

EFFECT OF INBREEDING ON PRODUCTION IN HOLSTEINS¹

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SUMMARY

Data collected over a 25-yr. period from the Iowa State College Holstein herd were used to study the effect of inbreeding on production. The inbreeding ranged from zero to 34% and averaged 7.4%. Records used were standardized to a 305-day-2 $\times$ -M.E. base. The number of cows used in each analysis varied but, at the most, 534 were available. Intra-sire regressions, using the average of each cow's records, were -1.74 ± 0.57 lb. of butterfat, -54 ± 17 lb. of milk, and $+0.003 \pm 0.003\%$ of butterfat for each increase of 1% in inbreeding. There was no evidence of curvilinearity in the effect of inbreeding on fat production. Differences among the individual sires' regressions were not significant. Inbreeding affects production mostly through channels other than reducing general size. This was shown by comparing the regression of production on inbreeding with and without holding heart girth constant. The partial regression was still about three-fourths as large as the simple regression. Partial regression of production on inbreeding, with the dam's production held constant, did not differ appreciably from the regression obtained when the dam's record was disregarded.

In certain situations, inbreeding is an unavoidable consequence of the breeding plan. Among these would be linebreeding programs, and when herds are thought to be of such high genetic merit that breeding animals of higher merit can be found within the herd than in other herds. The primary purpose of the present study was to assess the effect of inbreeding on production, so as to estimate whether the loss (if any) in average phenotypic merit, because of the inbreeding, is likely to exceed the gains which are sought in the plan.

Woodward and Graves (12,13) and Swett *et al.* (10) reported on the effect of inbreeding on production, in the experiment started by the USDA to determine if farmers' herds could be upgraded by using only one registered sire in a sire-daughter mating system. In the first few generations, the inbreeding effects were confounded with breed differences. However, after the cows became predominantly one breed, further inbreeding caused a decrease in milk and butterfat production.

Bartlett and Margolin (1) compared 39 outbred and 40 inbred Holstein cows and found that the outbreds were significantly higher in milk and butterfat yield, but the inbreds averaged 0.05% higher in butterfat test. Plum (8) found a significant intra-sire correlation of -0.24 between inbreeding and butterfat production in a Jersey herd of 181 cows.

The several experiments which were analyzed by calculating intra-sire regressions of production on inbreeding are summarized (Table 1). The regressions by Tyler *et al.* (11) were calculated with the dam's record held constant.

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TABLE 1
Average changes in production for each increase of one per cent in inbreeding

Authors	Type of record	Cows (No.)	B.F. (lb.)	Milk (lb.)	Fat (%)
Davis <i>et al.</i> (3)	305-2×-ME	630	-0.66	- 30.8	+0.003
Laben <i>et al.</i> (4)	305-2×Jr2	164	-4.88	-203.8	+0.008
Laben and Herman (5)	305-2×-ME	299	-2.07	- 66.1	+0.003
Nelson and Lush (7)	305-3×-ME	156	-4.5	-	
Robertson (9)	305-2 yr. 10 mo.	80		- 30.0	0.0
Tyler <i>et al.</i> (11)	305-2×-ME	89	-2.32	- 73.8	+0.005

SOURCE AND ADJUSTMENT OF DATA

The data came from the Iowa State College Holstein herd from 1930 to June of 1955. After 1930, the herd was almost closed to outside breeding. No outside bulls at all were used after 1934 and no females were introduced after 1937. The purpose of closing the herd was to determine the effects of selection, combined with such inbreeding as would necessarily arise in a finite population of this size. In the selections, production was considered roughly three times as important as type, and information on relatives was given some attention in the selection index. In the earlier years of the experiment, the selection differential for females could not be high because of many troubles, such as pneumonia and reaction to Bang's tests. Sons of the best cows were picked for sires and, as soon as they were of serviceable age, were bred to approximately 40 cows, then were sold with the option of repurchase. This option was exercised only twice.

The 534 cows with records were daughters of 69 sires. Among them they had 1,350 production records averaging 414 lb. of butterfat. The records were standardized to a 305-day, two-time milking, mature equivalent basis.

Most of the inbreeding was slight. The coefficients (Wright's) ranged from 0 to 34% with a mean of 7.4 and a standard deviation of 6.4. The average inbreeding of the cows which calved in 1954 was 11.8%. During the early years of the experiment only a few were inbred at all, and few of these more than 12.5%. In later years, as the background relationship became higher, the average inbreeding increased and the distribution of inbreeding coefficients became less extremely skewed, but the long tail of the curve remained in the direction of high inbreeding, because the bull in service could not have more than one dam and rarely had any full-sisters among his mates.

METHODS AND RESULTS

Simple regressions of production on inbreeding. An inbreeding experiment concerned with dairy cattle is necessarily a long-term project. This is especially so when there is no special effort to increase the inbreeding rapidly. The main reason for this is that the generation interval for dairy cattle is of the order of five years. One cannot hope to hold environmental conditions entirely constant during so long a period as this experiment. Even if it had been physically and

economically feasible to control feeding and management conditions, other extraneous factors, such as temperature, pasture quality, and incidence of disease, are impossible to control wholly. Some important effects of these may even be unknown. Furthermore, the mean genetic composition of the herd can scarcely have remained constant during the past 25 years. The selection for production is likely to have made some genetic changes, natural selection may have been effective in unknown ways, and the very nature of inbreeding permits gene frequency to drift randomly. These sources of change are in addition to any general effects of the inbreeding. The fact that more of the less inbred cows made their records in the earlier part of the experiment, whereas the more highly inbred cows were more frequent in the later years, confounds trends in average inbreeding with time trends in other factors.

Making the analysis on an intra-sire basis would bypass most of the effects of both genetic and environmental time trends, by removing the variance caused by trends and leaving that variance unanalyzed. This is because the comparisons then are only between daughters of the same sire. Since the sires in this herd were nearly always used for only about a year, their daughters were likely to have been nearly contemporary in their lives and production. The pooled intra-sire regression of production on inbreeding is a weighted average of the individual regressions for the daughters of the several sires.

The assumption, usual in the case of regressions, that for complete validity the X 's (the independent variable) are measured without error, need not be fulfilled in this case. The X 's used in the calculations are inbreeding coefficients calculated according to Wright (14). These are merely expectations of the probable loss in heterozygosis and, therefore, could be in error for any one animal because of the random chance in Mendelian segregation and recombination. However, such an error is merely the amount by which actual heterozygosis is more or less than the computed X . Provided that the only reason for there being any regression at all of production on inbreeding is the inbreeding itself, the true value of Y is correlated with these errors in X . This introduces a term in the numerator of the regression which cancels the effect of the denominator being too large. Berkson (2) has advanced a more comprehensive explanation of the reason the regression is unbiased in such cases. Some slight error in the independent variable could arise if differential mortality between the inbreds and noninbreds caused the actually more heterozygous animals to be more likely to live to production age than the less heterozygous ones, which had the same inbreeding coefficients. This would tend to make the regression coefficient a bit nearer to zero than it should be.

TABLE 2
Intra-sire correlations and the regressions of production on one per cent of inbreeding

	B.F.	Milk	Fat
			(%)
Regression	-1.74 ± 0.57	-54 ± 17	$+0.003 \pm 0.003$
Correlation	-0.14 ± 0.05	-0.15 ± 0.05	$+0.05 \pm 0.05$

All of the 534 cows were used in this part of the study. The simple intra-sire regressions and correlations are shown (Table 2). The correlations between inbreeding and production characters would all have been slightly smaller if single records instead of averages had been used.

The present estimates seem low, compared to the estimates Nelson and Lush (7) found, using part of these same data. The population would have had to behave quite differently since 1942, because there would certainly be some automatic resemblance in the regressions. To inquire into this, the data were divided into two parts: cows born before 1940 and cows born after 1940. The within-sire regressions of butterfat yield on inbreeding were then calculated for both periods. The regressions calculated for cows born before 1940 were not expected to correspond exactly to the figure from Nelson and Lush. It was not possible to use precisely the same cows and there were some differences in the records used. For instance, their data were on a three-time milking basis. The regression found here for cows born before 1940 was -3.89 lb. of butterfat and for cows born after 1940, -1.33 lb. The difference between the two regressions was not significant; however, it was nearly so ($t = 1.68$ with 462 degrees of freedom). If the regression from Nelson and Lush (-4.5 lb.) is corrected approximately for three-time milking by subtracting 20%, it becomes -3.6 lb.

Effect of inbreeding with dam's record held constant. Morley (6) suggested that the simple linear model, such as was used in the previous section, might be inadequate when the population had been subjected to selection. He reasoned that sires would be selected from the genotypically superior female families. The sires, thus being more closely related to the females in these superior families than to the rest of the herd, would tend to produce their more highly inbred offspring from females above average in transmitting ability. If this bias were important, the simple regression model would underestimate the real effect of inbreeding. The bias will be more when the heritability of the character concerned is high. The extent of this bias will depend on several things, especially on the family structure of the herd and whether the sires are, in fact, much more closely related to the higher-transmitting half of the cows than to the lower-transmitting half. The matings in the Iowa State College herd were made without any conscious attempt either to avoid or to favor inbreeding.

Morley recommended that the phenotype of the dam be considered as an additional independent variable. Then an intra-sire partial regression of production on inbreeding should give an estimate unbiased by any average relation between production of dam and inbreeding of daughter.

Only 484 cows were available for this part of the analysis, because some cows used in the simple regressions had no record available for their dams. This analysis was also on an intra-sire basis.

The correlations between dam's production and daughter's inbreeding are all very small. Only the one for butterfat percentage approaches significance. It is the smallness of these correlations which makes the partial and simple regressions so nearly alike and keeps Morley's argument unimportant in these data.

TABLE 3
Effect of inbreeding with and without considering dam's record

	Regression of daughter's production on each per cent of her inbreeding		Correlation between dam's production and daughter's inbreeding
	Partial	Simple	
Butter yield	-1.72 ± 0.57	-1.72 ± 0.58	-0.001 ± 0.05
Milk yield	-52 ± 17	-50 ± 19	0.05 ± 0.05
Butterfat percentage	0.003 ± 0.002	0.002 ± 0.003	-0.09 ± 0.05

Effect of inbreeding with heart girth held constant. According to Nelson and Lush (7), increased inbreeding caused a decrease in the cow's size in the Iowa State herd. They found that size was affected most at 2 yr. of age and that the effect decreased as the cows got older. At 5 yr. of age, the regression of size on inbreeding was positive. They postulated that inbreeding slowed down the growth rate but did not limit ultimate mature size. However, their data at the older ages were few. In the present analyses, it was thought desirable to find whether the depressing effect of inbreeding on production was due to decreased size of the more highly inbred cows, or if inbreeding was acting on production through channels other than its effects on size.

First records were used for this part of the analysis. When the cows started their first production records, their ages ranged from 21 to 36 mo. The records were converted to maturity, in order to eliminate differences caused by this range in ages. The cows were measured at as nearly 2 yr. of age as was practical. Seldom did the cow's age at measurement deviate more than 1 wk. from its second birthday. Measuring the cows at a fixed age, while they naturally varied in their age at first calving, allowed differences in the stage of gestation to introduce some extraneous variation in the measurements. Heart girth was used because it was thought to be the best measure of general size (among those measurements available) and was not likely to be influenced much by stage of gestation.

Multiple regression (intra-sire) was the method of analysis, just as in studying the dam's production. The 495 cows which also had a 2-yr.-old heart girth measurements were the progeny of 54 different sires. This and subsequent analyses were confined to butterfat production, because inbreeding seemed to have little or no effect on butterfat percentage.

The simple regression of production on inbreeding was -2.72 ± 0.63 lb. of butterfat; whereas, the partial regression of production on inbreeding with heart girth held constant was -2.05 ± 0.64 lb. The simple regression of heart girth on inbreeding was -0.30 ± 0.05 cm. for each increase of 1% in inbreeding. The simple correlation between heart girth and butterfat production was $+0.22 \pm 0.05$. All of these regressions and correlation coefficients are significantly different from zero at a probability level of less than 1%. The difference between 2.72 and 2.05 seems to indicate that the depressing effect of inbreeding on production is in part a consequence of its having depressed size or growth rate,

but the 2.05 indicates that much of its effect on production goes through one or more other channels.

Test for linearity and homogeneity of regressions. It seemed desirable to investigate whether the regression of production on inbreeding is, in fact, linear. If all the effects of the genes were simply additive, there is no apparent reason for inbreeding per se to have any effect on production. If all of the nonlinear effects of the genes are those due to some degree of dominance of genes for high production (even including overdominance), inbreeding would cause production to decrease, but the decrease should be linear with the inbreeding coefficient. Certain kinds of epistatic effects would cause a curvilinear decrease in production. For instance, those epistatic effects which involve the simultaneous presence of the heterozygote dominance deviations in at least two different pairs of genes would cause a curvilinear decrease. The more pairs of genes involved in such combinations, the faster inbreeding would break up the combinations. If inbreeding reached a level of 50%, theoretically only 1/16th of the 4-pair, one-eighth of the 3-pair, one-fourth of the 2-pair, and one-half of the 1-pair combinations would be left.

The regressions presented in the previous sections were average regressions for all sires. It seemed appropriate to find whether the regression coefficients of individual sires differed from each other more than would be expected by chance. Such differences might be expected if the inbreeding decline were due only to the uncovering of recessives and the sires varied much in the number of these they carried. To test these two things, the analysis of variance (shown Table 4) was calculated. In order to get a reasonable number of cows within

TABLE 4
Analysis of variance to test for linearity of the regressions and for homogeneity of the regressions of individual sires

Variation due to:	Sum of squares	Degrees of freedom	Mean square
Total	2,172,262	501	
Among sires	419,599	44	
Within sires	1,752,663	457	
Among F _x classes within sires	503,576	157	3,207
Pooled intra-sire regression	45,951		45,951**
Among regressions of individual sires	91,608	44	2,082
Deviations from linear regressions	366,017	112	3,268
Within F _x classes within sires	1,249,087	300	4,164

** Statistically significant beyond the .01 level.

each inbreeding class, the cows were grouped in intervals of 3% of inbreeding. Sires with only one or two daughters were discarded, because they did not contribute to the analysis. This left 502 cows by 45 sires. Again, the average of all of a cow's lactations was used as a measure of its butterfat production.

The surprisingly small mean square for differences among the regressions of individual sires seems to indicate that the decline in production caused by inbreeding is due to many genes, each of which would necessarily have a rather small effect. If this decline were due to inbreeding uncovering a very few major recessives with important detrimental effects, surely some of the sires would

have been heterozygous for more of these major genes than others. Thus, differences among sires should have been found. The smallness of this mean square also appears to indicate that the variation among sires in transmitting ability was small. A positive correlation between the inbreeding of a sire's daughters and their relationship to him is a necessity. Then, if a sire had an individual transmitting ability far above the level of the herd, his inbred daughters, being more closely related to him, should for that reason have higher production. Conversely, if some sires with transmitting ability far below average were picked by mistake, their more highly inbred daughters should be farther below the herd average.

The small mean square (3268) in Table 4 for deviations from linearity for each individual sire's regression line indicates that the true regressions are linear. Otherwise, this mean square would be expected to be larger than the mean square just below it. The data actually agree a little better than expected with the hypotheses that the regressions for individual sires are (a) equal and (b) linear.

DISCUSSION

The level of inbreeding reached in this herd, after more than 20 yr. essentially without introduction of outside blood, emphasizes that a herd of this size can be closed for a long time without the inbreeding reaching a high level. Actually, since production has been increased above starting levels, the accumulated inbreeding might be considered as an additional benefit, since that gives some promise that the cows would transmit their high level somewhat more uniformly. If the number of sires in use at any one time had been still larger, and an effort had been made to avoid mating highly related animals, the level of inbreeding could have been kept even lower.

Intra-sire regressions of -1.74 lb. of butterfat, -54 lb. of milk, and $+0.003\%$ butterfat, for each increase of 1% of inbreeding, are well within the range of the findings reported by other workers. Most of the investigations, including this one, have found a slight positive regression of butterfat per cent on inbreeding. It is well known that environmental conditions which affect milk and butterfat production adversely tend to raise butterfat percentage. Perhaps this is enough to explain the apparent slight effect of inbreeding on butterfat percentage.

Although not quite significant, the difference between the regressions for cows born before and after 1940 seems unduly large. There is approximately only one chance in ten that a difference this large would have been found, if, in fact, there were no true difference. Selection has been much stronger since 1940 than before, and it seems plausible that this might have had some influence on the effect of inbreeding. If the regression were curvilinear, there could be a difference in the two linear regressions, because the more highly inbred cows tended to make records after 1940. However, no evidence was found to indicate that the regression was not linear.

Holding the dam's record constant did not alter the regression coefficients appreciably. This happened because the correlations between the dam's pro-

duction and daughter's inbreeding were small and varied in signs. Considering that approximately one-tenth of the data had to be discarded, and that the simple and partial regressions were nearly alike, holding the dam's record constant seems not to have added enough information to be worth while in these data.

Reduction of the simple regression of -2.72 lb. to -2.05 lb. for the partial regression of inbreeding on first lactation fat production, when heart girth is held constant, indicates that inbreeding causes some of the decrease in production through its detrimental effect on body size. This would be expected from the a priori knowledge of the positive correlation between size and production and the negative correlation between inbreeding and size. Although this reduction is only of the order of one-fourth, perhaps it should be considered when assessing the effect of inbreeding on production, because the smaller cow is not necessarily less economical even though on the average it produces less.

A difference as large as the one between the regression of -2.72 for first records and -1.74 for average records seems too large to be written off as likely to have been caused by chance alone. A plausible explanation of the differences between the regressions for first and average records is that the depressing effect of inbreeding on size and production is materially reduced at older ages: i.e., that inbreeding acts more to lower the rate of development than it does to limit eventual size and production at maturity. Therefore, when average records are used some, but not all, of the adverse effect of inbreeding on production would be removed.

It would be interesting to know whether the effect of inbreeding on production is reduced or eliminated at maturity. Unfortunately, when the population has been subjected to selection, no way to evaluate the effect of inbreeding at different ages is apparent. If the cows are selected on their own performance (as was the main basis for their selection here), the older cows would tend to be the better producers, regardless of their inbreeding coefficients.

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