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The Incidence of Superfecundation and of Double Paternity in the General Population

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Abstract. It is estimated that at least one dizygotic (DZ) twin maternity in twelve is preceded by superfecundation (the fertilization of two ova by sperm from different coitions). Presumably this parameter varies from population to population eg. with coital rates and rates of double ovulation. Sometimes superfecundation occurs by two different men. The frequency with which this occurs must depend on rates of infidelity (promiscuity). It is suggested that among DZ twins born to married white women in the U.S., about one pair in 400 is bipaternal. The incidence may be substantially higher in small selected groups of dizygotic twin maternities, eg. those of women engaged in prostitution.

Key words: Incidence of superfecundation, Incidence of double paternity.

INTRODUCTION

Superfecundation is defined as the fertilization of two or more ova by sperm from different coitions. The existence of the phenomenon had long been suspected, because of the occasional occurrence of twins with features suggesting different racial backgrounds. More recently, testing with blood groups and other markers has confirmed the existence of bipaternal twins [20]. So one might wonder how often dizygotic twins *by the same father* are a consequence of superfecundation.

The following notes are offered towards a preliminary estimate. In the discussion, two numbered assumptions are made, and their plausibility is later assessed.

At one time, the author thought that superfecundation must be quite common [8]. This opinion was based on the facts that: (a) DZ twinning is more common in legitimate than illegitimate births to young women, and (b) when maternal age is controlled, DZ twin conceptions occur more commonly in the early months of marriage [6]. Both these factors are associated with high coital rates, and I inferred a relatively high rate of super-

fecundation. However, it appeared from these data that a doubling of coital rates very roughly corresponded to an increase of only 25% in the DZ twinning rate. And this was estimated to imply that the mean additional increment in the coital rate of DZ twin-bearers over singleton-bearers was of the order of only 6% [9]. DZ twin-bearers are substantially more fecundable than singleton-bearers: and the increment of 6% described seems inadequate to account for this. Accordingly, it was argued that the additional DZ twins in the legitimate pregnancies of young women, and in the conceptions in early marriage were not entirely explained by the associated higher coital rates. Instead it was inferred that erotic circumstances might sometimes cause multiple ovulations.

The Incidence of Superfecundation

For convenience, the main protagonists in a paternity dispute will here be called "husband", "the wife" and (where applicable, "the lover". It is true that reality is sometimes complicated by the existence of other men, and indeed apparently trizygotic triplets have been recorded with features suggestive of three different fathers [15]. However intercourse with three or more different men in the fruitful cycle is presumed to be rarer than with two men, so these rarer possibilities will be ignored here. Let p_1 be the proportion of paternity cases in which the child is proved not to be the husband's. Let us assume (1) that in such cases, a woman is, on the average equally at risk of conceiving by husband and lover. Then one might estimate that in a further proportion p_1, though the child was by the husband, it equally could have been by another man, but by chance was not. In other words, a proportion $2p_1$ of paternity suits are preceded by intercourse with two men.

Let p_2 be the proportion of DZ twins in paternity suits in which it is demonstrated that the children have different fathers. So, given that intercourse with 2 men has occurred, the proportion of resulting DZ twins which are bipaternal is estimated at $p_2/2p_1$. This is the rate of *identifiable* superfecundation (expressed as a proportion of those DZ twins in which it *could* have been identified). Let us assume (2) that when superfecundation occurs following intercourse with two men, monopaternal and bipaternal twins are equally likely. Then the total proportion of DZ twins which are preceded by superfecundation is estimated by P, where $P = p_2/p_1$.

Terasaki [19] estimated the non-paternity rate (p_1) in his series of 1000 paternity cases at 0.25: and I am grateful to Dr. R.E. Wenk (Baltimore) for informing me that in his sample of 39000 cases, the rate is about 0.3, and that in his DZ twins, the rate is similar, namely 36/124. The proportion of DZ twins that were bipaternal in Dr. Wenk's series was 3/124 [21]: so taking his estimate of p_1, one would estimate P at about 1 in 12.

The Incidence of Double Paternity

Using the assumptions outlined above, it is possible to estimate the frequency of double paternity among DZ twins in the general population (as opposed to those ascertained in paternity suits).

Let p_3 be the proportion of children in the general population who are not fathered by the mother's husband. Then the probability of double paternity in DZ twins is p_2p_3/p_1.

This parameter p_3, has been subject to much speculation but less study. It may be expected to vary with maternal age, social class, birth order, and in the U.S. it has been reported to vary by race [18]. The Table gives estimates of non-paternity rates in some (mainly Caucasian) populations. Data of this sort have been contrasted by some workers [4,13] with the high proportion of married women who report having extra-marital partners. However, the woman in the sample of Bellis & Baker [4] were self-selected readers of a (fairly) sophisticated magazine, and cannot be regarded as a random sample of married British women; the data cited by Macintyre and Sooman [13] were on the proportion of women who reported extramarital partners within the last *year*. A more useful datum would be the proportion of women who have had extramarital partners in the last *month*; if assumption (1) were correct, that in the proportion of paternity cases in which the child is proved not to be the husbands', a woman is equally likely to conceive by her husband as by her lover, then this latter proportion should be twice the non-paternity rate.

Bearing in mind all these considerations, the lower values in the table would seem to be the safest. As noted earlier, the proportion of children in the general population who are not fathered by the mother's husband ($p_3$must vary from one population to another. But for purely illustrative purposes, one might take a value of 0.03. The probability then that a randomly chosen pair of DZ twins is bipaternal is estimated at 1 in 400.

This estimate is based on data from (mainly Caucasian) U.S. sources. There is no obvious reason to suppose that the value would differ greatly in England and Wales. It may be noted again for illustrative purposes that there were 2341 live-born opposite-sexed twin maternities in England & Wales in 1990. So one might estimate about 4682 DZ twin maternities. And, very approximately, one might suppose that among them, there were 12 bipaternal pairs.

DISCUSSION AND CONCLUSIONS

Comment on the Assumptions Involved

The first assumption is that if a woman has intercourse with 2 men, she will be equally at risk of conception by each. However, there are reasons for wondering if there may a bias in favour of fecundation by lovers vis-a-vis husbands:

a) I have argued that particularly erotic circumstances may sometimes provoke or accelerate ovulations [9] and one might suppose that lovers have an advantage in this regard.

b) There is a substantial literature on sperm competition [16], and these authors speculate that it is a potent evolutionary force among mammals. However, few studies on sperm competition in the human female have been reported. An exception is a paper [2] whose authors conclude that (i) women are less likely to use contraception in extra-marital than marital coitus, and (ii) women are more likely to engage in extra-marital coitus during the fertile days of the cycle.

In a subsequent paper, the same authors buttressed their argument that (some) women act to maximize the possibility of sperm competition [4]. They report that on the average, 35% of sperms are ejected by females within 30 minutes of insemination. The occurrence and timing of female orgasm in relation to copulation and male ejaculation influenced the number of sperms retained at both the current and the next copulation. Moreover, they report that women adjust their orgasm pattern to favor the retention of sperm of the extra-pair male, thus presumably raising his chance of success in sperm competition with the female's regular partner. These authors also report that individual males inseminate more sperm when the pair has recently spent a small proportion of their time together (and hence the risk of sperm competition was greater) [3]. Thus, it would seem that women strive to promote sperm competition and their male partners strive to eliminate it, and, failing that, to win the competition.

If these suggestions are correct, then $2p_1$, defined as the proportion of paternity suits preceded by intercourse with 2 men, is an overestimate of the proportion of paternity cases preceded by intercourse with 2 men, and P, the total proportion of DZ twins which are preceded by superfecundation, is underestimated above.

The second assumption is that when DZ twins result from intercourse with 2 men and superfecundation, the twins are as likely to be bipaternal as monopaternal. Let that time interval from the beginning of viability of the first ovum to the expiry of viability of the second be called the fertile interval. If a woman has coitus more than once with equal probability with each of two men across this fertile interval, then it is equally likely that two randomly chosen coitions within the interval are with the same man as with different men. However, in most cases one must assume that women are not so even-handed in their choice of sexual partner: husbands and lovers have unequal access. So, even if a woman conceives twins by superfecundation after she has engaged in coitus with two men during the fertile interval, it is rather more likely that the twins will be monopaternal than bipaternal. It must be noted however, that except where there is substantial inequality of access, the probability of bipaternity (all other things being equal) does not depart greatly from 0.5. For instance, if a woman's coital rate with one man were twice that with the other, the probability that two randomly chosen coitions were with the same man is only 0.56.

It is interesting to consider the effects of sperm competition within the female tract. The viability of sperm and of ova are estimated to decline with time over mean periods of 1.5 days and 0.7 days respectively [17]. Moreover, human coitus typically does not occur more than once per day (though admittedly data on fruitful cycles — let alone superfecundation — are sparse). So, if two ova are released simultaneously, then one might suppose that if both are fertilized after two coitions have occurred within the fertile interval, both will be fertilized by sperm from whichever coition is more optimally timed (namely that superfecundation does not occur). Only as the interval between the release of the ova increases, would one expect superfecundation. Under such circumstances, when ova are released into a pool of competing sperms from two ejaculations, the competition would seem to be based more on the timing than on the intrinsic qualities of the two ejaculates. For sperm competition to be a powerful force, one would expect either higher coital rates, or a longer mean sperm viability. One may conclude that even though sperm from different men may differ in fertilizing power, this does not appear to greatly increase the chance that superfecundation will be monopaternal.

Table - Estimates of non-paternity rates in Caucasian populations

Author	Rate (%)	N	Place
Ashton [1]	2.3	2839	Hawaii
Brock & Shrimpton [5]	1.0	521	Edinburgh
Johnstone [10]	5.7	2578	London
Le Roux et al [11]	2.8	362	Nantes, France
Peritz & Rust [14]	2.1	6960	Oakland, California

Notes to Table

1. The estimate of Peritz & Rust [14] had 95% confidence intervals of 1.4% and 3.0%.
2. The estimate of Johnstone [10] was based only on parent-child ABO blood group anomalies. According to Edwards [7], such a system would be expected to detect only 18% of agamous children in England at that time. So Johnstone's estimate must have a large standard error. The estimate of 'more than 5%' frequently ascribed to Edwards [7] is based on Johnstone's data, and was evidently selected by Edwards because of its magnitude.
3. The data in the Table must refer not only to cases arising through wives' infidelity, but also those based on concealed adoption, and the occasional hospital error in which babies are 'switched'.
4. It is possible that infidelity may be underestimated in the data because unfaithful wives might be less willing to participate in testing.
5. Not all the samples in the Table were random: some were ascertained in the course of genetic screening. Le Roux et al [12] remark that some female fragile-X carriers are mentally impaired, and are thought to have many partners. So the non-paternity estimate of these authors may be high for the general population from which their sample was drawn.

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