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Offspring sex ratio: Coital rates and other potential causal mechanisms



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ABSTRACT

In recent years, scientists have begun to pay serious attention to the hypothesis that human parental coital rates around the time of conception causally influences the sexes of subsequent births. In this paper, the grounds of the argument are outlined. The point is important because, if the hypothesis were credible, it can potentially explain one of the best established (and otherwise unexplained) epidemiological features of sex ratio at birth – its rises during and just after World Wars 1 and 2 insofar as increased coital rates increase the ratio. Moreover, the greater the understanding of the variations of sex ratio at birth, the greater will be the understanding of the causes of those selected diseases associated with unusual sex ratios at birth (testicular cancer, hepatitis B, *Toxoplasma gondii*, and, perhaps, prostatic cancer).

1. Introduction

The main purpose of this paper is to summarize the evidence that human parental coital rates around the time of conception have a positive causal effect on subsequent offspring sex ratios (proportions male) at birth (SRB). The second purpose here is to describe two (noncompeting) hypotheses on the causes of the variations of SRB.

Hypothesis 1. Maternal stress-induced sex-selective foetal wastage lowers sex ratio at birth.

Up to circa two decades age, it was generally supposed – but without hard supporting evidence – that pregnant women exposed to adverse environmental circumstances were at increased risk of foetal loss, and that male foetuses were at greater risk than female foetuses; and that therefore the liveborn infants produced by stressed women contained a higher proportion of daughters. That hard evidence has now been accumulated in a series of papers by Catalano and colleagues, and others.

Using time-series analysis, it has been shown that the SRB briefly declined, slightly but significantly, some three to five months after many catastrophic and other adverse events e.g. the terrorist attacks on September 11th, 2001 [8,9]; the Troubles in Northern Ireland (1969–1998), the Breivik shooting in 2011 in Norway, the Sandy Hook shooting in 2012 in Connecticut [19]; the assassination of President Kennedy [21], [though the effect in this case was more marked in non-White than White births [20]].

Transient SRB reduction has also been reported following temperature oscillations [10]; severe maternal peri-conceptual life events

(death or admission to hospital for cancer in the partner or older children) [22], psychological stress during early gestation [46], maternal anxiety disorder [55]; economic stress in various countries [4,40,58]; mass layoffs [12]; the Kobe Earthquake [15], the Bam earthquake in Iran [51], the 'Tarapaca' earthquake in 2005 in northern Chile [56], the Eastern Marmara earthquake in 1999 [13] and the Great East Japan Earthquake [11].

Catalano's group demonstrated that these foetal losses involved selective culling of frail males rather than simply the random damage to foetal cohorts [6]. This demonstration showed that the male foetuses which survive such adverse circumstances have low mortality rates [2,7,5]. It was inferred by these workers that natural selection has conserved mechanisms by which stressed pregnant women cull frail males in utero (rather than that a dysregulated system should present equal risks to foetuses of both sexes). These workers also suggested that a similar explanation applies to the Bruce effect (in which pregnant female mice abort when exposed to danger e.g. a strange male), and that the Bruce effect applies to humans too [52]. The evolutionary rationale for this selective culling of frail males will be explained later in the discussion of the influential hypothesis of Trivers & Willard [57].

Thus there is overwhelming evidence that sex ratios at birth are partially controlled by maternal stress-induced selective culling of frail males in utero, resulting in a conception cohort with a low sex ratio at birth. It has also been postulated that the ratio may be skewed because of fertilization of non-optimally matured oocytes under these circumstances [39]. Moreover, it has also been hypothesized that higher coital rates will lead to ejaculation of newly formed spermatozoa cells, possibly leading to a preponderance of Y-sperm since it is also

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hypothesized that X-sperm age faster and are eliminated earlier [16].

However, it will be appreciated that selective culling of frail males during pregnancy cannot explain some of the established variations of SRB. First, it cannot explain why some reported sex ratios are higher than prevailing norms. Second, it cannot explain why these norms almost always exceed 0.5 (equal numbers of males and females). These points will now be examined.

Hypothesis 2. Parental hormone concentrations around the time of conception partially control offspring sex ratios at birth.

It has been hypothesized that human sex ratios at birth are partially controlled by the parental hormone levels of both parents around the time of conception [23,26,27,28,29,31,32,34,35]. *Ex hypothesi*, high levels of testosterone (in either parent) and/or of oestrogen (in the mother), are associated with subsequent male births. And high levels of gonadotrophins (in either parent) are associated with subsequent female births. Most of this evidence is observational and correlational, and is in accordance with the hypothesis of Trivers & Willard [57]. This will now be summarized.

It is commonly observed in many species (including man) that the variance of male reproductive success is greater than the variance of female reproductive success. In other words, most females have an average number of offspring, whereas in contrast, some males have many offspring and an appreciable proportion of males have no offspring. On the basis of this observation, Trivers & Willard [57] noted that the expected number of grandchildren would be maximized in all women if females in good 'condition' were to produce sons, and females in poor 'condition' were to produce daughters. Accordingly, in an intuitive coup, they predicted that this actually occurs. This paper has been influential, having attracted > 2000 citations (according to the Web of Science in August 2017). One prediction of the hypothesis has recently been the subject of measured support by a meta-analysis [1]. However, the best direct evidence for the Trivers-Willard hypothesis are the demonstrations [14,53] that (under natural conditions) the most fertile parents produce the highest proportion of male offspring.

Nevertheless, some of the citations of Trivers-Willard are by authors who claim to have failed to confirm the hypothesis. We suggest, following Cameron [3] that these 'failures' were occasioned by the failure of these authors to test the hypothesis as formulated. Cameron [3], on the basis of a meta-analysis, found that the Trivers-Willard hypothesis was consistently supported if the measure of 'condition' was made around the time of conception. The crucial point to note here is that Trivers & Willard defined 'condition' by two criteria viz. (1) heritable and (2) positively related to fertility.

The reason for emphasising this point is as follows. The underlying cause of high fertility (number of progeny produced under natural conditions) is high fecundability, the probability of conceiving in a month at risk. Fecundability is dependent on four (admittedly non-independent) parameters viz. P1, the probability that ovulation will occur in that month, P2, the probability that viable sperm will be delivered during the viable life of the ovum, P3, the probability that fertilization will occur, and P4, the probability that foetal loss will not occur.

The relevance of all this is that, as documented by James [36,37], the levels of two of the hormones that are proposed to control the sex ratio (testosterone in males and oestrogen in females) each correlates positively with all four of these parameters. Moreover, it was also documented in James [36,37] that testosterone levels correlate positively between fathers and sons; and that oestrogen levels correlate positively between mothers and daughters. In short, the criteria proposed by Trivers-Willard for the agents controlling sex ratio are fulfilled by the agents independently proposed by James. So the evidence that parental hormone levels control offspring sex ratios is now stronger since the synthesis of the evidence for TW with observational, correlational data adds credibility to the interpretations put on the original evidence for each.

One consequence of this synthesis is a renewed interest in the effect

of coital rates on sex ratios. This effect will now be described.

2. Parental coital rates and offspring sex ratios

Sex ratios rose (slightly but significantly) during, and just after, World Wars 1 and 2 in the belligerent, but generally not the non-belligerent, countries [44,50]. These changes were not due to changes in parental ages or birth order, and the latter authors opined that there was no more satisfactory explanation for these wartime sex ratio rises than Divine Providence. However, subsequent workers on this topic ([42]; [23]) made the more mundane proposal that increased coital rates might be responsible. This suggestion was originally met with caution, but it now seems to be gaining acceptance in some quarters. The subsequent thinking on the relationship between parental coital rates and offspring sex ratio will now be summarized.

The proposition that parental coital rates affect offspring sex ratios depends on the proposition that parental hormone levels (around the time of conception) affect offspring sex ratios. A meta-analysis [30] showed that the regression of offspring sex ratio on time of insemination within the menstrual cycle is U-shaped (p < 0.005). In other words, boys are conceived disproportionately often at the beginning and end of the 'fertile interval' (that period of time during which a woman is at a non-zero risk of conception). In contrast, girls are conceived more frequently in the middle of that interval. It may be shown mathematically that the time of conception during the cycle is dependent on coital rate, being earlier if the rate is higher [49]. In short, given these data, we would expect high coital rates at the time of conception to be followed by high sex ratios (more boys) at birth.

It was later suggested that the rises in sex ratio during, and just after, the World Wars had slightly different explanations, both involving coital rates. During those wars, servicemen were given embarkation leaves which were typically short. Under such circumstances couples knew that they might never see one another again. In the absence of documentation, it was speculated that coital rates then were high for that reason [33,38]. Moreover, since the duration of the leaves was limited, then, for pregnancy to have occurred at all, there must have been selection for high coital rates. In contrast, the argument that coital rates at the time of the Armistices were high is more intuitive. In Britain, there was public elation such as has never since been seen. Soldiers climbed the lamp-posts in Piccadilly Circus, and strangers kissed one another and danced in the streets. As a docile teenager, one of the authors (WHJ) witnessed charismatic jitterbugging U.S. soldiers whirl excited girls over their heads in the VJ Day celebrations in England. During 1941-46, the live-born sex ratios in England & Wales were higher than in any years previously recorded, registration having started in 1841 [41]. Illegitimacy rates were high and the illegitimate sex ratios increased more than the legitimate sex ratios in England & Wales during the Second World War [43], suggesting that irregular liaisons, in particular, were flourishing at that time.

In recent years, it has been confirmed that there have been brief rises in sex ratio associated with other selected times of public elation e.g. in England & Wales following the birth of Prince William in 1982 [17]; and in Hong Kong during 1975–6, 1988 and 2000, the auspicious Years of the Dragon [18]; and in South Africa following that country's success in the 2010 FIFA World Cup [45]. These observations lend some further credence to the suggestion that high coital rates are associated with the subsequent births of sons. Moreover, it has also been authoritatively speculated that the very slow reported decline in sex ratios across the long reign of Queen Victoria may have been due to a slow secular decline in coital rates [54].

Further support for this line of thinking is as follows. It has been shown that coital rates decline with duration of marriage. Roughly speaking, coital rates halve during the first year of marriage and then take another twenty years to halve again [24,25]. In conformity with the present argument, Renkonen [48] found a slight but significant decline in sex ratios at birth of a very large sample of first births by

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