Causes of variation in the frequency of monozygous and dizygous twinning in various breeds of cattle

IVAR JOHANSSON, BENGT LINDHÉ and FRANZ PIRCHNER

Swedish Association for Improvement of Animal Production (SHS), Hällsta, Eskilstuna, Sweden
Institut für Tierzucht an der Technischen Universität München, 805 Freising-Weihenstephan, Germany B.R.

A statistical investigation has been made comprising 12 European cattle breeds with a total of about 5.3 milj. calvings and 120,000 twin births. Season of conception has a marked influence on the frequency of twin births, one maximum corresponding to spring and another one to autumn conceptions. There are significant breed differences in the relation between age of the cows, measured in parities, and the frequency of monozygous (MZ) as well as dizygous (DZ) twin births. On an average, the DZ frequency increases more than the MZ frequency from the first to the fourth-fifth calving; then the age-curves show a plateauing tendency. After the first twin birth, the twinning frequency at the following calvings is 4-5 times higher than in the general population. Apparently, twinning depends on polygenic inheritance and also on various environmental influences, with a threshold for the phenotypic manifestation. It may be assumed that the underlying liability of the cows in a population to bear twins has an approximately normal distribution. The heritability of twinning has been estimated on the binomial p-scale as well as on the x-scale of the normal curve. On the p-scale the heritability of twinning was found to be about 0.02 which corresponds to 0.16 on the x-scale, although with some differences between breeds.

Bengt Lindhé, Swedish Association for Improvement of Animal Production (SHS), Hällsta, S-63184 Eskilstuna, Sweden

In 1932, the senior author published a treatise on "The sex ratio and multiple births in cattle", based mainly on data from a number of pedigree herds of Swedish dairy breeds. The herds were selected in order to obtain as accurate records as possible of all the calvings within the herds, without exclusions of any kind. Previous as well as more recent investigations by numerous authors have shown that herdbook data are, as a rule, unreliable for this kind of study, because of numerous omissions of cases of twinning, and the sex of calves, in the reports of breeders to the herdbook offices. With few exceptions, the investigations on twinning in cattle where this source of error has been recognized, have therefore been limited to some large herds where careful notations have been made on the reproductive performance of all the breeding animals, but such data are usually too limited for detailed studies of the problems involved. However, with the widespread use of artificial insemination, milk recording, and electronic data-processing, this situation has changed, at least for some types of investigations. Large amounts of data are now available for studying such effects as the influence of mating season and age of the cows on the twinning incidence, as well as the proportions between monozygous (MZ) and dizygous (DZ) twin births.

The first estimate of the frequency of MZ twins was made on data from various sources (JOHANSSON 1932) with the result that 11.6 % of all like-sexed twin pairs were monozygotic. Neither the effect of breed nor age of the dam was considered.

The age of the cow at the time of conception has a pronounced effect on the likelihood of her producing twins. Breed comparisons can give
reliable results only when the age distribution of the cows on parities is taken into consideration. This is particularly important as regards the total frequency of twinning but it also seems to be important for the estimation of the ratio of MZ to DZ twinning incidence. A new investigation of the twinning problems, based on large numbers of reliable and unselected data, would therefore appear to be justified.

The present study of twinning in cattle does not include the relation of twinning to milk yield or to the reproductive functions of the dams. These problems have been discussed recently in a comprehensive review by HENDY and BOWMAN (1970). The major topic considered here is the causes of variation in the frequency of MZ and DZ twinning.

Material and methods

The data on twinning in the Swedish breeds were obtained from the Swedish Association for Improvement of Animal Production (SHS), and the main tabulations of these data have been made at the Agricultural Center for Data Processing at Hällsta. The data for the Danish breeds emanate from the publication “Kaelvingsstatistik” by ELLEBY and MYGIND-RASMUSSEN (1971), although additional calculations from their tables have been made by the present authors. ELLEBY (1973) has provided some “fresh” data on twinning and triplet-births. Data for dairy breeds in South Germany (Bavaria) and in Niedersachsen have been placed at our disposal by the courtesy of Dr. H. Schumann, director of the “Landeskuratorium der Erzeugerringe fur Tierveredelung in Bayern” and by Dr. O. Vogt-Rohlf, “Rechenzentrum fur Förderung der Landwirtschaft in Niedersachsen”. We have also obtained data on the Swiss Simmental cattle from Mr. Claude Gaillard, director of the “Schweizerischer Verband fur künstliche Besamung”. Furthermore, data were obtained from a large breeding establishment for Hereford cattle in the U.S.A., viz. the Wyoming Hereford Ranch, Cheyenne Wy. With regard to the Charolais breed in France we have obtained permission to quote some data from an unpublished manuscript by Mr. Menissier, Département de Génétique Animal, Jouy-en-Josas. A small amount of data were also available in Sweden on the British beef breeds Hereford and Aberdeen-Angus and on the French Charolais, which are now used in Sweden and other Northern countries for crossing with dairy breeds for beef production. Practically all data for the European breeds relate to the period 1968–72.

The methods used in analysing the data are simple and follow traditional lines, employed in human genetics. However, the methods used in estimating the fraction of the total number of twin pairs which are probably monozygotic, and the standard deviation of the estimates, may need some discussion.

As early as 1902, the German physician-geneticist WILHELM WEINBERG devised his “differential method” for estimating the number of MZ twin pairs within a random sample of twins where the sex ratio was about 50 % males. The probability for the male and female sex would then be equal (p = q = 0.5), and with random distribution of the sexes within pairs, the distribution of the three possible sex combinations would be (p + q)² = 0.25p² + 0.50pq + 0.25q², i.e. equal numbers of like-sexed and unlike-sexed pairs. An excess of like-sexed pairs may then be used as an estimate of the number of MZ pairs in the sample. Where the number of twin pairs = n, the number of like-sexed pairs = n₁ and the number of unlike-sexed pairs = n₂, the estimated number of MZ pairs would be n - 2n₂. Because of the importance of MZ cattle twins for various types of experiments, their frequency is often expressed as a fraction (or percentage) of the number of like-sexed twin pairs:

\[ m = \frac{n - 2n_2}{n_1} \]

BONNIER (1946) preferred to use the observed sex ratios in the twin sample rather than the approximate ratio of 50 % males, thus estimating the value of m = \( \frac{2pqn - n_2}{2pq(n - n_q)} \). However, the gain in accuracy by introducing the term 2pq, where p and q are the observed frequencies of males and females in the twin sample, is very slight, as pointed out by MEADOWS and LUSH (1957). The intra-uterine and perinatal mortality, which is known to be selective against males, is much higher for twins than for single born animals, and the sex ratio of twins is seldom higher than 52 % males (cf. Table 3). With this ratio, the
term \(2pq = 0.4992\) instead of 0.50 for equal numbers of males and females. It is important, however, to define the stage at which the sex of the twins is determined. The secondary sex ratios of single born calves and twins, presented in Table 3, refer to calves born alive at full term. However, there may be some differences between countries in applying this general rule. It may be added that not only is the fraction \(m\) of interest in a twin study, but also the relation between the number of MZ pairs to the DZ's and to the total number of births.

In calculating the standard deviation of twinning percentages \((pt)\) we use the formula

\[
s_{pt} = \sqrt{\frac{pt(100 - pt)}{n}}, \]

where \(n\) = the number of calfings on which the twinning percentage is based. However, when calculating the standard deviation of an estimate of the frequency of MZ twins, it must be borne in mind that this estimate is based on the fractions of like-sexed and unlike-sexed twin pairs in the population, and each of these two samples has its sampling error. Bonnier (1946) derived the following formula for the standard deviation of the calculated fraction \((m)\) of MZ twins out of like-sexed twins:

\[
s_m = \sqrt{\frac{1}{2} \left(1 - 2pqm\right) \left(\frac{1}{n}\right)}. \]

Since \(2pq\) can be eliminated without any noticeable loss of accuracy, the formula can be simplified to

\[
s_m = \sqrt{\frac{1}{2} \left(1 - m\right) \left(\frac{1}{n}\right)}. \]

The method used in estimating the heritability of the twinning tendency will be discussed later (p. 219).

Results

1. Perinatal mortality and the sex ratio of twins and single born calves

Perinatal mortality and the secondary sex ratio of twins, compared to single born calves, are of interest from a breeding point of view, and they are important in estimating the relative frequency of MZ and DZ twinning. Our data relating to these problems are meager, but they will nevertheless be presented in order to illustrate the situation within some of the breeds studied.

It is well known from human genetics that the sex ratio of aborted and stillborn fetuses is considerably higher than that of children born alive at full term (cf. Stern 1960). Chapman et al. (1938) studied the sex ratio of cattle fetuses at different stages of development using slaughterhouse material. The data, comprising 2,044 fetuses on which the crown-rump length was measured, were grouped into ten classes with an interval of 10 cm. The material did not show a gradual decline in fetal sex ratio from the first to the tenth class but a rather sudden drop from the smallest fetuses with less than 10 cm crown-rump length, where the sex ratio reached 66\%, to 56\% in the next class (11–20 cm) and then a further decrease to about equality in the 80–90 cm class. The early stage of high male mortality corresponded roughly to the third month of pregnancy.

In the Swedish AI and milk recording associations, abortion is defined as delivery of the fetus before 260 days of gestation. Stillbirth includes not only calves dead at birth but also those dying within a day after birth. Therefore, the term perinatal mortality will be used rather than stillbirth. Calf mortality within a month after the date of birth is called “early death”. In practice, the sex of aborted calves is recorded only when abortion occurs during the later stages of pregnancy, and even here the records may be incomplete. The sex recording in perinatal mortality is fairly complete, although omissions may occur. The available data are examined and compared with similar data from Denmark, Germany and Switzerland.

In Table 1, data are presented on the sex ratio for perinatal mortality of single fetuses in four different breeds. The sex ratio of aborted calves in the Swedish breeds SRB and SLB is close to 70\% males, and the corresponding ratio for perinatal mortality is about 60\%. The sex ratio for “early deaths” is somewhat less than 50\% which probably is due to an after-effect of the high sex ratio for perinatal deaths.

The Swiss and German data in Table 1 are not quite comparable to the Swedish data, and therefore separate headings are used in the table. “Stillbirths” actually means here “dead at birth”, and the figures for calves dying within four weeks include mortality during the first day after birth. This explains, at least partly, the high sex ratios for post-natal deaths. Kräußlich (1972) has published data from 271,870 calfings of German Fleckvieh where he found the sex ratio for 3,769
stillbirths to be 69.9% males. DREYER (1973) has reported on mortality losses of calves in the Rheinland-Pfalz-Saar district of Germany for the years 1970–71. His data comprise 135,144 calvings, including 5,407 twin births. From the published figures we have calculated that the sex ratio of 3,827 stillborn calves was 74.2% males and that the ratio of 1,797 calves that died within four weeks after birth was 62.1%.

Comparable data in connection with twin pregnancies are difficult to obtain. The results from a one year sample of abortions in the Swedish breeds (1971) are presented in Table 2, together with data on perinatal deaths from a larger sample of twin births. If the figures for perinatal mortality at twin births are compared with those for single births in Table 1, it will be observed that mortality was on average 4.3 times higher for twins than for single born calves in the Swedish breeds. For 721,180 single births in the Niedersachsen Schwarzbunt, the mortality rate was 2.8% and for 14,773 twin births it was 13.1%, or 4.7 times as high as for single births. The sex ratio at perinatal deaths of twins in the Swedish breeds was somewhat lower, however, than that for the single-born calves. This is probably due to a higher rate of abortions during twin pregnancies.

Table 3 is designed to show the secondary sex ratio of single born calves and twins. The sex ratio of twins is expressed in two different ways, viz. for the total number of twin calves and for the like-sexed twin pairs only. Obviously, the sex ratio of unlike-sexed pairs is always 0.5, whereas the proportion of male and female pairs may vary to some extent. The figures in Table 3 do not indicate that the loss of male twin pairs is greater than that of female twin pairs at the time of delivery when the sex of the calves was determined.

### Table 2. Sex ratio of twins at abortions and perinatal mortality

| Breed | No. of twin births | Late abortions | Sex ratio of aborted fetuses, % | Total twin births | Perinatal deaths for twin births |
|-------|--------------------|----------------|---------------------------------|-------------------|---------------------------------|
|       |                    | No. | %    | No. | %    | No. | %    | No. | %    | No. | %    |
| SRB   | 2,459              | 303 | 12.3 | 58.7 | 9,914 | 2,550 | 12.9 | 53.1 |
| SLB   | 1,203              | 212 | 17.6 | 60.4 | 4,733 | 1,236 | 12.4 | 55.6 |

**Notes:**
1. Data from Schweizerischer Verband für künstliche Besamung
2. Calculated from DREYER (1973)
Table 3. Secondary sex ratio of single born calves and twins in seven European breeds

| Breed       | Single born calves | Twin pairs |
|-------------|--------------------|------------|
|             | Total births       | Male births | Sex ratio | Total no. of pairs | Same sexed pairs |
|             |                    |            |           |                  |               |
| Swedish     |                    |            |           |                  |               |
| SRB         | 661,084            | 350,774    | 53.1      | 2,801            | 51.1          |
| SLB         | 230,950            | 118,047    | 51.1      | 1,308            | 51.1          |
| Danish      |                    |            |           |                  |               |
| RDM         | 728,836            | 368,239    | 50.5      | 8,388            | 50.2          |
| SDM         | 641,393            | 314,665    | 49.1      | 6,601            | 49.0          |
| German      |                    |            |           |                  |               |
| Schwarzbutt | 721,364            | 375,580    | 52.1      | 4,370            | 52.6          |
| Fleckvieh   | 662,604            | 347,485    | 52.4      | 6,443            | 52.2          |
| Braunvieh   | 258,735            | 135,157    | 52.2      | 2,577            | 51.6          |
| Total and av. | 3,904,966       | 2,009,947  | 51.5      | 32,488          | 50.7          | 51.3|

1 Data for single calves from Tables 12 and 13 in Elleby and Mygind-Rasmussen (1971), twin data from Elleby (1973, pers. comm.)
2 Niedersachsen Schwarzbunt, Bavarian Fleckvieh and Braunvieh

It may be concluded that Weinberg's method for estimating the incidence of MZ twins births is valid for cattle as well as for man.

When comparing the sex ratios of different breeds, it is probably safest to make the comparisons only within the same organization for AI, milk recording, and data processing because the practice of sex recording may differ somewhat between the organizations. By doing so, it is interesting to find that the ratio is higher for the Red and White and the Danish Red (SRB and RDM) than for the Black and White (SLB and SDM) breeds. For single born calves the difference between SRB and SLB is 2.0 ± 0.038 % and between RDM and SDM 1.4 ± 0.028 %. With regard to twin births the sex-ratios are equal for the two Swedish breeds but there is a significant difference between the two Danish breeds (2.2 ± 0.408 %) when calculated on the like-sexed pairs.

One explanation for breed differences in the secondary sex ratio could be differences in intrauterine mortality and incidence of stillbirths. For the Swedish breeds there are some indications that these mortality figures are higher in the Friesians than in SRB (Table 1) but for the Danish breeds we know of no such indications.

2. Seasonal variation in twinning frequency

Only one environmental factor influencing the incidence of twinning can be studied from the available data, viz. the season of conception. No data are available on the nutritional level of the various herds, or of the individuals within the herds, but the milk records of the tested herds in Sweden and Denmark indicate that the plane of nutrition is on an average fairly high. In Sweden, the average yield of 4 % fat corrected milk of all recorded cows in the year 1971-72 was for SRB 5,394 kg (221,465 cows) and for SLB 5,704 kg (76,978 cows).

In earlier studies of twinning frequency in the Swedish breeds the senior author (Johansson 1932) found two yearly peaks, one corresponding to conceptions in the early spring and another, more pronounced, after conceptions in September-October. The causes underlying these seasonal variations were discussed, and it was assumed that the temperature changes, causing changes in metabolism, were important factors. Later investigations on farm animals, especially on sheep, have demonstrated the effect of changes in the length of daylight in the autumn on the reproductive functions, and this would probably also apply to the bovines, at least to some extent.
Fig. 1. Seasonal variation in the frequency of calvings in Swedish and Danish breeds and German Schwarzbunt in Niedersachsen, 1 = first calving, 2 ≤ = second and following calvings.
Fig. 2. Seasonal variation in the frequency of twinning in Swedish and Danish breeds and German Schwarzbunt (N), in relation to parity and month of conception.
The present study of seasonal variations in twinning is based on a larger amount of data from five dairy breeds, viz. the Swedish Red and White cattle (SRB) and Swedish Friesians (SLB), the Danish Red (RDM) and Black and White (SDM) cattle, and the German Schwarzbunt in Niedersachsen, altogether nearly 3.5 million calvings and about 73,000 twin births (cf. Tables 4–6).

The diagrams in Fig. 1 show the seasonal distribution of calvings for each of the Danish and Swedish breeds mentioned, and for the German Schwarzbunt in Niedersachsen. The Swedish and Danish data could be classified into the first and the following calvings only, but the German data were completely classified on calving number. In all the populations studied, the calving incidence of primiparous animals reaches a maximum in the autumn, although somewhat later in Niedersachsen than in Sweden and Denmark. The seasonal distribution of calvings in Niedersachsen changes gradually with increasing age of the cows from an autumn to a spring maximum, but the greatest change occurs from the first to the second calving. All data for the fourth and following calvings have been pooled, since the change in distribution from one calving to the next is very slight. Table 8 in the publication by Elleby et al. (1971) shows that the change in seasonal distribution of the calvings with increasing age of the cows is very nearly the same in Denmark as in Niedersachsen, and it is also about the same in Sweden.

Spring calving has been predominant in the Scandinavian countries for many centuries and it was probably the normal case among the aurochs. Feed was more scarce in winter than in summer, and the nutritional value of the feed was certainly superior in the summer. Under the present economic conditions, a relatively high incidence of autumn calvings is usually preferred. The mating of the heifers is timed by the breeders to result in autumn calving, but the cows tend to revert to the sexual season of their ancestors. One factor causing this change is probably the decreasing daylight hours in the autumn tending to favor not only conceptions but also multiple births (cf. Fig. 2) although a part is due to the length of the calving interval being about 13 months on an average.

Fig. 2 shows the seasonal variation in twinning frequency in the same five breeds as referred to in Fig. 1 and with the same classification on calving number. Multiple birth depends mainly on the number of eggs ovulated at a time when fertile spermatozoa are present in the oviducts, and therefore the diagrams relate the twinning frequency to the estimated month of conception.

At the first calving, the Swedish breeds show a slight tendency to increased twinning frequency after autumn conceptions. For the Danish breeds and the German Schwarzbunt, this increase is quite pronounced. For these last mentioned breeds there is also an increased twinning frequency after conceptions in May and June.

At the second and following calvings all the five breeds show two very distinct peaks in the twinning frequency, one after spring and the other after autumn conceptions. The first peak occurs after conceptions in May (for SRB May and June), with calvings in February the following year, and the other corresponds to autumn conceptions and calving in the spring. In the diagram it may be noted that the maximum twinning rate of the cows in the Scandinavian countries occurs about one month earlier than in Niedersachsen. This supports the hypothesis that the calving as well as the twinning incidence in a district is to a certain extent regulated by the seasonal changes in length of daylight.

In Table 4, the heifers are divided into two seasonal classes, autumn conceptions (September–November) and conceptions during the rest of the year (December–August). The twinning frequency is calculated for each class of the Swedish and Danish breeds. In each of the four breeds the seasonal difference in twinning frequency is highly significant.

Table 5 presents similar data for the second and following calvings in the same four breeds. Since the cows show two seasonal twinning peaks, the data are divided into three classes according to conceptions in the spring, autumn, and the rest of the year. The differences in twinning rate between the three seasons are highly significant.

The corresponding data for German Schwarzbunt in Niedersachsen are presented in Table 6, where classification is made on the first, second, third and fourth or more calvings. The seasonal differences in twinning rate are highly significant for all four parity groups.

The spring maximum in twin conceptions may be explained as an effect of "flushing" when the cows are turned out on plentiful and lush pasture.
**Table 4.** Relation of twinning frequency to season of conception in the Swedish and Danish dairy breeds. First calving

| Breed | Season of conception | September—November | December—August |
|-------|----------------------|--------------------|-----------------|
|       | No. of calvings      | Twin births        | No. of calvings | Twin births |
|       | No. | %     | No. | %     | No. | %     |
| SRB   | 41,389 | 243 | 0.59 | 162,297 | 633 | 0.39 |
| SLB   | 13,537 | 112 | 0.83 | 64,282 | 347 | 0.54 |
| RDM   | 36,927 | 501 | 1.36 | 214,543 | 1,503 | 0.70 |
| SDM   | 32,799 | 356 | 1.09 | 183,844 | 1,072 | 0.58 |

\( \chi^2 > 15.2 \) indicates that the deviation of twinning frequency from the yearly breed average is highly significant. \( P < 0.0005 \)

1. 12.6 corresponds to \( P < 0.0005 \)
2. Autumn conceptions comprise October—November

**Table 5.** Relation of twinning frequency to season of conception for the second and following pregnancies in the Swedish and Danish breeds

| Breed | Season of conception | 1. May | 2. September—October | 3. Rest of year |
|-------|----------------------|--------|----------------------|-----------------|
|       | No. of calvings      | Twin births | No. of calvings | Twin births | No. of calvings | Twin births |
|       | No. | %     | No. | %     | No. | %     |
| SRB   | 95,572 | 2,020 | 2.11 | 49,431 | 1,139 | 2.31 | 315,470 | 5,893 | 1.87 | 54.6 |
| SLB   | 13,811 | 492 | 3.56 | 13,935 | 417 | 2.99 | 126,800 | 3,356 | 2.65 | 41.6 |
| RDM   | 45,228 | 1,990 | 4.40 | 43,619 | 1,876 | 4.30 | 388,519 | 14,274 | 3.67 | 87.9 |
| SDM   | 49,070 | 2,012 | 4.10 | 41,906 | 1,443 | 3.44 | 333,774 | 10,137 | 3.04 | 159.9 |

\( \chi^2 > 15.2 \) indicates that the deviation of twinning frequency from the yearly breed average is highly significant. \( P < 0.0005 \)

1. \( \chi^2 > 15.2 \) indicates that the deviation of twinning frequency from the yearly breed average is highly significant. \( P < 0.0005 \)
2. Period 1 comprises May and June (cf. Fig. 2)
3. Period 2 comprises August and September (cf. Fig. 2)

**Table 6.** Relation of twinning frequency to season of conception in the German Schwarzbunt (Niedersachsen) at different parities

| Parity | Season of conception | 1. May | 2. October—December | 3. Rest of year |
|--------|----------------------|--------|----------------------|-----------------|
|        | No. of calvings      | Twin births | No. of calvings | Twin births | No. of calvings | Twin births |
|        | No. | %     | No. | %     | No. | %     |
| 1, 2   | 10,300 | 111 | 1.09 | 31,572 | 382 | 1.21 | 140,162 | 1,014 | 0.72 | 82.7 |
| 2.     | 18,958 | 362 | 1.95 | 14,262 | 310 | 2.17 | 108,944 | 1,818 | 1.67 | 21.4 |
| 3.     | 17,974 | 439 | 2.44 | 10,483 | 289 | 2.76 | 88,877 | 1,778 | 2.00 | 34.3 |
| 4 ≤    | 50,455 | 1,436 | 2.85 | 22,736 | 726 | 3.19 | 235,685 | 5,808 | 2.46 | 59.0 |

\( \chi^2 > 15.2 \) indicates that the deviation of twinning frequency from the annual breed mean is highly significant

1. \( \chi^2 > 15.2 \) indicates that the deviation of twinning frequency from the annual breed mean is highly significant.
2. The twinning maximum for first calvers occurs in June (cf. Fig. 2)
1.2

Fig. 3. Relation between the age at first calving and twinning frequency. The table below the diagram shows the percentage distribution of calvings in the age groups for each of the two Swedish breeds: SRB and SLB.

It would be expected that individual animals react differently to "flushing" as well as to change in daylight hours, but there are probably, on an average, very slight, genetic differences between the groups of cows which are inseminated during the different months of the year. We are therefore inclined to believe that the spring maximum in twinning is an environmental effect, which could probably be produced at any time of the year, and that the autumn maximum is caused by the animals' reaction to the decreasing daylight.

3. Effect of age of dam on twinning frequency

Numerous investigations have shown that the age of the cow has a pronounced effect on the probability of her bearing twins (cf. HENDY and BOWMAN 1970). With one major exception, the ordinal number of parity would seem to be a satisfactory measure of the age of the cows in a population, and it is certainly the most convenient measure. The age at first calving varies within and between breeds, and therefore the influence of this variable was the subject of a special study. It would have been interesting to follow up the problem of the combined effect of age and parity for the second and third calvings but this could not be done on the available data. With increasing number of parities, the need for taking calving age into special consideration will gradually disappear.

Fig. 3 presents in a general way the relation at age at first calving and the frequency of twinning in the two main Swedish breeds, SRB and SLB. The diagram is based on 202,468 SRB cows with an average age of 29.15 months at the first calving and 77,087 SLB cows with an average calving age of 29.78 months. The percentage distribution of the cows on four-months age-groups is shown below the diagram. Linear regressions have been fitted to the twinning frequencies. For the SLB, the fit is not very good, but the data for the highest age group indicated that some second calvers happened to be registered there. Therefore, no importance should be given to the deviation of this group average. The breed averages (y) are 0.584 for the SLB and 0.424 for the SRB breed. The regression coefficients (b) are 0.034 and 0.031, respectively. The breed averages for calving age (x) have been

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Table 7. Relation between parity and twinning frequency

| Parity | Total calves | Twin births | Total calves | Twin births | Total calves | Twin births |
|--------|--------------|-------------|--------------|-------------|--------------|-------------|
|        | No.          | %           | No.          | %           | No.          | %           |
| Swedish Red and White | | | | | | |
| 1.     | 179,034      | 873         | 0.49         | 67,849      | 426          | 0.63        |
| 2.     | 128,745      | 1,983       | 1.54         | 43,908      | 894          | 2.04        |
| 3.     | 84,906       | 1,795       | 2.11         | 27,138      | 816          | 3.01        |
| 4.     | 52,345       | 1,336       | 2.55         | 15,921      | 594          | 3.73        |
| 5.     | 29,276       | 753         | 2.57         | 8,580       | 357          | 4.16        |
| 6.     | 13,476       | 358         | 2.66         | 3,872       | 165          | 4.26        |
| 7.     | 4,666        | 138         | 3.17         | 1,279       | 51           | 3.81        |
|        | 492,448      | 7,236       | 1.47         | 168,547     | 3,303        | 1.96        |
|        | Corrected    | Basis of comparison | 492,448 | 7,236 | 1.47 | 168,547 | 3,303 | 1.96 |
| German Fleckvieh (Bavaria) | | | | | | |
| 1.     | 166,173      | 1,715       | 1.03         | 57,901      | 562          | 0.97        |
| 2.     | 131,381      | 4,391       | 3.34         | 47,407      | 1,262        | 2.66        |
| 3.     | 105,314      | 4,028       | 3.82         | 39,187      | 1,360        | 3.47        |
| 4.     | 83,909       | 3,199       | 3.97         | 32,530      | 1,261        | 3.88        |
| 5.     | 63,138       | 2,535       | 4.02         | 25,581      | 1,078        | 4.21        |
| 6.     | 46,006       | 1,910       | 4.15         | 19,104      | 870          | 4.55        |
| 7,3    | 34,044       | 1,437       | 4.22         | 14,137      | 677          | 4.79        |
|        | 629,965      | 19,335      | 3.07         | 235,847     | 7,070        | 3.00        |
|        | Corrected    | Basis of comparison | 629,965 | 19,335 | 3.07 | 235,847 | 7,070 | 3.00 |
| German Braunvieh (Bavaria) | | | | | | |
| 1.     | 37,076       | 211         | 0.54         | 26,335      | 462          | 1.75        |
| 2.     | 21,870       | 494         | 2.26         | 17,328      | 460          | 2.65        |
| 3.     | 12,641       | 335         | 2.65         | 12,641      | 460          | 2.65        |
| 4.     | 8,662        | 223         | 2.57         | 8,662       | 223          | 2.57        |
| 5.     | 5,977        | 164         | 2.74         | 5,977       | 164          | 2.74        |
|        | 129,889      | 2,349       | 1.81         | 129,889     | 2,349        | 1.81        |
|        | Corrected    | Basis of comparison | 129,889 | 2,349 | 1.81 | 129,889 | 2,349 | 1.81 |

1 Correction is made to the same distribution of calvings on parities as in the Swedish Red and White cattle
2 Pooled data for Bavarian Schwarzbunt, Rotbunt and Gelbvieh
3 The numbers of calving and twinning are estimated from pooled data for the seventh and following calvings

stated above. Both regression coefficients, as well as the differences between the breed means for twinning frequency at the first calving are highly significant.

Data on the relation of twinning frequency to age of dams, measured by number of parities are presented in Table 7 for the Swedish and German breeds, viz. Schwarzbunt (Black and White Lowland), Fleckvieh (German Simmental) and Braunvieh (German Brown cattle). In addition, pooled data are given for three Bavarian breeds where the number of cows was small. Only data for the first to the seventh calving inclusive are listed in the table. In the Swedish breeds, only a small number of cows had more than seven calvings, for the Bavarian breeds all data beyond the sixth calving were pooled at the data-processing, and classification on parity beyond this point was made only for Schwarzbunt in Niedersachsen. For the Bavarian breeds the number of cows at the seventh calving was estimated on the basis of the data from Niedersachsen.

There was a discrepancy in the methods of sampling between the Swedish and German breeds which might have had an influence on the data on which the age curves are based (cf. Fig. 4). The German data represent a cross-section of all the tested cows in the year 1971 (Bavaria) or 1972 (Niedersachsen), whereas the Swedish data represent all cows which were culled in the period 1969–71. The history of these cows was followed retroactively until they entered the herds as calving heifers. The average twinning frequency was practically the same for each year from which the samples were taken, but the sampling method might have led to an exaggeration of the preponderance of young cows in the samples. Taking a cross-section of all the tested SRB and SLB cows during the period 1960–70, the first calvers amounted to 31 % of the total calvings in SRB and 34 % in SLB; the
corresponding figures for the data presented in Table 7 are 36 and 40% respectively. The average twinning incidence for parities 1 to 7 across the samples was for SRB 1.49 and for SLB 2.03%, very close to the figures given in Table 7.

The culling rate among the young cows was apparently much higher in the Swedish than in the German breeds. The percentage first calvers in the total samples from the German breeds was for Fleckvieh 24%, Braunvieh 23% and for Schwarzbunt in Niedersachsen 26%. In the same breeds 13%, 17% and 5%, respectively, of the total number of calvings occurred at the seventh or later parities; the corresponding figure for the Swedish breeds was about one per cent.

The figures show that when breeds are compared with regard to average twinning frequency it is necessary to correct for differences in the distribution of calvings on parities. This has been done in Table 7 with the SRB distribution as standard. With this correction, there is a significant difference in twinning frequency between the Swedish Friesians and the Schwarzbunt in Niedersachsen (0.41 ± 0.038). The corresponding difference between Fleckvieh and Braunvieh is also significant (0.24 ± 0.037) and both these breeds show significantly higher twinning frequencies than any of the other breeds listed in Table 7. The twinning frequency at the first calving is higher for Niedersachsen Schwarzbunt (0.83%) than for the Swedish Friesians (0.63%). This depends at least partly on the 2.2 months higher freshening age (32.0 contra 29.8 months).

Fig. 4 presents a general picture of the relation between twinning frequency and age of the cows in the populations studied. Third degree polynomial curves have been fitted to the observed frequencies. Comparing Fleckvieh and Braunvieh there is a marked difference in the age at first calving. At the time when the records were made, the average age at first calving was 29.3 months for Fleckvieh and 31.7 months for Braunvieh. This difference and the higher twinning frequency for Braunvieh at the 5th–7th calvings suggest that this breed is later maturing and more “persistent” at higher ages than the Fleckvieh. In the Fleckvieh the twinning rate rises more rapidly from the first to the third calving than for any of the other breeds. In this breed the seasonal distribution of the calvings is more uniform than for the Braunvieh but it is not known what influence this difference has had on the age curves for twinning rate.

The Fleckvieh as well as the Niedersachsen Schwarzbunt and the Swedish Red and White cattle show a plateauing in twinning rate after the fourth calving and no tendency to decline at the 7th and later calvings. The decline in the Swedish Friesians was slight and not significant. The Niedersachsen Schwarzbunt were grouped by age up to the 11th and later calvings. The average twinning rate for the 9th–10th calving was 2.76% and for the 11th and later calvings 2.51%. The difference between these two percentages is significant (0.25 ± 0.022%) which indicates a decline in twinning rate for the highest age group.

It is interesting to find that for the 2nd–7th calvings the average twinning frequency is practically the same for the Swedish Friesians (2.86%) as for the Danish Black and White (2.85%) whereas for the Niedersachsen Schwarzbunt the corresponding figure is only 2.28. The difference (0.57%) is highly significant. This may be partly a genetical effect and partly an effect of higher nutritional levels of the cows in Sweden and Denmark than in Niedersachsen as indicated by a 600–800 kg higher average milk yield of the tested cows. The possibility of genetic differences is supported by the fact that the present-day black and white cattle, particularly in Denmark but also in Sweden, are based mainly on imports from Holland whereas the interchange of breeding stock between Germany and Holland has been rather small in recent times.

However, the conclusion may be drawn that genetic differences exist between most of the breeds listed in Tables 7 and 9 with regard to twinning frequencies.

4. The proportion of monozygous to dizygous twins and its relation to breed and age of dam

In the literature, the frequency of MZ births is expressed in three different ways:

1) as a percentage of all like-sexed twins, based on the fact that unlike-sexed twins are never monozygotic;
2) as a percentage of the total number of twin pairs; and
3) as a percentage of the total number of births which is useful for comparison with the
corresponding frequencies of DZ twins in the same sample.

Several human geneticists have expressed the opinion that the incidence of MZ twinning is "not appreciably influenced by the mother's age" (Penrose 1963). Bulmer (1970) has analysed human data from various countries and tried to separate the effect of age and parity on twinning rate. He concluded that the MZ twinning rate shows a "slight increase with maternal age, but fails to show any effect of parity". With regard to DZ twinning he found a clear increase in rate with parity but stated that this effect was smaller than that for age. Enders and Stern (1963) found, in studying large samples of the white and negro populations in the USA, a significant tendency for the frequency of MZ births to increase from the youngest group of mothers 15–19 years old to those approaching the climacterium, and this
### Table 8. Relation between age of dam and the frequency of monozygous and dizygous twinning

| Parity | No. of twin pairs | MZ twin pairs | DZ twin pairs | No. of twin pairs | MZ twin pairs | DZ twin pairs |
|--------|-------------------|---------------|---------------|-------------------|---------------|---------------|
|        | Like sexed | Unlike sexed | % of like sexed | % of total births | Like sexed | Unlike sexed | % of like sexed | % of total births |
| Sweden Red and White cattle (SRB) | | | | | | | | |
| I. 566 | 294 | 272 | 48.1 | 0.152 | 0.33 |
| 2. 1,097 | 874 | 223 | 20.3 | 0.173 | 1.36 |
| 3. 950 | 831 | 119 | 12.6 | 0.141 | 1.96 |
| 4. 728 | 600 | 128 | 17.6 | 0.245 | 2.30 |
| 5≤ 680 | 599 | 81 | 12.2 | 0.171 | 2.54 |
| Total and av. | 4,021 | 3,198 | 823 | 20.5 | 0.167 | 1.29 |

| Swedish Friesians (SLB) | | | | | | | | |
| 1. 258 | 164 | 94 | 34.6 | 0.139 | 0.48 |
| 2. 460 | 431 | 29 | 6.3 | 0.066 | 1.69 |
| 3. 427 | 389 | 38 | 8.9 | 0.140 | 2.87 |
| 4. 302 | 287 | 15 | 5.0 | 0.094 | 3.61 |
| 5≤ 322 | 260 | 62 | 19.2 | 0.442 | 4.09 |
| Total and av. | 1,769 | 1,531 | 238 | 13.5 | 0.141 | 1.81 |

| German Schwarzbunt (Niedersachsen) | | | | | | | | |
| 1. 943 | 564 | 379 | 40.2 | 0.210 | 0.62 |
| 2. 1,403 | 1,087 | 316 | 22.5 | 0.226 | 1.55 |
| 3. 1,425 | 1,081 | 344 | 24.1 | 0.300 | 2.13 |
| 4. 1,339 | 1,022 | 317 | 23.8 | 0.340 | 2.20 |
| 5≤ 3,162 | 2,447 | 715 | 22.6 | 0.344 | 2.36 |
| Total and av. | 8,272 | 6,201 | 2,071 | 25.0 | 0.281 | 1.69 |

| Three dairy breeds in Bavaria¹ | | | | | | | | |
| 1. 1,163 | 1,141 | 251 | 17.8 | 0.180 | 1.66 |
| 2. 1,289 | 1,288 | 251 | 17.8 | 0.180 | 1.66 |
| 3. 1,425 | 1,422 | 251 | 17.8 | 0.180 | 1.66 |
| 4. 1,571 | 1,570 | 251 | 17.8 | 0.180 | 1.66 |
| 5≤ 3,162 | 2,447 | 715 | 22.6 | 0.344 | 2.36 |
| Total and av. | 8,272 | 6,201 | 2,071 | 25.0 | 0.281 | 1.69 |

| German Fleckvieh | | | | | | | | |
| 1. 1,012 | 703 | 309 | 30.5 | 0.187 | 0.85 |
| 2. 2,375 | 2,016 | 359 | 15.2 | 0.273 | 3.07 |
| 3. 2,233 | 1,795 | 428 | 19.6 | 0.416 | 3.41 |
| 4. 1,894 | 1,425 | 469 | 24.8 | 0.558 | 3.40 |
| 5≤ 4,423 | 3,746 | 677 | 15.4 | 0.343 | 3.79 |
| Total and av. | 11,937 | 9,685 | 2,252 | 18.9 | 0.329 | 2.83 |

| German Braunvieh | | | | | | | | |
| 1. 330 | 232 | 98 | 29.7 | 0.169 | 0.80 |
| 2. 732 | 539 | 184 | 25.5 | 0.388 | 2.27 |
| 3. 781 | 579 | 202 | 25.9 | 0.515 | 2.96 |
| 4. 730 | 531 | 199 | 27.3 | 0.612 | 3.26 |
| 5≤ 2,316 | 1,817 | 499 | 21.5 | 0.553 | 4.03 |
| Total and av. | 4,880 | 3,698 | 1,182 | 24.2 | 0.442 | 2.77 |

¹ Schwarzbunt, Rotbunt and Gelbvieh

The trend was especially marked for the negro population.

With regard to the present investigation, it would have been desirable to study the effect of maternal age not only on the total twinning rate, as in Fig. 3, but also the separate effects on the MZ and DZ rates within the first, and preferably also within the second calvings, but this could not be done without a costly rearrangement of the data for processing. In cattle, the correlation between maternal age and parity is so high, and the twinning rate so stabilized after the second calvings, that further separation of the effect of maternal age and parity would probably be of no value (cf. JOHANSSON 1932).

In Table 8, data are presented for the same breeds as in Table 7, showing the relation between age of dam and the estimated frequencies of MZ and DZ twin births. The total number of twin births in the breeds is somewhat higher in Table 8 than in Table 7, because the former table includes all registered calvings of the cows, even after the seventh calving. In Table 8, all data from the fifth and following calvings have been pooled because of rapidly decreasing numbers with increasing age of the cows, especially in the Swedish breeds. Furthermore, the change in twinning frequency after the fourth calving is very slight.

There are two especially interesting features of the estimates of MZ twinning in Table 8. Firstly, when expressed in per cent of like-sexed twins, the MZ frequency is much higher for the first than for the following calvings. This is most
marked for SRB and German Schwarzbunt and least for the Braunvieh. After the first calving there is no clear trend in the percentages with increasing age of the dam. Secondly, when the MZ twinning frequency is based on the total number of calvings, there is a more or less marked tendency for an increase up to the fourth calving. This is most pronounced in the Bavarian breeds, Fleckvieh and Braunvieh, and least in the Swedish breeds. Fig. 5 gives a visual presentation of the breed differences in the relation between maternal age and the MZ and DZ twinning rates.

The two Bavarian breeds are very much alike in the average rates of MZ and DZ twinning and their relation to maternal age. Therefore the data for these two breeds were pooled and averages calculated on which their age curves are based. The two Swedish breeds, SRB and SLB, differ significantly in average DZ rate (0.52 ± 0.036) but they are rather similar in MZ twinning rate. For SLB the estimated numbers of MZ pairs in the various parities are very small, and the group averages behave therefore rather irregularly. For this reason the MZ data for SRB and SLB were pooled, but the DZ data were kept separate. The third breed-group is the Niedersachsen Schwarzbunt which is about intermediate to the other two groups in MZ twinning rate.

The group differences in MZ frequency are relatively small at the first calving but later on there is a rapid rise in the Bavarian breeds up to the fourth calving, followed by a decline at the fifth and sixth calvings. The difference between the MZ frequency, in the first and fourth calvings is highly significant (0.392 ± 0.037), and the following decline to the sixth calving is also highly significant (0.248 ± 0.029). In the Niedersachsen Schwarzbunt the trend is similar but much less pronounced. The rise in MZ frequency, from the first to the fourth calving is significant (0.130 ± 0.049), but the following decline to the fifth calving is barely significant (0.088 ± 0.046). On an average for the two Swedish breeds, the MZ twinning rate is significantly lower at the first three than at the following four calvings (0.076 ± 0.026). A rather peculiar phenomenon is, that in all three breed groups the MZ twinning incidence attains a relatively high level at the fourth calving, declines at the fifth and sixth calvings and then rises again for the older cows (7 ≤ calvings).

For the Swedish breeds, the total number of the seventh and following calvings was 7,304 with an estimated number of 59 MZ births (= 0.81%). The relation between maternal age and DZ frequency is nearly the same for SRB and the Niedersachen Schwarzbunt as shown in Fig. 5. The age curves for both breeds are plateauing after the fourth calving. The comparison between SLB and the Bavarian breeds is interesting. At the first three calvings the DZ frequency is higher for the Bavarian breeds (B + F) but then the age curves cross one another, and at the 5th–6th parities the DZ rate is higher for SLB than for F + B. The later downward and upward trends in the age curves are not significant.

Some additional data on the relative incidence of MZ and DZ twinning are presented in Table 9 for the Danish breeds and Swiss Simmental, where classification was made only on the first and the following parities. The incidences of MZ twinning, calculated in per cent of total births, are surprisingly low for the Danish Red and Black and White breeds but they are rather high for the Danish Jersey, even compared with breeds of large body size. The DZ rate is very low in the Jerseys, on an average for the total number of calvings 0.89 compared with 0.242% MZ twins. In the Swiss Simmental, the DZ and MZ frequencies are both high.

The conclusion may be drawn that not only the DZ but also the MZ twinning rate depends on the age of the mother. In the Fleckvieh and Braunvieh, the relative rate of increase from the first to the fourth calving is just as pronounced as the increase in DZ twinning rate, but in the Swedish breeds it is very slight. Apparently, there are genetic differences between cattle breeds in the rate of increase in both MZ and DZ twinning with increasing maternal age. On the whole, however, the MZ twinning rate tends to be more stable throughout the life of the cows than that of DZ twinning.

5. Incidences of triplet births

The records on triplet births in the Swedish breeds are incomplete, but records which seem to be fairly complete are available for Danish and German breeds and for Swiss Simmental. Multiple births of higher order than triplet have occurred but they have not been regularly registered, or in some cases registered as triplet births.

On the basis of human data Hellin (1895)

*Hereditas* 78, 1974
formulated the rule that when the ratio of twin births to the total number of births is $1:X$, triplet births occur according to the ratio $1:X^2$, quadruplets $1:X^3$, etc. Some later investigators have found fairly good agreement between observed ratios and Hellin's rule. However, more sophisticated methods have also been used (cf. Bulmer 1970) where the biologically different types of zygosity in sets of triplets, quadruplets, etc. have been considered. It is well known from human genetics that the multiple sets may be all MZ, all DZ, or any possible combination of zygosities. In cattle, several cases of monozygous triplets and at least one case of monozygous quadruplets (Donald et al. 1951) have been reported.

Table 10 presents our data on triplet births in seven European breeds of cattle. On an average, one twin birth has occurred on 41.4 total births, and one triplet birth on $(41.4)^{3^{1/3}} = 6,972$ total births. However, when the application of this ratio was tested on the various breeds, the fit was very poor. Apparently, Hellin's rule is not applicable to multiple births in cattle. This is not surprising since the relative incidence of MZ twin birth, in proportion to DZ, is much lower in cattle than in man. However, the figures in table 10 indicate, with some exceptions, that the
### Table 9. Frequency of monozygous and dizygous twin births in three Danish breeds and in Swiss Simmental

| Calving number | Breed                        | Total calvings | Twin births | MZ twin births | % of total births |
|----------------|------------------------------|----------------|-------------|----------------|------------------|
|                |                              |                | % twin births | Like sexed No. | % of total births |
|                |                              |                | % of total births | DZ pairs |
| First          | Danish Red 1                 | 394,910        | 0.77        | 1,648          | 14.75            | 0.062 0.71    |
|                | Danish Black and White       | 376,880        | 0.62        | 1,254          | 12.52            | 0.042 0.58    |
|                | Danish Jersey                | 125,906        | 0.43        | 355            | 48.73            | 0.137 0.29    |
|                | Swiss Simmental 2            | 13,585         | 1.12        | 69             | 43.48            | --- ---       |
|                |                              |                |             |                |                  |                |
| Second and     | Danish Red                   | 770,531        | 3.77        | 15,009         | 14.046           | 0.125 3.64    |
| following      | Danish Black and White       | 834,348        | 2.85        | 12,453         | 11.365           | 0.130 2.72    |
|                | Danish Jersey                | 322,104        | 1.39        | 2,716          | 1.762            | 0.296 1.09    |
|                | Swiss Simmental 2            | 38,563         | 5.60 1      | 727 2          | 560 2            | 167 23.00     |

1 Data for the Danish breeds for the period 1967—71 has been kindly placed at our disposal by F. Elleby, Husdyrbrugsudvalget, Viby, Denmark
2 The sex distribution of twin pairs is obtained in a special investigation and does not exactly correspond to the data on total calvings and total twin births

### Table 10. Frequency of triplet births in Danish and German breeds and Swiss Simmental

| Breed                        | % twin births of total births | X 1 | No. of triplet births | Triplet births in % of multiple births |
|------------------------------|-------------------------------|-----|-----------------------|----------------------------------------|
| Danish Red                   | 2.76                          | 36.3| 153                   | 0.474 0.013                            |
| Danish Black and White       | 2.16                          | 46.3| 127                   | 0.483 0.011                            |
| Danish Jersey                | 1.12                          | 89.3| 37                    | 0.732 0.008                            |
| German Schwarzbunt (N) 2     | 1.97                          | 50.8| 116                   | 0.795 0.016                            |
| Bavarian Braunvieh           | 3.21                          | 31.2| 36                    | 0.418 0.014                            |
| Bavarian Fleckvieh           | 3.16                          | 31.6| 172                   | 0.789 0.025                            |
| Swiss Simmental              | 4.43                          | 22.6| 24                    | 1.028 0.046                            |
| Total and average            | 2.41                          | 41.4| 665                   | 0.600 0.015                            |

1 \(X = \frac{\text{Total births}}{\text{Twin births}}\)
2 Niedersachsen Schwarzbunt

The frequency of triplet births increases with increasing frequency of twin births.

### 6. Twinning in beef breeds

Relatively few investigations have been made on twinning in specialized beef breeds. Jones and Rouse (1920) reported results of an analysis of data from the Hereford and Aberdeen Angus herdbooks in the USA. The average twinning incidence was found to be 0.45% for 527,000 calvings in the Hereford and 0.41% for 219,200 calvings in the Aberdeen Angus breed. The twinning frequency was very low for the youngest age groups of cows but rose gradually up to about 5 years of age, plateauing later on. Since
Table 11. Twinning frequency in the Charolais and Hereford breeds

| Calving number | Charolais | France | Hereford | Sweden | USA |
|----------------|-----------|--------|----------|--------|-----|
|                | Sweden    |        |          |        |     |
|                |           | % twinning | % twinning | % twinning | % twinning |
| % distribution of calvings | % twinning | % distribution of calvings | % twinning | % distribution of calvings | % twinning |
| 1.             | 36.2      | 1.96   | 22.4     | 1.11   | 25.0 | 0.46 |
| 2.             | 31.9      | 2.96   | 17.2     | 2.64   | 21.1 | 0.76 |
| 3—6           | 28.2      | 4.12   | 42.5     | 3.91   | 42.2 | 1.15 |
| 7≤             | 3.7       | 5.32   | 17.9     | 4.75   | 11.7 | 1.05 |
| Total calvings | 2,544     | 3.03   | 81,463   | 3.19   | 10,544 | 0.88 |
| % twinning Corrected for distribution on parities | 3.65 | 0.94 | 24,432 |

The data were extracted from herdbooks, it is likely that the actual twinning incidence was underestimated. JOUBERT (1952) reported on twinning frequency in the South African Beef Shorthorns and found it to be 0.72% for 6,133 calvings. These data were also extracted from herdbooks but supported by results from the Mara Research Stations where only 0.40% twinning occurred in 506 calvings of purebred cows belonging to the three British beef breeds Hereford, Aberdeen Angus and Beef Shorthorn.

With kind co-operation of the American Hereford Association, the senior author obtained very carefully kept calving records for the purebred Hereford herd at the Wyoming Hereford Ranch, covering the period 1931–64. In the 1960's this herd comprised about 800 cows. Further, some data on the French Charolais are quoted from an unpublished manuscript by Mr. F. Menissier, Jouy-en-Josas (cf. p. 202).

In recent years, breeding stock of three beef breeds have been imported to Sweden for crossbreeding purposes, viz. Hereford and Aberdeen Angus from Great Britain and Charolais from France. The number of purebred Aberdeen Angus cattle in Sweden is very small, and our data from this source comprise only 1,210 calvings with 18 twin births (1.49 ± 0.348 %) which is too limited to be a satisfactory random sample o° the breed. In Table 11, the twinning frequency in the Swedish Charolais is compared with corresponding records from France, and the Swedish Herefords are compared with data from the Wyoming Hereford Ranch. The distribution of calvings on parities is expressed as a percentage of the total calvings in order to facilitate the comparisons. The figures show that for both breeds the Swedish cows are on an average younger, than the cows in the comparable population samples. For the same ordinal number of parity, the Swedish Charolais cows tend to show a somewhat higher twinning frequency than the French Charolais, and if the Swedish average is corrected to the same distribution on parities as the French material, the Swedish average would be 3.65% twinning, compared to 3.19% for the French Charolais. The twinning frequencies for the Swedish Herefords are somewhat higher throughout than the corresponding figures for the Wyoming herd, but the difference between the averages is not significant. It might be expected that a herd under ranch conditions would show a relatively low rate of twinning. The difference between the Swedish Charolais and the Swedish Herefords, kept under the same environmental conditions, is highly significant in spite of the small numbers (2.15 ± 0.455).

Monozygous twinning occurs apparently with about the same relative incidence in the beef breeds as in the dairy breeds. By pooling the Swedish and the Wyoming data for the Herefords we find the following sex combinations of the twin pairs: 62♂♂ + 80♀♀ + 89♂♀. It may then be estimated that 53 of 142 like-sexed pairs, or
According to Menissier's study of the French Charolais, the sex combinations of 1,700 twin pairs were as follows: 450♂♂ + 506♀♂ + 744♀♀, and here the MZ estimate would be 212 pairs or 22.2% of the same-sexed pairs. For the first calving the percentage was almost twice as high, or 43.6%, thus agreeing with the situation in the dairy breeds (Table 8) that the relative incidence of MZ twinning is higher at the first than at the following calvings.

7. Inheritance of the twinning tendency

The inheritance of twinning has been extensively studied by human geneticists from family records or population samples. It has been shown in the U.S.A. that the frequency of twinning is higher for the black than for the white population. It is particularly low in Japan, and in Europe it is higher in the Fenno-Scandinavian than in the Mediterranean countries. Many researchers have considered it likely that the tendency to bear twins is a recessive trait with simple Mendelian inheritance (cf. Penrose 1963). However, Stern (1960) writes "If the genetic basis of twinning is a simple one, it must have a very low penetrance". Dahlberg (1952) found in a study of 2,222 births that after the first twin birth, repetitions of twinning were on average only 5.46 ± 0.49%.

In previous sections it was found that different cattle breeds sharing the same geographical area may show highly significant differences in twinning rate, whereas closely related breeds, existing in different areas, usually show rather similar twinning rates (Tables 7, 9 and 11). This leads to the assumption that the variation between individuals within the same breed is, at least to some extent, of genetic origin.

In accordance with the majority of present-day opinion, we assume that predisposition for twinning is a polygenic character with a discontinuous manifestation on the observed scale. The analysis of such characters can be performed on the observed (binomial) scale or according to the assumption of an underlying continuous variation. The problem has been discussed as regards other all-or-none or quasicontinuous characters by, among others, Lush, Lamoreux and Hazel (1948), and Falconer (1965, 1967). Since we use both approaches, the problems involved may be briefly discussed.

Following S. Wright, Lush et al. (1948) pointed out that heritability on the observed binomial scale (p-scale) will be influenced by the frequency of the character, due to the dependency of the variance on the mean, and by the coarseness of grouping which of necessity decreases the correlation between observation and genotype. They suggest that heritability on the two scales can be approximately interconverted by the following relation:

\[ h^2_p = \frac{h^2_x \cdot z^2}{pq} \]

where \( h^2_p \) = heritability on the observed scale

\( h^2_x \) = refers to the continuous underlying scale

\( q \) = frequency of the trait in the population, and \( p = 1 - q \)

and \( z \) = ordinate at the threshold point, which separates the two classes, assuming normal distribution of the twinning liability.

Falconer suggested a simple and elegant method to estimate heritability of the underlying variable for threshold characters. His model can be used for twinning which on the observed scale is an all-or-none character. Underlying this binomial distribution is the liability for twinning which not only includes the “individual’s innate tendency” to give birth to twins but also “the whole combination of external circumstances” influencing the rate of twinning, such as age, season of conception, etc. All individuals where the liability exceeds the threshold will exhibit twinning. The position of the mean liability of a population (\( \mu_p \)) can be expressed relative to this threshold, as can the difference between the mean liability of twin-bearers and the population mean (\( = z/q = a \)). If differences in liability are partly genetic, relatives of twin-bearing cows should have a higher mean liability (\( \mu_r \)) which will be closer to the threshold. Falconer suggests estimating heritability by the increase in mean liability of relatives of twin-bearers over the population mean in proportion to the mean superiority of liability of the latter, i.e. \( h^2_x = \frac{\mu_p - \mu_r}{r \cdot a} \), where \( r \) = coefficient of relationship between twin-bearers and relatives. This approach can also be used for estimating repeatability and the importance of herd influences for twinning liability.
Table 12. Repetition of twinning

| Repetition | Ordinal number of calving at first twin birth | Swedish Red and White (SRB) | Swedish Friesian (SLB) |
|------------|---------------------------------------------|-----------------------------|------------------------|
|            | Calvings after first twin birth              | Twin births                 |                        |
| After the first twin birth |                 |                             |                        |
| 1          | 47                                           | 344                         | 24                     | 6.98                   | 127                     | 401                     | 38             | 9.48                       |
| 2          | 166                                          | 652                         | 36                     | 5.52                   | 251                     | 760                     | 77             | 10.13                      |
| 3          | 156                                          | 440                         | 29                     | 6.59                   | 212                     | 547                     | 61             | 11.15                      |
| 4          | 131                                          | 262                         | 15                     | 5.72                   | 160                     | 297                     | 27             | 9.09                       |
| 5 ≤        | 144                                          | 148                         | 8                      | 5.41                   | 223                     | 213                     | 16             | 7.51                       |
| Total and av. | 644                          | 1846                       | 112                    | 6.07                   | 973                     | 2218                    | 219           | 9.87                       |

JOHANSSON (1932) | 1709 | 113 | 6.61 | 583 | 74 | 12.69 |

| After the second twin birth | Breed | Calvings after second twin birth | Twin births | Repetitions by the same cow (number of twin births per cow) |
|-----------------------------|-------|---------------------------------|-------------|----------------------------------------------------------|
|                             |       | No. | No. | % | 2 | 3 | 4 | 5 |
| SRB |                       | 131 | 186 | 20 | 10.75 | 214 | 16 | 2 | 1 |
| SLB |                       | 94  | 183 | 28 | 15.30 | 169 | 17 | 4 | 1 |

1 The SRB sample is here more than twice as large as in the upper part of the table. The SLB sample is the same in both cases.

A. Repetition and repeatability

A suitable starting point in studying the possible effect of heredity on twinning would seem to be the repetition of twinning after the first twin birth. Repetition refers to the twin-bearers only, whereas repeatability refers to the whole population of twinning and nontwinning cows (cf. Bowman and Hendy 1970). The rate of repetition shows simply the proneness of individual cows to repeat twinning at the following calvings regardless of the underlying causes. An attempt to explain the inheritance of the twinning tendency on a monofactorial basis would be justified only if the repetition rate was relatively high.

Table 12 shows the results obtained in an analysis of data from the two Swedish breeds SRB and SLB with regard to the repetition of twinning in different age groups and after the first and second twin births. It has been assumed that early twinning, at the first or second calving, is a stronger indication of genetic predisposition than when the first twins are born later in life, and therefore the data are classified according to the parity when the first twinning occurred. No significant differences appear between repetition rates at various parities when tested by $\chi^2$. However, in SRB 32% and 9% of the twin pairs born at first parity and later parities, respectively, were probably monozygotic and the corresponding figures for SLB are 22 and 5%.

According to Bulmer (1970) the tendency to repeat twinning in man is limited to DZ births, and the same probably applies to cattle. If the rate of repetition is estimated relative to dizygous twinning only, the repetition would be 9.4 and 5.8% respectively after heifer and later twinning for the SRB, the difference being significant ($\chi^2 = 4.1$). The corresponding figures for the SLB are 11.5 and 10%. Therefore it appears that the suggestion that the repetition of DZ twinning is higher for heifers than for cows is a valid one.

According to Table 12 there is a breed difference in the rate of repetitions after the first twin birth, and this difference is highly significant. The difference between the repetitions after one and two twin births is significant for SRB only (P < 0.05). For comparison, results from the
Table 13. Repeatability of twinning in milk-recorded cows of the Swedish Red and White cattle
The breeding history of cows eliminated from the herds 1969—71 has been followed until these cows entered the herds

| No of completed calvings | Components of variance | Repeatability |
|--------------------------|------------------------|---------------|
|                          | df Between cows       | df Within cows|               |
| 2                        | 89,078                 | 0.000009      | 89,079 0.010036 0.0009 |
| 3                        | 59,290                 | 0.000173      | 118,582 0.013728 0.0124 |
| 4                        | 36,790                 | 0.000214      | 110,373 0.016865 0.0126 |
| 5                        | 21,216                 | 0.000223      | 84,868 0.019008 0.0116 |
| 6                        | 10,703                 | 0.000289      | 53,520 0.020378 0.0140 |
| 7                        | 4,224                  | 0.000350      | 25,350 0.022372 0.0154 |

earlier study of the same breeds (JOHANSSON 1932) are quoted in Table 12. The repeat figures were higher in this study than those obtained from the present data which probably has two main causes, viz. the earlier first calving and the shorter life of the cows in recent years than in the 1920's.

Table 13 presents an analysis of variance of the population data for the Swedish Red and White cattle employing the same type of model as that used by BOWMAN and HENDY (1970). The repeatability of twinning (r_p) in the population was estimated and since the number of calvings is fairly high, especially in the lower age groups, the estimates show a continuous series of increasing values from two to seven completed calvings in the groups. This increase would be expected because of higher twinning frequencies in older cows.

Falconer's method (FALCONER 1965, 1967) involves a slight downward bias of the estimates. When corrections were computed they were found to be almost insignificant and therefore only the original values are reported.

Repeatability of liability of twinning (r_x) can be estimated from repetition rates:

\[
\text{Repeatability (r_x)} = \frac{x_p - x_R}{z/q}
\]

As is apparent from these figures the repeatability of twinning liability of the two breeds is significantly different, albeit the difference is relatively smaller than that of the repetition rates. When converted to the observed scale, the repeatability is a little larger than that of Table 13 but these latter values are probably too small, as evidenced by the fact that they are below the similarly estimated heritability figures (p. 223). On the other hand, since repetition rate was compared with the population frequency of twinning, the intraherd repeatability may have been overestimated if real herd differences in twinning frequencies exist. However, this could not have been very great as will become evident in the second paragraph to follow.

It may be stated that cows show differences in their predisposition to twinning and that these differences become more evident when cows with repeated records of twinning are compared with average animals. Breeds have different repetition rates but this may be largely caused by different levels of twinning. Repeatability values on the continuous scale show less differences between breeds than repetition rates. All this evidence
supports the model of continuous underlying variation with a threshold.

In the Bavarian data the twinning frequency of daughters was compared to that of their herd mates (cf. Table 17). The differences between the latter and the population average twinning frequency can be used for investigating the existence of real herd differences in twinning liability:

The b values indicate to what extent herd differences in the liability of cows are repeatable. It can be concluded that real herd differences do exist, probably mainly due to differences in feeding and management. Bar-Anan (1973) observed somewhat larger twinning differences between herds with different management but with the same bull progenies. Differences in twinning

| Parity       | I       | 2       | 3 ff.    |
|--------------|---------|---------|----------|
|              | F       | B       | F        | B       | F        | B        |
| Population twinning frequency | 1.03    | 0.97    | 3.34     | 2.66    | 3.82     | 3.47     |
| Herd-mates' twinning frequency  | 1.18    | 0.86    | 3.64     | 2.94    | 4.75     | 4.37     |
| b            | 0.044   | -0.016  | 0.017    | 0.019   | 0.045    | 0.062    |
| s_b          | 0.013   | 0.022   | 0.014    | 0.023   | 0.019    | 0.030    |

F = Fleckvieh; B = Braunvieh

Table 14. Variation in twinning frequency between paternal half-sib groups

| Ratio: Heifers | No. of bulls | 1st calving (heifers) No. of daughters per bull | Twin births No. % | $\chi^2 1$ | 2≤ calvings (cows) No. of daughters per bull | Twin births No. % | $\chi^2 2$ |
|---------------|-------------|-----------------------------------------------|-------------------|---------|-----------------------------------------------|-------------------|---------|
| Cows          |             |                                               |                   |         |                                               |                   |         |
| SBR           |             |                                               |                   |         |                                               |                   |         |
| 0.10          | 13          | 79                                             | 3                 | 0.292  | 6.53                                          | 1,800             | 577     | 2.466  | 105.6  |
| 0.11—0.30     | 19          | 465                                            | 41                | 0.463  | 56.18\(^{b}\)                                | 2,174             | 761     | 1.842  | 192.6  |
| 0.31—0.50     | 13          | 1,104                                          | 53                | 0.369  | 17.66                                        | 2,746             | 668     | 1.891  | 124.2  |
| 0.51—0.70     | 10          | 1,142                                          | 36                | 0.315  | 9.86                                          | 1,949             | 261     | 1.339  | 49.9   |
| 0.70<         | 11          | 1,797                                          | 62                | 0.314  | 21.11\(^{a}\)                                | 1,920             | 343     | 1.624  | 108.8  |
| Total and av. | 66          | 840                                            | 195               | 0.352  | 111.35                                       | 2,137             | 395     | 1.851  | 581.1  |
| SBL           |             |                                               |                   |         |                                               |                   |         |
| 0.11—0.30     | 14          | 388                                            | 38                | 0.700  | 14.11                                        | 1,958             | 774     | 2.824  | 175.3  |
| 0.31—0.50     | 8           | 536                                            | 20                | 0.467  | 17.80\(^{a}\)                                | 1,440             | 260     | 2.258  | 26.6   |
| 0.70<         | 12          | 972                                            | 50                | 0.429  | 36.55\(^{b}\)                                | 1,002             | 273     | 2.271  | 60.9   |
| Total and av. | 34          | 629                                            | 108               | 0.505  | 67.66                                        | 1,498             | 384     | 2.563  | 262.8  |

1 \(^a\) P<0.05; \(^b\) P<0.001
2 All \(\chi^2\) are highly significant

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rates between Hereford in the USA and in Sweden and between Black-and-White cattle in Niedersachsen and in Sweden may be other examples of environmental influences.

B. Heritability

A preliminary analysis was made of the records of AI bulls with large numbers of offspring. Regarding twinning averages of bull-progeny groups calculated from such data, herd differences are unimportant because the daughters of each bull are spread over a large number of herds, but the influence of age differences should be considered. The daughters of each bull were divided into two groups, viz. heifers and cows, and their ratio was used to divide the bulls into 5 subgroups (Table 14). A high ratio was assumed to indicate that the daughters that had reached cow stage (2 or more parities) were relatively young. The twinning averages for the cow groups indicate that at least part of the differences in age distribution of progeny groups was eliminated by this grouping. A \( \chi^2 \)-test of the differences in twinning frequency between the 5 cow-groups turned out to be highly significant (\( \chi^2 = 81.35 \)), while it failed to reach significance for the heifer groups (\( \chi^2 = 6.42 \)).

Table 14 is arranged so that daughters of the same bull are entered on the same row, but heifers and cows separately. Since the twinning frequency at the first calving is fairly low, the difference between sires with regard to twinning frequency at the first calving of their daughters surpasses the conventional level of significance only twice in each breed. However for later parities, the differences between bulls are highly significant in each one of the five groups. Using the \( \chi^2 \)-method (ROBERTSON and LERNER 1949) the following half-sib correlations (within groups) and heritability estimates were obtained:

| Half-sib correlations (r) | Heritability (h^2) |
|--------------------------|------------------|
|                          | Heifers          | Cows |
| SRB 0.0010               | 0.004 ± 0.0016   | 0.016 ± 0.0033 |
| SLB 0.0017               | 0.007 ± 0.0025   | 0.023 ± 0.0066 |

Additional data became available in autumn 1973 so that twinning frequencies of cow progeny groups of a total of 101 SRB bulls could be included because two progeny groups were available only for seven bulls. The correlation pertaining to the 25 SRB heifer-subgroups is small and not

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Fig. 6. Distribution of average twinning frequency for 101 SRB and 34 SLB sire progeny groups, each group comprising 1,000 second and following calvings of the paternal half-sib cows.

Table 15. Repeated progeny test of AI bulls for twinning frequency of their daughters
Each subgroup comprises 500 calvings for heifers and 1,000 for cows

| Breed | Dams of calves | Number of AI bulls | Mean twinning frequency \((1+2)\) | Standard deviation \((1+2)\) | Correlation between the subgroups \(r_{12}\) |
|-------|----------------|--------------------|-------------------------------|-------------------------------|---------------------------------|
| SRB   | Heifers        | 25                 | 0.410                         | 0.253                         | 0.114                           |
| SRB   | Cows           | 24                 | 1.620                         | 0.949                         | 0.809***                       |
| SLB   | Cows           | 8                  | 2.599                         | 1.491                         | 0.966***                       |

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significant. However, with 1,000 cows in each subgroup, the correlation coefficients are high and highly significant. Half-sib correlations (r) were calculated from the equation

\[ r_{12} = \frac{nr}{1 + (n - 1)r} \]

Half-sib \[ h^2_p \] estimate

|         | \[ h^2_p \] estimate |
|---------|----------------------|
| SRB heifers | 0.0020 0.008         |
| SRB cows    | 0.0042 0.017         |
| SLB cows    | 0.0276 0.110         |

Practically the same value of the half-sib correlation was obtained for SRB as from the data in Table 14. The SLB numbers (8 groups) are too small to attract any attention to the higher value. Many more bulls were used for the corresponding estimation from Table 14.

Four earlier reports on the heritability of multiple births in cattle may be mentioned, published by MAIJALA (1964), BOWMAN et al. (1970), GAILLARD (1973) and BAR-ANAN and BOWMAN (1974), all based on paternal half-sib correlations. MAIJALA had a large number of records from progeny testing of Ayrshire A I bulls at his disposal. The minimum number of daughters per bull was 10 or 20, but the average number was several times larger. With 20 daughters as a minimum, heritabilities of about 3% were obtained. BOWMAN et al. analysed records 2,862 British Friesian daughters (2nd and following calvings) of 63 A I bulls and estimated the heritability of twinning, based on single calvings, to be 0.043 ± 0.012. GAILLARD’s data for Swiss Simmental comprised 31 sire-progeny groups with an average of 111 daughters per sire. For the cow-groups the twinning frequency was on an average 4.18% and the heritability estimate was 0.023 ± 0.016. BAR-ANAN and BOWMAN’s data (1974) were derived from the Israeli-Friesians and comprised cow-progeny groups for 144 sires each with over 200 daughter calvings at parities 2–6. The heritability of twinning was estimated to be 0.024 ± 0.002.

To summarize, it can be said that the heritability of twinning frequency of cows as observed is real but small, and that the heritability for heifers is even smaller. This difference may be explained by the very low dizygous twinning rate in heifers.

For an estimation of twinning heritability on the continuous scale, we have two sets of data, a limited sample of cows from SRB and SLB and a fairly large amount of data from Bavarian Fleckvieh and Braunvieh.

The Swedish data were manually selected from the milk-record files, and therefore the breed samples are rather small. Cows with one or several twin births (propositi) were picked at random and then their daughters (or dams) were located for comparison with the twinning records in the general population. In order to eliminate the effect of age at calving on the twinning frequency, only records for the 3rd–5th parities were compared. However, the propositi were used whenever they had born twins in the 1st–5th parities. For the SLB, where the largest sample was available, a special comparison was made for daughters of dams with two or more twin births. In the other cases only one twin birth per dam, and daughter was considered.

Twinning frequencies of daughters and dams of propositi were computed, and the results are presented in Table 16. As expected, the heritability values estimated according to Falconer’s method are much higher than those computed from the observed p-scale. Estimates for SRB are somewhat higher than those for SLB which is the reverse of that found for estimates on the observed scale. When the \[ h^2_p \] estimates are transformed to the binomial scale, the results are very close to those estimated directly from the observed twinning frequencies of cow progeny groups in Tables 14 and 15. The transformed \[ h^2_p \] values are roughly equal to the similarly estimated repeatability of twinning in SRB but smaller than repeatability in SLB (cf. p. 221). Herd differences were not taken into account in any of these calculations.

For the Bavarian Fleckvieh and Braunvieh a greater amount of data were available. Both twinning dams and their daughters could be grouped according to parity and the daughters could be compared with unrelated, contemporary herdmates in order to exclude possible effects of herd environment on the twinning frequency. The results are shown in Table 17. The number of first parity daughters from first parity dams was rather small in both breeds and their relatively high twinning frequency does not deviate significantly from the average of the other first calving groups of daughters. Since the twinning rate of
Table 16. Twinning frequency at the 3rd–5th parities of daughters and dams of twinning cows, compared to the corresponding breed average

| Breed | Population mean (from Table 6) | Number of daughters and dams respectively | Daughters and dams of twinning cows |
|-------|-----------------------------|---------------------------------------|-----------------------------------|
|       | Corrected1)                |                                      | No. of calvings | No. of twin births2 | Per cent twin births |
|       |                            |                                      |                   |                    |                     |
| 1. SRB | (2.33) 2.34               | 302                                   | 616               | 22                  | 3.57                |
| 2. SLB | (3.42) 3.49               | 519                                   | 1,113             | 51                  | 4.58                |
| 3. SRB | (2.33) 2.36               | 235                                   | 530               | 22                  | 4.15                |
| 4. SLB | (3.42) 3.58               | 174                                   | 441               | 21                  | 4.76                |
| 5. SLB | Propositi with 2 ≤ twin births (3.42) 3.50 | 100                                   | 217               | 12                  | 5.53                |

Heritability estimates on the x-scale

| Breed       | Heritability transformed to the p-scale |
|-------------|---------------------------------------|
| SRB: 1 and 3 | 1) 0.155 ± 0.080 3) 0.200 ± 0.083 |
| SLB: 2 and 4 | 2) 0.115 ± 0.059 4) 0.0118 ± 0.078 |
| SLB: 5      | 5) 0.198 ± 0.056                       |

1 The observed percentages are shown within parentheses. Correction has been made to the same distribution of calvings on parities as for daughters and dams of twinning cows in the corresponding groups.
2 Only one twin birth per daughter and dam in the 3rd–5th parities is included.

The daughters seemed to be rather independent on how early their dams started twinning, averages were calculated for each parity group of daughters from twinning dams of all ages. The twinning averages for the total population samples are stated in parentheses below the corresponding average for the contemporaries. For Fleckvieh where the largest numbers were available, the twinning frequency of the daughters of dams with at least two twin births was also calculated for each one of the parity groups. It is interesting to note that the twinning frequency among the daughters of dams with two or several twin births is consistently higher than for daughters of dams with only one registered twin birth. This is reflected in higher h² values. It is in good agreement with the results presented in Table 12 showing higher repetition of twinning at calvings succeeding second twin births than when the cows had born twins once only. The heritability values of single twin births vary between parity and breed groups but no obvious pattern can be discerned.

Transformation of the h² values yields heritabilities fairly close to those reported by Gaillard (1972) from Simmental progeny groups, and to the Swedish results discussed above. Transformed h²p values of “double twinning” are about twice those of single twinning but still quite small in absolute terms.

The h² values from the Swedish Friesians (SLB) and the Bavarian breeds lie in the same range of values. The SRB estimates are slightly higher but the samples from this breed are rather small and the difference between SRB and SLB is not statistically significant. Moreover the large h² values for SRB are not reflected by large repeatability values (Table 12).

The transformation reduces the various h² values to estimates which are fairly close to the directly computed binomial heritabilities. No bias in any direction can be discerned. In contrast,
Table 17. Twinning frequency of daughters of twin-bearing dams, compared with unrelated and contemporary herd-mates, calving at the same age and approximately in the same season as the daughters

| Source of data | First parity | Contemporaries | Second parity | Contemporaries | Third parity | Contemporaries |
|---------------|--------------|----------------|--------------|----------------|--------------|----------------|
|               | Daughters    |                | Daughters    |                | Daughters    |                |
|               | No.          | % twin births | No.          | % twin births | No.          | % twin births |
| **Fleckvieh** |              |                |              |                |              |                |
| Dams with     | 21,242       | 1.39           | 37,476       | 1.18<sup>1</sup> | 12,300       | 4.49           |
| one twin      |              |                |              | (1.03)         |              |                |
| birth         |              |                |              |                |              |                |
| h<sup>2</sup><sub>x</sub> = 0.049±0.017; | h<sup>2</sup><sub>p</sub> = 0.004 | h<sup>2</sup><sub>x</sub> = 0.102±0.018; | h<sup>2</sup><sub>p</sub> = 0.018 | h<sup>2</sup><sub>x</sub> = 0.072±0.023; | h<sup>2</sup><sub>p</sub> = 0.014 |
| Dams with     | 2,395        | 2.20           | 5,187        | 1.23           | 1,739        | 6.44           |
| 2 ≤ twin      |              |                |              |                |              |                |
| births        |              |                |              |                |              |                |
| h<sup>2</sup><sub>x</sub> = 0.180±0.043; | h<sup>2</sup><sub>p</sub> = 0.013 | h<sup>2</sup><sub>x</sub> = 0.260±0.043; | h<sup>2</sup><sub>p</sub> = 0.044 | h<sup>2</sup><sub>x</sub> = 0.175±0.057; | h<sup>2</sup><sub>p</sub> = 0.033 |
| **Braunvieh** |              |                |              |                |              |                |
| Dams with     | 8,179        | 1.24           | 14,152       | 0.86<sup>1</sup> | 4,801        | 3.72           |
| one twin      |              |                |              | (0.97)         |              |                |
| birth         |              |                |              |                |              |                |
| h<sup>2</sup><sub>x</sub> = 0.102±0.028; | h<sup>2</sup><sub>p</sub> = 0.007 | h<sup>2</sup><sub>x</sub> = 0.093±0.030; | h<sup>2</sup><sub>p</sub> = 0.014 | h<sup>2</sup><sub>x</sub> = 0.022±0.040 | h<sup>2</sup><sub>p</sub> = 0.004 |

<sup>1</sup> The comparable twinning frequency in the general populations is stated within parentheses. h<sup>2</sup><sub>x</sub> = heritability of the normal scale; h<sup>2</sup><sub>p</sub> = transformed value on the binomial scale.
DEMPSTER and LERNER (1950) found higher heritabilities for egg production from direct estimation on the binomial scale than when the regular estimate was transformed by multiplication with \( \frac{pq}{z^2} \). However, in view of the standard errors, they felt that the agreement was satisfactory. Also VAN VLECK (1972) found from computer simulation experiments that heritabilities estimated directly from the binomial scale were larger than those obtained by transformation.

As indicated, we find the agreement satisfactory and without apparent bias. Falconer's method therefore appears to be a convenient and efficient way of estimating heritabilities for rare traits from large volumes of data. It directly estimates the liability for the trait which, after all, is responsible for the observed correlations between relatives. Of course, the latter are relevant for animal improvement but as our results indicate, they can be estimated sufficiently well from knowledge of the heritability on the underlying continuous variable. As will be shown later, \( h^2 \) can also be used for estimating genetic gain from selection.

**C. Genetic correlations**

Twin births in different parities are composed of varying fractions of MZ and DZ twins. As has been indicated above, it appears, that the frequency of MZ twins is more stable between breeds and parities than that of DZ ones, and that only the frequency of the latter shows appreciable heritable variation. The DZ twin frequency varies greatly with age. Therefore, the question may be raised, whether twinning at the different parities is genetically identical, i.e. whether the genetic correlations are 1. The large volume of Bavarian data permitted estimation of heritability of and genetic correlations between twinning liability in 1st, 2nd and later parities. Regression coefficients were computed for daughter—herdmate differences in liability at different parities on dam superiority for twinning liability in each parity group (1, 2 and later). The coefficients were not significantly different for the two breeds and therefore the estimates were combined. The genetic correlations \( r_{01} \) between parities and the heritability \( h^2 \) within parities were as follows:

| Parity | 1   | 2   | 3   |
|--------|-----|-----|-----|
| \( P \) |     |     |     |
| a      | 0.040 |
| r      | 1.0  | 0.122 |
| i      | 1.3  | 1.1  | 0.059 |

\( h^2 \) on diagonal; \( r_{01} \) off diagonal

The heritability estimates vary, but the genetic correlations between twinning liability in different parities appear to be 1. Obviously this refers to DZ twinning liability only. This seems reasonable if one assumes that MZ twinning liability has no, or very slight, genetic basis, and that it has no genetic connection with the predisposition for DZ twinning, which assumption agrees with most observations reported in the literature, as indicated above.

**D. Paternal influence on frequency and zygosity of twins**

A priori it seems unlikely that the sire of the calves has any influence on the DZ twinning rate, which primarily is determined by the number of eggs ovulated in connection with the heat period when insemination takes place, but it is quite possible that the sperm, as well as the egg, conveys genes to the zygote which makes it split at an early stage of development, thus producing monozygous twins, as suggested by DAHLBERG (1926). With the exception of the Jersey breed and the firstparity of the other breeds listed in Tables 8 and 9, the MZ twins constitute only a small part of the total number of twins produced, and they have therefore only a slight effect on the total twinning rate. However, for the sake of comparison we tested the variation in twinning rate after parturitions where the bulls were sires of the calves. This was done by the same type of progeny test as used in Table 15. The results are shown in Table 18.

In both heifer groups and also in the SLB cow-group the correlation between twinning rates of the duplicate samples are negative but not significant, but in the SRB cow-group the correlation is positive and significant at the \( P < 0.01 \) level.

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Table 18. Repeated tests of A I bulls, as sires of calves, for direct influence on the frequency of twins

| Breed | Dams of calves and no. of tested bulls | Av. twinning frequency for total no. of calvings | Standard dev. in the groups (twinning rate) | Correlation between subgroups r_{12} |
|-------|---------------------------------------|-----------------------------------------------|----------------------------------------|---------------------------------|
|       |                                       |                                               | (1 + 2)                                 |                                 |
|       | Heifers: 500+ 500 calvings             |                                               |                                        |                                 |
| SRB   | 22                                    | 0.419                                         | 0.297                                  | -0.162                          |
| SLB   | 11                                    | 0.593                                         | 0.250                                  | -0.214                          |
|       | Cows: 1,000+ 1,000 calvings           |                                               |                                        |                                 |
| SRB   | 51                                    | 1.829                                         | 0.550                                  | 0.491**                         |
| SLB   | 20                                    | 2.621                                         | 0.548                                  | -0.311                          |

We are not inclined to consider this as an evidence that some sires are predisposed to produce more twins than others. The deviation from the total sire average may be due to some unknown causes.

Another analysis was made of the distribution of like-sexed and unlike-sexed twins on 13 SRB sires that had each produced at least 100 twin pairs, with a range of 101 to 275 per bull. Of the total number of 2,138 twin pairs, 1,119 were like-sexed and 1,019 unlike-sexed. The estimated number of MZ pairs would therefore be 100 or 8.94% of the like-sexed pairs. The observed numbers of like-sexed pairs from the individual bulls were fairly close to the expected numbers. The deviations from the average for the 13 bulls were not significant ($\chi^2 = 11.54$ and $P \approx 0.50$). The results did not indicate that the sire has any influence on the production of MZ twins. This is in agreement with results obtained from analyses of human data, reviewed by Bulmer (1970).

Possibilities of selection

Twinning in cattle has some disadvantages as discussed in recent reviews by Hendy and Bowman (1970) and by Holz, Haring and Smidt (1970). The number of premature births increases, and the perinatal mortality is about four times higher than for single-born calves. The length of calving interval after twinning increases due to frequent complications during and after parturition. Furthermore, about 90% of all female calves born co-twins with bulls are sterile because of intersexuality.

Therefore, some natural and possibly also some artificial selection operates against twinning. Table 19 bears this out. Culling rates are higher after twinning than in the general population and elimination of cows after repeated twinning is especially high. The increase in culling may result from reproductive disturbances and/or conscious selection by the breeders. Syrstad (1973) found that in Norway the culling rate was about 5% higher after twinning than after single births. Thus, it is arguable whether selection for higher twinning frequency in dairy breeds would be profitable. However, the disadvantages are not so great that selection against twinning would be likely to justify the efforts, as was pointed out by Erb et al. (1960).

The situation is different in the dual purpose beef-milk breeds and in some specialized beef breeds. In spite of the larger losses among twin calves, more calves are produced than from single births. Bar-Anan and Bowman (1974) have estimated that from 100 twin births some 160–170 calves can be raised compared to about 95 from 100 single births.

The Hereford and Aberdeen-Angus breeds are characterized by low twinning frequencies, and the cows give so little milk that in some cases it is hardly sufficient for one suckling calf. Mechling and Carter (1964) have reported on an attempt by a private breeder to raise the twinning frequency in an Aberdeen-Angus herd by selection. Only twin bulls were used as sires in the herd, and the females used for breeding were born as twins or were daughters of twinning cows. After some 15–20 years the average twinning frequency in the herd was 1.71% in 585 calvings.
Table 19. Culling rate of cows from the herds after the first and second twin birth, compared with the average culling rate in the population after the same four calvings

| Parity | Swedish Red and White cattle (SRB) | Swedish Friesians (SLB) |
|--------|-----------------------------------|------------------------|
|        | Population\(^1\) Culled after twin birth | Population\(^1\) Culled after twin birth |
|        | 1st twinning | 2nd twinning | 1st twinning | 2nd twinning |
| 1      | 28.1 % | 30.7 % | -- | 35.3 % | 53.6 % | -- |
| 2      | 34.4 % | 41.4 % | 61.5 % | 38.2 % | 56.7 % | 85.7 % |
| 3      | 38.6 % | 47.9 % | 52.1 % | 41.3 % | 59.2 % | 39.7 % |
| 4      | 41.1 % | 57.5 % | 49.0 % | 46.7 % | 65.3 % | 55.7 % |
| Average per parity | 33.7 % | 45.1 % | 53.1 % | 38.3 % | 58.5 % | 52.1 % |

\(^1\) The ordinal number of calving after which culling occurred

\(^2\) The culling rates may be somewhat exaggerated due to the method used in data extraction (cf. p. 21). This does not, however, alter the relations between the culling rates of twinning cows and the corresponding population average.

If any real progress had been made, it was certainly very slight. Selection pressure and/or accuracy were too weak.

In Australia, experiments have been carried out at two research stations on the possibility of raising the rate of multiple births of Merino sheep by selection, and Turner (1966, 1968) has reported good results. The selection was carried out in the same environment over a period of 10–12 years, in one line for low and in one line for high rate of multiple births when the ewes had reached three years of age. At the conclusion of the experiment the difference between adult ewes of the two lines was at one of the stations 35 lambs per 100 ewes mated. Selection on the number of lambs when the ewes were two years old had little effect.

A selection procedure with the purpose of increasing the twinning frequency in cattle should preferably start with a dual purpose beef-milk breed with a high initial twinning frequency and a milk yield which is high enough for nursing two calves at the same time, for example the various Fleckvieh strains. Among the specialized beef breeds we have studied, the Charolais shows the highest twinning frequency but Fleckvieh and Simmental are superior in milk yield.

Since the heritability values are very small, reasonable accuracy can only be achieved when selection is based upon information from many observations. This leads immediately to progeny testing of bulls on large numbers of daughters with mature calving records. Accepting 2% as the heritability of twinning in adult cows would imply a repeatability of more than 0.8 for bulls with 1,000 daughters. On the female side the gain in accuracy is limited even when using repeated records. However, selection pressure will be strong when twin-bearing cows are selected or selection is restricted to cows with repeated records of twinning.

Let us assume that in a project aimed at increasing twinning frequency 20% of the bulls with the highest twinning rate in their daughters are selected, e.g. among the 101 SRB bulls, the selection differential would be (3.64 – 2.21%) = 1.43%. Assuming 1,000 daughters per bull and \( h^2 = 0.02 \), the repeatability of the progeny test will be 83% so that future daughters of the same bulls should have increased the adult twinning frequency by 1.19% to 3.40%. Cows with adult records involving two or more twin births would have a liability which is 2.38 standard deviations above the mean. A heritability of 2% on the binomial scale implies a heritability of liability of 0.156 when the population incidence is 2.21%. Progeny from such cows should be 0.186 standard deviations above the mean liability, which should raise their twinning rate to 3.73%, a gain of 1.52%.
Therefore, in a selection program which involves mating of the 20% best progeny-tested sires to cows with two or more twin records, the twinning rate should improve by more than 2% per generation (2.71% in our example). The first aim of such a program would be the production of young bulls for future breeding. It is not our intention to draw any detailed breeding plans but simply to show that an intense selection for increased twinning rate can be expected to yield quite satisfactory response. It seems likely that by selection through many generations it would also be possible to produce cows that are better adapted to multiple births than those existing today.

Discussion

Several investigations indicate that multiple ovulation in the cow is more common than multiple birth. Kidd et al. (1952) and Lahsetwar (1963) reported 6.1% multiple ovulations from 900 parities with 3,549 ovulations. Conception rate after single ovulation was 57.5% but only 26.8% after multiple ovulation. Out of 12 diagnosed pregnancies after multiple ovulations three involved twins (1952). Cystic ovaries were diagnosed in 62 parities involving 478 ovulations. In cystic periods multiple ovulations were about three times higher than in normal heat periods (1963).

Settergren (unpubl.) examined genital organs from slaughterhouse material of US Holsteins and SRB. In the Holstein material two corpora lutea (c.l.) were found in 58 (6.4%) and three in one of 901 organs with no detectable pregnancy. Forty of the 58 double c.l. were on the same ovary and of the remaining 18 one on each side. Out of 113 pregnant uteri seven contained twins and in five of these cases one c.l. was on each ovary. The SRB material comprised 198 non-pregnant uteri where in three cases two c.l. were on the same ovary and in four cases one on each side. Four of 88 pregnant uteri carried twins. In one case the two c.l. were on one ovary and both fetuses in the corresponding horn, in two cases the two c.l. and the two fetuses were distributed bilaterally and in the remaining case only one c.l. was present with like-sexed twins in the corresponding horn.

Settergren examined Graafian follicles by serial sections of about 50 ovaries and found only single ova in each follicle. His opinions was that intrauterine migration of fertilized eggs or blastocysts is rare.

Rowson, Lawson and Moor (1971) and Rowson (1973) found only two twin pregnancies out of 16 when two eggs were transferred into one uterine horn. Transfer of one egg into each horn resulted in 73% twin pregnancies. Low twinning rate upon egg transfer into one horn was attributed to lack of uterine migration and death of one embryo due to competition, usually at about 50 days post conception.

The Wisconsin investigations and a report by Erb et al. (1960) indicate a high frequency of multiple ovulations in service periods when ovarian cysts had appeared. Conception within 75 days of the appearance of the cyst caused 15.1% twin pregnancies, compared to 4.9% for later conception and to a 30 year's herd average twinning frequency of 4.1%. More than one fourth of the 266 twinning cows had short estrous cycles.

Henricson (1956) found in 149 SRB herds in Middle Sweden the frequency of cysts to increase from a low value in heifers to a maximum in 4–5 year old cows. The frequency had its seasonal peak November–February and its minimum May–September. This cycle is rather different from seasonal variations in twin conception (cf. Fig. 2) but it correlates with variation in non-return rate.

The reproductive processes of the cow represents a complex series of inter-related events, the sequence of which is hormonally regulated. In the majority of cases only one ovulation occurs at one heat period and smaller follicles degenerate. The regulation of ovulation is not perfect, however, and in some cases two or more follicles ovulate at the same time. The hormonal equilibrium necessary for single ovulation is apparently more labile in some cows than in others and this may lead to repeated multiple ovulations in certain animals. Their ovulatory mechanism is less well canalized, to use a genetic term. This may be considered quite normal but the distance may be short to pathological conditions where no ovulation occurs and ovarian cysts are formed. Erb and Morrison (1959) found a 3–5 fold increase in frequency of retained placentas after twin births compared to single births. Also, ovarian cysts and persistent c.l. became more

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frequent, obviously a result of hormonal imbalance. Thus twinning may sometimes be a cause for the immediate repetition of twinning.

MZ twinning is a biologically different phenomenon. Twins arise from one fertilized egg. BULMER (1970) concludes, from a survey of statistics, that "propensity to MZ twinning is the same in all women" but that "propensity to have DZ twins varies from woman to woman". The validity for cattle within a breed, of the first part of this statement may be an open question although it agrees with our own findings (cf. p. 229). BULMER further concludes that there are no genetic differences between human races for MZ twinning frequency. ENDERS and STERN (1948), however, found the increase in MZ twinning frequency with maternal age in US negroes and whites to be significantly different. BULMER'S statement certainly does not apply to cattle where highly significant breed differences have been found (cf. Tables 8 and 9 and Fig. 5) and breeds differ also in the age-related increase of MZ twinning rate (Fig. 5).

We conclude from our investigations that DZ twinning frequency is a polygenic character with a threshold. The rather complex physiological mechanisms which determine single or double ovulation, and the complexity of the further course of events such as migration of ova, success of implantation, competition etc. would support this contention and lend plausibility to the genetic model we have used. Whether a single locus in a given genetic situation can play a major role may be left as an open question.

Summary

Cow-testing records from 10 European dairy breeds and two specialized beef breeds were analysed. The main results may be summarized as follows.

1. The sex-ratio for abortion and perinatal mortality for single-born and twin-born calves is 60–70 % males. The mortality of twin-born calves is 3–4 times higher than for single-born ones (Tables 1 and 2).

2. Season of conception has a pronounced influence on the frequency of twinning. Primipara reach the highest frequency after conceptions in October, whereas cows (2 ≤ calvings) show two yearly maxima, viz. after May and autumn conceptions (Fig. 2).

3. Twinning frequency is low at the first calving but gradually increases up to the 4th–5th parities and flattens out later on (Fig. 4).

4. The frequency of monozygous twinning, expressed in percent of total calvings, varies between breeds and parities. In the Bavarian Fleckvieh and Braunvieh there is a marked increase up to the fourth parity with a decrease later on. For the Swedish breeds the frequency is approximately constant for the first three parities, and the later increase is relatively small (Fig. 5). On the whole, the frequency of MZ twinning is less age-dependent than DZ twinning.

5. The repetition of twinning after the first twin birth was found to be 6.07 % for Swedish Red and White cattle (SRB) and 9.72 % for the Swedish Friesians (SLB). After the second twin birth the corresponding figures were 10.75 and 15.30 % respectively (Table 12). The repeatability of twinning was estimated for the SRB population only. It rose from 0.0009 for completed first and second calvings to 0.0154 with seven completed calvings (Table 13).

6. The variations in twinning rate are probably dependent on many genes with complicated interactions between the genotype and a multitude of environmental influences, especially nutritional and seasonal variations. Phenotypically, twinning is an "all-or-none" trait, but it is likely that the underlying liability to bear twins has an approximately normal distribution.

7. Highly significant differences were found between AI bulls with regard to the twinning frequency of their daughters (Table 14). The correlation between progeny subgroups from the same sires, each subgroup comprising 1,000 cow-daughters, was approximately 0.8 (Table 15). When measured on the observed phenotypical scale, the heritability of twinning frequency was estimated to be about 2 %, based on one twin birth per cow. When measured on the continuous x-scale the corresponding estimate was about 10 % for one and 20 % for two twin births per cow (Table 17).

8. Paternal influences upon total twinning frequency are probably unimportant, and no

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Evidence was found for the suggestion that sires influence the rate of MZ twinning.

(9) Intensive selection for increased twinning rate could be expected to yield a gain of at least 2 percentage units per generation.

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