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Variation in Sex Ratio between Progeny Groups in Dairy Cattle

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Summary. Highly significant differences between progeny groups have been found in the Israeli-Frisian breed of cattle. The standard deviations between groups in the proportion of males was estimated to be 1.5% . Significant correlations between sire and son and between half-sibs in the sex ratio of their progeny suggest that the differences may have a genetic basis.

The existence of variation between families in sex ratio, whether in humans or in farm animals, is a widely held notion. In humans, the classical data is that published from Saxony by Geissler (1889) which has recently been subjected to a comprehensive statistical analysis by Edwards (1958). In cattle, McWhirter (1956) has published an analysis of 37,515 calvings from a single artificial insemination centre in Scotland, finding significant difference between progeny groups by the same bull in sex ratio.

Materials and Methods

The present material comprises 157,255 single births, the progeny of 107 bulls, from October, 1964 to October, 1970 in the Israeli-Frisian dairy breed. The breed is bred as a single unit from two artificial insemination stations and the data are therefore uniform both in farm background and in recording method. The results are given separately for calves born to heifers and to cows. The number of calvings per bull varied from 50 to 9203 to heifers, from 135 to 6045 to cows. This variation is a consequence of the progeny testing programme. The first use of a young sire is aimed to produce about 300 calvings from which will come enough daughters in milk for a progeny test for yield. If the bull returns to use because of his progeny test, he is used extensively and will usually have several thousand calvings. As a further consequence of the breeding programme, sixteen of the bulls had sons in AI so that we could compare sex ratio on father and son as well as those of half brothers.

Results

The proportion of males was 52.24 ± 0.24% in calvings from heifers and 52.54 ± 0.17 % in those from cows. Combining together the results from the two groups of females, the heterogeneity χ^2 for the proportion of males was 217.12 with 106 d.f. There are thus highly significant differences between bulls in sex ratio. These may be quantified as the variance between bulls in their "real" sex ratio. We used two methods to estimate this. In the first, we estimated the variance from the distribution of overall sex ratio for the individual bulls. In the second, we treated the sex ratio from the two groups of females as independent measures and estimated the covariance between the two. In the first method, we in essence subtract the binomial variation from the observed variance between bulls. The binomial variation only enters in the second in the consideration of the relative weights to be given to the information from each bull.

The problem of weighting is important because of the great variation in the size of the progeny groups. The solution was based on the following principle, illustrated for the first method. Let us assume that the true mean proportion of males, p, is known accurately and that a given bull has a proportion p_1 based on N calvings. Then this gives an estimate of V_b, the variance component between bulls, of $(p_1-p)^2-p(1-p)/N$ and has variance equal to $2(V_b + p(1-p)/N)^2$, if we assume normal distributions. We then use the reciprocal of this expression as the correct weight to be given to each squared deviation and the final estimate has sampling variance $1/\Sigma(1/V)$. The process then proceeds by iteration from an initial value of V_b of zero.

In the estimation of the covariance, C, between sex ratio in the two groups of calvings, we make use of the known expression for the variance of the covariance from a bivariate normal distribution of x and y as $C_{xy}^2 + V_x \cdot V_y$ where C_{xy} is the true covariance and V_x and V_y are the two variances. In the present analysis we can write the expression approximately as

$$C^2 + (C + p(1-p)/N_h)(C + p(1-p)/N_c) .$$

where N_h and N_c are the number of calvings in the two groups. In this, we assume that the same factors affect sex ratio in the two groups of calvings so that the covariance between the two equals the component between sires. Again the process was one of iteration with an initial value of C of zero.

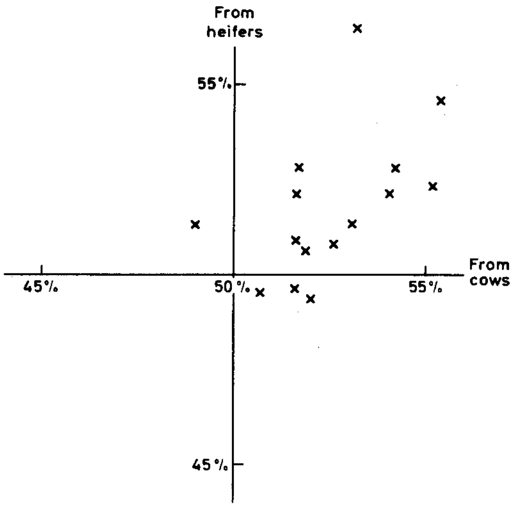

Fig. 1. The percentage of males in progeny groups by the same bull out of heifers and cows respectively, restricted to those bulls with more than 500 calves out of heifers

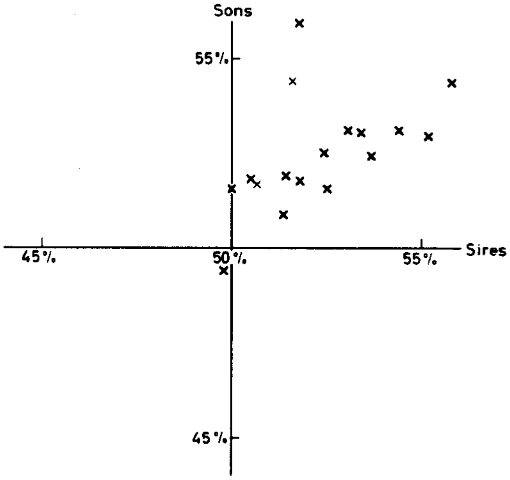

Fig. 2. The average percentage of males in all calvings from groups of sons plotted against that of their fathers. All son groups have more than 700 calvings, with the exception of the two fainter points

The final estimate of the variance between bulls in the proportion of males was 2.26 ± 0.76 × 10^{-4}, implying a standard deviation of the real proportion from different bulls of 1.5 %. The covariance between the proportion of males in the two groups of calvings was 1.85 ± 0.81 × 10^{-4}. This would indicate that the same factors were operating in the two groups. In agreement with this, the summed heterogeneity χ^2 within bulls between the two groups of mates, for the 93 bulls having two groups, was 101.37 for 93 d.f., indicating no heterogeneity. Fig. 1 shows the results for those bulls with more than 500 calvings from heifers.

Because the population is fairly closed on the male side, many of the bulls had sires in common and for the majority the sex ratio of the sire's progeny was also available. It was therefore possible to do not only a sire-son but also a half sib analysis. In the first, sixteen sires, all with more than 500 calvings, had a total of 69 sons. The majority of the sons had between 200 and 600 calvings. The data are presented in Fig. 2. An analysis of correlation and regression was carried out between the observed sex ratio on the father and the average value for his sons, weighted according to the number of calvings that the latter had. The observed correlation of 0.50 is just significant at the 5% level. The regression of son's sex ratio on that of his father was 0.43. The estimate of the covariance in sex ratio in sire and son was 1.37 ± 0.66 × 10^{-4}.

A further nine groups of half-sibs could be added for which there was no information on the sire. A half-sib analysis was then carried out on these 25 groups. The ratio of the mean square between sires to that within sires was 1.96, in between the 5% and 1% levels of significance. An estimate of the variance component between sire groups was obtained of 0.87 ± 0.54 × 10^{-4}.

As an extreme example from the data, we may choose the bull Thor with an average percentage of sons in his 3345 calves of 49.81% and of 49.45% in the 4194 calves of his eight sons. At the other extreme is Nezer with 55.8% males in 5991 calves and 54.4% in the 3949 calves of his 7 sons.

Discussion

The observed differences between bulls in the sex ratio of their progeny appear to be real. This might be a purely phenotypic effect in the sense that the relative survival of the groups of sperm carrying X and Y chromosomes varied between bulls. The second part of the analysis would suggest, however, that there is perhaps a genetic basis to the differences. This could be due to genetic differences between bulls in the relative survival of X and Y bearing sperm before fertilisation or to differential survival of the zygotes of the two sexes. This might be a consequence of autosomal genes or, more speculatively, it could be due to the Y chromosome. Variations in the length of the Y chromosome are certainly known in cattle populations (Darre et al., 1974). The expectations on the first model would be the classical ones, that the covariance between sire and son would be twice that between half sibs and it would be one half the genetic differences between bulls in the population. On the other hand, if the effect were due solely to the Y chromosome, the expected covariance between sire and son and between half brother and half brother would be equal to the whole of the genetic variation in the population since sire and son have the same Y. On the other hand, genes on the X chromosome cannot contribute the correlations between sire and son or between half brothers. The present data are too limited to distinguish between these possibilities.

McWhirter (1956) found a highly significant χ^2 of 123 between bulls based on 31 degrees of freedom. From this result we cannot make a direct estimate of the variance component between bulls since the χ^2 value depends on the variation in progeny group size. But a minimum estimate, assuming all progeny groups to be equal, would be 6.2×10^{-4} or a real between sire standard deviation of 2.5%, rather larger than we have found.

The ratio of the variance within bulls, the usual binomial variance, to that between bulls was approximately 1,000 in our data. If these effects are accepted as real, progeny group sizes of four times this would be needed to make adequate judgements of bulls.

In Edwards' analysis of Geissler's data, he too made an estimate of the variance component between families. He found a consistent increase in the component with family size but the average value over all of the data was approximately 25×10^{-4}. It is not surprising that he should find effects much larger than ours because, in families with a common mother, the variation in sex ratio must also contain effects due to recessive lethal or semilethal genes on the X chromosome.

Literature

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