

TWINNING IN CATTLE: I. FOUNDATION ANIMALS AND GENETIC AND ENVIRONMENTAL EFFECTS ON TWINNING RATE^{1,2,3,4}

K. E. Gregory⁵, S. E. Echternkamp⁵, G. E. Dickerson⁵, L. V. Cundiff⁵,
R. M. Koch⁶ and L. D. Van Vleck⁵

U.S. Department of Agriculture, Clay Center, NE 68933

ABSTRACT

Foundation cows were selected using prior records from one of two sources, private herds or other projects at the Research Center. Comparing twinning rates before and after selection, the repeatability was lower for those from the first (.08) than for those from the second (.16) source with a combined value of .12. Realized heritability of single-parity twinning rate estimated from selection of parents and response in daughters of foundation females was .06. Paternal half-sib estimate of heritability of twinning rate was $.02 \pm .07$. Estimates of repeatability computed from calving records of females born in the project indicate that permanent environmental effects on twinning rate in cattle are small. Mean calving rate of females born in the project was 1.11 in the data set that included all data and 1.09 in the data set that excluded females from highly selected parents. Twinning rate was greater ($P < .05$) in fall than in spring calving (1.13 vs 1.06). Data on twinning rate of a sample of the Swedish Friesian breed were summarized. Mean twinning rate of the Swedish Friesian breed is 2.57%. Age adjusted mean twinning rate of daughters of 32 half-sib sons of one particular Swedish Friesian sire averaged 5.4% and ranged from .9% to 13.6%. There was no indication of a bimodal distribution, which would be expected if a single gene with a major effect on twinning rate were segregating. The estimated genetic standard deviation ($\sigma_{\bar{x}_n}$) for mean twinning rates of the 32 sire progeny groups was 1.8%. Observed range among son progenies was .127 or $7.2 \sigma_{\bar{x}_n}$, in reasonable agreement with the hypothesis that twinning rate in this population is inherited as a quantitative trait. (Key Words: Cattle, Twinning, Heritability, Repeatability, Selection.)

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Introduction

More than 50% of the feed units used by the national beef herd are needed to meet maintenance requirements of reproducing females; comparable requirements in meat-type chickens are about 3% (Gregory and Dickerson, 1989). Small differences in reproduction rate of beef cattle can have a major effect on cost of production and on production resources for which beef cattle are competitive. Results from experimentation and computer simulation suggest that input costs per unit of beef output could be reduced by from 20 to 30% for the proportion of the herd producing twins relative to singles (Dickerson et al., 1988). Several analyses of field data and review papers on

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⁵Roman L. Hruska U.S. Meat Anim. Res. Center, ARS, USDA, Clay Center, NE 68933.

⁶Anim. Sci. Dept., Univ. of Nebraska, Roman L. Hruska U.S. Meat Anim. Res. Center, Clay Center, NE 68933.

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twinning rate in cattle have been published (Bowman and Hendy, 1970; Hendy and Bowman, 1970; Johansson et al., 1974; Rutledge, 1975; Maijala and Syvajarvi, 1977; Cady and Van Vleck, 1978; Morris, 1984; Syrstad, 1984). Generally, most studies involving analysis of field data have reported that heritability of single-parity twinning rate is low ($<.04$). Further, these studies document large differences among breeds in twinning rate. Twinning rates in the Hereford and Angus breeds average less than 1%, but in the Holstein breed they exceed 4% (Rutledge, 1975). The objectives of this study were to estimate heritability and repeatability of twinning rate, to estimate the effects of environmental factors such as age of cow and season of calving on twinning rate and to determine the mode of inheritance of twinning rate in a specific population of cattle. This study is part of a long-term effort designed to determine the effectiveness of selection for dizygotic twinning in cattle and to develop selection criteria and procedures to increase the rate of genetic improvement for twinning rate of cattle.

Materials and Methods

In the late 1970s and early 1980s, experiments were implemented in Australia (Bindon et al., 1982), New Zealand (Morris and Day, 1986), France (Frebling et al., 1982) and at the Roman L. Hruska U.S. Meat Animal Research Center (Gregory et al., 1988) to study twinning in cattle. A primary objective of these experiments was to determine the potential for genetic improvement in twinning rate of cattle. In each experiment, foundation female populations were established by screening large populations of cattle from breeds that twin at a relatively high frequency to identify females with a record of producing twins.

Our experimental population was established from industry and Research Center sources. A foundation of 96 cows with records of two or more twin calvings was acquired from industry from 1976 to 1977 (46) and from 1981 to 1982 (50) (Table 1). An effort also was made to identify some foundation sires whose daughters produced twins at a high frequency. Semen of three Swedish Friesian sires and two Norwegian Red sires whose daughters had produced twins at a rate of about 10% was introduced in 1983 and 1984, respectively. In 1988, semen was introduced

from three additional Swedish Friesian sires whose daughters produced twins at a frequency of about 10%.

A total of 211 females with a record of twinning in other projects at the Research Center were transferred into the Twinning Project (Table 1). Semen from a Pinzgauer sire and a Charolais sire whose daughters produced 8 to 10% twins in other projects at the Research Center also contributed to the foundation. Unproven bulls by a random sample of sires but out of 36 foundation cows with a record of producing twins (e.g., 1.68 calves per parturition) were used as foundation sires in the project. Multiple ovulation and embryo transfer from cows with a relatively high twinning frequency bred to sires with a relatively high estimated breeding value for twinning were used to augment the first generation.

Twelve breeds are represented in the experimental population: Holstein, Simmental, Charolais, Brown Swiss, Braunvieh, Pinzgauer, Gelbvieh, Swedish Friesian, Norwegian Red, Shorthorn, Hereford and Angus. An effort was made to sample breeds with an average twinning rate of at least 2%. The Shorthorn, Hereford and Angus breeds do not meet this criterion, but they gained entry as contributors to the foundation as residuals in grade-up programs to other breeds that have a higher twinning frequency.

To the extent possible, matings made in the early generations limited the contribution of a single breed to 50% or less in any individual. The intent was to limit the eventual contribution of any single breed in order to achieve and maintain high levels of heterozygosity.

Females in the Twinning Project calve in approximately equal numbers in spring and fall. Breeding seasons are about 45 d in virgin heifers and 60 d in females 2 yr old and older. For heifers, the spring breeding season is from late May until mid-July, and the fall breeding season is from late October until mid-December. For females 2 yr old and older, the spring breeding season is from mid-June until mid-August, and the fall breeding season is from late October until late December. All virgin heifers (either 1 or 1.5 yr) were bred by natural service. Spring matings of females 2 yr old and older were by artificial insemination (40 d) and natural service (20 d) throughout the study. Fall matings were by natural service until 1985. Starting in 1985, fall matings were by a

TABLE 1. TWINNING RECORDS OF COWS USED AS FOUNDATION FOR TWINNING PROJECT

Item	Purchased cows, n = 96	
	Records before purchase	Records after purchase
Progeny	622	289
Progeny/cow	6.5	3.0
Parturitions	368	246
Parturitions/cow	3.8	2.6
Progeny/parturition ^a	1.73	1.20
Mean calving age	5.3	8.1
Cows from other projects, n = 211		
	Records before transfer	Records after transfer
Progeny	726	766
Progeny/cow	3.4	3.6
Parturitions	550	661
Parturitions/cow	2.6	3.1
Progeny/parturition ^a	1.39	1.15
Mean calving age	3.6	6.3
All foundation cows, n = 307		
	Records before purchase/transfer	Records after purchase/transfer
Progeny	1,348	1,055
Progeny/cow	4.4	3.4
Parturitions	918	907
Parturitions/cow	3.0	2.9
Progeny/parturition ^a	1.50	1.17
Mean calving age	4.1	6.9

^aCows given equal weight.

combination of artificial insemination (40 d) and natural service (20 d).

Calves were weaned at an average age of 100 d, about midway through the breeding season. Fall-born calves were offered feed (creep feeder) before weaning, but spring-born calves did not receive supplemental feed before weaning. Calves were fed a diet of 2.63 mcal ME/kg DM and 14.4% CP from weaning to 200 d. The experimental protocol was to cross foster only if, in the judgment of support staff, there was high probability of losing a calf if both members of a set of twins were left on their dam. There were two sets of triplets. Triplets were included in analyses as twins.

No attempt was made to identify cows gestating twins and to feed and manage them according to their higher requirements. All cows were managed in a relatively favorable nutritive environment for beef cows producing singles. Cows birthing and rearing twins were separated and fed on a higher plane of nutrition subsequent to calving than cows birthing singles.

Progeny of foundation cows either in utero or nursing at the time a dam was added

became part of the project. The general practice was to retain open foundation cows for either one or two breeding seasons. Cows with highest estimated breeding value for twinning generally received two additional chances to become pregnant before removal from the project. Cows open from fall breeding were exposed in spring breeding and open spring-bred cows were exposed in fall breeding.

Superovulation and embryo transfer were done in two seasons (i.e., May and September). The general practice was to hold fall calving donor cows open for superovulation and embryo transfer in May and spring calving donor cows open for superovulation and embryo transfer in September. Donor cows were generally exposed to normal breeding in the breeding season immediately after the May or September superovulation and embryo transfer protocol. All embryo collections and transfers were nonsurgical.

Because of the diversity of questions addressed and specificity of analytical procedures used to address each question, statistical methods used for data analysis are described

under the appropriate heading in the section on Results and Discussion.

Results and Discussion

Analyses were applied to all females born in the project, including the progeny of selected sires. This was justified because the foundation cow population also was selected; the complete data set reflects the potential of selection for twinning in cattle. Two data sets were analyzed for paternal half-sib estimates of heritability and for estimates of repeatability of twinning rate. One data set included the progeny of selected sires and the other data set excluded data on the progeny of highly selected sires and dams.

Records of Twinning in Foundation Females. A total of 96 cows with records of two or more twin calvings were acquired from industry sources from 1976 to 1977 (46) and from 1981 to 1982 (50). Prior records of the 96 cows, based on information provided by owners, averaged 3.8 parturitions per cow and 1.73 progeny per parturition (i.e., $[.73] \times [3.8] = 2.8$ twin sets per cow). Records after entering the project averaged 2.6 parturitions per cow and 1.20 progeny per parturition (Table 1). Approximate mean calving ages were 5.3 and 8.1 yr, respectively, before and after purchase. In cases for which exact ages were not known, they were estimated based on supplementary circumstantial information provided by the owner. Records on twinning rate prior to purchase may be subject to downward bias because of younger mean age effects on twinning rate, or perhaps to upward bias because of a dairy production environment.

Assuming a population twinning rate of .03 (adapted from Rutledge, 1975), "repeatability" of mean twinning rate based on 3.8 records per cow can be estimated

$$\left[\frac{1.20 - 1.30}{1.73 - 1.03} \right] = \left[\frac{.17}{.70} \right] = .24.$$

In this sense, repeatability is the proportion of superiority at time of selection that is retained in subsequent records. Repeatability (r) of a single observation for twinning may be estimated from "repeatability" based on 3.8 calving records using the formula presented by Lush (1945), $nr/[1 + (n - 1)r] = .24$ and solving for single record repeatability, $r = .08$.

A total of 211 females in other projects at

the Research Center with a record of producing twins were transferred into the Twinning Project. Before transfer, these cows averaged 2.6 parturitions per cow and 1.39 progeny per parturition ($[.39] \times [2.6] = 1.01$ twin births per cow). Records in the project averaged 3.1 parturitions per cow and 1.15 progeny per parturition (Table 1). Mean calving age was 3.6 and 6.3 yr, respectively, before and after transfer into the Twinning Project. Again, the records before transfer into the project may be subject to downward bias because of the younger ages. "Repeatability" of mean twinning rate based on 2.6 records per cow prior to entering the project was estimated to be .33, and repeatability of twinning rate for a single observation was estimated to be $r = .16$.

A total of 307 females from both sources were used as foundation cows in the project (Table 1). Before selection as foundation, these cows averaged 3.0 parturitions per cow and 1.50 progeny per parturition ($[.50] \times [3.0] = 1.5$ twin sets per cow). Their records in the project averaged 1.17 progeny per parturition (Table 1). Mean calving ages were 4.1 and 6.9 yr before and after selection as foundation for the project. "Repeatability" of mean twinning rate based on 3.0 records per cow before selection was estimated to be .30, and repeatability (r) of twinning rate for a single observation was estimated to be .12.

The low precision of these estimates for repeatability of twinning rate is recognized. However, there does appear to be a difference in estimates of repeatability between cows purchased based on their twinning records and cows born and reared at the Research Center and transferred into the Twinning Project based on their record of twinning in other projects. Even though every effort was made to validate records of twinning of the cows purchased, their records before purchase are probably subject to greater error than those from cows born and reared at the Research Center. Cows born and reared at the Research Center had a similar environment before and after transfer to the Twinning Project and should provide unbiased estimates of repeatability. There was a major change in the environment with movement of most of the purchased cows to the Research Center. Many of the purchased cows were Holstein and had been in conventional dairy programs.

Realized Heritability. Heritability was estimated based on selection response in twinning

rate of daughters to selection of all foundation dams, and of dams of foundation sires (e.g., paternal grand dams), using all records made before selection. Twinning rates of dams and of sires' dams were weighted based on number of daughters born in the project that produced progeny from 1985 through 1988. Daughters of the progeny-tested foundation sires were excluded. Included were 389 daughters with 837 parturitions, or 2.2 parturitions per daughter with a twinning rate of 1.09 unadjusted for the effects of age. No selection was practiced among the daughters.

Dams of the daughters included 191 cows with 518 parturitions, or 2.7 parturitions per dam before selection for the project. Twinning rate of dams before selection, weighted based on number of daughters, was 1.55 calves per parturition.

$$\hat{h}_n^2 = \left[\frac{1.09 - 1.03}{1.46 - 1.03} \right] = \left[\frac{.06}{.43} \right] = .14 \text{ for 2.8 parturitions,}$$

the mean number of parturitions for foundation dams and of dams of foundation sires prior to selection. With the use of the formula of Lush (1945), heritability of twinning rate based on a single parturition can be estimated as $nh^2/[1 + (n - 1)h^2] = .14$ (assuming $h^2 = r$) with $\hat{h}^2 = .06$. This estimate of realized heritability is subject to some downward bias because of age effects on twinning rate, i.e., parturitions per daughter averaged 2.2, and parturitions for foundation dams and paternal grand dams prior to selection averaged 2.8.

Records of Females Born in the Project. Records were analyzed using least squares mixed model procedures (Harvey, 1977). For the data set when all data were included, twinning rate was observed on 710 females in 1,374 parturitions for a mean of 1.9 parturitions per female. These females were either born in the project or were nursing their dams when they entered the project. They were either daughters or granddaughters of foundation cows. These females were the progeny of 58 sires. Observations were made for both spring and fall calving for the years 1985 through 1988. Females ranged in age from 2 to 10 yr. Mean twinning rate was 1.11 calves per parturition when all females born in the project were included (Table 2).

Breed was not considered in these analyses. Although differences in twinning rate exist among the breeds contributing to the foundation, most of the females born in the project

were crossbreds of two or more breeds. Further, we are interested in genetic effects on twinning rate contributed by between-breed and within-breed sources of genetic variation.

Some of the females were produced by embryo transfer from both dams and sires thought to be superior genetically for twinning rate; others were by sires selected on twinning rate of their daughters; and some involved both of these situations. Thus, two data sets were analyzed to obtain estimates of genetic and environmental effects (Table 2).

The model used to estimate fixed effects (season of calving, year of record and age of cow) and random effects (sires and daughters within sires) is indicated by Table 2. Interactions among the fixed effects were not significant in a preliminary analysis; thus, they were deleted from the final analysis. Even though the effects of year and age of cow were not significant in the analysis of either data set, they were included in the final analyses because year means are of interest and other analyses involving some of these data have shown age of cow effects on twinning rate to be important (Gregory et al., 1988). Records on 64 cows calving in 1983 and 112 cows calving in 1984 were deleted from both data sets in the final analyses because most of the twins were out of 4-yr-old dams in these two calving years, resulting in an aberrant structure of the data.

Season of calving (spring or fall) was significant in the analysis of one of the data

TABLE 2. ESTIMATES OF GENETIC AND ENVIRONMENTAL EFFECTS ON TWINNING RATE OF FEMALES BORN IN THE PROJECT

Item	All data	Minus daughters of embryo-transfer dams and of progeny-tested sires
No. of sires	58	51
No. of daughters	710	465
No. of parturitions	1,374	894
Parturitions/daughter	1.94	1.92
Analysis of variance		
Sires (S)	**	NS
Daughter/S	NS ^a	NS
Season	NS	*
Year	NS	NS
Age of cow	NS	NS
Least squares means		
Mean	1.11	1.09
Season of calving		
Spring	1.09	1.06
Fall	1.13	1.13
Year of record		
1985	1.13	1.12
1986	1.13	1.12
1987	1.10	1.07
1988	1.08	1.06
Age of cow		
2 yr	1.06	1.06
3 yr	1.11	1.08
4 yr	1.13	1.12
5+ yr	1.14	1.11
Estimates of heritability (h^2) and repeatability (r)		
h^2	.09 ± .07	.02 ± .07
r	.04	.05

^aNS = not significant.

* $P \leq .05$.

** $P \leq .01$.

sets. Records involving unadjusted means have been consistent in showing twinning rate in fall calving to be 50% or more greater than in spring calving. Further, ovulation rate in postpartum cows is greater in fall than in spring breeding (Echtemkamp et al., 1990). Differences in twinning rate between spring and fall calving generally were consistent for the two data sets (Table 2) and are considered to be real.

Even though effects of cow age on twinning rate were not significant in either of the data sets, age of cow and season were significant in a model that included sires as a random effect but excluded daughters within sires as a random effect. Thus, even though age of cow effects were not statistically significant in the analysis of variance, the differences in least

squares means reported (Table 2) are interpreted to be real in view of prior estimates (Gregory et al., 1988).

Paternal half-sib estimates of heritability (h^2) of twinning rate were small (Table 2). The estimate obtained from the analysis of the data set that included all data (.09 ± .07) is subject to upward bias from two sources; i.e., some daughters of dams used in embryo transfer were by sires thought to be superior, and some daughters were by sires selected as superior based on twinning rate of their daughters. The estimate of heritability (.02 ± .07) obtained from analysis of the data set that excluded both of these classes is less subject to bias. Bias associated with daughters of embryo-transfer dams results from mating of those dams to superior sires; this inflates the sire component of variance ($1/4 \sigma_g^2$). If embryo-transfer dams had been mated to a random sample of sires, only the daughter-within-sire component of variance ($3/4 \sigma_g^2 + \sigma_{pe}^2$) would be increased with some negative bias in the paternal half-sib estimate of heritability.

From daughter-within-sire and residual variance components from the analysis of variance model in Table 2, the estimates of repeatability (r) were small from both data sets (.04 and .05). This suggests that permanent environmental effects on twinning rate were not important in these populations. In a supplementary analysis, sires were deleted from the model and repeatabilities were computed from cow and residual variance components. They did not differ from values shown in Table 2.

The daughter-within-sire component of variance ($3/4 \sigma_g^2 + \sigma_{pe}^2$) was small (.00197) relative to the sire component of variance ($1/4 \sigma_g^2$) for Model 1 (.00196) with all data included. The mating plan was to mate sires to breeds of females different from the sire. Breeds contributing to the foundation differ in their twinning rate. Thus, because of crossbreeding, the among-sire component of variance would tend to include breed differences in twinning rate to a higher degree than breed differences would be reflected in the daughter-within-sire component of variance. Thus, the mating procedure may account for the higher than expected estimates of the sire component of variance relative to the daughter-within-sire component of variance in the data set that included all data.

The increase in twinning rate of daughters of foundation cows relative to the assumed population mean twinning rate of .03 suggests that the foundation cows were indeed genetically superior for twinning rate to the population from which they were sampled. As indicated earlier, the realized heritability was .06 for a single parturition using twinning rate response of daughters relative to selection for twinning rate practiced in their dams and paternal grand-dams. Thus, selection for twinning rate appears to be more effective than is indicated by the less biased paternal half-sib estimate of heritability (.02) presented in Table 2. The two estimates, however, do not differ significantly.

Mode of Inheritance of Twinning Rate. Semen from six sires of the Swedish Friesian breed was sampled based on twinning rate of their daughters. A Swedish summary to identify sires whose daughters produced twins at a high frequency revealed that 9 of the top 10 sires of the Swedish Friesian breed included the sire Sailor and 8 of his sons. The 10th sire identified in this screening had the same dam as 1 of the 8 sons of Sailor (personal communication, Dr. Göran Malmberg). On further review, we determined that 32 sons of Sailor produced daughters on which records of twinning were available. These records included 11,467 daughters producing 29,427 parturitions with 1,690 twin sets (adjusted to a

mature basis) for a sire mean twinning rate of 5.4% and a range of from .9 to 13.6% among the 32 sire progeny groups (Table 3). Mean twinning rate of the Swedish Friesian breed on a mature basis is 2.57% (personal communication, Dr. Göran Malmberg).

The frequency distribution of mean twinning rates for 32 sons of Sailor is shown in Figure 1. Sailor produced 7,463 daughters with 26,293 parturitions and a mean twinning rate of 9.96%, adjusted to a mature basis. Of the 32 sons, 21 had daughter averages at or below the average for daughter-mean twinning rates (5.4%) of Sailor sons (Table 3). This skewed distribution for daughter-means of Sailor sons may suggest some degree of dominance for genes favoring single births, in harmony with the reduced proportion of twin births from crossbred vs purebred cows reported by Majjala and Syvajarvi (1977). For 3,720 purebred and 271 reciprocal crossbred cows of the Ayrshire, Finncattle and Friesian breeds, frequency of twinning averaged approximately one-third less for crossbred cows than for straightbred cows at all ages. However, if one assumes that the underlying genetic liability for twinning is normally distributed (Falconer, 1981), the degree of negative heterosis for deviation from the liability threshold for twinning was only about 10% of the parental purebred mean, or about one-third as large as for heterosis of the observed frequencies and

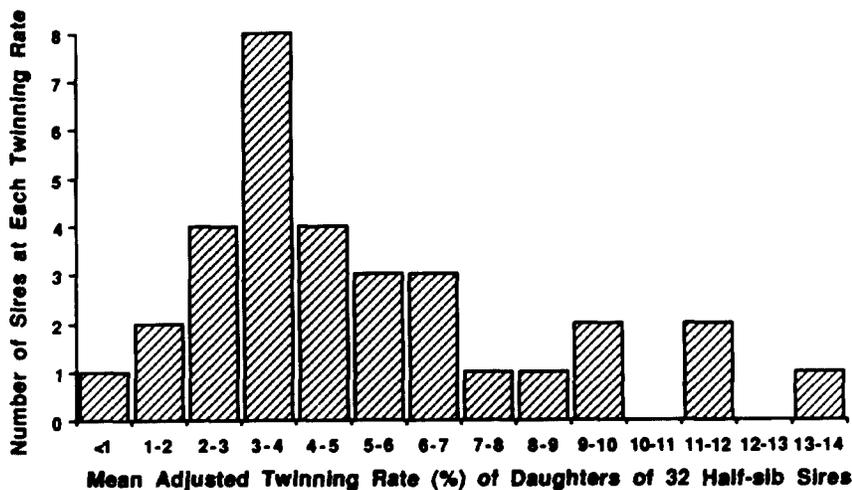


Figure 1. Frequency distribution for adjusted twinning rate of daughters of 32 sons of one sire.

TABLE 3. TWINNING RATES OF DAUGHTERS BY 32 SONS OF THE SIRE-SAILOR

Sire number	No. of daughters calving	Adjusted no. of twin sets at first parity ^a	Total no. of calvings	Adjusted total no. of twin sets	Adjusted twinning rate, %	Mean deviation from threshold liability for twinning ^b
35603	166	0	533	5	.9	-2.366
73010	62	0	237	3	1.3	-2.227
37802	155	2	511	10	2.0	-2.054
35960	108	0	388	8	2.1	-2.034
36664	90	2	328	9	2.7	-1.927
73045	160	0	562	16	2.8	-1.911
36621	126	2	412	12	2.9	-1.896
73026	137	4	435	14	3.2	-1.852
35913	147	2	379	13	3.4	-1.825
36698	144	2	496	17	3.4	-1.825
73002	650	12	2,060	73	3.5	-1.812
36653	100	0	278	10	3.6	-1.799
73014	63	0	242	9	3.7	-1.786
35973	98	5	371	14	3.8	-1.774
35912	1,080	14	2,662	109	4.0	-1.751
35586	124	7	423	19	4.5	-1.695
35902	89	2	286	13	4.5	-1.695
73020	119	0	325	15	4.6	-1.685
36631	1,904	68	3,902	182	4.7	-1.675
35906	124	2	419	24	5.7	-1.581
36684	117	7	350	20	5.7	-1.581
73011	46	2	152	9	6.0	-1.555
35926	109	0	351	22	6.3	-1.530
37813	118	4	306	20	6.5	-1.514
35931	3,813	159	8,689	606	7.0	-1.476
73004	269	9	752	60	8.0	-1.405
35966	113	4	315	28	8.9	-1.347
36642	124	7	341	32	9.4	-1.317
35918	691	35	1,696	165	9.7	-1.299
36644	118	9	316	37	11.7	-1.191
35907	156	5	433	51	11.8	-1.185
73027	147	14	477	65	13.6	-1.098
Totals or means	11,467	379	29,427	1,690	5.4	-1.677

^aTwinning rate of heifers was adjusted to a mature basis by multiplying first-parity twinning rate by 1.75. This estimate of age effects was computed from data collected in the Twinning Project.

^bSee Falconer (1981). Threshold = 0.

can probably be accounted for by sampling error. Also, when the daughter means for 32 sons of Sailor are scaled in liability standard deviations from an assumed threshold of zero units for twinning (Table 3), their distribution (Figure 2) is no longer obviously skewed toward a low twinning rate. Syrstad (1984) reached a similar conclusion based on analyses of a larger data set in the Norwegian Red breed.

The range in mean twinning rates for daughters of Sailor's sons (.9 to 13.6%, Table 3) raises the question of whether this range is consistent with the expected standard deviation among mean twinning rates for daughters of the 32 half-sib sons of Sailor. If the mean

twinning rate of the Swedish Friesian breed is $P = 2.57\%$, the expected standard deviation among progeny means of sons can be calculated as follows: Phenotypic variance, $\sigma_P^2 = p(1-p) = (.0257)(.9743) = .025$. If heritability, $h^2 = .06$, $\sigma_g^2 = h^2 \sigma_P^2 = .06(.025) = .0015$. For half-sib variance of sons within sire, $\sigma_S^2 = (.75) \times (.25 \sigma_g^2) = .00028125$. Variance within sire progenies, $\sigma_e^2 = (.025) - (.25 \sigma_g^2) = .024625$. Thus, variance of half-sib sire progenies, $\sigma_{\text{sn}}^2 = \sigma_S^2 + \sigma_e^2/n = .00028125 + \frac{.024625}{920} = .000308$, because mean $n = 920$ for these sons. The

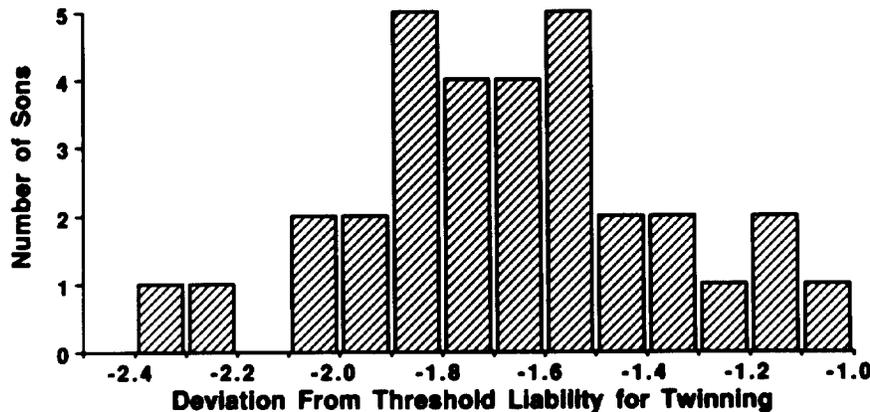


Figure 2. Distribution of mean liability deviations (based on Falconer, 1981) from threshold for twinning for daughter-means of 32 sons of Sailor.

standard deviation ($\sigma_{\bar{x}_n}$) would then equal .01755. The observed range among son progenies was .127 or 7.2 $\sigma_{\bar{x}_n}$ and the best son's daughters were 4.7 $\sigma_{\bar{x}_n}$ above the mean of .054 for all sons.

In terms of the calculated underlying normally distributed genetic liability of twin production, the range among the 32 sons of Sailor would be 1.27 σ (Table 3). The heritability of .06 (realized heritability) on the observed scale would correspond to heritability of .42 on the continuous and normally distributed liability scale; i.e., to .06 $(.9743)/i^2$ $(.0257) = .42$, where $i = 2.32 =$ mean deviation for the 2.57% of twins from the population mean in standard units (Falconer, 1981). On this scale $\sigma_g^2 = .42$, $\sigma_e^2 = 1 - .105 = .895$, $\sigma_S^2 = .07875$, $\sigma_{\bar{x}_n}^2 = .07875 + .895/920 = .07972$, $\sigma_{\bar{x}_n} = .282$.

The range among sons of 1.27 σ on the liability scale would be 4.5 $\sigma_{\bar{x}_n}$ units, and the best son's progeny would be 2.0 $\sigma_{\bar{x}_n}$ above the mean liability deviation from the threshold of 1.677 σ for all progenies (Table 3). On the normalized scale (Figure 2) the range among the 32 son's progenies is no wider than would be expected from matings of Sailor sons to a random sample of cows in the breed; thus, there is little indication of any major gene effects. The distribution of sire progeny means for liability of twinning do not show an effect of possible partial dominance of single births suggested in the crossbreeding comparisons by

Maijala and Syvajarvi (1977). There is no indication of a bimodal distribution, which would be expected if a single gene with a major effect were segregating. Thus, we conclude in this population that twinning rate likely is inherited as a quantitative trait.

Implications

Foundation animals selected on the basis of twinning rate (e.g., 1.5 calves per parturition) continued to produce twins at a rate of 1.17 calves per parturition in the experimental population. Daughters of foundation animals produced twins at a rate of 1.09 calves per parturition. Thus, first-generation animals in the experimental population produced twins at a frequency three times greater than the unselected contributing populations. Realized heritability of single-parity twinning rate estimated from selection of parents and response in daughters of foundation females was .06. Results suggest that twinning rate is inherited as a quantitative trait.

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