

DEPARTMENT OF AGRICULTURE
 MILK AND DAIRY BRANCH

Results of Inbreeding Grade Holstein-Friesian Cattle¹

By T. E. WOODWARD, *dairy husbandman*,² and R. R. GRAVES, *head, Division of Dairy Cattle Breeding, Feeding, and Management Investigations, Bureau of Dairy Industry, Agricultural Research Administration*

CONTENTS

	Page		Page
Introduction.....	1	The transmitting ability for level of production of the six sires.....	22
Breeding of bulls.....	2	Sire 1.....	22
Breeding of foundation cows.....	6	Sire 2.....	24
Results of inbreeding.....	7	Sire 3.....	26
Services required for conception.....	7	Sire 4.....	27
Normality of calves.....	9	Sire 5.....	28
Birth weight of calves.....	10	Sire 6.....	29
Mortality of calves.....	11	Effect on level of production of the close inbreeding to sire 2.....	32
Rate of increase in weight of calves.....	11	The effect of outbreeding on level of production.....	34
Changes in body weight after 2 years of age.....	13	Summary and conclusions.....	36
Conformation and vigor.....	14		
The production of milk and butterfat.....	15		

INTRODUCTION

This investigation on inbreeding grade Holstein-Friesian cattle was the outgrowth of a breeding experiment begun in 1912, at the dairy experiment station at Beltsville, Md., to determine whether a good dairy herd could be bred up from an ordinary one by the use of a good bull. The plan was to mate the bull with the foundation cows and also with all his female offspring throughout his entire useful life. Inasmuch as the results of such a breeding experiment would depend on the individuality of the bull used, the experiment was started with two bulls of different breeds. Some of the foundation cows were mated with one bull and some with the other; but each bull was mated with his own daughters for all the following generations.

A well-bred Guernsey bull and a registered Holstein bull were used to start the experiment with 27 foundation cows of mixed breeding. The experiment proceeded substantially as planned until the herd became infected with Bang's disease in 1914. By 1918 the disease,

¹Submitted for publication January 18, 1946.

²Retired July 31, 1944.

coupled with the efforts to eradicate it, had nearly terminated experiment. The females of the Guernsey group were breeding with such uncertainty that the work with that group had to be discontinued but enough females of the Holstein group were salvaged to continue with this breed.

By the time the first Holstein sire—Johan Woodcrest Lad 11th 103987—had become impotent, a fair start had already been made in the inbreeding of grade Holsteins. As no injurious results from inbreeding were yet apparent, it was decided to continue the experiment for the purpose of determining the effects of close inbreeding on the health and size of the cattle and on milk production. The general plan of the inbreeding experiment was to mate a bull with his own spring as long as he retained his potency, then follow in the same way with a highly inbred son of the preceding bull, and so on. As a check on the inbreeding results, each cow was to be mated with an unrelated registered Holstein bull after she had produced two daughters by the inbred bull. For one reason or another, however, a number of the cows were bred to an unrelated bull before they had produced their heifer calves.

The final results of the experiment with the Guernsey group were published³ in 1933, and some tentative conclusions from the unfinished work with the Holstein group were also included, which were brief as follows: Inbreeding had no adverse effect on the fertility or on the normality of the calves. The birth weights were reduced and the mortality in early life was increased. Inbreeding appeared to depress the rate of growth and to reduce mature size. There was no definite evidence that the moderate amount of inbreeding practiced up to that time was detrimental to the production of milk and butterfat.

The 1933 progress report did not include data beyond the F_3 generation. This bulletin gives data on growth for animals up to the F_4 and F_5 generations, and on production for some animals in the F_5 generation.

The data in this investigation were assembled with reference to Wright's coefficient of inbreeding. Because the inbred bulls became impotent or died at an early age, it was difficult to get many animals with a coefficient of inbreeding beyond 50 percent.

Since the appearance and behavior of the animals indicated that inbreeding at high levels of intensity for successive generations was having a noticeable effect, the data were assembled also with reference to the number of generations of experimental breeding. The offspring of the foundation cows were counted as the first generation although they were not inbred.

BREEDING OF BULLS USED

The first Holstein bull used in the work (sire 1) was Johan Woodcrest Lad 11th 103987. He was by Johan Woodcrest Lad 52145 and cow of Lillian Walker Nudine 16229, a cow with an advanced-register record of 16,229 pounds of milk and 518 pounds of butterfat at 2 years 4 months of age.

³ WOODWARD, T. E. and GRAVES, R. R. SOME RESULTS OF INBREEDING GRADE GUERNSEY AND GRADE HOLSTEIN-FRIESIAN CATTLE. U. S. Dept. Agr. Tech. Bull. 339, 32 pp., illus. 1933.

The second bull used (sire 2) was an 87.5 percent inbred son of sire 1. Sires 3 and 4 were 75 percent inbred sons of sire 2. Sire 5 was a son of sire 3. Sire 6 was the result of mating sire 3 with his own dam, and sire 7 was the result of mating sire 6 with his own dam. Sire 8 was a son of sire 6 out of a cow by sire 3.

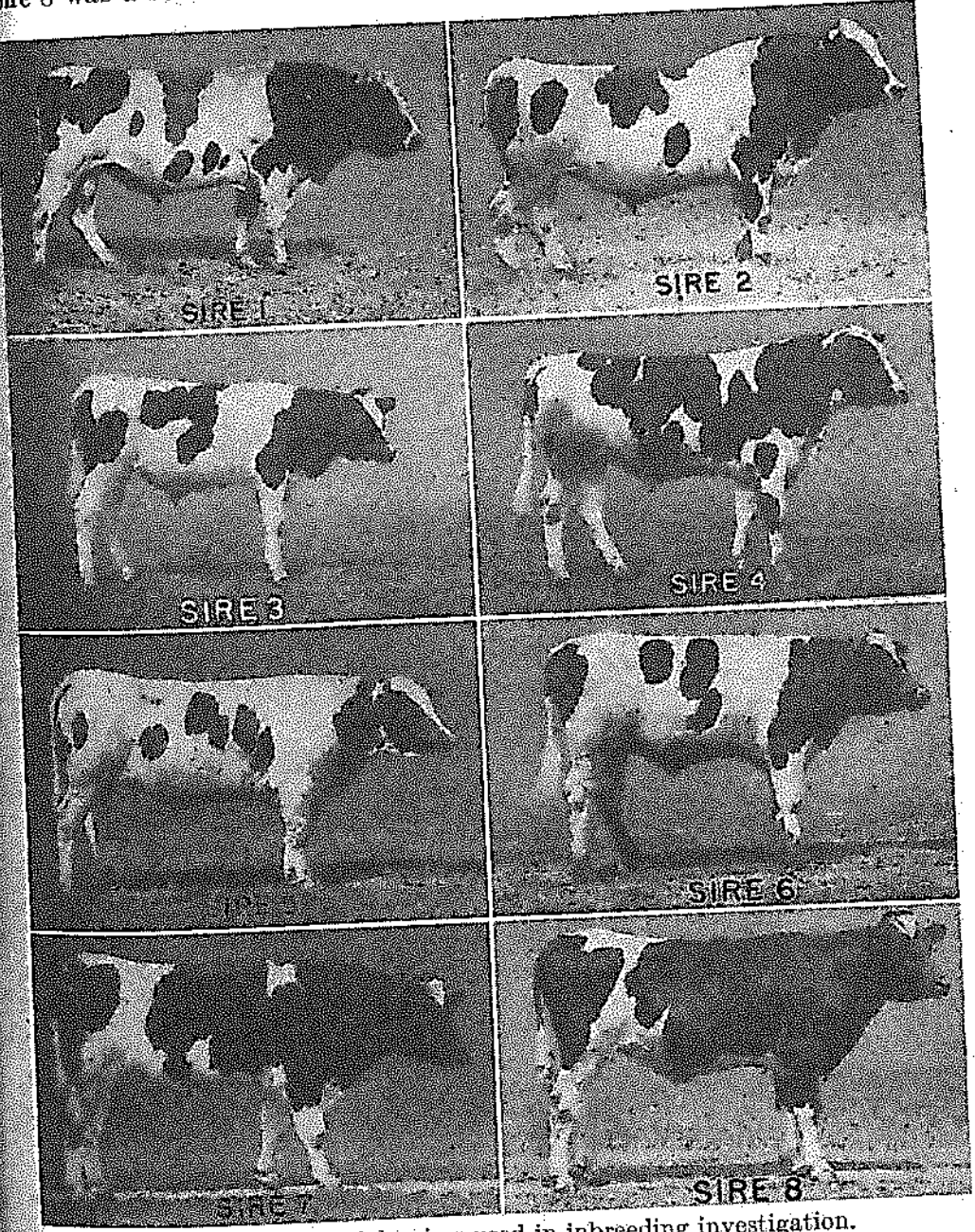


FIGURE 1.—The eight sires used in inbreeding investigation.

Figure 1 shows the eight sires used in this investigation, and table 1 gives the coefficients of inbreeding according to Wright's formula and other information regarding these sires.⁴ The pedigrees of the sires are shown on pages 4-6.

⁴ WRIGHT, S. COEFFICIENTS OF INBREEDING AND RELATIONSHIP. Amer. Nat. 56: 330-338. 1922.

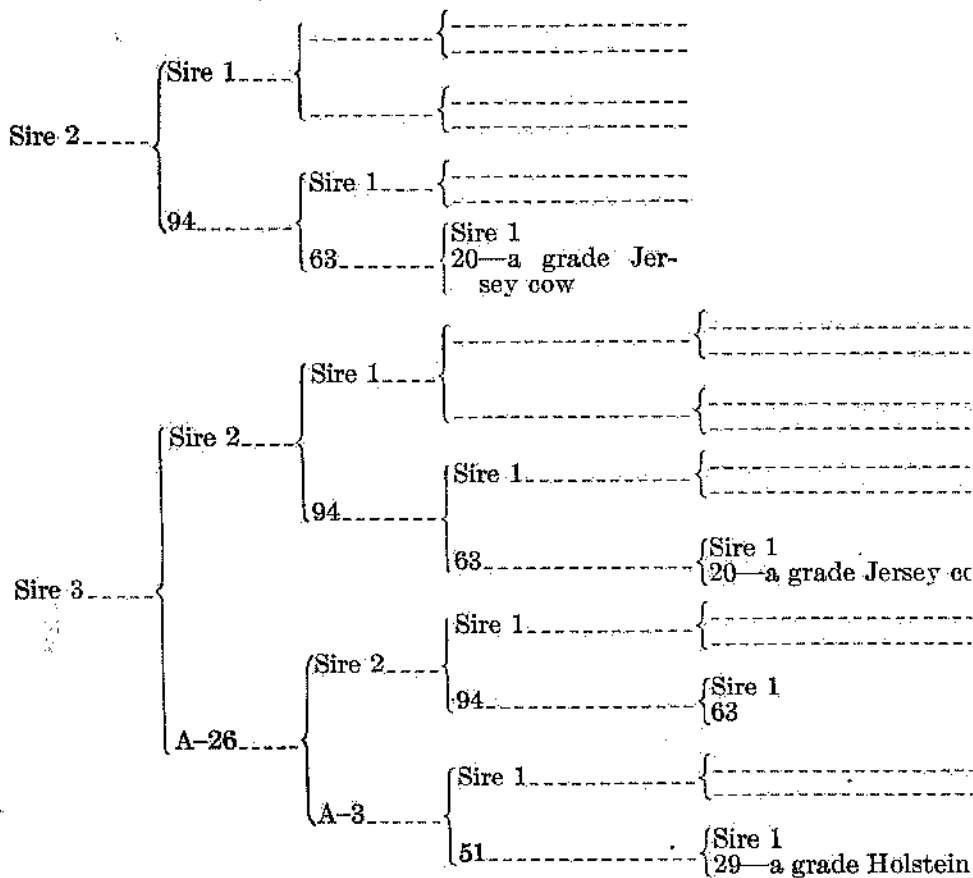
Table 1.—Coefficients of inbreeding, breeding efficiency, and transmitting ability of the bulls used in this investigation

Sire No.	Sire's coefficient of inbreeding ¹	Age at time of death or impotence	Services per conception	Male and female get	Daughters completing at least 1 year's record	Average production of daughters ²		
						Milk	Butterfat	
	Percent	Yrs. Mos.	Number	Number	Number	Pounds	Percent	Pou
1	0	11 0		55	19	11,609	3.70	
2	37.5	8 0	2.80	74	29	13,244	3.48	
3	50.8	2 6	2.40	21	10	13,118	3.53	
4	34.4	3 6	2.08	29	10	12,256	3.43	
5	29.9	3 0	2.05	18	5	11,752	3.51	
6	50.4	8 6	3.32	70	18	11,137	3.34	
7	58.4	2 6	3.25	6	1	7,729	3.27	
8	47.9		2.45	9	0			

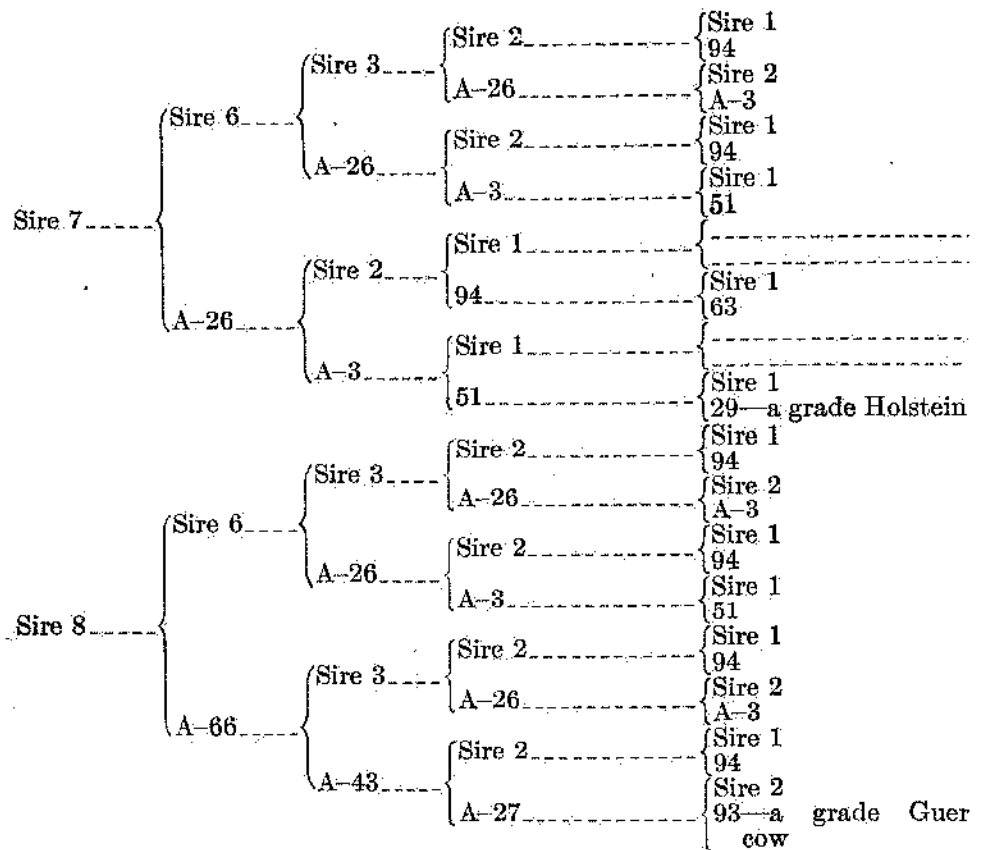
¹ Wright's formula.
² 365-day records as junior 2-year-olds.

PEDIGREES OF THE EIGHT SIRE

Sire 1 (Johan Woodcrest Lad 11th 103987) -- {Johan Woodcrest Lad 52145
 Lillian Walker Nudine 16229



PEDIGREES OF THE EIGHT SIRES—continued



BREEDING OF FOUNDATION COWS.

The immediate ancestry of nine of the foundation cows listed below is unknown. The opinion on their breeding is based upon their appearance. The other five cows were by sires of known breeding.

Cow No.	Breeding
7	A red brindle cow weighing about 1,100 pounds, probably Jersey Shorthorn.
18	Typical Jersey color, probably carried at least 75 percent Jersey blood.
20	Do.
21	Do.
23	Do.
25	Do.
A-6	Color black and white, probably 50 percent or more Holstein.
A-7	Typical Holstein color, probably 75 percent or more Holstein.
29	Color black, dam a large red cow, sire a registered Holstein.
33	Fawn color, dam a small red roan cow, sire a registered Guernsey.
34	Dam a grade Jersey, sire a grade Jersey.
84	Dam a grade Jersey, sire a registered Guernsey.
93	75 percent inbred Guernsey.
A-13	Dam A-7 above, sire a registered Holstein.

RESULTS OF INBREEDING

SERVICES REQUIRED FOR CONCEPTION

Table 2 shows the average number of services required per conception for all females of breeding age in the experiment. The females are grouped according to the degree of inbreeding of the fetus, as measured by Wright's formula.

TABLE 2.—Influence of the degree of inbreeding on the number of services required for conception

ALL SIRES INCLUDED

Coefficient of inbreeding (percent) ¹	Pregnancies	Services ²	
		Total	Average per conception
	Number	Number	Number
	113	226	2.00
	41	101	2.46
0 to 24.9	24	54	2.25
1 to 29.9	37	115	3.11
2 to 34.9	28	79	2.82
3 to 39.9	58	154	2.66
4 to 44.9	48	152	3.17
5 to 49.9	55	197	3.58
6 and above			

SIRE 6 OMITTED

	113	226	2.00
	38	98	2.58
0 to 24.9	24	54	2.25
1 to 29.9	34	97	2.85
2 to 34.9	21	64	3.05
3 to 39.9	29	71	2.45
4 to 44.9	25	60	2.40
5 to 49.9	29	85	2.93
6 and above			

SIRE 6 ALONE

	0		
	3	3	1.00
0 to 24.9	0		
5.0 to 29.9	3	18	6.00
10.0 to 34.9	7	15	2.14
15.0 to 39.9	29	83	2.86
20.0 to 44.9	23	92	4.00
25.0 to 49.9	26	112	4.31
30.0 and above			

¹ Refers to the fetus resulting from the conception rather than to either parent.
² Statistical analysis shows the probability of chance occurrence of the increase in services required for conception was less than one in a hundred.

Sire 6 was an uncertain breeder. Whether this was because he was intensely inbred (50.4 percent) or whether it was the result of other causes could not be determined. If inbreeding caused the condition, then the data representing all sires in tables 2 and 3 accurately represent the influence of inbreeding upon the services required for conception and the conclusion that inbreeding adversely affected the fertility seems justified. Most of sire 6's daughters appear in the groups having coefficients of inbreeding of 35.0 percent and above.

However, since there was a possibility that some factor other than intensity of inbreeding was responsible for sire 6 being an uncertain breeder, the data were reassembled leaving out sire 6. These are also

shown in table 2. Aside from the first group, which was not inbred there is no definite indication that the higher degrees of inbreeding affected the fertility. But if the breeding record of sire 6 alone is examined (table 2) it is evident that the number of his services per conception did increase with the intensity of inbreeding.

When the data, including those of sire 6, are assembled with reference to the effect of the number of generations of inbreeding on the number of services per conception (table 3) it is evident that continuous inbreeding increased the services required. If sire 6 is omitted (table 3) the data are not consistent, the number of services per conception for the fourth and fifth generations being out of line with the number for the other generations; but if the record of sire 6 alone is considered (table 3), it is plain that fertility declined with each succeeding generation of inbreeding. It is apparent that the fertility of sire 6 was affected more adversely by close and continuous inbreeding than was that of the other sires.

TABLE 3.—Influence of the generation of inbreeding (female side) on the number of services required for conception

Generation of inbreeding ¹	Pregnancies	Services	
		Total	Average concept.
	<i>Number</i>	<i>Number</i>	<i>Number</i>
First ²	84	183	
Second.....	66	157	
Third.....	87	242	
Fourth.....	68	191	
Fifth.....	38	127	
Sixth and seventh.....	23	105	
GET OF SIRE 6 OMITTED			
First ²	82	181	
Second.....	65	156	
Third.....	55	148	
Fourth.....	44	105	
Fifth.....	12	22	
Sixth and seventh.....	17	70	
GET OF SIRE 6 ONLY			
First ²	2	2	
Second.....	1	1	
Third.....	32	94	
Fourth.....	24	86	
Fifth.....	26	105	
Sixth and seventh.....	6	35	

¹ Generation of inbreeding on the female side.

² Offspring of the foundation cows are counted as first generation, although not inbred.

Further information on this point was obtained by comparing results of mating inbred cows to related inbred bulls and also to related outbred bulls. Twenty-eight cows became pregnant to related inbred bulls and at other times to unrelated outbred bulls. There were 228 services by the inbred bulls and 76 pregnancies—average of 3.00 services per pregnancy. There were 100 services by outbred bulls and 52 pregnancies—an average of 1.92 services

pregnancy. Omitting the cows served by sire 6, the average number of services per pregnancy by the inbred bulls was 2.65 and by the outbred bulls, 1.95.

Fertility was not adversely affected in this experiment as early as one might expect it to be. The earlier generations of inbred animals appeared to be affected very little. The number of generations of close inbreeding appears to have had a more pronounced adverse effect on fertility than did the degree of inbreeding. This is probably because some of the most closely inbred animals were in the earlier generations of inbred animals. Some of sire 2's daughters had higher coefficients of inbreeding than those of any of the other sires except sire 6. The inheritance for vigor of fertility of sires 1 and 2, whose germ plasms were most intensified in this experiment, must have been very good. It was not until the closely inbred sire 6 and his closely inbred get were reached that the vigor of fertility declined at an alarming rate.

NORMALITY OF CALVES

More complete gestation and calving records have been kept since January 1, 1926, than were kept previously. In the period from that date to June 1, 1942, 289 calves were born in this experiment, of which 204 were inbred and 85 were outbred. Of the calves carried for the full gestation period, all the outbred calves and all but 1 of the inbred calves were normal. The abnormal inbred calf is shown in figure 2.

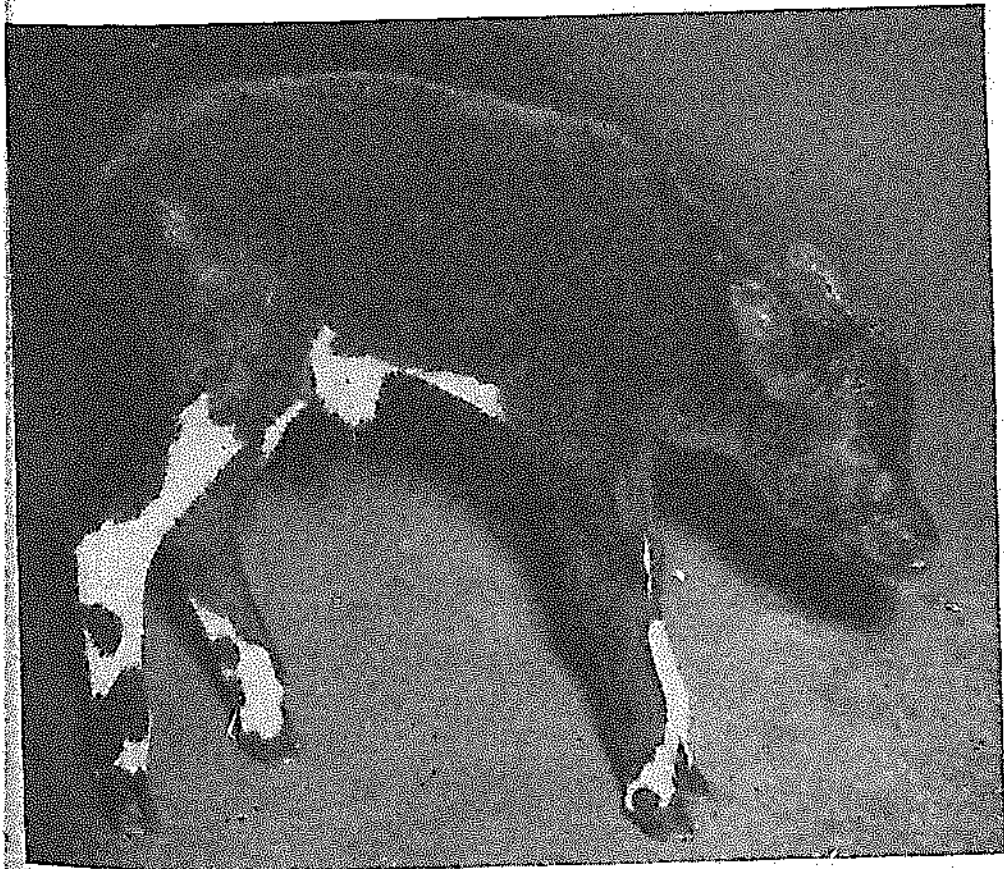


FIGURE 2.—Abnormal inbred calf.

It had an overshot lower jaw, no eyeballs, no tail, and weighed only 48 pounds at birth. Although weak, it lived and grew normally for several weeks before it was slaughtered. This calf was the result of mating sire 8 with his dam. Previous to 1926, another inbred calf was born deformed. It was dead at birth and the posterior part of the spinal column, including the tail, was missing. It was the result of mating sire 1 with one of his 50-percent daughters.

Since only 2 of the 204 inbred calves were malformed, it seems unlikely that these malformations were the result of hereditary defects. At any rate, they probably were not the result of a simple recessive gene, as are many malformations, such as hairless calves and bulldog calves. If these 2 malformations had been caused by a recessive gene, at least 1 in 8 of the inbred calves would have been malformed—provided all the sires carried the recessive gene. Since sire 1 was the sire of the first malformed calf, and the bulls and heifers used subsequently traced many times to him, it seems that many of the inbred calves would have received such a recessive gene through his progeny if he possessed it. Then too, the second malformed calf (by sire 8) appears to have had a different type of malformation than the first malformed calf.

BIRTH WEIGHT OF CALVES

An examination of the birth weights of all the calves showed that the calves from 2-year-old cows averaged 7 pounds lighter than calves from older cows and that male calves averaged 6 pounds heavier than female calves. To make the birth weights comparable for studying the effect of inbreeding, all birth weights were adjusted to the same weight basis as female calves from older cows, by adding 7 pounds to the weight of calves from 2-year-old cows and subtracting 6 pounds from the weight of all male calves. Table 4 shows the influence of the coefficient of inbreeding and also the influence of succeeding generations of inbreeding on the birth weight.

TABLE 4.—Influence of the degree of inbreeding and the generation of inbreeding (female side) on the birth weight of the calves¹

Coefficient of inbreeding	Calves	Average birth weight	Generation of inbreeding	Calves	Average birth weight
Percent	Number	Pounds		Number	Pounds
0.....	47	81.5	First.....	32	81.5
0.1 to 24.9.....	34	84.4	Second.....	70	82.5
25.0 to 29.9.....	37	80.5	Third.....	67	77.5
30.0 to 34.9.....	29	77.8	Fourth.....	47	77.5
35.0 to 39.9.....	24	74.0	Fifth.....	32	69.5
40.0 to 44.9.....	33	69.4	Sixth and seventh.....	19	69.5
45.0 to 49.9.....	38	72.7			
50.0 and above.....	43	65.9			

¹ Includes get of sires 1 to 8, inclusive; does not include get of outbred registered bulls.

In table 4, it will be seen that the outbred calves (represented by 0 coefficient of inbreeding and by the first generation) are smaller than the moderately inbred calves (represented by an inbreeding coefficient less than 25 percent and by the second generation). The reason for this is that about two-thirds of the foundation cows carried a preponderance of Jersey or Guernsey blood and naturally produced

smaller calves than Holsteins. The upward pull of the Holstein breed, for which heavy calves are characteristic, exceeded the downward pull of inbreeding for the second generation. As the second-generation cows carried about as much Holstein blood as the bulls to which they were mated, the upward pull of the breed in succeeding generations was diminished; and the longer inbreeding was practiced, the less was the influence of the breed. The consistent downward trend in birth weight, beyond 25 percent inbreeding and the second generation, can be attributed almost entirely to the influence of inbreeding. It should be mentioned also that the absence of any bad results when the extent of inbreeding was less than 25 percent is in harmony with the results at the New Jersey Agricultural Experiment Station.⁵

Further evidence of the influence of inbreeding was obtained by comparing the weights of the inbred calves produced by 24 cows with the weights of outbred calves produced by the same cows. There were 69 inbred calves and 43 outbred calves. The average weight of the inbred calves was 72.0 pounds and that of the outbred calves was 80.5 pounds, a difference of 8.5 pounds. A part of this difference, but probably not all of it, could properly be attributed to the influence of breed since all of the outcross calves were sired by registered Holstein bulls while most of the inbred calves were sired by grade Holstein bulls.

MORTALITY OF CALVES

From January 1, 1920, to September 1, 1941, 108 inbred female calves and 41 outbred female calves were born in this experiment. Sixteen of the inbred calves died within a year, or 15 percent. None of the outbred calves died. During the same period, 300 outbred female calves were born in the herd of registered Holsteins at Beltsville and 29 of them died within a year, or approximately 10 percent. It appears that the inbred calves were not as vigorous as either the outbred grade calves or the outbred registered calves. Of course, the epidemics of infectious diseases that occurred during this period, such as scours and pneumonia, had a great influence on calf mortality. Inbred calves may have less resistance to infection, or outbred calves from inbred dams may possibly possess a hybrid vigor that makes it possible for them to offer greater resistance to infection. Whether all calves had the same opportunity to be exposed to infections could not be determined.

RATE OF INCREASE IN WEIGHT OF CALVES

The method of raising calves was to feed whole milk for about 3 weeks, then change to skim milk, taking a week or 10 days to make the change and to continue feeding skim milk until the calves were 6 months old. Grain and hay were fed as soon as the calves would eat these feeds. The quantity of grain was limited to about 4 pounds a day until the heifers reached calving age. There was no limit on the quantity of hay allowed at any time. Silage was fed after the calves reached 6 months to a year of age.

⁵ BARTLETT, J. W., REECE, R. P., and LEPARD, O. L. THE INFLUENCE OF INBREEDING ON BIRTH WEIGHT, RATE OF GROWTH, AND TYPE OF DAIRY CATTLE. Jour. Anim. Sci. 1: 206-212. 1942.

1.8
2.3
5.1
1.8
17.3
13.9

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As nearly all the male calves in this investigation were disposed at an early age, the data on increase in weight are for the female calves only. Tables 5 and 6 show the weights of calves at birth and at stated intervals thereafter up to 24 months of age. The birth weights are not adjusted for the age of the dams.

TABLE 5.—Increase in weight of heifer calves as influenced by the intensity of breeding and by the number of generations of inbreeding

Coefficient of Inbreeding	Average weight of calves					
	At birth	At 3 months	At 6 months	At 12 months	At 18 months	At 24 months
	Pounds	Pounds	Pounds	Pounds	Pounds	Pounds
Percent						
0.1.....	85	195	376	685	883	1101
Under 24.9.....	87	194	351	607	706	1001
25.0 to 29.9.....	73	164	317	587	761	951
30.0 to 34.9.....	76	172	323	599	770	961
35.0 to 39.9.....	73	163	300	596	772	961
Average.....	75	169	314	598	771	961
40.0 to 44.9.....	66	161	298	574	730	911
45.0 to 49.9.....	72	182	322	602	780	971
Average.....	70	174	312	590	759	941
50.0 and above.....	64	146	287	562	723	901

GENERATION OF INBREEDING						
First.....	85	195	376	685	883	1101
Second.....	77	176	335	600	769	951
Third.....	75	171	319	601	765	941
Fourth.....	70	163	304	587	747	921
Fifth.....	66	158	304	585	766	941
Sixth and seventh.....	57	125	266	540	726	901

¹ This group is composed mostly of daughters of inbred cows by registered Holstein bulls.

At 24 months of age there was a difference of 100 pounds or more between the outbred heifers and the moderately inbred ones. The difference after, the decline in weight through more intensive inbreeding was less, but it was nevertheless significant. The disproportionately heavier weight of the outbred heifers (represented by 0 inbreeding and the first generation in table 5) can be attributed mostly to the higher percentage of Holstein blood, since by far the greater number were sired by registered Holstein bulls. Only a few of the offspring of the foundation cows are included because weights of the young stock were not being taken regularly in the early years of this investigation.

Another factor that should be considered in the interpretation of these weights is the change in feeding practice that took place during the course of the study. There was a gradual tendency over the many years to feed the heifers to heavier weights at calving time. The more highly inbred animals on the average have had a better opportunity to grow than the less highly inbred animals of the earlier generations. If there were any way of evaluating this factor, the weight of the highly inbred animals would perhaps be even lower. The

ferences in weight at 2 years are less perhaps than would have been expected, when one considers the great difference in birth weights. The weights of the first generation animals shown in table 5 are on an evaluation of 100 percent, the relative weights of those with greater number of generations of inbreeding would be as shown in table 6.

TABLE 6.—Relative weight of animals in the first and subsequent generations

Generation	At birth	At 12 months	At 24 months
	Percent	Percent	Percent
First	100	100	100
Second	88.2	87.7	86.6
Third	77.6	85.4	85.6
Fourth and seventh	67.0	78.8	80.4

The animals with three generations of inbreeding made no change in relative weight from birth to 24 months of age (table 6); but those with five generations of inbreeding had made a gain at 12 months and this gain was maintained at 24 months. Those with six and seven generations of inbreeding made a large gain by 12 months and some further gain at 24 months. The latter animals were 33 percent lighter at birth than the first-generation animals but only approximately 20 percent lighter at 24 months of age.

CHANGES IN BODY WEIGHT AFTER 2 YEARS OF AGE

The more highly inbred animals were distinctly lighter at 2 years of age than the outbred or less highly inbred animals. In order to find out how the cows developed as they gradually approached maturity, data were assembled for cows that had dropped their first and second calves in consecutive years, for the same or other cows that had dropped their second and third calves in consecutive years, and so on for the third and fourth calves. An examination of the monthly weights of lactating cows had indicated that the weight 6 months after calving would be as satisfactory as any for use in determining the actual weight. Cows at that stage of lactation have had an opportunity to recover much of the flesh lost after calving, and they are not far enough along in the period of gestation to make the weight of the fetus a disturbing factor.

The number of cows calving in consecutive years became less and less as the cows approached maturity, and it was because of the small numbers that the data were assembled for only two groups—one below and one above 30-percent inbreeding. The results are given in table 7.

The figures in table 7 confirm our observations that inbreeding reduced the size of the animals, but the reduction in size at maturity was not nearly as noticeable as the reduction in birth weight. As the comparisons in table 7 are of two groups composed wholly or in part of inbred animals, the differences probably are not as pronounced as they would be if the comparison were between an outbred group and those inbred over 30 percent.

TABLE 7.—Weights of cows at 2 years of age and at 6 months after successive calving.

Coefficient of inbreeding	Cows	Age	Weight	Age	Weight	Gain in weight
		Years	Pounds	Years	Pounds	
0 to 30 percent.....	52	2.0	1,040			
More than 30 percent.....	58	2.0	952			
		6 months after first calving		6 months after second calving		
0 to 30 percent.....	29	2.70	1,049	4.03	1,109	
More than 30 percent.....	24	2.73	992	4.13	1,028	
		6 months after second calving		6 months after third calving		
0 to 30 percent.....	20	4.04	1,107	5.33	1,182	
More than 30 percent.....	15	4.08	1,042	5.29	1,116	
		6 months after third calving		6 months after fourth calving		
0 to 30 percent.....	17	5.35	1,178	6.75	1,256	
More than 30 percent.....	13	5.12	1,132	6.35	1,172	

CONFORMATION AND VIGOR

The inbred cows and heifers in this investigation were kept in the same herd with registered outbred and linebred Holsteins. They could, in nearly every instance, be readily identified by the shape of the head and face and the setting of the ears. Figure 3 shows a typical head of an inbred grade Holstein. There is a tendency for the poll to be high and for the ears to have a peculiar setting that gives them the appearance of drooping. There is nothing about the conformation in other ways that would definitely distinguish the inbred grades from the outbred registered Holsteins except that the inbreds are smaller.

In the winter some of the inbreds develop rough coats and this condition is sufficiently pronounced to identify them as inbred. Probably the most outstanding characteristic of the inbred animals is their sluggishness. When the herd is driven to and from pasture the inbreds are always in the rear. They have a peculiar walking gait with a tendency to drag their feet—a sort of shuffling walk. They are definitely less active and less alert to what is going on around them than the outbred Holsteins, and the attendants say that they are more stubborn to handle. Rough hair, sluggishness, dull appearance, and perhaps even stubbornness may be considered as evidences of lack of vigor.

due entirely to the effect of inbreeding or in part to poorer germ plasm. However, the gradual decrease in production level transmitted by each sire used after sire 2, together with the appearance of the animals, causes us to believe that the cumulative effects of intensive inbreeding were a major factor in the decline in production level and in the poor showing of sire 6.

TABLE 16.—*The variation in production by generations*

Generation	Cows	Average coefficient of inbreeding	Average coefficient of variation in—		
			Milk yield	Butterfat test	Butterfat yield
	<i>Number</i>	<i>Percent</i>			
Foundation cows.....	15	0	28.1	8.6	
F ₁	23	1.1	19.0	8.6	
F ₂	25	26.7	18.8	7.7	
F ₃	18	38.4	17.6	5.1	
F ₄	15	44.5	15.2	6.2	
F ₅	8	44.0	14.7	6.0	
F ₆	3	59.9	23.3	6.3	

EFFECT ON LEVEL OF PRODUCTION OF THE CLOSE INBREEDING TO SIRE 2

Perhaps the decline in production level transmitted by the sire is best illustrated by table 17, which shows the comparative results of breeding a sire back to his own daughters and of breeding other closely related sires to that same sire's daughters.

The production records have been mentioned briefly in the discussion of each sire's transmitting ability, but the data are brought together in table 17 to facilitate comparison. Note the uniformity in average yield by the five groups of dams (sire 2's daughters) which the different sires were mated. On the basis of this comparison sire 2 was the best of the sires used. His inbred daughters show the smallest percentage decline in yield of any group, and a high percentage of them were better than their dams than in any other group. Sire 3 was the next best sire. There is considerable difference between the production records of his daughters and those of sires 5, and 6—particularly in butterfat test and in butterfat yield. There appears to be very little difference between sires 4 and 5, but sire 6 is clearly the poorest.

The most astonishing feature of this record of production, in addition to the appearance of the animals and their decline in size, is that production did not decrease even more rapidly as a result of the intensive inbreeding. Everything considered, production has held up remarkably well and this is no doubt due to the splendid germ plasm possessed by sires 1 and 2. Had the inbreeding been to sires who possessed a poorer germ plasm than sires 1 and 2, less favorable results would no doubt have occurred in the early generations. Unfortunately there is no way of determining accurately, other than by a long and laborious breeding test, whether any given animal possesses a germ plasm that will stand up under intensive inbreeding.

THE EFFECT OF OUTBREEDING ON LEVEL OF PRODUCTION

A limited amount of data is available from this experiment for study of the effect, on level of production, of outbreeding on the intensely inbred cows. From time to time, some of the inbred grade cows have been bred to registered, unrelated Holstein bulls. Several of the inbred grade cows that have tested daughters that were sired by the closely related bulls used in this experiment also have tested daughters that were sired by unrelated registered bulls. Table 18 lists these 7 cows and shows the production records of their 11 inbred grade daughters sired by related bulls and of their 7 daughters sired by unrelated, registered bulls.

TABLE 18.—Production records of inbred and outbred daughters of the same cows

Dam	Daughters by related inbred bulls	Production records			Daughters by unrelated registered bulls	Production records		
		Milk	Butterfat			Milk	Butterfat	
		Pounds	Percent	Pounds		Pounds	Percent	Pounds
A-19	A-53	14,440	3.57	516	A-77	15,832	3.32	
	A-90	14,092	3.09	435				
	A-104	12,207	3.01	367				
A-26	A-80	13,513	3.28	443	A-55	15,315	3.48	
	A-93	7,923	2.27	259				
A-36	A-108	10,601	3.58	358	A-54	10,293	3.94	
A-57	A-85	9,162	3.51	322	A-117	8,922	3.24	
A-71	A-96	11,625	3.26	379	A-139	16,580	3.52	
A-97	A-143	12,424	3.39	422	A-130	6,879	3.80	
A-106	A-129	10,428	3.63	379	A-150	13,370	3.45	
	A-142	7,729	3.27	253				
Total or average	11	11,231	3.35	376	7	12,456	3.51	

Six of the inbred daughters were by sire 6, three by sire 4, one by sire 2, and one by sire 5. Only two of the inbred daughters were better in milk yield than their respective outbred sisters, one was better in butterfat yield, and three were better in butterfat test. The outbred sisters were better in average milk yield by almost 11 percent, in butterfat test by 5 percent, and in butterfat yield by 16 percent.

It is difficult to determine whether the difference in yield was due to depression in the production of the inbreds resulting from inbreeding (coefficient of inbreeding 42.5); heterosis in the outbreds resulting from the mating of the inbred grades to unrelated sires; or to a difference in the germ plasm for level of production of the inbred sires and the registered sires. We are inclined to credit the latter possibility for the greater part of the difference in production, since sire 6 sired 6 of the 11 inbred sisters and it has been shown that he had the poor record of transmission of any of the 6 inbred sires used.

Another indication of the effect of outbreeding is a comparison of production records of the daughters of four registered sires. Some of the daughters were out of inbred grade cows in this experiment and some were out of registered cows in the Beltsville herd. Table 19 includes the data for this comparison.

TABLE 19.—Relative production of outbred grade daughters and registered daughters of the same sires

Sire's herd No.	Outbred grade daughters out of inbred grade cows			Average production of registered daughters out of registered cows				
	Herd No.	Butterfat		Daughters' records averaged	Milk		Butterfat	
		Pounds	Percent		Pounds	Percent		Pounds
93	A-54	10,293	3.94	405	13	12,642	3.45	437
	A-77	15,832	3.32	523				
	A-55	15,315	3.48	533				
99	A-150	13,370	3.45	462	22	14,754	3.90	573
	A-115	11,283	3.46	391				
	A-116	10,939	3.40	372				
97	A-117	8,922	3.24	289	6	12,752	3.79	483
	A-118	11,743	3.56	418				
	A-130	6,879	3.80	261				
	A-133	15,154	3.96	600				
	A-135	15,715	3.77	593				
	A-139	16,580	3.52	583				
Total		152,025		5,433	60	1,802,548		1,291,431
Average		12,669	3.57	453		18,377	3.67	491

† Total for 60 records.
‡ Weighted average.

The weighted average production of all daughters of the registered cows, as compared with that of the daughters of inbred grade cows, was 5.6 percent greater in milk yield, 2.8 percent greater in butterfat test, and 8.4 percent greater in butterfat yield. However, three of the registered bulls used had only four daughters out of inbred grade cows. The best comparison is for the bull No. 947. (See table 20.) He has eight tested outbred daughters out of inbred grade cows and six tested inbred daughters out of registered cows. This comparison should offer the best measure of the occurrence of heterosis; the daughters out of the inbred grade dams being radical outcrosses.

TABLE 20.—Relative production of the daughters of sire 947 and their dams

Number of comparisons	Average production per cow		
	Milk	Butterfat	
	Pounds	Percent	Pounds
8 daughters	12,152	3.60	438
8 dams	12,387	3.54	439
Increase (+) or decrease (-) by daughters	-235	+0.06	-1
Daughters better than dams (percent)	50.0	75.0	50.0
INBRED DAUGHTERS OUT OF REGISTERED DAMS			
8 daughters	12,752	3.79	483
8 dams	12,158	3.63	442
Increase (+) or decrease (-) by daughters	+594	+0.16	+41
Daughters better than dams (percent)	67	50	67

The inbred grade dams and the registered dams had almost the same level of production, but sire 947's inbred daughters out of the registered dams had a higher level of production than his outbred daughters out of the inbred grade dams.

There is no evidence here of heterosis. However, there are two possible reasons for the lower level of production of the daughters out of the inbred grade dams. One is that several of these cows had some mastitis during their lactation periods, and the other is that the registered daughters of sire 947 have shown evidence of late maturity in production level. Some of the records for his registered daughters in the above tabulation are second-lactation records, while the records given for the grade daughters are first-lactation records.

Possibly another generation outcross on these outbred animals would have developed the full effect of heterosis. Limited facilities for keeping the animals in this experiment did not permit the keeping of the outbred animals to secure a second outbred generation.

SUMMARY AND CONCLUSIONS

This experiment in inbreeding grade Holstein-Friesian cattle was started with a group of 14 grade cows, of which 10 were predominantly Jersey or Guernsey breeding and 4 were predominantly Holstein breeding, and a registered Holstein sire, Johan Woodcrest Lad 11 103987. This sire was mated to the foundation cows and also to his own daughters. Subsequently seven sires were used in the experiment. All these sires were inbred to Johan Woodcrest Lad 11th and outcross dams that were bred in the herd and that had descended from foundation cows and Johan Woodcrest Lad 11th. Cows representing several filial generations from the foundation cows have production records. Data have also been obtained from some outcrosses—the progeny of unrelated registered sires and inbred grade cows.

The data were analyzed to determine the influence of inbreeding on fertility; on normalcy, birth weight, and mortality of calves; on growth as measured by weight; on the conformation and vigor of the cows; and on the production level for milk and butterfat. Wright's coefficient of inbreeding was used to measure the degree of inbreeding in the analysis of the above characteristics. The influence of the number of generations of inbreeding on these characteristics was also studied.

Fertility was not adversely affected in this experiment as quickly as might be expected. The number of generations of inbreeding had a more pronounced adverse effect than did the degree of inbreeding, perhaps because some of the most closely inbred animals appeared in the early generations. It was not until the closely inbred sire 6 that his closely inbred get became a factor in the experiment that vigor and fertility declined at an alarming rate. When the inbred cows were mated to unrelated sires the average number of services per conception was appreciably less than when they were mated to the closely related bulls.

There were 2 malformed calves among the 204 inbred calves in the experiment. Several generations elapsed between the appearance of the malformed calves. Also the malformations appeared to be of different types. Apparently they were not the result of sire

recessive genes, as is the case with many types of malformations, or they would have occurred with greater frequency.

Birth weights of the calves declined from an average of 81.5 pounds for the outbred calves resulting from unrelated matings to 65.9 pounds for inbred calves having a coefficient of inbreeding of 50.0 percent or over. Likewise the birth weights declined from an average of 81.8 pounds for the first generation calves to an average of 63.9 pounds for the calves that were the product of 6 and 7 generations of inbreeding.

The percentage of mortality was greater among the inbred calves than among the outbred calves in this experiment and also in the registered herd at the same station. Apparently the inbred calves were not as vigorous or as resistant to calfhoo infections as the calves that were not closely bred.

The rate of growth of the calves, as influenced by the degree of inbreeding and the number of generations of inbreeding, was analyzed by comparing their average weights at 3, 6, 18, and 24 months of age. The comparisons based on the number of generations of inbreeding showed that the first-generation animals (outbred) were the heaviest group at all ages and that the sixth and seventh generations combined were the lightest group at all ages. However, the difference in weight between the first-generation group and the sixth-and-seventh generation group was not as great at 1 year of age as at birth, nor as great at 2 years as at 1 year. Up to 1 year of age, the first-generation calves made an average daily gain of 1.64 pounds, the second-generation calves gained 1.43 pounds, the third generation 1.44 pounds, the fourth generation 1.44, the fifth generation 1.42, and the sixth and seventh generations 1.32. Up to 2 years of age, the average daily gains for the same groups were 1.41, 1.24, 1.22, 1.21, 1.21, and 1.14 pounds, respectively. The more closely inbred animals continued to gain on the less intensely inbred animals to some extent until they reached maturity.

The intensely inbred animals in this experiment had a characteristic shape of head and setting of ears that gave them a drooping appearance, which distinguished them from other animals in the herd. They also had rough coats and were sluggish in their movements. Their walking gait was peculiar, a tendency to drag their feet. They were less active and less alert than other cattle in the herd and attendants thought they were very stubborn.

The F_1 generation cows, composed largely of outbred daughters of sires 1 and 2, produced on the average 31 percent more milk and 13 percent more butterfat than the foundation cows that were their dams, but the milk they produced contained a much lower percentage of butterfat. The F_2 cows, inbred daughters of sires 1, 2, 3, 4, and 6, with an average coefficient of inbreeding of 26.3 percent, produced on the average 2.7 percent less milk and 8.5 percent less butterfat than their dams (the F_1 cows) and their butterfat test was also lower by 6.1 percent. The F_3 cows, inbred daughters of sires 1, 2, 3, 4, 5, and 6, with an average coefficient of inbreeding of 32.9 percent, produced on the average 8 percent more milk than the F_1 cows, but their butterfat test was lower by 10.7 percent and their butterfat yield was lower by 3.3 percent. The F_4 cows, inbred daughters of sires 2, 3, 4, 5, and 6, with a coefficient of inbreeding of 43.9 percent, produced on the average 6.6 percent less milk and 17.7 less butterfat

than the F_1 cows and the butterfat test was lower by 12 percent. The F_3 cows, inbred daughters of sires 5 and 6, with an average coefficient of inbreeding of 44.7 percent, produced on the average 7.1 percent less milk and 16.3 percent less butterfat than the F_1 cow and the butterfat test was 8.3 percent lower. The three cows in the F_6 generation, all daughters of sire 6, with an average coefficient of inbreeding of 59.9 percent, produced on the average 31.6 percent less milk and 38.4 percent less butterfat than the F_1 cows, and the butterfat test was lower by 10.1 percent.

Thus it will be seen that the milk yield was not seriously lowered by inbreeding until the F_6 generation; the percentage of fat reached the lower levels in the F_3 and F_4 generations (the lower fat percentage probably was brought about more by the increased concentration of Holstein-Friesian inheritance than by the effect of inbreeding); the butterfat yield reached a noticeably lower level in the F_4 generation and a decidedly lower level in the F_6 generation.

In view of the intensity of the inbreeding in this experiment the moderateness of the depression in milk and fat yields in the F_2 and F_3 generations, and in milk yield in the F_4 and F_5 generations, is surprising. It is less than that observed in some of the other breeding experiments at the same station.

Analysis of the transmitting ability for level of production of each of the six sires shows that sires 1 and 2 possessed excellent germ plasm. Sire 3 was the next best sire in this respect. There was very little difference between sires 4 and 5. Sire 6 was clearly the poorest of the sires used. The fact that the production level has been fairly well maintained despite the intensity of inbreeding and the decline in size of the animals is no doubt due to the excellent germ plasm of sires 1 and 2, to which the sires that were subsequently used were inbred.

Inbreeding has long been thought to be one of the best "tools" for bringing about uniformity among the offspring, that is, for decreasing variation in the inherited characters. In this experiment the greatest decrease in variability in milk yield occurred in the F_1 generation (outcross). From the F_1 to the F_5 generation there was a gradual decline in variability, but in the F_6 generation (only three animals but intensely inbred) the variability in milk yield increased to a point second only to that in the foundation group. In butterfat percentage variability declined from the F_1 to the F_3 generation, then increased to a level that was quite constant through the F_4 to the F_6 generation. The variability in butterfat yield was similar to that in milk yield.

Seven outbred daughters that were out of seven inbred dams had an average milk yield that was 11 percent greater, and an average butterfat yield that was 16 percent greater, than that of 11 inbred daughters out of the same dams. However, 6 of the 11 inbred daughters were by sire 6, whose daughters had a low level of production.

Sire 947, a registered and unrelated sire, had eight tested outbred daughters out of inbred grade dams. He also had six inbred daughters out of registered dams. There was little difference in average production between the inbred and the registered dams. The daughters out of the registered dams had the highest level of production. His daughters out of the inbred dams represented a radical outcross and, according to the theory of heterosis, should have been the better pro-

lacers. Mastitis infection may have prevented the outbred daughters from producing up to their inherent capacity.

This inbreeding experiment was originally started with the simple objective of determining whether a dairy farmer with a small herd might safely breed a bull back to his daughters and thus avoid having to obtain another sire to mate to the first sire's daughters. That question was answered early in the experiment. A bull that carries no lethal factors in his germ plasm, or factors for malformed calves, may safely be bred back to his daughters. But the results of this experiment do not show how the farmer would know whether his bull did, or did not, carry such undesirable hereditary factors without actually breeding the bull back to his daughters and judging by the results obtained.

Generally speaking farmers should not practice inbreeding. The results are harmful when inbreeding progresses beyond 25 percent (first mating of sire and daughter), even if one starts with widely dissimilar animals. If one starts with similar animals it is probable that less intensive inbreeding also will be harmful.

An important exception to the general rule should be noted. If a farmer has an outstanding cow or bull he is justified in inbreeding to the cow or bull in order to obtain a bull or bulls for breeding that will carry a higher percentage of the characteristics of the outstanding cow or bull. This course is justified because the fertility of the inbred bull is not likely to be seriously impaired; and any lack of size and vigor in the inbred bull is not likely to be transmitted to the offspring if he is mated with unrelated females. Continued inbreeding of whole herds, however, is almost certain to be disastrous.

As the experiment progressed interesting questions from the standpoint of the student of breeding arose. What would be the effect of continued close breeding on fertility, size, conformation, and producing ability? Could a fairly uniform level of production be attained? The results of the experiment, bearing on these questions, have been discussed. They are of greater interest and value to the student of breeding than to the farmer seeking information concerning the best method of breeding to follow, because of the inability of the farmer to determine whether any bull is free from undesirable genetic characters without resorting to the inbreeding test.