

JOURNAL OF ANIMAL SCIENCE

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J Anim Sci 1996. 74:522-528.

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Genetic Trend and Environmental Effects in a Population of Cattle Selected for Twinning

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ABSTRACT: A selection experiment was established in 1981 to increase twinning rate in cattle. Results reported are through 1993 calf crops. Estimates of genetic parameters for a two-trait twinning and ovulation rate model with genetic groups were as follows: heritabilities of .03 for twinning and .07 for ovulation rates with a genetic correlation of nearly 1.00 and fractional permanent environmental variances of .06 for twinning and .05 for ovulation rate. Corresponding estimates when group effects were ignored were as follows: heritabilities of .08 and .08 and fractional permanent environmental variances of

.02 and .04 for twinning and ovulation rates, respectively. Twinning rate (percentage) in the project at the U.S. Meat Animal Research Center has increased in all cows born in the project by year of calving from 3.4% in 1982 to 28.5% in 1993, a phenotypic increase of 25.1%. The estimated genetic change in twinning of cows by year of calving using the groups model has been 15.2%. The increase in average genetic value by year of birth has been 18.2% in twinning and 15.0% in ovulation rate from 1980 through 1991. Solutions for seven selected groups of foundation animals ranged from -6.0 to 33.1% and influenced genetic trend.

Key Words: Reproduction, Breeding Value, Age Differences, Seasonal Variation

J. Anim. Sci. 1996. 74:522-528

Introduction

A selection project was started in 1981 at the US Meat Animal Research Center (MARC) to increase economic efficiency of beef production by increasing twinning frequency. Earlier papers from the project have described the foundation animals, effects of twinning on other traits, potential of ovulation rate as a selection guide, and preliminary estimates of heritabilities of, and genetic correlation between, twinning and ovulation rates and the development of a multiple-trait animal model for predicting breeding values as a tool for selection (Echternkamp et al., 1990; Gregory et al., 1990a,b; Van Vleck et al., 1991a,b). The objectives of this study were to re-estimate genetic parameters with a much larger set of records using the model implemented for predicting breeding values, to estimate genetic improvement due to selection, and to re-examine effects of year-season of calving and age at calving.

Materials and Methods

Breeds represented in the experimental population included Holstein, Swedish Friesian, Simmental, Pinzgauer, Charolais, Swedish Red and White, Norwegian Red, Hereford, and Angus with small contributions from several other breeds. Mean breed composition of calves born in 1992 and 1993 is shown in Table 1. The Hereford and Angus breeds were introduced as residual from grade-up programs to breeds that were introduced into the project.

About 750 cows calved each year in the project. Calving was both spring and fall. Mating seasons were 70 d. About one-fourth of females (heifers and cows) with the highest predicted breeding value for twinning (PBV) were mated by artificial insemination (AI) to progeny-proven sires. These matings resulted in high PBV young sires that were candidates for progeny testing. The remaining heifers were mated by natural service to young high PBV but unproven sires for the full mating season. The remaining cows were mated by AI to young high PBV, unproven sires for 40 to 42 d and cleaned up by natural service mating to young high PBV, unproven sires for 28 to 30 d. Breeding assignments to young high PBV, unproven sires were made with the intent of obtaining 8 to 10 daughter progeny and 8 to 10 son progeny.

Received April 17, 1995.

Accepted October 25, 1995.

Table 1. Mean breed composition of calves born in 1992 and 1993

Breed	Percentage contribution
Holstein	20.0
Swedish Friesian	19.0
Simmental	16.5
Pinzgauer	13.5
Charolais	6.5
Swedish Red and White	4.0
Norwegian Red	6.0
Hereford and Angus	8.5
Other	6.0

Calves were weaned at an average of 140 to 150 d, late August for spring-born calves and late January for fall-born calves. Calves were creep-fed and both sexes were fed a growing diet from weaning to an average age of 200 d.

At an average age of 200 d candidate males (about 50 per year with highest PBV) were identified and fed a diet of 2.69 Mcal ME/kg of dry matter and 12.88% CP for 140 d, at which time final decisions were made on bulls (about 30 per year) to be retained for progeny testing.

Heifers were developed on a standard breeding heifer development program. Heifers were mated first at an average age of about 1.6 yr. Fall-born heifers were mated in the spring and spring-born heifers were mated in the fall to produce their first calves at an average age of 2.5 yr.

Twinning rate is number of calves for a cow that calves. The 10 triplets in the data set were recorded as three calves for those 10 calvings. Number of corpora lutea are for those animals with at least one.

Parameters initially used in the multiple-trait mixed model for prediction of breeding values for twinning and ovulation rate were from a mixture of analyses of relatively limited data. These estimates of parameters were then applied to a model that contained groups to account for selection of seven groups of foundation animals. The groups model was used to combine twinning and ovulation records for prediction of breeding values in 1990. Computing techniques have advanced since then so that the full groups model could be used in this study to re-estimate the parameters. The two-trait model included year-season (fall or spring) of calving by age of cow (2, 3, 4, ≥ 5 yr) effects ($12 \times 2 \times 4 = 96$ subclasses) for twinning rate and year-season of birth effects ($8 \times 2 = 16$ subclasses with the first season in the fall of 1984), five classes of age in months at measurement (≤ 11 to > 18 mo) and calendar month effects (12) for ovulation rate. Seven selection group effects were included as phantom parents of foundation animals (Quaas and Pollak, 1981; Westell et al., 1988). Random effects were animal genetic and animal permanent environmental that also account for genetic and environmental correlations between twin-

ning and ovulation rate on the same cow. The remaining temporary environmental effects were assumed to be uncorrelated. A total of 3,503 animals including foundation cows were included in calculation of the inverse of the numerator relationship matrix; 2,087 animals had 6,411 parturitions for measurement of twinning; and 2,194 heifers had number of ovulations measured in 18,687 estrous cycles. The order of the mixed-model equations was 13,365 when groups were included.

The MTDFREML program (Boldman et al., 1993) that uses a derivative-free algorithm was used to obtain (co)variance components by REML for models with and without group effects. The program was restarted several times to ensure global maximization of the likelihood. At convergence, solutions for predicted breeding values were obtained for twinning rate and ovulation rate and used to calculate genetic averages by year of calving and by year of birth. Solutions for fixed effects were also obtained for examination.

Results and Discussion

Variances and Covariances

Estimates of variance matrices, variances as proportions of total variance (h^2 , genetic; c^2 , permanent environmental; e^2 , temporary environmental) and correlations are given in Table 2. Temporary environmental variances were similar for the models with and without group effects. A likelihood ratio test showed a large difference between the two models ($-24775.94 - (-24894.99) = 119.05$ with 7 df). The genetic variances were substantially less, as might be expected, for the model including group effects, particularly the genetic variance for twinning (h_t^2 of .03 vs .08 and h_o^2 of .07 vs .08). The genetic correlation, however, was larger with the groups model (nearly 1.00 vs .76). With the groups model, the fraction of variance due to permanent environmental effects increased with the decrease in genetic variance (c_t^2 of .06 vs .02 and c_o^2 of .05 vs .04 with $r_c = .53$ vs .84). The earlier estimates used in genetic evaluations since 1990 (Van Vleck et al., 1991b) were $h_t^2 = .07$, $h_o^2 = .10$, $r_g = .89$ and $c_t^2 = .001$, $c_o^2 = .01$, $r_c = .19$. The main differences between the results of the new analysis with the groups model compared with what has been used for genetic evaluation are the reductions in genetic variance and increases in permanent environmental variance. The estimate of heritability for twinning rate with groups ignored is somewhat larger than most other estimates from populations with lower frequencies of twinning (e.g., Morris, 1984; Ron et al., 1990), which are more similar to that with group effects in the model. The heritability and repeatability estimates for ovulation

Table 2. Estimates of components of (co)variance and parameters for models with and without genetic groups: numbers of births per parity (t) and ovulations per estrous cycle (o) both multiplied by 100

Component	Groups		Parameter	Groups	
	Yes	No		Yes	No
Genetic					
$\sigma_{g_t}^2$	43.2	112.2	h_t^2	.03	.08
$\sigma_{g_t g_o}$	60.8	80.6	r_g	1.00	.76
$\sigma_{g_o}^2$	85.7	100.4	h_o^2	.07	.08
Permanent environment					
$\sigma_{c_t}^2$	88.9	34.8	c_t^2	.06	.02
$\sigma_{c_t c_o}$	41.7	37.2	r_c	.53	.84
$\sigma_{c_o}^2$	68.9	56.4	c_o^2	.05	.04
Temporary environment					
$\sigma_{e_t}^2$	1,316.1	1,321.6	e_t^2	.91	.90
$\sigma_{e_o}^2$	1,108.9	1,123.4	e_o^2	.88	.88

rate with groups ignored are slightly larger than those reported by Morris et al. (1992).

Genetic Trend

Trends as described by averages for year of calving and year of birth of cows born in the project are presented in Table 3. The unadjusted twinning rate of 3.4% for cows calving in 1982 or before increased to 28.5% for 1993 parturitions, an increase of 25.1%. The yearly estimates of genetic means for twinning increased by 15.2%, or approximately 60% of the phenotypic change. Genetic mean ovulation rate increased by 13.1%. Another measure of genetic trend is that shown by changes in genetic averages by year of birth (Table 4). The change in average predicted genetic value for twinning rate was 18.2% in 11 yr and 15.0% for ovulation rate. When the model ignoring groups was used, the estimated genetic trend was less for both twinning and ovulation rates despite the larger heritabilities. The solutions for genetic groups shown in the footnote of Table 3 were involved in all predicted breeding values with the groups model. Part of the difference between phenotypic means by year adjusted for year-season-age effects and the estimated genetic means with the groups model is due to an increase in average permanent environmental effects because selection leads to a temporary increase in average permanent environmental effects as well as an increase in average genetic effects. The estimated genetic means for cows by both year of calving and year born were, as expected, approximately the averages of predicted genetic values of their sires and dams (Tables 3 and 4). Comparison of the sire and dam averages show that most of the progress is coming from selection of sires.

The largest difference in solutions for genetic group effects was much larger for twinning rate than for ovulation rate, 39.1 vs 24.1%, with the same groups involved for both traits. Ranks of solutions for group effects were also different. For example, for twinning rate, the contrast of Group 1 minus Group 7 was -6.6% and for ovulation rate the contrast was 4.0%. The young age of heifers for measurement of ovulation rate may account for the reduction in group differences compared with twinning rate measured one or more years later. The standard errors of the group differences are relatively large: 7.6 and 8.5% for the Group 1 minus Group 7 contrast for twinning and ovulation rates, respectively. The standard errors of paired contrasts ranged from 2.8 to 7.7% for twinning rate and from 3.3 to 10.0% for ovulation rate.

Choice of model and variances and covariances affected estimates of change in average genetic value for twinning and ovulation rate. Table 5 for year of calving and Table 6 for year of birth show that the group model with previous estimates for genetic variances corresponding to larger heritabilities seems to overestimate genetic improvement relative to the groups model with the new estimates of genetic variances. Somewhat surprisingly, the model without group effects but with much larger estimates for genetic variances than for the groups model resulted in the smallest estimates of total genetic improvement in twinning and ovulation rate. This result indicates the importance of selection of foundation animals and subsequent incorporation of genes of the best groups of foundation animals into the twinning population.

Estimates of Fixed Effects

The effects of years, seasons, and ages at calving on twinning rate are difficult to interpret. Table 7 lists

Table 3. For cows born in the twinning project, mean phenotypic twinning rate (calves per cow calving, %) and mean predicted genetic values for twinning and ovulation rates (%) and those of their sires and dams by year of calving estimated from a genetic model including genetic groups^a and parameters estimated jointly

Year calving	No. of cows	Phenotypic mean	Genetic mean for twinning rate			Genetic mean for ovulation rate		
			Cows	Sires	Dams	Cows	Sires	Dams
≤1982	88	103.4	0.0	-.1	.1	.0	.5	-.4
1983	61	109.8	-1.0	.3	-2.1	-.8	.8	-2.2
1984	109	105.5	-.4	1.4	-1.8	-.5	1.4	-1.9
1985	215	106.5	1.5	2.7	.4	.8	2.1	-.2
1986	292	108.6	2.7	4.0	1.7	1.8	3.1	.7
1987	446	110.0	4.0	6.1	1.9	2.8	4.6	1.0
1988	435	111.7	5.8	8.7	2.8	4.3	7.0	1.5
1989	555	114.8	6.7	10.1	3.1	5.2	8.0	2.0
1990	654	119.3	8.2	11.4	4.3	6.5	9.0	3.1
1991	763	123.5	9.8	13.2	5.4	8.0	10.2	4.5
1992	793	124.3	11.9	16.0	6.9	10.0	12.7	5.9
1993	733	128.5	15.2	19.8	9.0	13.1	16.1	7.9

^aSolutions for genetic groups 1 to 7 are as follows. For twinning rate, 26.5, 2.3, 10.8, 6.5, -6.0, 5.3, and 33.1; for ovulation rate, 16.7, 0.0, 5.1, 1.7, -7.4, -1.9, and 12.7.

the solutions for the 96 combinations in the model. The solutions were adjusted for predicted genetic values for twinning of animals included in those subclasses. The standard errors for those solutions are extremely large due to small numbers of observations per subclass. Nevertheless, the trend was that later years had larger solutions than earlier years, which may indicate an improvement in management for twinning. At the same time, however, the average genetic value for twinning also increased, which may have allowed for greater expression of year effects.

The solutions for fixed effects in Table 7 were used to obtain contrasts between age of cow effects by season of calving for twinning rate. The contrasts and standard errors for pairs of effects of age by season combinations are shown in Table 8. Although the standard errors are relatively large, the trend was

that older cows had more twins. That trend was much more pronounced in the fall season than in the spring season of calving; the difference between cows 2.5 yr old and older (≥ 5 yr) cows was twice as large in the fall as in the spring, 10.4 vs 4.8%. The differences due to age for spring calving seemed particularly small and are similar to those observed in populations at MARC, where twinning is nearly non-existent in young cows. Averaged over all ages and years, the contrast in solutions for twinning rate between spring and fall seasons is $3.6 \pm 1.3\%$ in favor of the fall season of calving, in agreement with an earlier analysis (Gregory et al., 1990a).

Tables 9 and 10 summarize solutions for fixed effects on ovulation rate. Solutions for year-season of birth as a difference from fall of 1984 are shown in Table 9 along with the unadjusted phenotypic means.

Table 4. For cows born in the twinning project, mean predicted genetic values for twinning and ovulation rates (%) and those of their sires and dams by year of birth estimated from a genetic model including genetic groups and parameters estimated jointly

Year born	No. of cows	Mean for twinning rate			Mean for ovulation rate		
		Cows	Sires	Dams	Cows	Sires	Dams
≤1980	42	0.0	.8	-.9	0.0	1.1	-1.2
1981	26	-.7	1.1	-1.9	-.8	1.3	-2.0
1982	65	1.7	3.1	.8	1.1	2.5	.2
1983	120	3.7	4.8	2.7	2.4	3.6	1.4
1984	171	4.3	5.4	3.2	3.1	4.3	1.9
1985	223	7.0	11.0	2.6	5.3	8.8	1.5
1986	153	9.6	15.0	3.6	7.3	11.8	2.1
1987	190	11.2	15.0	6.3	9.5	12.0	5.3
1988	187	13.9	16.7	9.3	11.8	12.9	8.3
1989	210	15.1	19.8	9.6	12.8	15.6	8.7
1990	195	16.5	21.2	10.6	14.3	17.8	9.2
1991	115	18.2	23.8	12.3	15.0	19.3	10.2

Table 5. By year of calving, means of predicted genetic values for twinning and ovulation rates (%) for cows born in the twinning project with predictions from three models: group effect, new parameter estimates (G-NEW); no group effects, new parameter estimates (NG-NEW); group effects, previous parameter estimates (G-OLD)

Year calving	Mean twinning rate			Mean ovulation rate		
	G-NEW	NG-NEW	G-OLD	G-NEW	NG-NEW	G-OLD
≤1982	.0	.0	.0	.0	.0	.0
1983	-1.0	-.9	-.9	-.8	-.8	-.8
1984	-.4	-.5	.0	-.5	-1.0	-.3
1985	1.5	.7	2.0	.8	-.1	1.2
1986	2.7	1.5	3.4	1.8	.4	2.1
1987	4.0	2.6	4.8	2.8	1.2	3.3
1988	5.8	4.2	6.8	4.3	2.6	5.0
1989	6.7	5.3	8.1	5.2	3.4	6.1
1990	8.2	6.6	9.7	6.5	4.8	7.7
1991	9.8	8.4	11.6	8.0	6.2	9.5
1992	11.9	10.4	14.0	10.0	8.0	11.6
1993	15.2	13.9	17.9	13.1	11.1	15.3

Table 6. By year of birth, means of predicted genetic values for twinning and ovulation rates (%) for cows born in the twinning project with predictions from three models: group effect, new parameter estimates (G-NEW); no group effects, new parameter estimates (NG-NEW); group effects, previous parameter estimates (G-OLD)

Year born	Mean twinning rate			Mean ovulation rate		
	G-NEW	NG-NEW	G-OLD	G-NEW	NG-NEW	G-OLD
≤1980	.0	.0	.0	.0	.0	.0
1981	-.7	-1.5	-.9	-.8	-1.6	-1.2
1982	1.7	.9	2.4	1.1	-.2	1.5
1983	3.7	1.9	4.1	2.4	.7	2.6
1984	4.3	2.7	5.1	3.1	1.3	3.5
1985	7.0	4.6	7.8	5.3	3.2	5.9
1986	9.6	7.5	11.0	7.3	4.9	8.1
1987	11.2	9.7	13.2	9.5	7.3	10.9
1988	13.9	11.9	15.9	11.8	9.6	13.5
1989	15.1	12.8	17.2	12.8	10.3	14.4
1990	16.5	14.6	19.2	14.3	11.8	16.4
1991	18.2	15.8	20.7	15.0	12.2	16.7

Table 7. Solutions for year-season-age of calving subclass effects of twinning rate (%)

Year calving	Spring season age, yr				Fall season age, yr			
	2	3	4	≥5	2	3	4	≥5
≤1982	6.1	5.6	13.3	11.1	.0	5.3	.0	18.5
1983	.0	.0	5.9	8.5	.0	.0	33.3	19.0
1984	2.6	16.7	4.4	8.9	.0	13.3	.0	21.2
1985	4.4	0.0	6.9	7.3	6.4	18.8	.0	12.5
1986	4.4	6.2	8.3	15.1	7.4	13.0	17.2	20.0
1987	9.3	7.8	7.9	7.7	7.8	12.0	18.5	14.8
1988	9.5	11.1	.0	12.8	6.9	14.0	22.9	16.4
1989	14.3	12.1	11.1	10.4	20.3	15.4	19.5	15.5
1990	20.2	19.6	20.2	13.0	28.3	29.5	11.9	15.5
1991	24.5	26.4	28.6	20.1	17.8	35.2	33.3	18.8
1992	10.1	33.0	34.1	19.0	18.8	25.3	34.0	27.2
1993	32.3	26.1	23.8	28.9	27.0	30.0	32.2	26.4

Table 8. Contrasts (above diagonal) and standard errors (below diagonal) between solutions (diagonals) for age effects on twinning rates averaged over years by season (%) of calving

Age of cow, yr	Spring season ^a				Fall season ^a			
	2	3	4	≥5	2	3	4	≥5
2	.0	-3.4	-4.3	-4.8	-.2	-7.4	-9.4	-10.6
3	2.2	3.4	-.9	-1.4	2.7	7.2	-2.0	-3.2
4	2.4	2.5	4.3	-.5	2.7	3.0	9.3	-1.2
5	2.0	2.1	2.3	4.8	2.1	2.5	2.4	10.4

^aAverage difference in solutions for contrast between fall and spring season of calving effects is $3.6 \pm 1.3\%$.

In all except 1 yr, the fall effect of birth for cows measured for ovulation rate 12 to 18 mo later was greater than the spring effect. The phenotypic means were in the same direction but the differences in solutions for the mixed-model equations were larger (i.e., after adjustment for predicted genetic values and other effects in the model). The advantage of fall over spring season of birth was $3.5 \pm 1.0\%$.

No trend in the calendar month solutions shown in Table 10 was apparent. The standard errors of the contrasts are in most cases as large as the contrasts.

Solutions for ages in months at measurement of heifer ovulation are given in Table 10 and show that the expected patterns of ovulation rate increase from first measurements at approximately 10 to 11 mo up to 18 mo when most measures are completed. These results suggest that measurements should not be taken before 12, and possibly 14, mo of age. In fact, measurement before 12 mo of age has already been discontinued at MARC. The original grouping of ages at measurement was to reduce the number of classes. The increases with age in months suggest that perhaps more classes should be added. The counter arguments are that all heifers are measured through nearly the same ages and that the 21-d estrous cycles do not match monthly age classes very precisely. Perhaps a linear or quadratic regression on age in days would be an alternative.

Conclusions

The level of twinning achieved in this selection project exceeds that reported in another experiment (Frebling et al., 1982) and levels found in unselected populations (e.g., Rutledge, 1975) but is similar to that projected by Land and Hill (1975) with selection for increased ovulation rate based on more limited records of relatives. They also raised the question of whether one heritability is appropriate for different mean levels of ovulation rate. Even with relatively low heritability on the observed scale, the rate of increase in average breeding value has become greater over time. The change in ovulation rate was somewhat less than for twinning rate, probably because ovulation rate was measured at a young age on heifers. Indirect selection for twinning based on ovulation rate averaged over about eight estrous cycles seems to be as effective in practice as in theory because heritability of mean ovulation rate is much larger than for twinning and the genetic correlation with twinning seems to be near unity. Much of the success is likely due to fortuitous availability of semen from Swedish and Norwegian sires (group 1) and of two sires from another MARC project (group 7); the solutions for these two groups were much greater than those for the other five groups. Thus, the predicted breeding values

Table 9. Phenotypic means and solutions for year-season of birth effects for ovulation rate (%)

Year born	Spring season ^a		Fall season ^a	
	Mean	Solution	Mean	Solution
1984	—	—	109.0	0.0
1985	109.3	-3.2	111.3	0.0
1986	107.5	-8.2	111.9	-1.9
1987	115.8	-.3	115.3	1.4
1988	114.7	-1.5	117.2	1.5
1989	112.4	-4.5	118.3	-.7
1990	113.9	-4.7	117.4	-3.1
1991	113.8	-8.2	115.3	-6.3
1992	117.8	-7.1	—	—
Average	113.2	-4.7	114.5	-1.1

^aThe contrast for fall season minus spring season solutions averaged over years is 3.5 ± 1.0 .

Table 10. Solutions and phenotypic means for age in month classes at measurement and calendar months on ovulation rate (%)

Age in months	<u>≤11</u>	<u>12-13</u>	<u>14-15</u>	<u>16-17</u>	<u>≥18</u>	
Solution ^a	.0	2.8	5.5	7.0	7.5	
Mean	106.1	111.4	115.3	116.3	117.9	
Calendar month						
	<u>Jan</u>	<u>Feb</u>	<u>Mar</u>	<u>Apr</u>	<u>May</u>	<u>Jun</u>
Solution ^b	-1.5	.7	-.1	2.4	-.0	3.4
Mean	114.8	114.0	111.6	113.4	112.6	116.9
	<u>Jul</u>	<u>Aug</u>	<u>Sept</u>	<u>Oct</u>	<u>Nov</u>	<u>Dec</u>
Solution	.5	1.1	3.6	1.1	.6	.0
Mean	114.2	114.6	117.6	115.8	116.1	115.8

^aStandard errors of contrasts with ≤ 11 mo are approximately 1.7; standard errors of other contrasts range from .8 to 1.7.

^bStandard errors of contrasts range between 1.2 and 1.5.

of bulls in these groups are much higher than predicted breeding values of foundation animals from other groups. Twinning rate did not change in other contemporary populations at MARC that were not selected for twinning. Some of the difference between the phenotypic and genetic trends is likely due to more genetic variation in the underlying distribution than is shown on the observed binomial scale.

Implications

After only 12 yr of selection, twinning rate increased by a factor of approximately 10. Increased twinning rate would be likely to decrease the cost of producing feeder calves. The rate of twinning may be reaching the range needed for commercial use of twinning technology. The rapid increase in twinning, a trait with low heritability, also demonstrates the power of indirect selection using a trait such as ovulation rate with higher effective heritability and with a large genetic correlation with the trait of economic value.

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