

Effects of Inbreeding and Selection in a Closed Holstein-Friesian Herd¹

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Abstract

The effects of mild inbreeding and selection were measured in the Iowa State University Holstein herd. Inbreeding of all animals born in the herd from 1930 through 1964 ranged from zero to 47% and averaged 10.2. Selections were made primarily on an index based on the milk fat production and type of the individual and its close relatives. Intra-sire partial regressions and standard errors of production on inbreeding, holding the dam's production constant, were -23 ± 11 and $-.78 \pm .36$ kg for milk and milk fat, respectively. Inbreeding appeared to have little effect on the percentage of milk fat. Type score and percentage of white coloration were essentially unaffected by increased inbreeding. Analyses of weight and body measurements both showed a detrimental effect of inbreeding, but the reduction of weight and measurements due to inbreeding decreased with increasing age. This may be due, in part, to the indirect selection of larger cows that tend to have lower coefficients of inbreeding.

Genetic gain through the selection of parents was estimated to be 0.52 and 0.54% of the mean yield for milk and milk fat, respectively. About 80% of this gain came from the selection of dams of sires.

The genetic constitution of a herd of cattle at any given time is the result of many factors: mutation, migration, selection, chance, and the breeding system followed. Of these, selection and the choice of a breeding system are the only factors over which the breeder, in a closed herd situation, has any control. The purpose of this investigation was to evaluate the genetic and phenotypic consequences of selection and such inbreeding as occurred with selection in a closed herd.

Description of Data

The data for this study were collected in the Iowa State University Holstein herd from

1930 through 1964. The herd was initially closed in 1930, but outside sires were used in 1932, 1933, and 1934. Several heifers were added in 1932. In 1937, the university veterinary and experimental herds were combined. From 1937 on, the herd has been a completely isolated breeding unit.

Selection within the herd, since 1940, has been based on an index. This index utilizes information from the individual, its dam, its daughters, and its maternal and paternal sisters for type and milk fat production in the first 243 days of the lactation. Production is weighted approximately three times as heavily as type. Bulls were selected from the highest indexing dams and were each used for about one year. All heifers were kept for the major part of at least one lactation, unless it was impossible to do so for reasons of sterility, death, etc.

Inbreeding of all animals born in the herd, calculated as Wright's (13) coefficient of inbreeding, ranged from zero to 47%, with a mean of 10.2 and standard deviation of 7.3. The average inbreeding of all animals born in the herd in 1964 was 19.8%, and the average inbreeding of all cows that calved in 1964 was 16.3%.

All production records were standardized to a 243-day, two-time milking, mature-equivalent basis, using factors developed by Kendrick (5). Records of less than 243 days were extended if it was clear that the short lactation was not due to an inherent lack of persistency. These records were extended to 243 days by factors given by Lush (7). Madden et al. (8) have shown that in this herd 243-day records are as good an indicator of inherent productive ability as 305- or 365-day records. The use of 243-day lactations also avoids a large share of the effects of differences in stage of pregnancy.

Methods

The effects of inbreeding on production, type, body weight, measurements, and percentage of white coat color were measured by the within-sire partial regression of the trait on the inbreeding coefficient of the individual, holding the same measure of the trait on the dam constant. Only first lactations were used to study production traits. Body weight, measurements, and type were analyzed at six months, one, two, three, four, five, and seven years of

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age. Percentage white was an average of all estimates made at the same ages that the animals were weighed and measured.

Genetic improvement through selection was evaluated as suggested by Rendel and Robertson (10); i.e., selection of dams of cows, selection of dams of bulls, selection of sires of cows, and selection of sires of bulls. The genetic superiority of each dam was estimated by the formula:

$$\frac{(1 + F)nh^2}{1 + (n-1)r + nh^2F} \cdot \sum_{j=1}^n \left[\frac{\text{dam's } j^{\text{th}} \text{ record} - \text{adj.HA}_j}{\text{adj.HA}_j} \right] \frac{100}{n},$$

where F = coefficient of inbreeding of the dam, n = number of lactations of the dam, h^2 = heritability (assumed to be .25 for both milk and milk fat), r = repeatability (assumed to be .40 for both milk and milk fat), and adj.HA_j = adjusted annual herd average when the dam's j^{th} record was made.

The genetic superiority of each sire was estimated by:

$$\frac{\frac{1}{2} \left[1 + \frac{\bar{F}_d + F_s}{2} + 2\bar{F}_p \right]}{1 + \frac{(n-1)r}{nh^2} + \bar{F}_p + \frac{p-1}{4} \left[1 + \frac{\bar{F}_d + F_s}{2} + 6\bar{F}_p \right]} \cdot \sum_{i=1}^p \left\{ \sum_{j=1}^{n_i} \left[\frac{D_{ij} - \text{adj.HA}_{ij}}{\text{adj.HA}_{ij}} \right] 100/n_i \right\} / p,$$

where D_{ij} = the i^{th} daughter's j^{th} record, $\bar{F}_d$ = average coefficients of inbreeding of the mates of the sire, F_s = inbreeding of the sire, $\bar{F}_p$ = average inbreeding of the daughters, $\bar{n}$ = average number of records of the daughters, h^2 = heritability, r = repeatability, p = number of daughters, n_i = number of records of the i^{th} daughter, and adj.HA_{ij} = adjusted herd average when the i^{th} daughter made her j^{th} record.

The adjusted herd averages (adj.HA) used in the preceding two equations were corrected to account for the inbreeding depression and for previous selection. Each record was corrected to zero inbreeding by adding to the record the product of the cow's coefficient of inbreeding (expressed to the nearest 1%) and the inbreeding depression per unit increase in the coefficient of inbreeding. The yearly herd average can be visualized as a number of first lactations plus a number of later lactations.

The cows making first lactations were an unselected group. However, those cows contributing to the herd average that have had more than one lactation are the survivors of the selection practiced in previous years. To account for this selection the following formula was used:

$$\text{adj.HA}_a = \frac{n_{1,a}}{n_a} [\text{HA}_{1,a}] +$$

$$\frac{n_{>1,a}}{n_a} [\text{HA}_{>1,a} - E(SD_{a-1})_a]$$

where:

n_a = the number of cows having lactations in year a ,

$n_{1,a}$ = the number of cows having first lactations in year a ,

$n_{>1,a}$ = the number of cows having lactations, other than first, in year a ,

$\text{HA}_{1,a}$ = average of first lactations (corrected to zero inbreeding) in year a ,

$\text{HA}_{>1,a}$ = average of lactations, other than first (corrected to zero inbreeding), in year a ,

$E(SD_{a-1})_a$ = the expected value, in year a , of the selection differential for cows selected in year $a-1$.

If selection is based on current production alone, the selection differential for any year would be expressed as the difference between the average production of selected cows and the average production of all cows. However, if selection is based on all records of a cow, the selection differential must take into account the previous production of all selected cows. The expected value of the selection differential in the next year must also take into account imperfect repeatability. Thus, $E(SD_{a-1})_a$ is:

$$\sum_{i=1}^{P_a} \frac{r}{1 + (n_i - 1)r} \frac{\sum_{j=1}^{n_i} (Y_{ij} - \text{HA}_{ij})}{P_a}$$

where:

P_a = number of cows selected in year $(a-1)$ to have another record in year a ,

r = repeatability (assumed = .40 for both milk and milk fat),

n_i = number of lactations of the i^{th} selected cow up to and including her lactation in year a ,

Y_{ij} = j^{th} record of the i^{th} selected cow,

HA_{ij} = herd average when the i^{th} cow made her j^{th} record (all records corrected to zero inbreeding).

Results and Discussion

A total of 709 cows sired by 58 bulls had first lactations. The intrasire partial regression of milk production on inbreeding, holding

dam's record constant, was -23 ± 11 kg of milk for each increase of 1% in the coefficient of inbreeding. The similar figure for milk fat production was $-.78 \pm .36$ kg. Both of these regressions were significant ($P \leq .01$). Percentage of milk fat was decreased .0004% for each increase of 1% in the coefficient of inbreeding. Similar results were reported by Davis et al. (2), Laben and Herman (6), Hansson et al. (3), and Mi et al. (9).

Estimation of percentage white is a visual appraisal of the amount of white coloration on the animal when the profile is viewed from both sides. A correlation of .98 was calculated between these estimates of percentage white and planimeter measurements of a random sample of 50 pictures of two-year-old cows. Estimates from 912 animals in 62 sire groups were available. All available estimates were averaged to give one value for each animal. The intrasire partial regression of percentage white on inbreeding was $.03 \pm .26\%$. Percentage of white coat color is of interest, to determine any genetic drift that may have accompanied inbreeding. No selection was practiced for or against white color, except as this prevented registry. Only 24 animals out of 2,383 were culled for this reason.

The effects of inbreeding on type and measurements are shown in Table 1. The values shown are intrasire partial regression coefficients, where the phenotype of the dam was held constant. The type score of each animal was recorded to the nearest one-third of a classification rating. These were then placed on a scale from zero to 17, corresponding to ratings of low poor to high excellent. The average score over all ages was about eight, or a high good. Except for wither height and body length, which showed maximum inbreeding depression at six months to one year of age,

the inbreeding depression for weight and measurements was most pronounced at four years. After that age it diminished sharply and was essentially nonexistent at seven years. This suggests that the individuals may outgrow the depressing effects of inbreeding, or that inbreeding has the effect of slowing down or postponing maturity. However, in these data selection could enter into the results. If larger, less highly inbred cows were being inadvertently selected (perhaps a correlated response to index selection), the older cows that remained in the herd would tend to be larger and have lower coefficients of inbreeding. This would tend to negate the supposition of delayed maturity. Since all cows were not kept to maturity, it is not possible to clarify this question. The results of these analyses generally confirm other work concerned with inbreeding.

The total genetic improvement per year through the selection of parents, expressed as a percentage of the annual herd average, was estimated to be .52% for milk and .54% for milk fat yield. This is based on the assumption that heritabilities for milk and milk fat yield are .25 and the repeatabilities for both are .40. Table 2 shows the fractionation of this gain from the four paths of selection. In Table 2, L is the generation interval in years, and I is the estimated genetic superiority in percentage of the herd average. The subscripts CC , CB , BC , and BB refer to dams of cows, dams of bulls, sires of cows, and sires of bulls, respectively. The most important source of genetic gain was through the selection of dams of bulls. The selection of sires of cows would not be expected to be particularly strong, since only one sire was used at a time. The reason these values are negative, however, is not fully understood.

Genetic progress was evaluated before the

TABLE 1
Change in type, weight, and measurements per 1% increase in coefficient of inbreeding

	Age (in years)						
	1/2	1	2	3	4	5	7
No. of cows	831	821	760	506	274	143	24
No. of sires	57	57	58	55	44	36	10
Type score	-0.01	-0.02	-0.01	-0.03	+0.02	-0.02	+0.09
Weight (kg)	-0.29 ^b	-0.60 ^b	-1.40 ^b	-1.38 ^b	-1.88 ^b	-1.04	+0.49
Wither height (cm)	-0.07 ^b	-0.07 ^b	-0.05 ^b	-0.05 ^a	-0.04	-0.03	+0.04
Chest depth (cm)	-0.04 ^b	-0.05 ^b	-0.06 ^b	-0.04 ^b	-0.06 ^a	-0.08	+0.04
Body length (cm)	-0.08 ^b	-0.10 ^b	-0.10 ^b	-0.07 ^a	-0.07	-0.06	-0.04
Heart girth (cm)	-0.09 ^b	-0.14 ^b	-0.19 ^b	-0.13 ^b	-0.29 ^b	-0.13	+0.16
Paunch girth (cm)	-0.08	-0.13 ^b	-0.30 ^b	-0.30 ^b	-0.44 ^b	-0.14	+0.52

^a $p < .05$.

^b $p < .01$.

TABLE 2
Evaluation of selection practiced

Years	Generation interval (years)					Selection intensity (% of annual herd average)				ΣI
	L_{CC}	L_{CB}	L_{BC}	L_{BB}		I_{CC}	I_{CB}	I_{BC}	I_{BB}	ΣL
1930-41	3.89	4.27	3.96	4.96	M	-0.26	4.40	-0.27	1.82	0.33
					F	0.22	5.42	-0.48	0.64	0.34
1942-62	4.03	5.18	2.94	3.09	M	1.83	7.20	-0.79	0.92	0.60
					F	1.75	8.06	-0.58	0.12	0.61
1930-62	4.00	4.80	3.44	3.62	M	1.30	6.44	-0.63	1.16	0.52
					F	1.36	7.34	-0.63	0.43	0.54

introduction of the selection index in 1940, as well as after its introduction. The effectiveness of selection was nearly doubled in the years following 1941. Part of this is probably due to the use of the selection index. However, the herd size increased from about 40 cows to nearly 80 cows about then. Also, involuntary losses were less after 1941.

In a previous study on the effectiveness of selection in the Iowa State University Holstein herd, Walton (12) estimated genetic improvement to be .59% per year and .58% per year for milk and milk fat, respectively. Rendel et al. (11) estimated that a genetic gain of between .3 and .4% of the mean per year was made in 22 British herds. Hillers and Freeman (4) estimated that a .33% increase in milk yield and a .57% increase in milk fat yield resulted from selection in a small closed Guernsey herd. An average of .7% increase per year was estimated by Arave et al. (1) as the genetic gain in fat-corrected milk yield in 12 California Jersey herds. All these figures fall short of the 1% of the mean suggested by Rendel and Robertson (10) as the maximum rate of genetic improvement without progeny testing or artificial insemination.

Conclusions

The average effect of inbreeding was detrimental for milk and milk fat production. This was also true for all measures of growth, particularly at the early ages. There was little, if any, real change associated with inbreeding in type score or percentage of white in the coat color, a trait for which little selection was practiced.

Selection for yield of milk fat in this closed herd was effective, but not as effective as seems theoretically possible for single trait selection.

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