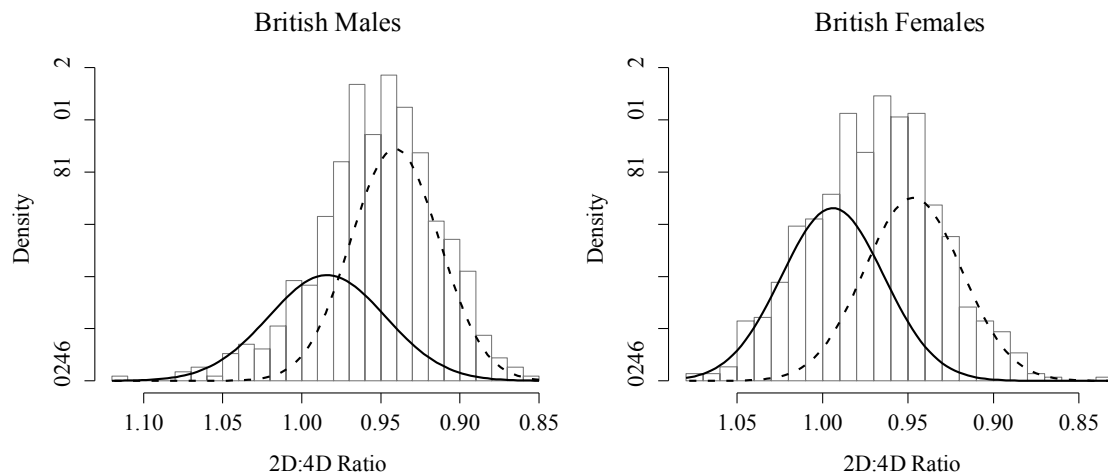


Figure 2. Modelled and actual distributions of 2D:4D ratio in British sample.

Modelled within-sex distribution mixtures of 2D:4D ratio (reversed x-axis) in a British sample, plotted against a histogram of the data. Total sample size = 1314. Curves display best-fit models estimating underlying mixture distributions: solid lines representing low-testosterone (high-2D:4D ratio) phenotype, dashed lines high-testosterone (low-2D:4D ratio) phenotype (reproduced from Wlodarski et al. (2015) with permission from the Royal Society).

¹ The 2D:4D digit has been found to be a physiological marker for foetal testosterone exposure and testosterone receptor-site density, reflecting prenatal testosterone effects in the adult phenotype (Manning et al., 2000; Zheng & Cohn, 2011) and in primates found to be related to mating strategy and mating systems (Nelson et al., 2011).

PHENOTYPES AS EVOLUTIONARY STABLE STRATEGIES?

Competing mating strategies can exist under frequency-dependent selection if the value of a particular strategy decreases as its relative frequency increases, keeping both strategies viable in a particular environmental setting (Allen & Clarke, 1984). Early research into male mating strategies implied that frequencies of long-term and short-term mating strategies in a Canadian population may be inversely related to their respective payoffs (Dunbar, 1993).

If the strategy-pair results from Wlodarski et. al. (2015) represent an Evolutionary Stable Strategy (ESS), then their frequencies should also inversely mirror their payoffs. A linear regression of fertility on 2D:4D digit ratios interpolated for a British population (Manning & Fink, 2008; Manning et al., 2000) shows that number of children born (fertility, F) is positively related to 2D:4D Digit Ratio (DR) in women, but negatively related in men:

$$F_{\text{male}} = 6.775 - 4.828 \text{ DR}_{\text{male}} \quad [N=117]$$

$$F_{\text{female}} = -2.614 + 4.486 \text{ DR}_{\text{female}} \quad [N=183]$$

Inserting the mean 2D:4D ratios of males and females found by Wlodarski et al. (2015) into the above equation gives fertility values of 1.845 and 1.634 children, respectively, for restricted and unrestricted women, and 2.024 and 2.232, respectively, for men. The payoff ratios for each sex thus match rather than mirror reciprocally (as would be expected under simple within-sex ESS solutions) the frequencies of their two strategies: 0.52 and 0.48 in favour of the restricted strategy for females and males, respectively, compared to the average actual strategy frequencies noted above of 0.53 and 0.43, respectively. Nonetheless, such an outcome might arise from some form of stabilizing selection between the two sexes: modest selection pressure favouring the restricted strategy in women and a rather stronger pressure favouring the unrestricted strategy in men, with the observed ratios being the outcome of the rather complex frequency dependence balance between these.

Two-way ESSs are analytically more complex than conventional one-way ESSs (the conventional Hawk-Dove variety) and no analytical solution exists for these at present. To explore this possibility, we calculated the fitness payoffs for the four strategies (two for each sex). Nonetheless, because the number of offspring produced is ultimately limited by the reproductive rate of the females, the left and right sides of the equation must be equal (males cannot sire more offspring than females can give birth to). Hence, if the four strategies form an ESS, the average male and female payoffs should be equal, and we can write a standard ESS equation as:

$$(p \times \theta u_{\text{♂}}) + ((1-p) \times \theta r_{\text{♂}}) = (q \times \theta u_{\text{♀}}) + ((1-q) \times \theta r_{\text{♀}})$$

where $\theta u_{\text{♂}}$ is the mean fertility of unrestricted males, $\theta r_{\text{♂}}$ that for restricted males, $\theta u_{\text{♀}}$ that for unrestricted females and $\theta r_{\text{♀}}$ that for restricted females, and $p = 0.57$ and $q = 0.47$ (the observed proportions of unrestricted males and females, respectively). In other words, the average fitness of males (left hand side, averaged across the two male phenotypes) must

equal the average fitness of the females (right hand side, averaged across the two female phenotypes).

It will be evident from the above that the two strategy sets are not in balance: overall, males have more children on average than women (2.134 vs. 1.746, respectively), perhaps suggesting that, at least in this sample, more women than men fail to reproduce. A similar sex difference has repeatedly been noted in respect of number of sexual partners and has invariably been interpreted as male inflation of sexual performance (Liljeros, Edling, Amaral, Stanley, & Aberg, 2001), though some of this may be due to gender role accommodation (Alexander & Fisher, 2003). This cannot be the explanation in this case, since these data refer to attested offspring. This perhaps suggests that the original claims on mating frequencies should be taken at face value.

There are three possible explanations that would allow the strategy set to be an ESS. First, there are more reproductively active females than males in the population, so that unrestricted males can pursue a polygamous or serially monogamous strategy. If only unrestricted males sire offspring with these surplus females, then the two phenotypes could be an ESS providing there are at least $0.57/0.43 = 1.325$ more females than males in the population. The second possibility is that unrestricted females produce 1.325 times more offspring in a lifetime than restricted females: in other words, rather than there being more females than males in the population, those females that pursue an unrestricted strategy are proportionately more fertile, allowing their males in turn to sire more offspring. The third possible explanation is that unrestricted males sire some of the offspring attributed to restricted (or monogamous) males: the ESS equation would be in balance if $50-43 = 7\%$ of the offspring produced in the mating relationships of restricted males were in fact sired by promiscuous males in extra-marital relationships.

The first is unlikely, given the fact that males remain reproductively active longer than females due to the menopause. Moreover, women are less willing (Starks & Blackie, 2000) or less able (Volland, 1988) to remarry after divorce or partner-death than men, and, in any case, are likely to be less valuable in the mating market because of their age (Pawlowski & Dunbar, 1999). The second is also implausible: in the Manning et al. (2000) dataset, the distribution of fertility is more left-skewed among women than men: 45.7% of women reported having only 0 or 1 child, whereas only 34.1% of men did so (Figure 3). Thus, by elimination, the most likely option is that unrestricted males steal conceptions from restricted males. In fact, the implied non-paternity rate of 7% is very close to the frequency of non-paternity of ~9% estimated for contemporary societies (Baker & Bellis, 1994) (though it must be noted that reliable estimates of non-paternity are notoriously difficult to obtain (e.g. Anderson, 2006)).

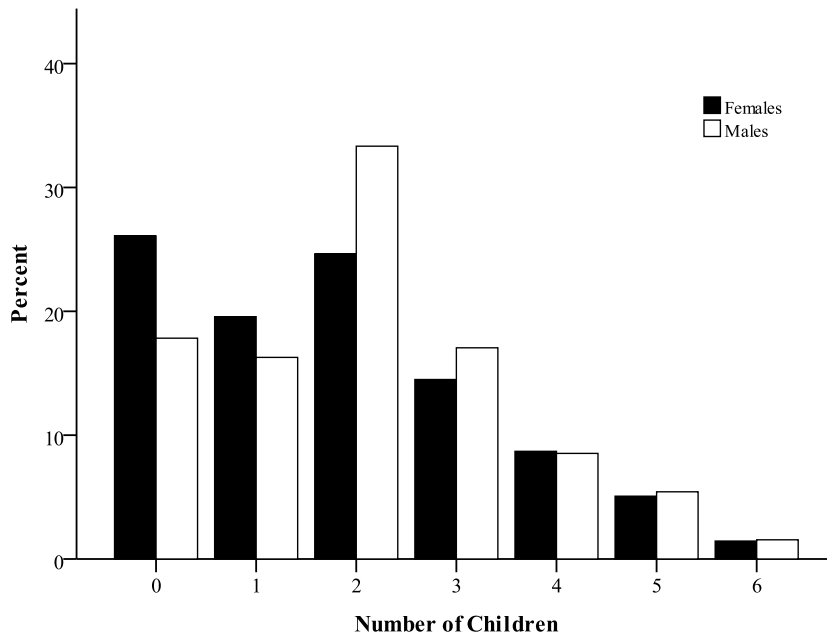


Figure 3. Distribution of Fertility

Distribution of mean fertility among females and males in subjects from England, Germany, Spain, Hungary (ethnic Hungarians and Gypsy subjects), Poland, and Jamaica (women only). Source Manning et al. (2000).

If so, this suggests that the selection pressure favouring a short-term strategy in males is opportunities for extra sirings at the expense of long-term mating. Any extra sirings in a short-term context, however, might come at the cost of reduced offspring survival, since the chances of offspring reaching maturity are greatly increased in the presence of bi-parental care (for a review see Geary, 2000). Furthermore, the availability of extra mating opportunities is always likely to be limited: long-term mating males may be expected to use mate defence tactics (Buss, 2002) (otherwise there would be runaway selection for the short-term mating strategy) and long-term mating females would be resistant to exploitation if their optimal strategy is to search for partners who are willing to invest over the rearing period. Hence, it may be no surprise that the proportional split in favour of the long-term mating strategy is modest. Indeed, the (weak) negative relationship between 2D:4D and fertility in men (Manning et al., 2000) suggests that there is a degree of stabilizing selection preventing runaway selection for super-promiscuous males. Seen against a background of universal polygamy in recent ancestral hominin populations (as judged by 2D:4D ratios in fossil archaic humans and Neanderthals: (Nelson, Rolian, Cashmore, & Shultz, 2011), these results would seem to reflect significant selection pressure in anatomically modern humans in favour of long-term mating in males which was presumably imposed by females (implying a significant degree of female choice).

CONCLUSION

The presence of two mating phenotypes implies that these competing mating strategies may be under frequency-dependent selection, thus forming a pair of Evolutionary Stable Strategies. We suggest that these data reflect selection pressure in modern humans which favours male long-term mating, presumably imposed by females.

It is worth noting that there is significant cross-cultural variation in adult 2D:4D ratios, with some suggestion that lower (more testosterone) ratios occur in both sexes in more polygamous cultures (Manning et al., 2000). This indicates directional selection as historical and cultural opportunities for polygamy increase, since foetal testosterone titres (and hence 2D:4D ratios) are known to have a genetic component (Manning et al., 2000). Nonetheless, comparison of the data in Wlodarski et al. (2015) suggests that the underlying biological predisposition (as represented by the 2D:4D values) can be influenced by cultural or contextual factors acting on psychological attitudes and desires (as represented by the sociosexuality values). In this respect, the ESS balance between the phenotypes will always be in dynamic equilibrium, since it will depend on the contingent costs and benefits that individuals encounter in real life.

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