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Twinning and the r/K Reproductive Strategy: A Critique of Rushton's Theory

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Abstract. The theory of r selection, favoring population growth, as opposed to K selection, favoring more efficient utilization of resources, has in recent years been applied by Rushton to contrast human ethnic groups in terms of their r/K reproductive strategies, suggesting the existence of a continuum from r groups, producing many offspring but providing little parental care, to K groups, producing few offspring but providing much parental care. Rushton's theory, which is largely based on ethnic differences in twinning rates, is here critically examined. It is pointed out that twinning rate differences are not necessarily genetic in origin since various environmental factors clearly play a role, and also that twinning, as a mode of reproduction, is not necessarily an r strategy, considering the high prenatal and perinatal selection to which it has been, and still is, associated. Moreover, Rushton misinterprets a number of relevant aspects related to the biology of twinning. The claim that ethnic differences in twinning rates provide evidence for an r/K typology in human populations with respect to reproductive strategies does not appear to be warranted.

Key words: Reproductive strategy, Selection, Litter size, Twinning, Ethnic differences

THE r/K SELECTION THEORY

In 1967, in their book, "The Theory of Island Biogeography" [18], MacArthur and Wilson made an effort to develop a theory that would start "the growth of a mathematical tradition... comparable to the tradition in physics" in the field of biogeography. While the original idea was to stick to small islands such as the Galàpagos, they hoped

that the theory would be able to cover the entire earth, with all its plants and animals. Two of the important concepts they developed were “ r ” selection and “ K ” selection, which they defined as follows:

- r selection favors a higher population growth and higher production (of individuals). This form of selection will come forth during the colonizing episode or in species which are frequently engaged in colonizing episodes and hence must frequently build back up to K .
- K selection is, by contrast, selection favoring a more efficient utilization of resources, such as a closer cropping of the food supply. This form of selection will be more pronounced when the species is at or near K .

K is defined at the outset as “the carrying capacity of the environment”, ie, the number of individuals in a population of a given species at the population equilibrium. A population with more than K individuals will decline. In contrast, r is defined as “the intrinsic rate of increase”, the per capita rate of net increase in a given environment. The general scheme is very complex and these are only 2 of a set of 39 basic concepts (eg. A = the area of an island, B = the age of an organism at which first offspring are produced, I = the immigration rate in a species per unit time, J = the total of individuals in a taxon at a given time, etc). The whole effort seems almost too grandiose and would require data on many variables that are difficult to quantify, while it is not known to what extent one can lift out some of the measures and apply them to a small area or to a single species.

Some sociobiologists have contrasted species that produce large quantities of offspring with species that have only a single offspring at one time but protect and care for this single young until it is able to take care of itself. This contrast between the r and K selection — or, as others refer to them, the two reproductive strategies — has become an important, but controversial, idea. First of all, one should keep in mind that the original treatment by MacArthur and Wilson does not anticipate lifting just two concepts out of the theory. More specifically, however, the r/K typology is especially controversial, not when it is used in the total scheme of MacArthur and Wilson, but when it is applied to humans as a potentially quantifiable entity which can be used to contrast ethnic groups that are also contrasted on behavioral measures. This is what has been done in recent years by Rushton [22,24] and his theory is the object of the present critique.

LITTER SIZE IN MAMMALS

The litter size in mammals varies within and between species, from one in horses to up to 24 in dogs. The usual number of human babies is one per pregnancy, but multiple maternities do occur. Sextuplets hardly ever survive but quintuplets are no longer rare — due primarily to the use of fertility drugs or to the use and subsequent disuse of birth control pills. In Nigeria, the incidence of multiple maternities was increased by consumption of a type of yam that contains a substance which acts as a fertility drug. The varying number of babies per pregnancy, as well as the total number of offspring (which can be very large for wealthy Arabs with many wives and concubines, and occasionally

can reach into the thirties and higher), is indeed of some interest. It would be instructive to summarize the information. Information on multiple maternities in primates is available and can be related to their lifestyles.

It is not clear to what extent the data on animals in captivity are representative of the situation in the wild. In many species the rate of pregnancies that carry to term is very low, while in other species it is high.

RUSHTON'S THEORY AND TWINNING RATES

Now we turn to twinning rates, which form one end of Rushton's thesis [22,24] — keeping in mind that r/K contrast is reduced in Rushton's theory to simple frequencies of twin maternities, whether MZ or DZ. It seems that the lifetime number of twins might be more valuable for sociological research, but this information is not readily available. However, the numbers of triplets, quadruplets, and the rarer cases of quintuplets would still be a more suitable measure than twins alone. Such studies should statistically control for the age of the mother, as well as the father's age and socioeconomic status, and ideally should take into account whether there are other sexual outlets for the father and also for the mother. Most reports in the literature on twinning rates are probably not of equal quality and are unavailable for some countries; spontaneous abortions, for example, are not considered.

To do a more effective critique of Rushton's idea about differences in r/K reproductive strategies, we would first of all need to summarize data on the various animals that have these strategies, working up to mammals and primates and finally humans. Then we would like to summarize the incidence of multiple maternities in various ethnic groups as completely as possible, including, if practicable, ethnically similar groups in different countries in Europe, South America, etc, as well as different ethnic groups in the same country (eg, USA, India, etc). Figures on triplet, quadruplet, and quintuplet maternities would be especially interesting. Then we want to look for differences in age of mother, SES, and so on. On the other end of Rushton's continuum, we may wish to look for summary statistics about criminality, sex, etc, in the various countries and look for changes in SES and other correlates. The Arab countries would be especially interesting in that respect.

Rushton [22,24] bases his r/K racial typology in part on observed racial differences in twinning rates, which he takes to be genetic and clearly an r -trait and which he links to differences in behavior, also alleged r -traits.

Rushton's papers have been critically reviewed by other authors, particularly Zuckerman and Brody [27] and Lynn [17]. We will direct our attention mainly to those statements related to twinning rates, and with twinning rates as example, to Rushton's more general interpretation of individual differences. All or nearly all the statements cited were in the 1987 article [23], which was principally about twins and twinning.

1. The racial differences in twinning which Rushton uses in his typology may be environmental rather than genetic in origin

Most recent statistics on twinning seem to support racial differences in the direction of Rushton's thesis: Negroid > Caucasoid > Mongoloid, going from r to K if higher twin-

ning rate is an r -trait. However, variation within races and even within populations is so great that twinning cannot be considered a stable genetic characteristic. Other factors are known to play a role, and twinning rates can increase by 300% from maternal age below 20 to maternal age around 37. Environmental effects are known to be strong. Racial differences in any trait are inevitably associated with cultural and environmental differences not only in the native lands of those races, but in their adopted lands. In the United States, where relative twinning rates may be crucial to Rushton's argument, even when Negroes and Caucasians, "blacks" and "whites", live in the same apartment houses, they often differ in economic status and lifestyle. As national populations on which the racial statistics are based, American blacks and American whites exhibit very large average environmental and cultural differences.

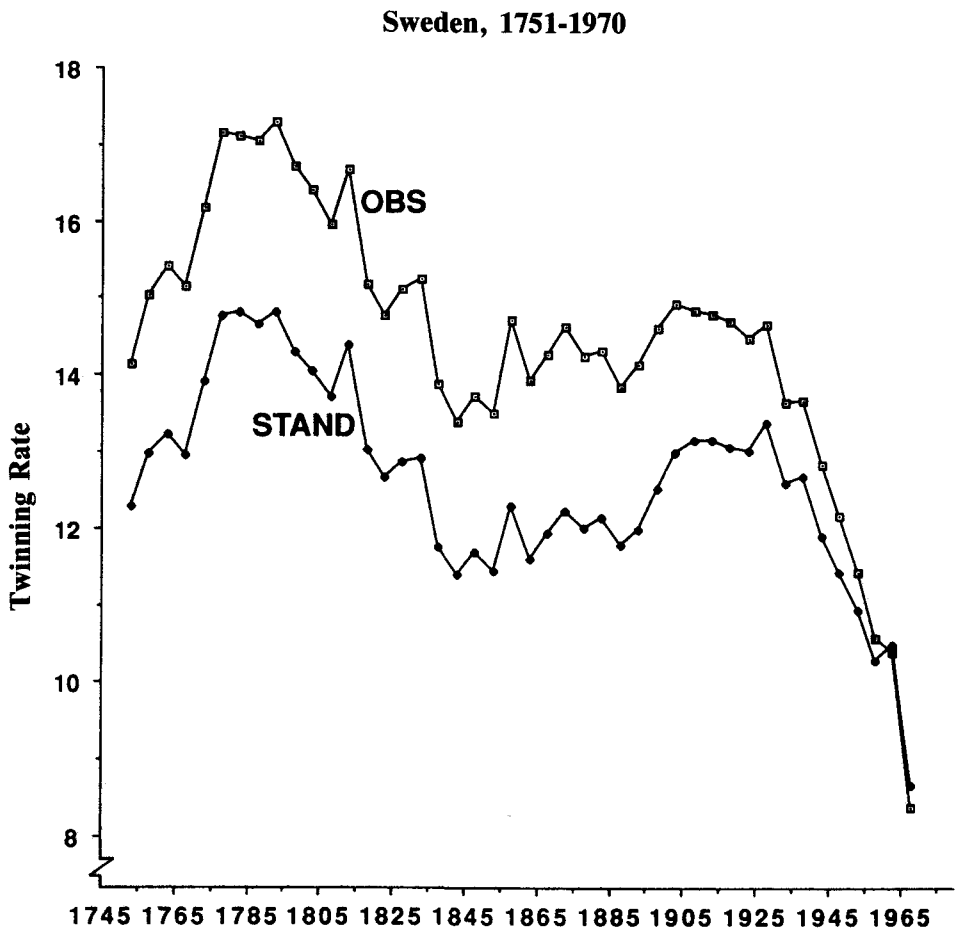


Fig. 1. The twinning rate in Sweden, 1751-1970. Observed and standardized values. (After Fellman and Eriksson, 1990).

The difference in twinning frequency between US blacks and whites is as much as 44% of the lower figure: 13.7% in blacks and 9.5% in whites [13]. However, this is not much greater than differences over time in the same population. In Sweden the twinning rate was 14.8% in 1901-1910 and 11.0% in 1951-1960, a 35% difference (Fig. 1), and in the 1960s the rate was hardly 60% of what it had been during the last three decades of the 18th century, with a corresponding fall to 30% in the triplet and quadruplet maternities [10]. Very similar variations were observed in Italy (Fig. 2) [20] and in other countries.

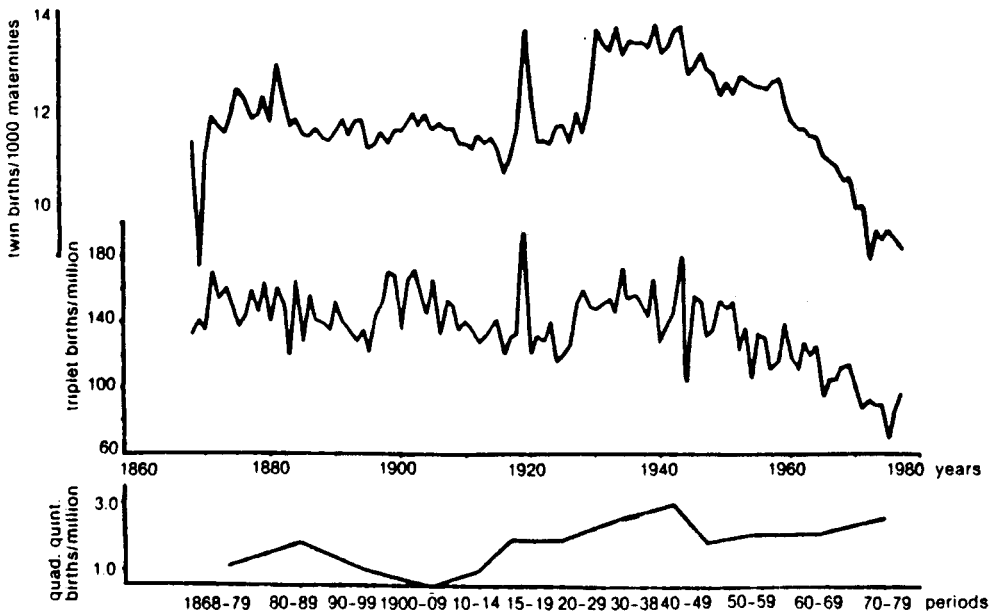


Fig. 2. Twin, triplet, and higher multiple births in Italy, 1868-1977. (After Parisi and Caperna, 1982).

Such comparisons, both between races and over time, may be misleading without adjustment for maternal age and parity, both of which affect the twinning rate. Actually, adjustment does not have much effect on the changes over time: analysis of Italian data [2] shows a decline in DZ twinning from 8.9% to 6.0% between 1949-53 and 1978-81 after full adjustment for maternal age and parity [Fig. 3]. Also, irrespective of the standardization method, the changes in the maternal age explain only about 50% of the strong temporal variations in the twinning rate [11,12]. Thus, even apart from the effect of maternal age, the twinning rate in Sweden has been falling. Other factors must decrease the rate, such as declining mean parity and probably also industrialization and urbanization [20] with breaking up of isolates and more sedentary occupations of women, leading to a poorer physical condition of women and higher risks of spontaneous abortion in an early phase of gestation [10].

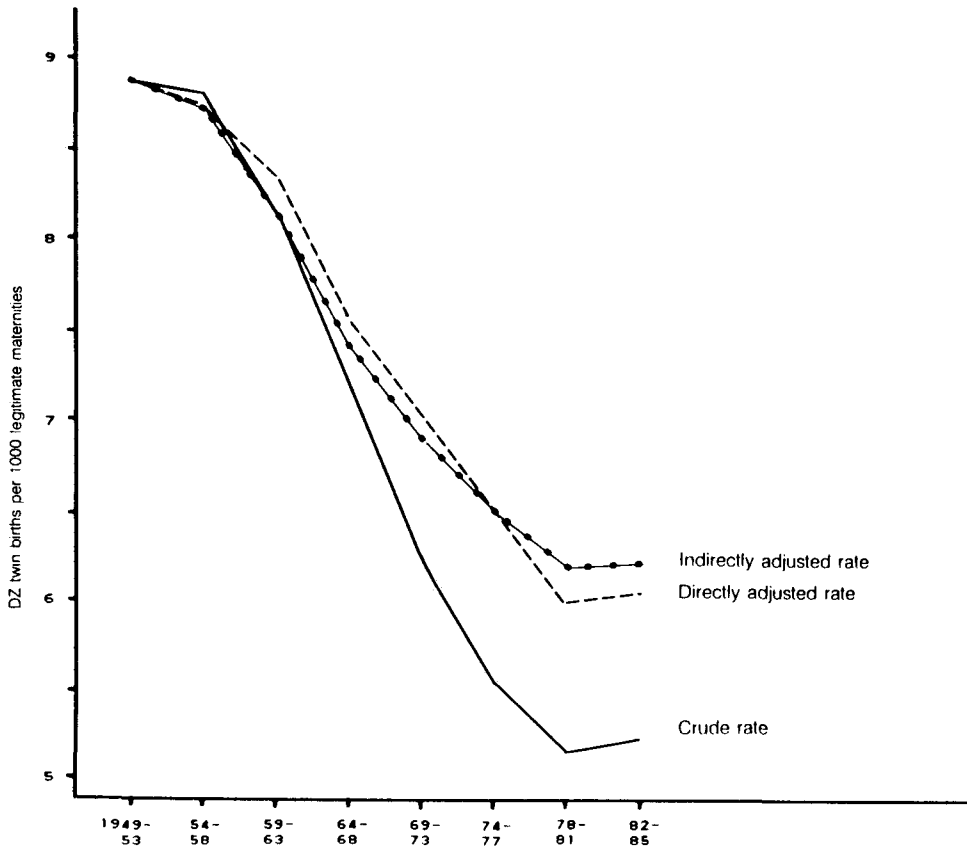


Fig. 3. DZ twinning rate in Italy, 1949-1985: effects of adjustment. The crude rate is compared with rate adjusted directly and indirectly for maternal age and birth order. (After Allen and Parisi, 1990).

Recent studies [4] on survival of natural twin pregnancies, estimated from published values, suggest that at least 73% of natural single conceptions have no real chance of surviving six weeks of gestation and that pregnancies with multiple embryos may constitute more than 12% of all natural conceptions, of which, only 2% survive to term as twins and 12% result in single births. This indicates that interracial differences in twinning rates reflect differences not only in polyovulation tendency but also in survival probability of conceptions from fertilization to term, particularly before clinical detection of pregnancies.

Some white Caucasian populations have exhibited twinning rates as high as those commonly reported in American Negroes; for example, the higher figure given above for Sweden. The highest reported rate in Caucasians, 23.7% in the Aland Islands [10] is similar to rates Bulmer [5] found for most of Africa, though short of some extraordinary figures from Nigeria [19]. Dr. Trefor Jenkins of the South African Institute for Medical Research has kindly supplied twinning rate figures from two different series of

“Negro” maternities in Johannesburg, both for 1976-1977, which are lower than most of Bulmer’s rates for Africa including Johannesburg: 14.8 and 16.3.

With such a wide overlap between races, and such great variation within races, twinning rate is probably no better than intelligence as an index of genetic status for racial groups.

2. Twinning, as a mode of reproduction, is not necessarily an r strategy

The number of eggs produced may be a suitable indicator of r reproductive behavior in fish or birds, but for mammals the corresponding parameter is litter size. In either of these terms, twinning and other multiple maternities must be called an r -strategy. But an even more general criterion is parental investment in each offspring; if twinning does not on average increase the number of infants surviving the neonatal period, it does not significantly reduce parental investment per child. Even under modern medical conditions, and more so under primitive conditions, twin pregnancy is hazardous for the mother and the fetuses. The effect of this mortality must be evaluated before twinning is assigned an r/K designation. Twinning may not have been an r -trait during human evolution, its frequency having been maintained by selection for physiological traits which are necessary for reproduction and incidentally sometimes produce twins.

Fig. 4 indicates that in the 16th and 17th centuries, even in ruling families, the perinatal mortality of twins was four times that of singletons and that hardly $\frac{1}{3}$ of the twins survived childhood [21]. In the sibships with 2 or more multiple maternities from the Aland Islands, 1740-1915, there were on average twice as many stillbirths among the twins as among the singletons. After twin children had attained the age of 6 months they had about the same chances of survival as singletons. Only 23% of the children born in multiple maternities in Aland attained the age of 15 years, whereas 47% of their singleton sibs reached adolescence. Furthermore, maternal mortality was in the past considerably higher in maternities with twins and triplets than in maternities with singletons. These results indicate that from the reproductive point of view, at least until present times, with better treatment during pregnancy, better care of prematures and lower infant morbidity, the twinning mechanism does not seem to have been of selective advantage [7].

3. A history of r - or K - selection cannot explain individual differences within a Mendelian population, and cannot be inferred from such differences

Twin-proneness may depend, partly, on a single gene or a small number of genes, but women with those genes have not themselves been selected for their r - reproductive behavior, and there is no reason to expect them to show other r - traits. Rushton’s examples [24], supposed to illustrate this phenomenon in nonhuman organisms, were based on populations of individuals who had survived a process of r - or K - selection, so the association among traits was due to this history of selection. Such traits are indeed expected to covary *between* species, sometimes even between populations within a species, but not within a population that shares a common history of selection. The fact that each genotype may be said to have a value on the r/K continuum [3] does not imply that each individual has an ancestral selection history different from those of its siblings. Every

Chances of survival of single births (---) and twins (—) in
 1) ruling families of Europe in the 16th and 17th centuries (R), (Peller 1944),
 2) sibships with at least two multiple maternities in Åland, 1740-1915 (Å).

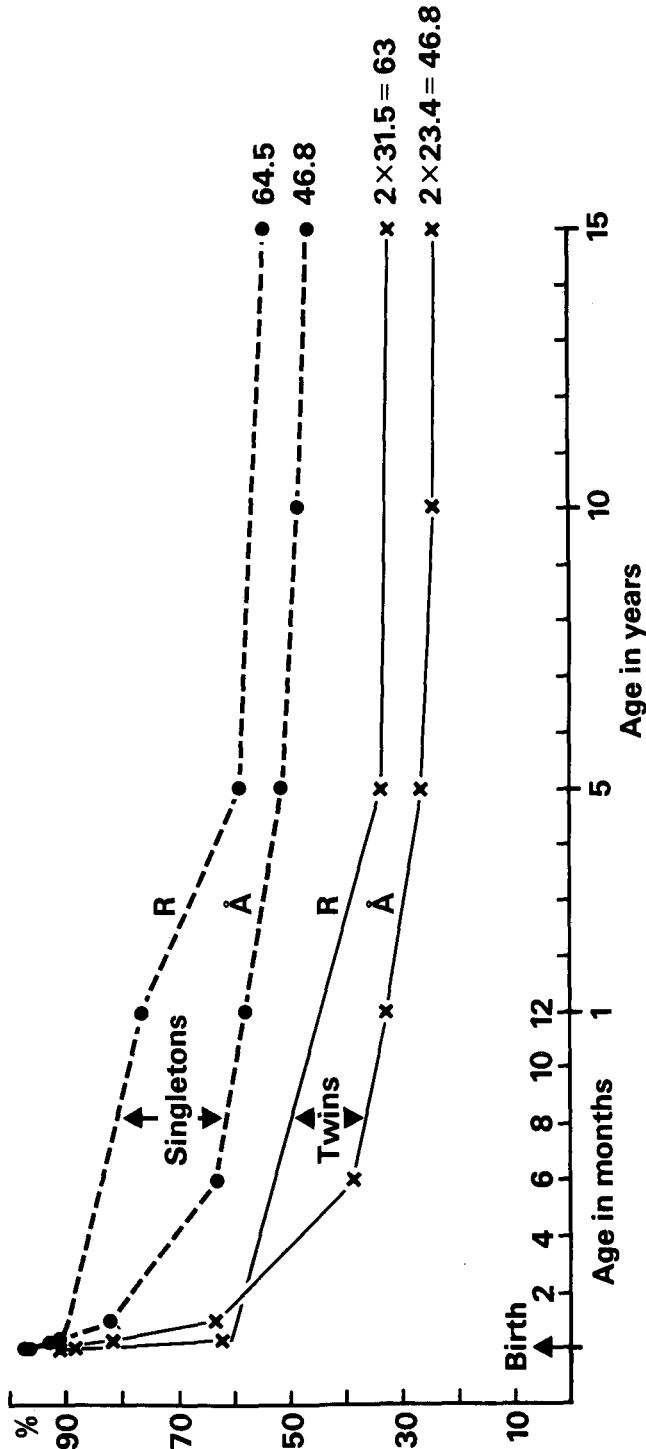


Fig. 4. Comparison of the chances of survival of singletons and twins up to 15 years of age in sibships of ruling families of Europe in the 16th and 17th century and in sibships in Åland, 1740-1915, with more than one set of multiple maternities. Note that these series also include the stillbirths and therefore the starting points are below 100%.

genotype has both r and K characteristics to varying degrees, and the interaction of the two kinds of selection determines the population structure during the approach to equilibrium.

4. Rushton has misinterpreted several traits that are in various ways associated with twinning

1) The association of DZ twinning with large family size is statistical, not genetic. It is probably entirely explained by birth-order effect and the obvious fact that a woman's chance of having twins increases with the number of times she tries. Weinberg (1901-02) compared family size for DZ twins with that for MZ twins, expecting to demonstrate greater fertility in the former, but he found no difference [25]. Subsequent studies have revealed some family size advantage for the DZ twin families, but this can be explained by the greater frequency of DZ twinning in higher birth orders, which tends to favor large families.

2) Rushton cites Wyshak [26] for statements that mothers of DZ twins have shorter menstrual cycles on average and an earlier menarche than mothers of singletons. The first observation may be a true r -trait, but it requires confirmation in other material and might have offsetting physiological correlates. The second observation is vitiated by Wyshak's finding that these DZ twin-prone mothers reported a later first birth, on average, and a greater delay from marriage to first birth. Rushton does not mention Wyshak's finding that the mothers of opposite-sex twins reported greater difficulty in conceiving than mothers of singletons, and they more often sought therapy for this problem (nearly all twin maternities in these families occurred before the common use of fertility drugs). Wyshak's report of greater pregnancy wastage among these mothers is taken by Rushton as an r -trait, but its effect is to *reduce* reproduction. Even neonatal deaths would reduce r provided they were not due to population density.

3) Wyshak reported that mothers of DZ twins had more marriages, and Rushton classified this as an r -trait. It might indicate higher sexuality, which is probably not an r -trait [17:p.4], but it is more likely an effect of the extra strain which twins place on a marriage. The difference was very small, 1.07 marriages per mother of opposite-sex twins and 1.05 per mother of singletons. For mothers of triplets and higher multiples (only 56) the average number of marriages was 1.12, consistent with the hypothesis that multiple births tend to destabilize families.

4) Rushton cites a statement taken out of context that mothers of DZ twins have more closely spaced maternities than other women [see 1:p.6]. This spacing depends entirely on the statistical association of DZ twinning with large families and high parity, discussed above, not on ease of conception. However, there is evidence that DZ twins are conceived more promptly after marriage or at the beginning of a sexual relationship. This may not mean that women who are twin-prone generally conceive more promptly, but that *when* they conceive promptly, they are more likely to bear twins than when they conceive later. This interpretation was supported (short of statistical significance; Allen 1981, Table 3) by an analysis designed to test it.

5) Rushton makes a similar error when he interprets the high frequency of twins among illegitimate births in Finland [9] to mean a high frequency of illegitimate births

to mothers of twins. It may mean simply that *when* twin-prone women have illegitimate births (probably no more often than other women), these pregnancies are more likely *than their legitimate pregnancies* to produce twins. This phenomenon has been discussed by Eriksson and Fellman [9], Allen [1], Parisi and Caperna [20], and James [15]. Erotic stimuli are known to raise women's gonadotropin levels [16], and gonadotropin level is correlated with double ovulation. This appears to explain the association of twinning with illegitimate births in Finland without implying higher illegitimacy rates in twin-prone women. In fact, during 1905-1954 the rate of extramarital maternities among mothers of triplets in Finland was not higher than in the general population, around 6-7% [8].

6) Finally, Rushton says that mothers of DZ twins have more frequent coitus than mothers of singletons, citing James [15]. James did not compare mothers known to be twin-prone with other mothers, but all mothers who conceived early after marriage with all mothers who conceived late. Coitus is more frequent early in marriage, and early conceptions include more twin pregnancies, but James gave no evidence that the mothers of twins have more frequent coitus than other mothers at the same period of marriage.

To summarize the six parts of point 5, individual twin proneness and its correlates do not provide Rushton's desired picture of a many-faceted *r*-strategy (even if such individual variation could have evolutionary meaning). With the exception of shorter menstrual cycles found in one study, the traits Rushton cites as *r*-selected in association with twinning are either statistical artifacts of no reproductive value or figments of misinterpretation.

It might be informative to summarize the litter sizes of many animals — especially those of dogs, monkeys, apes, and, finally, the various races of man. For example, because dogs have been bred for many different tasks, they show much more extreme differences which are mostly genetic in origin.

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