Twinning rate in Norwegian cattle: Frequency, (co)variance components, and genetic trends

A. Karlsen, J. Ruane, G. Klemetsdal, and B. Heringstad

Department of Animal Science, Agricultural University of Norway, N-1432 Ås, Norway

ABSTRACT: The overall twinning rate was shown to increase from .6% in the first parity to 4.0% in the sixth parity, and a positive phenotypic trend for twinning rate was observed during the time period considered (1978 to 1995). The distribution of bulls according to the average percentage of multiple births of daughters in first and second parity showed that some bulls had an extremely low twinning frequency and others exceeded the population mean by approximately six times. (Co)variance components were estimated for twinning in first and second parities using a linear sire model. The analysis included either first- and second-crop daughters (1.4 and .9 million records for first- and second-parity cows, respectively) or first-crop daughters only (.6 and .4 million records for first- and second-parity cows, respectively) from 2,043 sires. Heritability estimates were .7 to .8% in the first parity and 2.8% in the second parity. The genetic correlation between twinning in the first and second parities was approximately 1. Part of the phenotypic trend observed can be explained by a genetic trend for twinning rate.

Key Words: Twinning, Norwegian Cattle, (Co)variance Components, Genetic Trend

©2000 American Society of Animal Science. All rights reserved.

Introduction

In cattle, increasing the twinning rate is one alternative for increasing beef production. The genetic potential for improving twinning is large (e.g., Gregory et al., 1997), and this highlights the importance of increased knowledge on the inheritance of twinning.

Syrstad (1984) estimated a heritability for twinning of .006 in the first parity, increasing to approximately .04 in parities 3 to 5 using Norwegian data collected from 1978 to 1981. One objective of this study was to reestimate variance components for twinning in first and second parities using all data from 1978 onward. Heritability estimates were .7 to .8% in the first parity and 2.8% in the second parity. The genetic correlation between twinning in the first and second parities was approximately 1. Part of the phenotypic trend observed can be explained by a genetic trend for twinning rate.

Materials and Methods

Data

Phenotypic data from the Norwegian dairy recording service (NDRS) have been used to construct a database on an individual cow basis (Ruane et al., 1997). This database contains information on calving, embryo transfer, abortion, multiple births, and many other traits. Data are available from 1978 onward. In total, the database contains almost 6.5 million calving records. In addition to the data file, a pedigree file is available that contains more than 3 million cows, of which the first were born in 1958, and approximately 4,000 bulls (Ruane et al., 1997).

A first data set (Data Set A) with information on multiple births was constructed from the phenotypic records. In this file, all cows with first calving between September 1, 1978, and December 31, 1995, were included.
cluded with calving information up to the seventh parity. To be included in the data file, age at first calving had to be between 450 and 1,200 d. All intervals between subsequent calvings had to be from 250 to 730 d. Calvings resulting from embryo transfer and pregnancies ending in abortion were excluded. After editing, information on 1,824,745 first-parity cows was available. Of the first-parity cows, 66% were recorded with a second parity, and 42, 24, 12, 6, and 3% calved a third, fourth, fifth, sixth, and seventh time, respectively. The phenotypic records contained information on both twins and triplets, which, owing to the extremely low frequency of triplets (.002% in first calving), were grouped together in the subsequent analysis. Data Set A was used for describing twinning rate by parity, year, and month of calving.

A second data set (Data Set B) contained information only on first- and second-parity cows and was constructed using the same restrictions as Data Set A. In addition, Data Set B was limited to include only daughters of bulls that had been progeny-tested with more than 30 daughters between 1978 and 1995, restricting the data to 1,376,069 first-parity and 923,506 second-parity records. Bulls had, on average, 674 first-parity and 452 second-parity daughters. Data Set B was initially used for describing the frequency distribution of the average percentage of multiple births among daughters in sire progeny groups. Variance components were estimated in a univariate analysis for both first- and second-parity cows using Data Set B. In these analyses the number of herd × year subclasses was 345,713 and 301,700, respectively, and the average twinning frequencies were .6 and 2.3% for first- and second-parity cows. Genetic trend for twinning rate was estimated using Data Set B.

To avoid potential selection bias, a third data set (Data Set C) was constructed including first-crop daughters only (i.e., only including daughters of young bulls). It contained 573,648 first- and 392,511 second-parity cows, and the number of herd × year subclasses was 265,835 and 219,436, respectively. The average twinning frequency was .6 and 2.1%, respectively. The genetic correlation between twinning in first and second parity was also estimated in a bivariate analysis using Data Set C.

The pedigree file was constructed from sires of cows in the data, and their pedigrees were traced back as far as possible. The pedigree file contained information on 2,159 AI bulls, of which 2,043 had daughters with calving records. The number of bulls with an unknown sire (i.e., base animals) was 50.

Model

First-parity records were analyzed using a linear sire model: \( Y_{ijklm} = A_i + M_j + HY_k + S_l + E_{ijklm} \), where \( Y_{ijklm} \) = observation of number of calves born \( (Y = 1, 2) \); \( A_i \) = fixed effect of the \( i^{th} \) level of age at calving, in seven classes with intervals of 2 mo, the first class is \(< 22 \) mo and the last class is \( \geq 32 \) mo; \( M_j \) = fixed effect of the \( j^{th} \) level of month of calving in 12 classes; \( HY_k \) = random effect of the \( k^{th} \) herd × year class; \( S_l \) = random effect of the \( l^{th} \) sire; and \( E_{ijklm} \) = random error term. Second-parity records were analyzed assuming the following linear sire model: \( Y_{ijklmn} = A_i + M_j + HY_k + D_l + S_m + E_{ijklmn} \), where \( A_i \) = fixed effect of \( i^{th} \) age at calving, in five classes with intervals of 2 mo, the first class is \(< 35 \) mo and the last class is \( \geq 41 \) mo; and \( D_l \) = fixed effect of the \( l^{th} \) time span from first to second calving, in six classes of monthly intervals with the first class \(< 11 \) mo and the last class \( \geq 15 \) mo. The effects of M, HY, S, and E are as defined previously.

A relationship matrix containing the relationship between sires was included in both models. (Co)variance components were estimated using a REML procedure in the program VCE4 (Neumaier and Groeneveld, 1998). Breeding values for bulls were estimated using the program PEST (Groeneveld, 1990).

Results

Descriptive Analyses. Figure 1 shows the rate of twinning in different parities from Data Set A. Frequency of twinning increased from .6% in parity 1 to 4.0% in parity 6 and then showed a slight decrease in parity 7. A separate analysis of the 3% of the cows that had completed all seven calvings showed slightly lower twinning rates for the first six parities and a steady increase over all seven parities. Phenotypic rate of twinning increased slightly from 1978 to 1995, both for first (from .3 to .9%) and second (from 1.4 to 2.6%) calving (Figure 2). For first-parity cows, a maximum frequency of twinning was observed in July, and second-parity cows showed peaks in both March and June to July (Figure 3).

Figure 4 presents the frequency distribution of bulls according to average percentage of twin births among
Genetic parameters for twinning rate

Figure 2. Twinning rate by year of calving for first- and second-parity cows.

Figure 3. Twinning rate by month of calving for first- and second-parity cows.

Figure 4. Frequency distribution of bulls according to percentage of multiple births among daughters in the first parity using Data Set B including both first- and second-crop daughters. Although the majority of the bulls were distributed around the mean (.6%), there were bulls with no twin births in progeny groups of several hundred daughters. Daughters of the most extreme bull had a twinning rate of 4.1%. Figure 5 shows the corresponding frequency distribution for daughters in second parity. The large variation of twinning rates was again found, but at a higher mean (2.3%). Some bulls had several hundred daughters with no multiple births, and the top bull had daughters with a twinning rate of 12.9%.

(Co)variance Components. Estimates of variance components based on the first- and second-crop daughters (Data Set B) are shown in Table 1. Estimates based on first-crop daughters only (Data Set C) are presented in Table 2. The estimated variance components using the two data sets were approximately similar and resulted in heritabilities of .008 and .007 for first parity and .028 for second parity. The estimated genetic correlation between twinning rate in first and second parities (Data Set C) was .9883 (Table 3).

<table>
<thead>
<tr>
<th>Item</th>
<th>Parity 1</th>
<th>Parity 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sire variance</td>
<td>1.213e−5 a</td>
<td>1.545e−4 a</td>
</tr>
<tr>
<td>Herd × year variance</td>
<td>1.563e−5 b</td>
<td>7.710e−5 b</td>
</tr>
<tr>
<td>Error variance</td>
<td>6.164e−3 c</td>
<td>2.179e−2 c</td>
</tr>
<tr>
<td>Phenotypic variance</td>
<td>6.191e−3</td>
<td>2.205e−2</td>
</tr>
<tr>
<td>Heritability</td>
<td>.0078</td>
<td>.0281</td>
</tr>
</tbody>
</table>

Standard error on variance ratio (sire/phenotypic): approximately 0.

Standard error on variance ratio (herd × year/phenotypic) for first and second calving, respectively: approximately 0. and .001.

Standard error on variance ratio (error/phenotypic) for first and second calving, respectively: approximately 0. and .001.
breeding value of .003 and .016 was estimated for to the curves for genetic trend, an increase in estimated increased, average over time. Fitting a linear regression in Figure 6. The breeding values of bulls by year of birth are presented ning rate.

parity, a longer interval had a negative effect on twin-

Table 2. Estimates of variance components and heritability of twinning rate in first and second parity based on Data Set C with first-crop daughters only

<table>
<thead>
<tr>
<th>Item</th>
<th>Parity 1</th>
<th>Parity 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sire variance</td>
<td>1.082e-5</td>
<td>1.457e-4</td>
</tr>
<tr>
<td>Herd × year variance</td>
<td>1.618e-5</td>
<td>5.112e-5</td>
</tr>
<tr>
<td>Error variance</td>
<td>5.896e-3</td>
<td>2.063e-2</td>
</tr>
<tr>
<td>Phenotypic variance</td>
<td>5.923e-3</td>
<td>2.083e-2</td>
</tr>
<tr>
<td>Heritability</td>
<td>.0073</td>
<td>.0280</td>
</tr>
</tbody>
</table>

*Standard error on variance ratio (sire/phenotypic): approximately 0.

*Standard error on variance ratio (herd × year/phenotypic): approximately 0.

*Standard error on variance ratio (error/phenotypic): approximately 0.

**Genetic Trends and Fixed Effects.** Mean estimated breeding values of bulls by year of birth are presented in Figure 6. The figure shows a very flat, but slightly increased, average over time. Fitting a linear regression to the curves for genetic trend, an increase in estimated breeding value of .003 and .016 was estimated for first and second calving, respectively. Solutions for month of calving reflected the phenotypic tendencies in Figure 3, showing an advantage of calving in July for first parity and in March and July for second parity. Solutions for age at calving for first and second parity demonstrated that cows older at calving are more likely to have twins. For the interval between first and second parity, a longer interval had a negative effect on twinning rate.

**Discussion**

The phenotypic increase in twinning over parity has been reported in earlier studies (for review, see Rutledge, 1975). Reasons for this may be that young cows are not able to maintain a twin pregnancy and, thus, they abort one or both fetuses, or that cows that are

Table 3. Estimates of (co)variance components and heritability of twinning rate in first and second parity from a bivariate analysis of Data Set C containing only first-crop daughters

<table>
<thead>
<tr>
<th>Item</th>
<th>Parity 1</th>
<th>Parity 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sire variance</td>
<td>1.119e-5</td>
<td>1.448e-4</td>
</tr>
<tr>
<td>Herd × year variance</td>
<td>1.565e-5</td>
<td>4.800e-5</td>
</tr>
<tr>
<td>Error variance</td>
<td>5.897e-3</td>
<td>2.064e-2</td>
</tr>
<tr>
<td>Phenotypic variance</td>
<td>5.924e-3</td>
<td>2.083e-2</td>
</tr>
<tr>
<td>Heritability</td>
<td>.0076</td>
<td>.0276</td>
</tr>
<tr>
<td>Genetic correlation</td>
<td>.9883</td>
<td></td>
</tr>
</tbody>
</table>

*Standard error on variance ratio (sire/phenotypic): approximately 0.

*Standard error on variance ratio (herd × year/phenotypic) for first and second calving, respectively: approximately .001 and 0.

*Standard error on variance ratio (error/phenotypic) for first and second calving, respectively: approximately .001 and 0.

older are more likely to ovulate several oocytes (Cady and Van Vleck, 1978). Results by Morris et al. (1992) demonstrate that older cows have a greater ovulation rate. As Figure 1 shows, cows that had completed at least seven parities had a lower frequency of twinning in the first six parities than that observed in the population as a whole. This suggests that farmers may practice slight selection against cows giving birth to twins. This selection could be due to increased frequencies of dystocia or retained placenta, reduced conception rate, and increased number of days open, all of which are reported to be effects of increased twinning (e.g., Hendy and Bowman, 1970).

The observed phenotypic trend in twinning over time could partly be explained by a corresponding genetic trend (compare Figures 2 and 6). A possible explanation for the increasing genetic trend is indirect selection on milk production, because twinning rate has been found to have a positive genetic correlation with milk yield (e.g., Maijala and Osva, 1990). Improved nutrition might also be an important factor influencing twinning rate. Hendy and Bowman (1970) concluded in their review that an increase in the quality and quantity of feed will improve fertility and, presumably the manifestation of twinning in a cow genetically predisposed to twinning.

Differences in twinning frequency between month of calving (Figure 3) have also been reported previously. Johansson (1932) observed a maximum in June and July using Finnish and Swedish data and suggested that this was due to a decrease in temperature in autumn, resulting in increased ovulation rate. Cady and Van Vleck (1978) found a small, although not significant, majority of twinning in May, June, and July, which they suggested to be due to better feeding in autumn. Johansson et al. (1974) observed seasonal variation that they explained to be due to changes in duration of daylight. The literature also shows that photoperiod physiologically regulates the onset of puberty in
cattle (Schillo et al., 1992), and photoperiod could have a similar effect on twinning rate.

In Norway, the observed maximum frequency of twinning in June and July could be seen in connection with reduced temperature, reduced amount of daylight, and change from pasture to indoor feeding at conception in autumn. The observed peak in March for second-calving cows is more likely due to the turnout on pasture in early summer.

The finding that some bulls had an extremely high or low percentage of multiple births among daughters compared with the others was in accordance with earlier studies in this population (Syrstad, 1984).

This is the largest data set that has been used to estimate (co)variance components of twinning. Heritabilities on the linear scale for twinning in first and second parities were very similar to those found previously by Syrstad (1984). He found estimates of .6 and 2.1% for twinning in first and second parities, respectively. Similarly, in second- and third-parity Israeli Holstein cows, with a frequency of twinning of 4.8 and 6.9%, respectively, estimated heritability was 2.2% (Ron et al., 1990). In a population selected for twinning, a heritability of 3% was estimated by Van Vleck and Gregory (1996).

Heritability estimates of twinning rate, when analyzed with a linear model, depend on the frequency of the trait (Gianola, 1982). It is, therefore, not straightforward to compare estimates from different populations. However, all previous estimates indicate heritability of twinning rate on the observed scale is low. On the underlying scale, however, estimates have been found to be higher, increasing for example from 2.2 to 10.1% in the Israeli population (Ron et al., 1990). When transforming the estimates based on Data Set B to the underlying scale by use of the formulae of Dempster and Lerner (1950), heritabilities of close to 20% (increase from .78 to 16.10% in first and 2.81 to 21.65% in second parity) were obtained for both first and second parities.

Heritabilities based on first-crop daughters only were very similar to those based on all daughters (compare Tables 1 and 2). This indicates that selection bias due to correlated responses from traits included in the breeding goal is not a major problem for variance component estimation in a univariate analysis with our data. Twinning has never been included directly in the Norwegian breeding goal, and, because of its low heritability and its expected low genetic correlation with traits in the breeding goal, the result is not surprising. Similar conclusions have been drawn from an analysis of mastitis resistance in the same population (Heringstad et al., 1999). Including all daughters in an analysis resulted in a greater number of records in each subclass and slightly increased heritability estimates. This may result from greater orthogonality between sire and contemporary group effects compared with using first-crop daughters only.

The genetic correlation of approximately 1 between twinning in first and second parity is higher than the corresponding genetic correlation of .6 estimated by Syrstad (1984). The high genetic correlation indicates that twinning rate in first and second parities should be considered the same trait. Theoretically, the genetic correlation between two binary traits estimated by use of linear methodology is expected to equal estimates on the underlying scale (Gianola, 1982). Mäntysaari et al. (1991) found a slight downward bias for the genetic correlation at a low incidence level using linear methodology. Even though the frequencies in this study were extremely low, the genetic correlation estimated in this study did not indicate such a downward bias.

Implications

Twinning rate in cattle is heritable. Heritability, on the linear scale, is approximately four times greater for twinning in the second than in the first parity. An estimated genetic correlation of close to 1 indicates that twinning in first and second parity should be considered the same trait, despite the low frequency of twinning in first compared to second parity. In Norway, the genetic trend of twinning rate in both first and second calving increased during an 18-yr period, showing that selection for the Norwegian breeding goal, with a large weight on milk production, will increase twinning rate.

Literature Cited


