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Effects of Inbreeding on Milk and Fat Production, Stayability, and Calving Interval of Registered Ayrshire Cattle in the Northeastern United States

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ABSTRACT

Inbreeding coefficients of 30,794 registered Ayrshire cows were calculated from relationships between sire and maternal male ancestors. Average inbreeding coefficient of all cows was less than 1% and of the 5,202 inbred cows was 5.4%. Fewer than 2% of inbred cows had coefficients greater than 15%. Percent of inbred cows increased from 23% of cows born in 1972 to 43% in 1980. Over the same period average inbreeding coefficient of all cows increased from 1.2 to 2.0%, but average coefficient of inbred cows decreased from 5.6 to 4.7%.

Effects of inbreeding on first lactation, 305-day, 2 \times , mature equivalent milk and fat production (kg), 48-mo stayability (proportion of cows surviving to 48 mo of age), and first calving interval (days) were estimated by a model that included fixed effects for herd-year-seasons, sire-maternal grandsire groups, inbreeding, and random effects for sires and maternal grandsires within groups. Inbreeding was included in the model as a classification (six classes according to inbreeding coefficient: 0, 0⁺ to 5⁻%, 5 to 10⁻%, 10 to 15⁻%, 15 to 25⁻%, and 25 to 35⁻% and one class for cows with indeterminate inbreeding). Estimates of differences between inbreeding classes 0⁺ to 5⁻% through 25 to 35⁻% and the zero inbreeding class indicated that milk and fat production decreased with increased inbreeding. Effects of inbreeding on stayability and calving interval were small. Inbreeding was fitted also as a linear covariate. Regressions of milk, fat,

stayability, and calving interval on inbreeding coefficients were -23, -1, -.008, and -.095 per 1% increase of inbreeding coefficient.

INTRODUCTION

Inbreeding of dairy cattle reduces milk and fat production, increases calf mortality, and adversely affects heifer and cow reproductive ability (15). The small number of sires necessary to maintain an artificially-bred dairy population theoretically can result in high inbreeding. In the Holstein breed, inbreeding is not high (1, 3), and current relationships among sires are not cause for concern (13), although (13) cautions that "the trend toward increasing relationships . . . may be indicators of future problems". However, extensive use of Selwood Betty's Commander, 117936, (Betty) and of his sibs and descendants has led to concern about inbreeding in Ayrshire cattle. Although Betty semen has not been available since December 1975, current worries are exemplified by eight of nine Ayrshire bulls listed in the June 1981 Northeast Artificial Insemination Sire Comparison (NEAISC) report being related to Betty, of which two were sons of Betty. Objectives of this study were to determine the extent and percent of inbreeding in registered Ayrshire cattle in the northeastern United States and to estimate effects of inbreeding on milk and fat production, stayability to 48 mo of age, and first calving interval.

DATA

First lactation, 2 \times , 305-day, mature equivalent (ME) milk and fat records and calving dates of registered daughters of both artificial insemination (AI) and natural service Ayrshire sires were obtained from New York Dairy Records Processing Laboratory (DRPL) in Ithaca, NY. Each cow had to have both sire and

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dam identified. Data were subjected to edits in Table 1.

Stayability records were 1 if a cow survived to 48 mo of age and were 0 otherwise. Cows sold for dairy purposes prior to 48 mo and cows in herds that terminated enrollment on test prior to the date at which the cow reached or would have reached 48 mo were not included in the analysis of stayability.

The final data set contained records on 30,794 cows sired by 2,532 bulls in 1,495 herds. Year of first freshening ranged from 1959 to 1981. Valid first calving intervals were available on 22,443 cows, and 21,880 cows had the opportunity to stay to 48 mo.

Estimation of Inbreeding

Inbreeding coefficients of cows were estimated from relationships between sire and dam's male ancestors. The procedure involved six steps.

- 1) Identify sire and dam of all cows with records.
- 2) Trace the dam pedigree back along the female line only, recording the sire of all such identified females. In this manner, a pedigree for each cow with data was built that consisted of sire, maternal grandsire (MGS), maternal great-grandsire, etc. Pedigrees were traced up to and including the seventh generation from DRPL files.
- 3) Obtain sire and MGS information for all males listed in steps 1 and 2 from the United States Department of Agriculture (USDA) format 380 file and from the

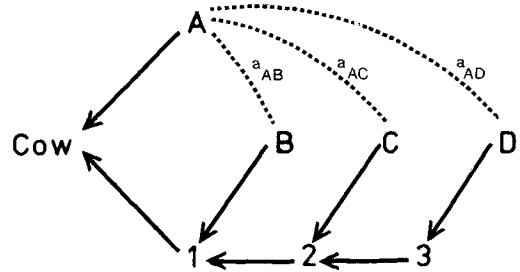


Figure 1. Hypothetical pedigree for inbreeding calculation. (Letters denote males; numerals denote females; a_{ij} = numerator relationship between animals i and j .)

DRPL AI sire pedigree file. Maternal grandsires of non-AI bulls were not identified unless the bull-dam either had a record or had a descendent with a record, in which case the sire of the bull-dam already had been recorded as a cow-sire. This omission was because the USDA pedigree file identifies only bull-sire and bull-dam. The DRPL AI sire pedigree file, however, records bull grandparents as well.

- 4) Repeat step 3 for all new males identified therein. Thus, steps 3 and 4 create a male pedigree for all male ancestors from steps 1 and 2.
- 5) Compute relationships among and inbreeding of all identified males based on sire-maternal grandsire information as described by Hudson et al. (9). This procedure will underestimate relationships in certain cases; two are: a) Two bulls, with the same dam but unrelated sires, will have a calculated relationship of zero if the dam's sire (i.e., bull maternal grandsire) is unrecorded. If dam's sire is recorded, calculated relationship is .0625. True relationship (half-sibs) is .25. This error occurs because the algorithm fails to recognize the dams as the same animal and performs the calculation as if the dams were half-sibs. b) Two bulls with unrelated sires and maternal grandsires but the same maternal grandam have a true relationship of .0625, but the calculated coefficient will be 0. Similarly

TABLE 1. Data edits.

Edit	Acceptable range
First calving age	20 to 34 mo
ME ¹ milk	907 to 15,875 kg
ME fat	32 to 680 kg
ME test	2.2 to 6%
Calving interval ²	10 to 20 mo

¹ ME = mature equivalent.

² Production records of cows with calving interval outside acceptable range were retained, but those cows were not included in the analysis of calving interval.

two maternal half sibs will have a relationship coefficient calculated as 0 if their dam's sire is unrecorded. The frequency of occurrence of errors of this type is unknown. Calculated inbreeding coefficients will be affected only if two bulls with incorrectly computed relationship appear on different sides of a cow's pedigree.

- 6) For each cow, steps 1 and 2 generate a pedigree shown in Figure 1. Relationships, a_{ij} , between the sire of cow and maternal male ancestors are calculated in steps 3 to 5. The inbreeding coefficient, F , of each cow then is estimated by:

$$F_{\text{cow}} = a_{AB}/4 + a_{AC}/8 + a_{AD}/16 + \dots$$

Pedigrees such as in Figure 1 actually were not generated or stored in the computer. Relationships among males were stored as described by Hudson et al. (9), and cow pedigrees were traced from a list of cows, sires, and dams. Each inbreeding coefficient was accumulated as maternal male ancestors were identified as being related to the sire of cow.

Sources of underestimation of inbreeding coefficients include inaccurate calculation of relationship among males as described and lack of pedigree information for cows born in early years. Pollak and Ufford (10) used a similar procedure for estimating inbreeding coefficients in a closed herd of beef cattle. Their method incorporated relationships between sire and dam or sire and maternal grandam, if known (i.e., a_{A1} and a_{A2} in Figure 1), and terminated with sire of maternal grandam. The highest error due to a single pathway that their procedure could have caused was 6.25%, but only 1 out of 3481 coefficients had an error of this magnitude. Erroneous inbreeding coefficients were calculated for only 3.3% of the animals, and 87% of the errors were .02 or less. Only errors due to the approximate nature of the method were counted by Pollak and Ufford (10) and not those due to missing ancestral information for the cows.

MODEL

The model was a modification of the maternal

grandsire model (4, 12) currently used for the NEAISC (11). The model is

$$y = Xh + (Z_s + Z_m)(Qg + s) + e \quad [1]$$

where y is the data vector,

h is a vector of fixed herd-year-season effects,

s is a vector of random sire effects,

g is a vector of fixed sire group effects, X is an incidence matrix of 0's and 1's referring herd-year-seasons to records,

Q is an incidence matrix of 0's and 1's referring sires to genetic groups,

Z_s is an incidence matrix of 0's and 1's referring sires to daughter records,

Z_m is a matrix of 0's and .5's referring MGS to granddaughter records, and

e is a vector of random residual effects.

Both s and e were distributed with null means and variance-covariance matrices $Ah^2\sigma^2/4$ and $I(1-5h^2/16)\sigma^2$ if all cows had both sire and MGS identified, with A = matrix of additive relationships among the sires, I = identity matrix, h^2 = heritability, and σ^2 = variance of a single record.

Inbreeding effects were incorporated into [1] by two procedures. First, inbreeding was analyzed as a classification variable with records assigned to classes depending on the associated inbreeding coefficient. Cows with records fell into two distinct categories: those with both sire and MGS identified and those with only sire known. Inbreeding coefficients could not be calculated for cows without known MGS. The calculated inbreeding coefficient of some cows with both sire and MGS identified was 0, but this is distinctly different from indeterminate inbreeding from lack of ancestral information. Thus, the model had a class for cows with unknown inbreeding (f^*) and a class for cows with 0 inbreeding (f_0). Five other classes (f_i) were for cows with inbreeding coefficients (F) in the ranges $0 < F < 5\%$, $5 \leq F < 10\%$, $10 \leq F < 15\%$, $15 \leq F < 25\%$, and $F \geq 25\%$.

The model with inbreeding incorporated as a classification variable was:

$$\begin{bmatrix} y_k \\ y_u \end{bmatrix} = \begin{bmatrix} X_k \\ X_u \end{bmatrix} h + \begin{bmatrix} Z_k Q & 0 \\ Z_u Q & Z^* Q^* \end{bmatrix} \begin{bmatrix} g \\ g^* \end{bmatrix} + \begin{bmatrix} Z_k \\ Z_u \end{bmatrix} s + \begin{bmatrix} B & 0 \\ 0 & 1 \end{bmatrix} \begin{bmatrix} f \\ f^* \end{bmatrix} + \begin{bmatrix} e_k \\ e_u \end{bmatrix} \quad [2]$$

In [2], y and X of [1] have been partitioned to correspond to cows with known MGS (subscript k) and those with unknown MGS (subscript u). Each row of Z_k contains a 1 and a .5 corresponding to sire and MGS of cows with records, whereas Z_u contains no .5, because corresponding records are from cows with unknown MGS.

For cows with unknown MGS, the MGS effect was incorporated into the residual e_u . Group effects of unknown MGS's were included in the model by defining groups for unknown MGS by year of birth of their granddaughters. Thus, Z^* in [2] is a design matrix of 0's and .5's that conceptually refers unknown MGS to records. The Q^* refers unknown MGS to groups g^* .

In [2], $f = (f_0 \ f_1 \ \dots \ f_5)'$, B is an incidence matrix referring inbreeding class effects to records of cows with known sire and MGS, and 1 is a unit vector. The variance-covariance matrix of e_k is $K(1-5h^2/16)\sigma^2$ and that of e_u is $I(1-h^2/4)\sigma^2$.

Inbreeding effects also were incorporated into the model as a linear covariate. The procedure was simplified by utilizing only records of cows with both sire and MGS identified. The model was:

$$y = Xh + (Z_s + Z_m)(Qg + s) + bc + e \quad [3]$$

where terms are defined as for model [1] and c is a vector of regressors (inbreeding coefficients) and b is the regression of milk, fat, stayability, or calving interval on inbreeding coefficient.

For both models [2] and [3], mixed model equations were set up as described in (4) and solved by modified Gauss-Seidel iteration. For model [2] estimates of inbreeding depression were calculated by $f_0^0 - f_1^0$ for $i = 1, \dots, 5$,

where superscript 0 indicates solutions to the mixed model equations. Procedures for estimating standard errors of estimates in both models [2] and [3] are in the appendix.

As presented, models [2] and [3] ignore the different residual variances for cows with different inbreeding coefficients. For a non-inbred cow with noninbred sire and MGS, the residual variance is:

$$\sigma_e^2 = (1-5h^2/16)\sigma^2 \quad [4]$$

and the variance component ratio used in the mixed model equations is:

$$\theta = 4/h^2 - 5/4 \quad [5]$$

For a cow with inbreeding coefficient F , the residual variance is:

$$\sigma_{e(F)}^2 = [1 + (F-5/16)h^2] \sigma^2 \quad [6]$$

and the corresponding variance ratio is

$$\theta_F = 4/h^2 + 4F - 5/4 \quad [7]$$

If θ of [5] is used erroneously instead of θ_F of [7], the absolute error in the ratio is $\theta_F - \theta = 4F$ and the relative error is $(\theta_F - \theta)/\theta_F = Fh^2/[1 + (F-5/16)h^2]$. For $F = .25$ and $h^2 = .25$, the relative error is less than 7%. If both sire and MGS are inbred with coefficients F_s and F_m , then the relative error is:

$$\begin{aligned} & [F_m h^2/16 - F_s(1 - 9h^2/16)] / \\ & [1 - (5 - 4F_s - F_m)h^2/16] \end{aligned}$$

For $F_s = F_m = h^2 = .25$, this error is as high as 22%. However, few bulls were inbred, and only a small proportion of cows had both sire and MGS inbred. Hence, inbreeding coefficients were ignored in calculation of the variance component ratio for the mixed model equations.

For both models [2] and [3] herd-year-season categories were based on date of first freshening for all traits. Seasons were December to April and May to November. Numbers of herd-year-seasons were 8,717 for milk and fat, 6,670 for stayability, and 7,114 for calving interval. Sires were grouped by registration number in groups of 25. Daughters and grand-

daughters of sires without a US registration number were excluded.

RESULTS AND DISCUSSION

Inbreeding

Of 2,726 bulls used to calculate the relationship matrix 49, or 1.8%, were inbred. The average inbreeding coefficient was 7.5% for inbred bulls and .13% for all bulls. This low inbreeding contrasts sharply with the range of .66 to 6.66% found by Fowler (6) in Scottish Ayrshires. However, Fowler used 1877 as the base year for inbreeding calculations, which was the year of first publication of the *Ayrshire Cattle Herd Book*. During the 60 yr covered by Fowler's study, inbreeding was actively practiced to consolidate "breed type". The earliest date of birth available for bulls in our study was 1950, thus an approximate "base" date. No bull was inbred more than 12.5% (Table 2), which is equivalent to the offspring of a half-sib mating. Of the inbred bulls, 23 were inbred to Betty or his sire, and two were inbred to both Betty and his sire by different pathways.

Table 3 shows that 237 (8.7%) bulls were related to Betty, of which 99 were sons, 124 were descendants other than sons, and the remaining 14 were relatives other than descendants (e.g., sire, half-sibs, etc.). The bull most related to Betty was Selwood Royal Welcome, 129931, a Betty son out of a Betty half-sib. The relationship of Royal Welcome to Betty was .625. However, the average relationship of Betty relatives to Betty was .354, and the average relationship of Betty to all bulls was only .031. Average relationship of all cows to Betty was .15; thus, the average relationship from Betty of cows to bulls was $(.031)(.15) = .0046$. Random mating in the sample would produce an offspring with inbreeding coefficient from Betty of $.0046/2$ or .23%. This inbreeding is an average for the whole sample and does not account for increasing influence of Betty over time. For example, of cows born from 1974 to 1978, 83% were related to Betty, and average relationship to Betty of all cows born in that period was .20. Average relationship of bulls listed in the June 1981 NEAISC was .319. Thus, inbreeding from Betty of an offspring from random mating of a cow born 1974 to 1978 to a bull listed in the June 1981 NEAISC would be only 3.2%.

TABLE 2. Distribution of inbred bulls by inbreeding percent.¹

Inbreeding	Bulls
(%)	(n)
12.5	19
6.25 - 12.4	16
1.00 - 6.24	8
< 1.00	6

¹Total number of bulls = 2,726.

TABLE 3. Distribution of bulls related to Selwood Betty's Commander by relationship.

Relationship	Bulls
(%)	(n)
< 10	5
10 to 20—	15
20 to 30—	102
30 to 40—	10
40 to 50—	2
50 to 60—	102
≥ 60	1
Total	237

TABLE 4. Distribution of inbred cows by inbreeding percent.

Inbreeding	Cows	Percent of total cows
(%)	(n)	
0+ to 5—	2,754	8.9
5 to 10—	1,721	5.5
10 to 15—	637	2.1
15 to 20—	36	.1
20 to 25—	2	0
25 to 30—	51	.2
30 to 35—	1	0
Total	5,202	16.9

Table 4 shows that of the 5,202 inbred cows, less than 2% had inbreeding coefficients of 15% or greater. Average inbreeding coefficient of all cows was less than 1% (Table 5). Inbred cows represented 17% of the total with

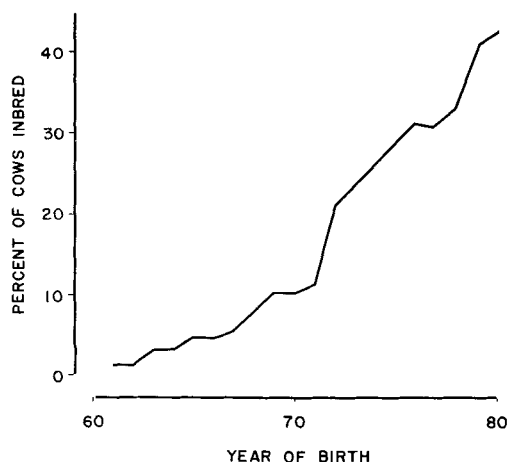


Figure 2. Percentage of inbred cows by year of birth.

inbreeding coefficients averaging 5.4%. Daughters of Betty and daughters of sons of Betty constituted 25% of all cows, but over 38% of inbred cows were daughters or granddaughters of Betty. Average inbreeding coefficient of daughters of Betty was less than that of all cows, but the average inbreeding coefficient of granddaughters of Betty was three times as great as the average inbreeding coefficient of all cows. Betty has had substantial influence on the Ayrshire breed, but daughters of his sons have contributed more to total inbreeding in the sample than have Betty's own daughters as probably would be expected because there would be few matings of Betty to daughters of Betty's sire, and matings of Betty to his own daughters would be avoided because of the high

inbreeding of the ensuing progeny.

Inbreeding coefficients in Tables 4 and 5 represent averages over the whole sample, regardless of year of birth. Figure 2 shows that fewer than 10% of cows born prior to 1972 were inbred. Since 1972 the percent of inbred cows has increased from 23% to 42.4% of cows born in 1980.

Figure 3 shows that although the average inbreeding coefficient of all cows increased from .16% in 1961 to 2.0% in 1980, the average inbreeding of inbred cows dropped from 11.3% to 4.7% over the same period.

Betty entered AI service in April 1958 and left service in December 1975. In the June 1981 NEAISC report, nine Ayrshire bulls were listed, of which two were sons of Betty and only one was unrelated to Betty. Betty's influence has been and still is substantial. He has sired numerous daughters, and his many sons have produced a substantial proportion of the Ayrshire breed. No breed as small in numbers as the Ayrshire can have such an influential bull without some increase in inbreeding. Over 40% of cows born in 1980 were inbred, but average inbreeding coefficient in that year was only 2%. Serious concern over inbreeding in the Ayrshire breed is unjustified in light of the small relationship to Betty and in view of the low inbreeding in the breed today.

Inbreeding Effects

Table 6 shows results for fitting inbreeding as a classification variable. For each of the four traits, the analysis was repeated with two heritabilities. Heritabilities of .43, .45, and .024 for milk, fat, and stayability are from Hudson

TABLE 5. Inbreeding of all cows and of daughters and granddaughters of Selwood Betty's Commander (Betty).

	Total	Inbred (n)	Inbred (%)	Average inbreeding	
				All cows	Inbred cows
				(%)	
All cows	30,794	5,202	16.9	.9	5.4
Betty daughters	3,568 (11.6) ¹	283 (5.4) ¹	7.9	.7	8.5
Daughters of Betty sons	4,137 (13.4) ¹	1,705 (32.8) ¹	41.2	3.0	7.2

¹ In parentheses is number of daughters as a percentage of the "all cows" row.

and Van Vleck (8). Heritabilities of .25, .25, and .10 for the same traits are those used in the NEAISC (R. W. Everett, personal communication, 1982). For calving interval, heritabilities represent extremes of the range reviewed by Foote (5). Differences in estimates of inbreeding effects due to different heritabilities were small.

Table 6 shows differences between each of five classes of inbreeding and the noninbred class. For example, cows in the 10 to 15% inbred class produced 346 kg less milk than noninbred cows. As inbreeding increased, both milk and fat production decreased. The estimate for the 15 to 25% inbred class is positive but smaller than the standard error. There were only 35 records in the 15 to 25% class. A similar number of records, 37, were in the 25 to 35% class, but estimates for that class were negative and, thus, compatible with the theory of inbreeding depression. Bar-Anan (personal communication, 1982) suggested that increased days open of cows in the 15 to 25% class may have increased milk yield.

Stayability to 48 mo was reduced by inbreeding, but estimates for all classes were small, and only in the 10 to 15% class was the estimate larger than the standard error. For example, the estimates for stayability are interpreted as 15% fewer cows in the 10 to 15% class will survive to 48 mo of age as compared with noninbred cows.

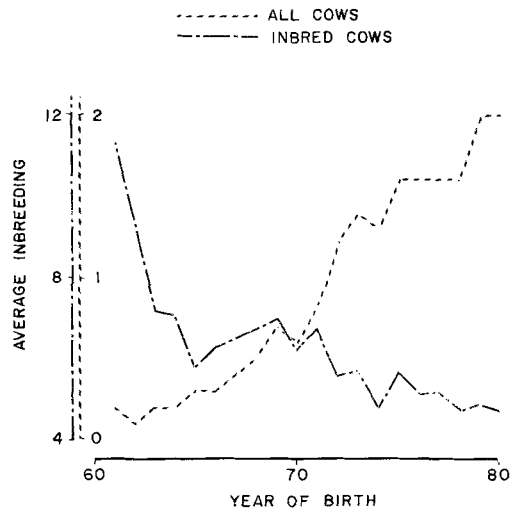


Figure 3. Average inbreeding coefficient of inbred cows and of all cows by year of birth.

For the high relationship between first lactation milk and stayability (7), a greater effect of inbreeding on stayability might have been expected. A review of work in the North Central (NC) cooperative project (15) reported that inbreeding adversely affects pre- and post-natal mortality and disposals prior to first calving. A heifer must initiate a first lactation

TABLE 6. Differences and standard errors (in parentheses) of milk and fat production, stayability, and calving interval (C.I.) between five classes of inbred cows and noninbred cows.

Inbreeding	Assumed heritability							
	Milk		Fat		Stayability		C.I.	
	.43	.25	.45	.25	.024	.10	.01	.10
	(kg)				(pts)		(days)	
0+ to 5—%	—66.2 (24.8)	—69.4 (25.0)	—2.8 (1.0)	—2.9 (1.0)	—0.01 (.01)	—0.01 (.01)	—0.3 (1.6)	—0.42 (1.6)
5 to 10—%	—163.9 (29.8)	—164.6 (30.0)	—7.4 (1.2)	—7.5 (1.2)	—0.03 (.02)	—0.04 (.02)	—1.5 (1.9)	—2.0 (1.9)
10 to 15—%	—346.2 (45.9)	—345.8 (46.2)	—14.3 (1.9)	—14.3 (1.9)	—0.15 (.03)	—0.16 (.03)	—1.1 (3.0)	—2.0 (3.0)
15 to 25—%	87.5 (181.0)	82.6 (182.3)	1.5 (7.3)	1.6 (7.3)	.15 (.10)	.15 (.10)	10.1 (10.3)	9.3 (10.2)
25 to 35—%	—416.0 (172.5)	—407.1 (173.8)	—17.4 (6.9)	—17.2 (7.0)	—0.21 (.10)	—0.21 (.09)	—12.3 (11.7)	—12.6 (11.6)

TABLE 7. Regression coefficients of milk and fat production, stayability and calving interval on percent inbreeding.

	Milk	Fat	Stayability	Calving interval
	(kg)		(pts)	(days)
Regression estimate	-23	-1.02	-.0081	-.095
Standard error	3.3	.13	.0017	.20
No. of records	20,430	20,430	14,894	14,435

to appear in the data set in this study; thus, in this study stayability does not account for deaths prior to first calving. Animals with reduced livability because of high inbreeding possibly do not appear in the data, and inbreeding may not affect mortality after first calving.

Cooperators in the NC project reported reduced conception rate, more services per conception, delayed puberty, and more abortions in inbred cattle compared to outbreds. However, intervals from parturition to uterine involution and to first heat were shorter in inbred cattle than in noninbred (15). Calving interval is a conglomerate trait incorporating all of the traits just mentioned, except that a cow must have two calvings to have an interval between calvings. A substantial fraction of culling is based on reproductive performance (2) so only proven reproducers will have recorded calving intervals. Cows with fertility problems from inbreeding may not have had a first or second calving. Examination of estimates of effects of inbreeding on calving interval and the associated standard errors (Table 6) indicates average calving interval is not affected by inbreeding.

Regressions of milk and fat production on inbreeding coefficient (Table 7) were similar to the majority of published estimates (1, 15). In agreement with results of Table 6, regressions of stayability and calving interval on inbreeding coefficient were both close to zero.

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REFERENCES

- 1 Allaire, F. R., and C. R. Henderson. 1965. Inbreeding within an artificially bred dairy cattle population. *J. Dairy Sci.* 48:1366.
- 2 Allaire, F. R., H. E. Sterwerf, and T. M. Ludwick. 1977. Variations in removal reasons and culling rates with age for dairy females. *J. Dairy Sci.* 60:254.
- 3 Bonczek, R. R., and C. W. Young. 1980. Comparison of the ancestry and inbreeding of two lines of Holstein cattle and the Holstein breed. *J. Dairy Sci.* 63 (Suppl. 1):107. (Abstr.)
- 4 Everett, R. W., R. L. Quaas, and A. E. McClintock. 1979. Daughters' maternal grandsires in sire evaluation. *J. Dairy Sci.* 62:1304.
- 5 Foote, R. H. 1970. Inheritance of fertility - facts, opinions and speculation. *J. Dairy Sci.* 53:936.
- 6 Fowler, A. B. 1933. The Ayrshire breed of cattle: A genetic study. *J. Dairy Res.* 4:11.
- 7 Hudson, G.F.S., and L. D. Van Vleck. 1981. Relationship between production and stayability in Holstein cattle. *J. Dairy Sci.* 64:2246.
- 8 Hudson, G.F.S., and L. D. Van Vleck. 1982. Estimation of components of variance by Method 3 and Henderson's new method. *J. Dairy Sci.* 65:435.
- 9 Hudson, G.F.S., R. L. Quaas, and L. D. Van Vleck. 1982. Computer algorithm for the recursive method of calculating large numerator relationship matrices. *J. Dairy Sci.* 65:2018.
- 10 Pollak, E. J., and G. R. Ufford. 1978. Effect of inbreeding on within-herd genetic evaluation of beef cattle. *J. Anim. Sci.* 47:853.
- 11 Quaas, R. L., and R. W. Everett. 1980. Sire evaluation - 1980 style. *In Proc. 1980 Dairy Days*. Dept. Anim. Sci. Mimeo Ser. 46, Cornell Univ., Ithaca, NY.
- 12 Quaas, R. L., R. W. Everett, and A. E. McClintock. 1979. Maternal grandsire model for dairy sire evaluation. *J. Dairy Sci.* 62:1648.
- 13 Rutter, C. R., and R. E. Pearson. 1981. Breeding structure in artificial insemination Holsteins. *J. Dairy Sci.* 64(Suppl. 1):74. (Abstr.)
- 14 Searle, S. R. 1971. Linear models. John Wiley and Sons, Inc. New York, NY.
- 15 Young, C. W., W. J. Tyler, A. E. Freeman, H. H.

Voelker, L. D. McGilliard, and T. M. Ludwick. 1969. Inbreeding investigations with dairy cattle in the North Central region of the United States. North Central Reg. Res. Publ. 191, Tech. Bull. 266, Agric. Exp. Stn., Univ. Minnesota, St. Paul.

APPENDIX

In the linear model:

$$y = W\beta + e, e \sim (0, R\sigma_e^2) \quad [A-1]$$

the estimate of some estimable linear function $k'\beta$ is:

$$\hat{k'\beta} = k'\beta^0 \quad [A-2]$$

where $\beta^0 = (W'R^{-1}W)^{-1}W'R^{-1}y$ is any solution to the equations $W'R^{-1}W\beta^0 = W'R^{-1}y$ and $(W'R^{-1}W)^{-}$ is a generalized inverse of $(W'R^{-1}W)$. The variance of the estimate in [A-2] is (14):

$$\text{Var}(\hat{k'\beta}) = k'(W'R^{-1}W)^{-}k\sigma_e^2 \quad [A-3]$$

Applying [A-3] to the model [2] requires the generalized inverse of the coefficient matrix of the mixed model equations. That generalized inverse was not calculated because solutions were obtained iteratively because of the large coefficient matrix. Instead, $(W'R^{-1}W)$ in [A-3] was replaced by $B'(H^{-1} - X_k(X_k'H^{-1}X_k)^{-1}X_k)B$, which is that part of the mixed model equations (after absorption of herd-year-season equations) corresponding to f . The H is a diagonal matrix with elements dependent on ancestral information available for each cow (4).

The error variance required in [A-3] was estimated by

$$\hat{\sigma}_e^2 = (y'y - \text{reduction due to fitting complete model}) / (\text{no. of observations} - \text{rank of fixed effect equations})$$

When inbreeding was fitted as a covariate, the variance of the estimated regression coefficient could be estimated exactly. In the linear model with covariate:

$$y = W\beta + b\mathbf{c} + e \quad [A-4]$$

the sum of squares $R(b|\beta)$ is used as the numerator of an F statistic to test the hypothesis $Hb = 0$ (See Searle (14), p. 346). $R(b|\beta) = R(\beta, b) - R(\beta)$, which is the difference between reduction in sum of squares due to fitting the model [A-4] with and without the covariate. Each reduction was calculated as the sum of products between solutions and right-hand sides of the mixed model equations with and without the equation for the covariate. The $R(b|\beta)$ can also be calculated as:

$$R(b|\beta) = \hat{b}^2 \left\{ \begin{pmatrix} 0 & 1 \end{pmatrix} \begin{bmatrix} W'R^{-1}W & W'R^{-1}\mathbf{c} \\ \mathbf{c}'R^{-1}W & \mathbf{c}'R^{-1}\mathbf{c} \end{bmatrix}^{-1} \begin{bmatrix} 0 \\ 1 \end{bmatrix} \right\} \quad [A-5]$$

Note that the term inside the braces in [A-5] is a scalar and is equal to $\text{Var}(\hat{b})/\hat{\sigma}_e^2$. Thus, $\text{Var}(\hat{b}) = R(b|\beta)\hat{\sigma}_e^2/\hat{b}^2$.