RELATIONS BETWEEN WEIGHT AT FIRST CALVING AND MILK PRODUCTION DURING THE FIRST LACTATION

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RELATIONS BETWEEN WEIGHT AT FIRST CALVING AND MILK PRODUCTION DURING THE FIRST LACTATION

By

Robert H. Miller

AN ABSTRACT

Submitted to the College of Agriculture
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MASTER OF SCIENCE

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ABSTRACT ROBERT H. MILLER

First lactation milk and fat production records (including age and weight at calving) for 4677 Holsteins, 1001 Guernseys, and 501 Jerseys compiled in the Michigan DHIA-IBM program over a three and one-half year period were analyzed to ascertain the relation between weight and production.

Least squares estimates of the independent influences of age and weight at calving on first lactation production were derived. Maturity, as measured by age, was negatively related to the economy of first lactation production. The expected change in production associated with a change in weight at first calving was dependent upon the level at which a change in weight occurred. In all three breeds, there were instances where a decrease in production was associated with increased weight. The production response to level of development appeared to reach a maximum at weights 300-400 pounds above the breed average for the age. When the value of added production accompanying increased weight was contrasted to the added expense involved, heavier heifers had little or no advantage in the first lactation. It was concluded that dairy heifers should be bred as soon as sufficient size is attained to minimize harmful effects on the length of productive life.

Partial regressions of production on age and weight were computed on overall and intraherd bases. Weight was a more important source of variation in production records in a group of many herds than age. Large standard errors of estimate suggested that the linear regression equation was inefficient in predicting individual production records in the group studied. Weight was only about one-half as important in predicting within-herd production as compared to production in a group of many herds. The intraherd regressions of milk production on age and weight were of the order of 75 lb. per month and 200 lb. per 100 lbs., respectively. Partial correlations indicated that age had little or no role in the association of weight and production in a group of many herds but was important in the intraherd relationship.

Large between herd correlations of weight with production indicated that differences between herds contributed significantly to the association. Irregular results were obtained for Jerseys and Guernseys.

Estimates of the genetic correlation between weight and production for Holsteins were of the order of .3, indicating significant genetic contribution to the association between weight and production.

Individual differences in weight at first calving were found to be heritable to the extent of .3 to .5. Heritabilities of first lactation milk and fat production ranged from .2 to .3 and .2 to .4, respectively.

ABSTRACT ROBERT H. MILLER

It was concluded that, while differences between herds indicated that environmental factors were of primary importance, genetic contribution to the weight-production relationship was large enough to result in indirect increases in weight through selection for milk production.

It was further concluded that correction for weight differences may remove a fraction of the genetic variation in production.

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TABLE OF CONTENTS

LIST OF TABLES

Table		Page

LIST OF FIGURES

INTRODUCTION

How body weight and milk production are related has received prominent attention by many workers. However, the emphasis which body size, as measured by weight, should receive in dairy cattle selection and management programs and how it should be used have not been definitely ascertained.

In practice, large animals are favored by breeders of dairy cattle. Body size is a factor often considered important in both inter- and intra-breed evaluation of dairy cattle. The Unified Score-Card of the Purebred Dairy Cattle Association (44) subjects cows and bulls lacking size desired for the breed to "slight to serious discrimination" in the show ring. Small animals are penalized in type classification. Such evaluation is usually based on the theory that a deficiency in size is to a large extent reflected in a deficiency in the capacity for the consumption and storage of nutrients. Size is also an important consideration in selecting the parents of the next generation. However, the importance of size to milk production and the factors responsible for the association are obscure.

If the relation of body weight *per se* to milk and fat production is not large enough to be economically important, size, as measured by weight, should be considered only in the management of the dairy cow. If a close association of milk and fat production with weight exists, but this connection is primarily conditioned by environmental differences, selection for gross size should not be a prominent consideration in a dairy cattle selection program, except insofar as there may be a genetic relation between size and other factors, such as longevity. However, differences in size can be used to remove environmental differences from production records. If a close relationship between weight and production exists and the genotype is important to the association, size should receive attention in evaluating the genetic ability of animals for milk production.

Closely associated with possible influences of weight on milk yield is the energetic efficiency of milk production, a topic which has been rigorously treated by Brody (6,7,8). While the efficiency of production is an important subject not necessarily synonymous with gross rate of production, a discussion of its aspects is beyond the scope of the present paper.

The objectives of this investigation are: (1) To assess the direct quantitative effect of body weight upon milk and butterfat production in the first lactation, and (2) To determine the genetic or environmental nature of any association which may exist.

A REVIEW OF THE LITERATURE

The general subject of the relationship of body size to milk production has been reviewed by Beck and Turk (3) and by Pfau and Bartlett (43). In each case the conclusion was that large cows tend to produce more than small cows. Gowen (20), in a review of early work on the subject, concluded that the large cow is a more economical producer than the small cow because the small cow needs proportionately more feed for maintenance. A review of work concerning the productive efficiency of milk production has been made by Brody (7).

Various analytical methods have been employed in an effort to discern any existing connection between live weight and the amount of milk and butterfat produced by dairy cattle.

Edwards (14) arranged the milk production data for 2400 cows of various breeds tested at the London Dairy Show between the years 1922-1934 according to body weight. He concluded that within the breed there was a slight tendency for live weight and the economy of production to be inversely related.

Various workers have examined milk production and body weight data for significant phenotypic correlation. Davis and Willet (13) found no correlation between weight gain from birth to two years of age with milk or fat production for the first lactation or for the lifetime average when the records of 76 Holstein females were analyzed. Davis *et al*. (12)

reported correlations of .24, .45, .58, .60, and .83 for Guernsey, Ayrshire, Jersey, Holstein, and all breeds, respectively, between fat-corrected milk (FCM) for the first eight months of the lactation and body weight measured in the first month of the lactation of cows of various ages. Gaines (15) found a correlation of .70 between the yield of 4% FCM during the first eight months of the lactation and body weight measured in the first month of the lactation of 11 Holstein cows of various ages. This correlation decreased as weight was measured at successive stages of the lactation. Gowen (21) reported correlations of .51 for both milk and fat with weight in a study of Jersey Registry of Merit (ROM) data for 840 cows of various ages. In the same paper, Gowen analyzed 365-day milk and fat records from the Jersey ROM for 1371 cows whose weights were known and 10,547 cows whose weights were estimated. This sample exhibited correlations of .47 and .48 of weight with milk and fat, respectively. Gowen's data were obtained from animals of diverse ages. Hofmeyr (27), in a study of 934 records of Red Dane heifers from 748 different herds, found a correlation of .30 between weight at calving and the first lactation yield of 4% FCM. Touchberry (48), in an analysis of data for 187 Holstein dam-daughter pairs in one herd, found phenotypic correlations of -.04 and -.08 for milk and fat, respectively, with weight. The records studied by Touchberry were those which began nearest the cow's third year of age, but the data were corrected to a mature-equivalent basis. Turner (49) reported correlations of .32 and .33 for weight with milk and fat, respectively, in an analysis of Advanced Registry (AR) records of 2700 Guernsey cows of various ages for which actual and estimated body weights were available. Turner (50) also reported a correlation between weight and fat of .11 in a study of 8422 Jersey ROM records of cows of various ages (the data were corrected for age differences).

The above estimates of the phenotypic correlation between weight and production range from -.1 to .7. Most values obtained appear to have been of the order of .4. While there are many differences in ages of the animals studied and treatment of the data in these investigations, there is strong evidence of an important phenotypic relationship between weight and production.

A number of workers have computed regression coefficients of milk and fat on body weight. Gowen (21), in an analysis of 840 Jersey ROM records of cows of various ages, reported regressions of milk and fat (pounds) on weight (pounds) of 9.5 and .5, respectively. When the data were corrected for age differences, the corresponding regressions were only 6.1 and .4. In the same paper, Gowen analyzed 1371 Jersey ROM 365-day records of cows of various ages. This sample exhibited regressions of milk and fat on weight of 7.2 and .4, respectively. Johansson (29) found a regression of first lactation 250-day butterfat yield (kg.) on weight at calving (kg.) of .15 in an analysis of records of Red Dane heifers tested in special progeny testing stations. Turner (49), in a study of AR butterfat records and body weights (actual and estimated) of 2700 Guernsey cows of various ages, reported a regression of fat on weight of .77 where fat and weight were measured in pounds and age at calving was ignored. When only three to four year-old animals were considered, the regression was .22. In earlier work, Turner <u>et al</u>. (51) computed a regression value for butterfat (pounds) of 1.02, from Jersey ROM data. From the results of these workers, the regression of production on weight appears to be decreased when age differences are removed.

Work of the preceding nature has been questioned on several grounds, but the chief point of dissension lies in the problem of whether production is truly a linear function of body weight. Brody (8), Kleiber (33), and Kleiber and Mead (34,35) maintain the negative position, while Gaines and his associates (16,17,18) upheld the affirmative. Brody has advanced the "power formula," $Y = aW^b$, as more closely representing the relationship between the two quantities (Y = milk energy produced, W = body weight, b = slope of the fitted line on the logarithmic grid). To the exponent b, Brody assigns the value 0.7 ± 0.1, the magnitude of the standard error depending upon the "dairy merit" of the animal (presumably the inherited productive capacity). This argument is based on the assumption that maintenance requirement increases with body weight raised to an exponential value less than 1.0 (9), rather than with simple body weight. This represents a reversal on Brody's part, for in earlier work with Jersey ROM data (10), butterfat yield was expressed as a linear function of body weight. As a basis for the linear relation, it was asserted that increase in milk secretion with age follows the same course as the increase of body weight with age, and that, therefore, the two should be linearly related or directly proportional for a group of animals of all ages during the growing period. To express the common course of the two quantities with increasing age, the function $X = A(1 - e^{-kt})$ was presented, where X = body weight or milk secretion at any age t, A is a constant, e is the base of the natural logarithm system, and k is the velocity constant. (The above is also the function expressing the course of a monomolecular chemical reaction.) Kleiber and Mead (34,35) employed a modification of the "power formula," terming Brody's $(W)^b$ the "metabolic body size" of the cow. Kleiber and Mead have contended that lactation rate is proportional to (body weight in kilograms)$^{3/4}$. The basis of this expression is the theory that "the capacity for rate of production in animals is in general proportional to their rate of metabolism, or in terms of the 3/4 power of their body weight." (35) This expression was formulated from data obtained from 24 Holstein and 42 Jersey cows at the California station. As a measure of the "inherent ability of cows for milk production," Kleiber and Mead (34) proposed the ratio of average daily milk production during a ten-month period (FCM or milk energy basis) to mean "metabolic body size" of the animal in kilograms $^{3/4}$. Gaines (16) tested another productive efficiency measure (FCM_8/W_1, where FCM_8 = 4% fat-corrected milk production for the first eight months of the lactation, W_1 = live weight measured in the first month following parturition) against Kleiber's efficiency ratio described above, by equating both to the expression $a + bW_1$ (a = a constant, b = least squares regression coefficient) and comparing the goodness of fit. From such a comparison on actual data, the metabolic body size hypothesis was rejected.

A second objection to phenotypic correlation and regression measurements of the association between weight and production is that they fail to consider the role of age with respect to weight and production. Several workers have measured this relationship by correlation. Hofmeyr (27) reported a correlation between age and weight at first calving of .32 in data from 934 Red Dane heifers from 748 different herds. Johansson (29) found a correlation of .26 between age and weight at first calving for Red Dane heifers tested in Danish progeny stations. Gowen (21) reported a correlation of .38 in Jerseys, while Turner (49) found .32 in AR data from 2700 Guernsey cows (when both age and weight were measured at the end of the test period). Animals of various ages were studied in the latter two investigations.

Much of the confusion in determining the direct influence of body weight on milk and butterfat production arises from the lack of agreement by workers concerning valid methods of disentangling the combined effects of age and weight. When production data are converted to a mature-equivalent basis, some of the effects of weight are eliminated also (17, 18). From a linear regression analysis (17), Gaines et al. concluded that the contribution of age to production with weight held constant was negligible compared to that of weight with constant age, and that, therefore, the correction of production data for age differences is "biologically unsound." Some workers (48,49,50) have attempted to assess the relationship between weight and production utilizing age-corrected data.

Multiple linear regression (2,17,18,21,29) has been employed to estimate the change in production associated with a change in weight, independent of age. The results of these studies will be compared in a later section. However, in general, the findings have indicated that weight is much more important to production than age.

To determine the association of weight and production independent of the influence of age, the method of partial correlation has been used (21,27,29,49). The results of these studies suggest that the association between weight and production is little influenced by age, but that the correlation between age and production is much smaller when weight is constant.

Where body weight has been found to have a direct bearing on the production of milk and butterfat, a few attempts have been made to ascertain the primary nature of the relationship, i.e. environmental or genetic. Bailey and Broster (2) compared regressions between sire-groups and concluded that selection for live weight would improve production only by chance. Gowen (22) deduced that, in Jerseys, the weight of the sire was of slight importance in predicting the daughter's probable production. In another paper (23), Gowen, on the basis of parent-offspring and sibship correlations in Jersey cattle, stated that "inheritance accounts for most of the variation in size of these cattle, such environmental differences as do exist playing but little part in the ultimate constitution of these animals" (the relationship of weight to production was not discussed). Mason et al. (40), in a study of records of Red Dane cattle in special progeny testing stations in Denmark, found a significant between-sire relationship of weight and milk-yield, and concluded that selection for yield or efficiency would result in a slight increase in body size. Blackmore (4), in a study of 334 Holstein dam-daughter pairs, concluded that selection for milk production and meat-type conformation simultaneously would be impractical. Pfau and Bartlett (43) found no evidence of a genetic relation between size and milk production from a review of the literature. Shrode and Lush (47), in a review of the inheritance of economic characters in farm animals, indicated that the extent of pleiotropic action of genes controlling weight and production might prove large enough to be important. Touchberry (48) found no evidence for a positive genetic connection between size and production, but the data studied had been corrected for differences in age. Turner (50) inferred, from a study of Jersey ROM fat records and body weights, that the sire could cause significant changes in the daughter's fat production over that of the dam, without materially changing the level of the daughter's body weight over the dam's.

Thus, correlation and regression studies have indicated that there is an important association between weight and production. The results of these investigations have been questioned on the basis of whether production is actually a linear function of body weight. An exponential expression has been proposed as a more accurate expression of the relationship. The exponential relationship is based on metabolic and energetic considerations from the standpoint of physiology. Applications of the exponential formula to empirical data have not yielded conclusive results.

Partial correlation and regression have been employed to separate the influences of age and weight on production. Results of these studies indicate that weight is more important than age in predicting production.

Efforts to ascertain the role of the genotype in the relationship between weight and production have not yielded conclusive results.

SOURCE OF DATA

DESCRIPTION

The data were records completed in the Michigan DHIA-IBM program during the period from January, 1954, through May, 1957 (no corrections for yearly differences were made). The following measurements were obtained from individual first lactation records: (1) actual milk production, (2) actual fat production, (3) age at calving, and (4) body weight at calving. Only completed lactations of 305 days or less were used; lactations continuing beyond 305 days were cut off at 305 days.

Numbers sufficient for analysis were available for only three breeds. The breeds studied and the number of records for each were: (1) 4677 Holsteins, (2) 1001 Guernseys, and (3) 501 Jerseys.

To facilitate computation, milk was coded in hundreds of pounds, while fat and weight were coded in tens of pounds. Age was recorded in months.

Weight was estimated by means of taped chest girth measurements based on the relationship between the two published by the Bureau of Dairy Industry (32). Chest girth was measured by the DHIA supervisor on his first visit following the date of calving (within 30 days following parturition). This method of estimation is in wide use under practical conditions due to the lack of cattle scales on commercial dairy farms (18).

Although there is a lack of data on the subject, estimates of weight based on chest girth appear to provide suitable approximations. Touchberry (48) reported phenotypic and genetic correlations of .81 and .88, respectively, between weight and heart girth in Holstein cattle. Ragsdale and Brody (45) and Davis *et al.* (11) reported a standard error of seven per cent for weights estimated by chest girth measurements. On the other hand, scale weights may show considerable variation within a relatively short period of time. Lush *et al.* (38) found an "experimental error" of single scale weights in cattle of six to twelve pounds. Johansson and Hildiman (31) reported a standard error of scale weights in cattle of one to two per cent.

DISTRIBUTIONS AND MEANS

Tables 1 and 2 exhibit the distributions of age and weight, respectively, in the samples studied.

TABLE 1

DISTRIBUTION OF AGE AT FIRST CALVING

Age Group	Holstein		Guernsey		Jersey	
	%	No.	%	No.	%	No.
16-19	.5	24	.9	9	1.0	5
20-23	6.3	296	5.7	57	15.2	76
24-27	34.1	1597	40.3	403	49.7	249
28-31	31.2	1459	29.4	294	21.0	105
32-35	18.1	846	15.1	151	7.8	39
36-39	7.1	334	6.1	61	3.8	19
40-43	2.0	92	2.0	20	1.2	6
44-47	.4	21	.2	2	0.0	0
48 & above	.2	8	.4	4	.4	2

1

TABLE 2

DISTRIBUTION OF WEIGHT AT FIRST CALVING

Weight Group	Holstein		Guernsey		Jersey	
	%	No.	%	No.	%	No.
600-699	.1	4	1.2	12	17.8	89
700-799	.5	25	9.1	91	38.5	193
800-899	3.6	168	29.6	296	28.9	145
900-999	12.8	599	31.4	314	9.8	49
1000-1099	27.5	1286	20.5	205	3.4	17
1100-1199	26.9	1260	6.4	64	1.0	5
1200-1299	17.8	833	1.7	17	.2	1
1300-1399	7.9	369	.2	2	.4	2
1400-1499	2.1	98	---	0	---	0
1500-1599	.4	21	---	0	---	0
1600-1699	.3	14	---	0	---	0

Table 3 displays the means and standard deviations for the four measurements studied. Milk, fat, and weight are in coded units.

TABLE 3

MEANS AND STANDARD DEVIATIONS

OF AGE AT CALVING, WEIGHT AT CALVING,

MILK AND FAT PRODUCTION FOR THE FIRST LACTATION*

Breed	Age		Weight		Milk		Fat	
	M	S	M	S	M	S	M	S
Holstein	29	4.6	112	13.9	99	20.4	36	7.4
Guernsey	29	4.7	93	11.6	71	16.0	34	7.6
Jersey	27	4.2	79	12.0	62	13.5	32	6.9

* M = Mean, S = Standard Deviation.

METHODS AND RESULTS

LEAST SQUARES ESTIMATES OF INFLUENCES OF AGE AND WEIGHT ON PRODUCTION

There is a need to estimate the change in production accompanying a given change in the weight of the dairy cow. From a management standpoint, information of this nature is needed for the formation of sound decisions in such matters as the level of development at which heifers should be bred to achieve the most economical production during the first lactation. Even if the genotype proves to be important in the association of weight and production, the economic importance of weight to milk production will have some bearing on how weight is used in selection for milk production. Although the analytical tools required for a study of this type have been available for some time, the literature does not disclose any estimates of this nature. The technical details of the application of the method of least squares to non-orthogonal data of the present nature have been well described by Harvey (24). The procedure of the present analysis has closely followed that outlined by Harvey.

Since the effect of weight on production is closely associated with that of age, to obtain an estimate of the direct effect of weight on production requires that effects of age be analyzed also.

Let y_{ijkl} be the record made in the i^{th} herd by the l^{th} animal in the j^{th} age group and the k^{th} weight group. If the effects are additive and interaction is not an important source of variation (an examination of the age-weight two-way tables indicated such to be the case), the relationship between these observations is $y_{ijkl} = \mu + h_i + a_j + w_k + e_{ijkl}$, where μ is the unknown population mean, h_i is an effect common to all observations in the $i^{\underline{th}}$ herd, a_j is an effect for all records in the $j^{\underline{th}}$ age group, w_k is an effect for all observations in the $k^{\underline{th}}$ weight group, and e_{ijkl} is a random element peculiar to the individual record.

The reduced normal equations were obtained with the above model by the procedure described by Harvey (24). For ease of computation, age was grouped in four-month intervals and weight in intervals of 100 pounds. The equations were solved simultaneously to estimate age and weight effects (see Tables 4 and 6, respectively). The constants are given in coded units and are presented as deviations from the overall mean production for milk and fat, respectively, for each breed (for the mean production values, see Table 3).

TABLE 4

INFLUENCE OF AGE OF FIRST CALVING

ON MILK AND FAT PRODUCTION IN THE FIRST LACTATION

	Holstein			Guernsey			Jersey		
Age Group	No. in Group	Milk	Fat	No. in Group	Milk	Fat	No. in Group	Milk	Fat
16-19	24	-13.8	-5.4	9	-10.1	-4.8	5	-10.5	- 5.9
20-23	296	- 7.5	-3.2	57	- 4.1	-2.7	76	- 6.0	- 3.5
24-27	1597	- 4.8	-2.3	402	- 3.5	-1.9	249	- 3.4	- 1.7
28-31	1459	- 2.2	-1.2	294	- 1.7	-0.9	105	- 0.4	- 0.2
32-35	846	0.2	-0.2	151	0.3	0.0	39	1.8	0.5
36-39	334	4.0	1.0	61	2.2	1.9	19	- 1.9	- 0.3
40-43	92	6.1	2.2	20	7.2	2.6	6	- 5.4	- 3.1
44-47	21	7.4	3.2	2	13.3	7.5	0	---	---
48-up	8	10.5	5.8	4	- 3.6	-1.8	2	25.8	14.2

The number of observations in many of the groups is rather small. The estimates for such classes must be used with caution since sampling errors may be expected to be rather large. Thus the classes on both extremes, especially in Guernseys and Jerseys, are likely to be somewhat less reliable than the central classes.

Although the age estimates were made primarily to separate age effects from those of weight, some discussion of the magnitude and behavior of the age effects seems appropriate. Such effects, being independent of weight, may be interpreted as representing the influence of the degree of maturity of body functions upon production. In general, the age constants for production exhibit a continuous positive direction with succeeding age groups. The small numbers in the older age classes for Jerseys and Guernseys may account for the exceptions noted in those cases. The age constants for milk production are plotted in Figure 1. Departures from linearity are rather large in the extreme classes for Jerseys and Guernseys; however, the approximation to a linear relationship is quite striking in the Holstein example.

In Holsteins the largest increase in production between two successive age classes occurs between the 18-22 and 22-26 month classes. In this instance delaying the calving of an animal four months within this age range would be expected to yield increases of 630 pounds of milk and 22 pounds of fat in the first lactation. In Holsteins the increase in production expected for animals calving in the median age group (28-31 months) as compared to those calving in the 16-19 month group, is only 1170 pounds of milk and 43 pounds of fat. This is a rather small increase in view of the 12 months delay in commencement of production required to obtain it. Similar observations may be made for the Jersey and Guernsey age constants.

Since age correction factors are usually not derived independently of weight, the estimates in Table 4 can be compared with those obtained when weight is not considered in Table 5.

TABLE 5

INFLUENCE OF AGE ON MILK AND FAT PRODUCTION IN THE FIRST LACTATION, DISREGARDING WEIGHT

Age Group	Holstein		Guernsey		Jersey	
	Milk	Fat	Milk	Fat	Milk	Fat
16-19	-17.3	-6.5	-13.6	-5.9	-12.7	-6.2
20-23	-10.2	-4.1	- 5.9	-3.5	- 7.0	-4.0
24-27	- 6.1	-2.7	- 4.6	-2.4	- 4.0	-2.0
28-31	- 2.4	-1.3	- 2.3	-1.2	0.2	-0.1
32-35	0.7	0.0	0.5	0.0	2.2	0.7
36-39	5.2	1.4	2.8	2.1	- 0.6	0.0
40-43	7.5	2.6	8.1	2.9	- 3.7	-2.7
44-47	9.6	4.0	17.9	9.5	---	---
48 & above	12.9	6.6	- 3.0	-1.5	25.6	14.1

The differences between the estimates of the effect of age on production in Table 5 and the corresponding entries in Table 4 may be interpreted as due to the joint effects of age and weight on production. The joint contribution of age and weight is generally quite small in the 28-31 month age group but is progressively larger in the classes above and below this group. The estimates for ages less than 28 months in Table 5 are numerically smaller than the corresponding values in Table 4. This may be interpreted as due to the fact that animals in these classes are smaller than average. Estimates for ages greater than 32 months in Table 5 are numerically larger than the corresponding entries in Table 4. This is probably due to the fact that animals in these groups are larger than the average. Table 5 indicates that when weight is not considered, the estimates of the influence of age on production carry some correlated effects due to the animal being smaller or larger than the average.

TABLE 6

INFLUENCE OF WEIGHT AT FIRST CALVING ON MILK AND FAT PRODUCTION IN THE FIRST LACTATION

	Holstein			Guernsey			Jersey		
Weight Group	No. in Group	Milk	Fat	No. in Group	Milk	Fat	No. in Group	Milk	Fat
600-699	4	-7.6	-2.8	12	-7.4	-3.4	89	-4.4	-3.8
700-799	25	-7.0	-2.9	91	-4.9	-2.4	193	-0.9	-2.2
800-899	168	-7.4	-2.2	296	-0.4	0.1	145	1.0	-1.1
900-999	599	-3.2	-1.1	313	2.4	1.0	49	1.8	-1.3
1000-1099	1286	-0.7	-0.2	205	1.8	0.7	17	3.6	-1.6
1100-1199	1260	1.7	0.6	64	5.9	2.7	5	8.4	4.9
1200-1299	833	4.3	1.5	17	2.5	1.3	1	-22.2	1.2
1300-1399	369	4.0	1.3	2	---	---	2	12.5	3.9
1400-1499	98	7.4	2.9	0	---	---	0	---	---
1500-1599	21	2.8	1.4	0	---	---	0	---	---
1600-1699	14	5.6	1.6	0	---	---	0	---	---

The significance of the weight constants (Table 6 and Figure 2) is somewhat more difficult to assess in view of there being no continuous positive increase in production with

FIGURE 1. INFLUENCE OF AGE AT FIRST CALVING ON FIRST LACTATION MILK PRODUCTION

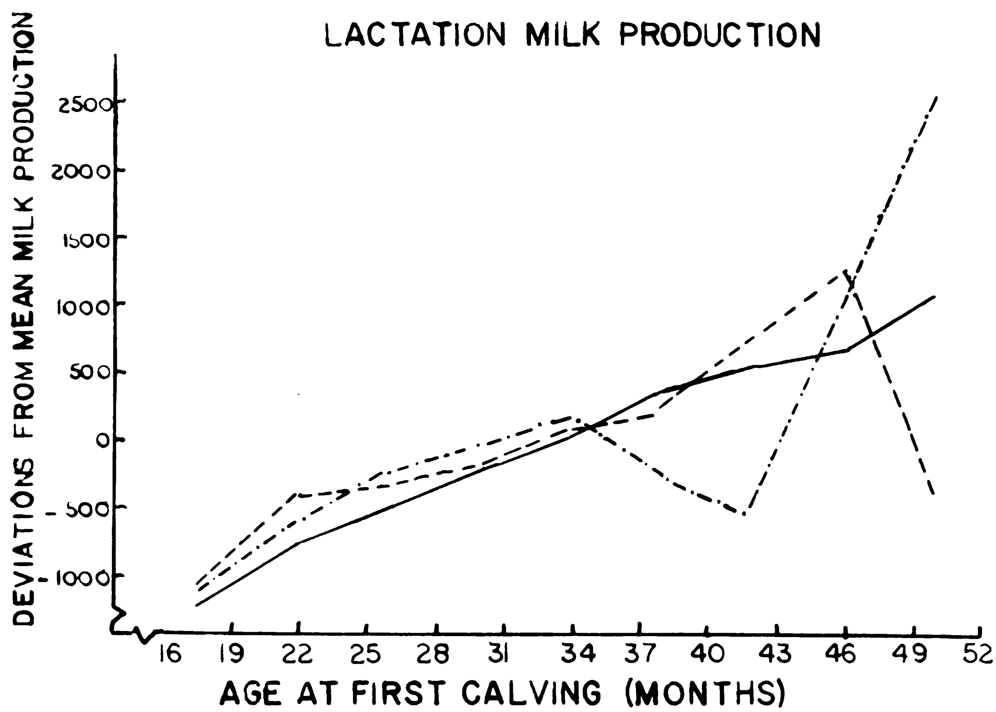
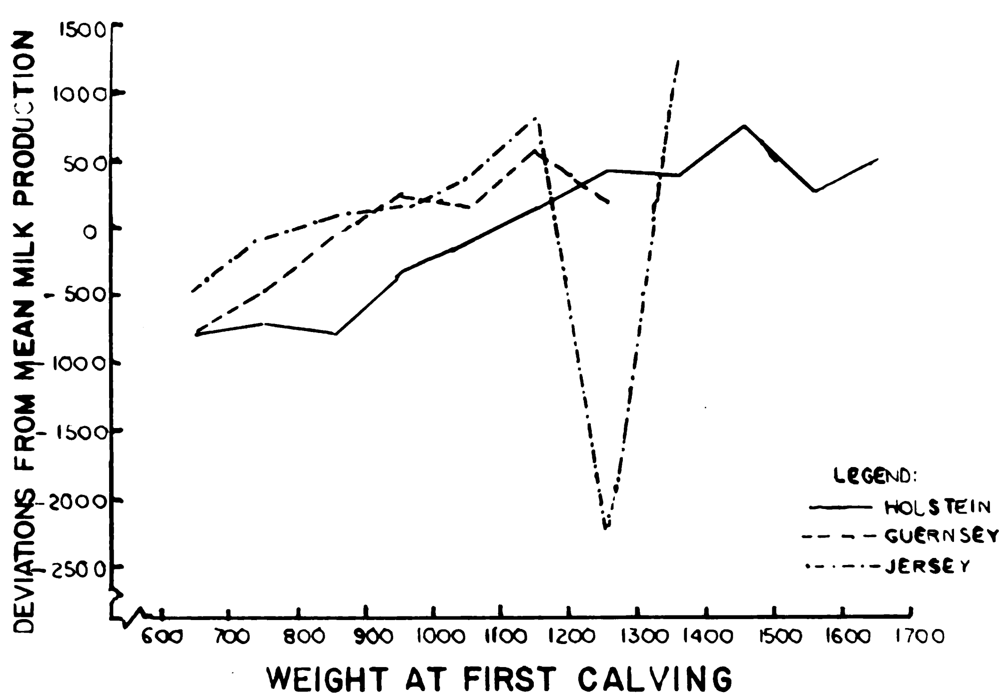


FIGURE 2. INFLUENCE OF WEIGHT AT FIRST CALVING ON FIRST LACTATION MILK PRODUCTION



successive weight increments. Where the numbers in the classes concerned are small, this phenomenon may be attributed in part to sampling error. However, in the case of the negative increment of production associated with an increase from 1200-1299 pounds to 1300-1399 pounds in Holsteins, sampling error would be expected to be small.

Close examination of the graphic portrayal of the constants in Figure 2 yields two observations: (1) the departure from a linear increase is not large over the range of 600-1000 pounds for Jerseys and Guernseys and from 800-1400 pounds in Holsteins, and (2) if the Jersey and Guernsey curves are shifted 200 pounds to the right on the weight axis, the three curves behave in a similar manner over the same general range of increasing weight. More severe deviations of the Jersey and Guernsey curves from the behavior of the Holstein curve in Figure 2 may be attributed in part to smaller numbers in the former breeds. In each breed, there is a consistent, almost linear increase in production over a wide range, then a slight decrease, followed by an increase over a small range, and finally, a rather sharp decrease.

The flatness of the Holstein curve between 600-900 pounds indicates that weight has little or no effect on production at this level of development. While the estimates undoubtedly contain some sampling error, there appears to be a type of threshold at the 900-1000 pound weight level. This may indicate a level at which growth needs no longer hold complete priority over milk secretion requirements--above this level a larger proportion of the nutrient intake may be channeled to milk secretory usage. If more data were available, perhaps the other breeds would exhibit similar responses at weights less than 600 pounds.

The aberrations in the curves at higher levels of development are more difficult to explain. The sharp decline in production may indicate a level at which there is an increasing tendency for the conversion of nutrients into fatty tissue and storage. If such a condition interfered in some way with milk secretion, one might expect to see a steady decline in production beyond this weight level. Larger numbers would need to be available in the extreme weight classes to determine this. Certainly, one would not expect the production to show a continuous increase with weight. At high levels of weight, interference with foraging ability and a tendency to sluggish activity might be expected.

Based on the above observations, the following behavior may generally be expected of the effects of weight on milk production: first, a region of little or no response at relatively low levels of development in size, then a rather constant increase (approaching linearity) to a maximum level at a weight of perhaps 300-400 pounds above the breed average for the age, and finally, a rather steady decrease in production. Fat production would be expected to follow a similar course.

A clearer picture of the importance of the independent influences of age and weight on production may be obtained by placing economic values upon them and contrasting these with the cost of obtaining the added production. Tables 7 and 8 will serve to give a rough approximation of the economic worth of the added milk production in the first lactation through increased age and weight at the time of first calving (economic values were placed only on the age constants independent of weight). In Table 7, the left column lists the midpoints of the two successive age classes between which a four-month increase is made. For each breed, the first column shows the value of the increment of production obtained by delaying age at calving from the first age group to the second. The second column under each breed shows the feed cost of maintenance of the animal over the four-month period required to obtain the increased production.

TABLE 7

VALUE OF INCREASED MILK PRODUCTION IN THE FIRST LACTATION FROM OLDER FRESHENING AGES, CONTRASTED TO MAINTENANCE COST INCURRED**

Change In Age at Calving	Holstein		Guernsey		Jersey	
	Value of Add. Prod.	Cost of Maint.	Value of Add. Prod.	Cost of Maint.	Value of Add. Prod.	Cost of Maint.
18-22	$25.83	$27.72	$25.01	$23.23	$18.45	$21.65
22-26	11.07	27.72	2.05	24.82	11.07	23.23
26-30	10.66	29.26	7.79	26.14	12.30	24.82
30-34	9.84	29.26	8.20	26.14	9.02	24.82
34-38	15.58	29.26	7.79	26.14	14.76*	26.14
38-42	8.61	29.26	20.50	26.14	14.35*	26.14
42-46	5.33	29.26	25.01	27.72		
46-50	12.30	29.26	69.29*	27.72	128.33	52.27

* Value of Production Lost
** Age independent of weight

TABLE 8

VALUE OF CHANGES IN MILK PRODUCTION IN THE FIRST LACTATION DUE TO INCREASED WEIGHT CONTRASTED TO COST OF GAIN AND MAINTENANCE

Changes In Weight	Cost of Gain	Cost of Add. Maint.	Value of Added Product Holstein	Guernsey	Jersey
650-750	$7.77	$4.70	$ 2.46	$10.25	$ 14.35
750-850	7.77	4.70	1.64	18.45	7.79
850-950	7.77	4.70	17.22	11.48	3.28
950-1050	7.77	4.03	10.25	2.46*	7.38
1050-1150	7.77	4.03	9.84	16.81	19.68
1150-1250	7.77	4.03	11.07	13.94*	125.46*
1250-1350	7.77	4.70	1.23*		142.27
1350-1450	7.77	4.70	13.94		
1450-1550	7.77	4.03	18.86*		
1550-1650	7.77	4.70	11.48		

* Value of Production Lost

Table 8 compares the value of the increased production accompanying increased weight with the feed cost of obtaining the increase in weight. The left column gives the midpoints of the two weight classes in which a 100-pound increase occurs. The second column lists the cost of obtaining this 100 pound gain in weight. The third column presents the cost of maintaining the 100 pounds additional weight for a 305 day lactation period. Under each breed is listed the value of the difference in production between the two successive weight classes.

Both Tables 7 and 8 were computed using the 1956 average price received by Michigan farmers for fluid milk ($4.10) and the 1956 average price paid by Michigan farmers per ton of alfalfa hay ($21.75). (1) Maintenance and growth requirements were determined from the standards of Morrison (41) and Knott et al. (36), respectively.

From Table 7 it is seen that in all but two cases, the maintenance cost exceeds the value of the added product from the four-months delay in first calving. In Table 8, while there is some variation, the value of increased production due to 100 pounds larger weight is generally slightly less than the feed cost for the gain and maintenance of the added weight. Thus, it appears that the production gained through older age at calving is uneconomical, while that obtained through increased weight at calving is slightly unprofitable. These comparisons are intended to provide only a rough idea of the economy of the increase in production due to increased age and weight at calving. Many factors have not been considered, of course, so in actual practice the costs involved are expected to be greater than is shown here.

In making use of Tables 4-8 and Figures 1 and 2 for other groups of animals, these estimates of the effects of age and weight should be applied as deviations from the average actual production of the group in which they are to be used. Of course, it is necessary to integrate the separate effects of age and weight in actual application. Time is required to obtain increased weight and, conversely, weight increases will usually accompany increases in age over this range. The problem is one of determining the most advantageous level of age and weight in regard to economical first lactation production.

ANALYSIS OF VARIANCE AND COVARIANCE

Before the association between weight and production can be measured, the variation and covariation of age, weight, and production must be determined.

Let y_{ijk} signify the first lactation record made in the i^{th} herd by the k^{th} daughter of the j^{th} sire. Then, the linear model is

$$y_{ijk} = \mu + h_i + hs_{ij} + p_{ijk},$$

where μ is common to all observations, h_i is a characteristic of all records in the i^{th} herd, hs_{ij} is common to all observations of daughters of the j^{th} sire in the i^{th} herd, and p_{ijk} is peculiar to the record of the k^{th} daughter of the j^{th} sire in the i^{th} herd.

Table 9 lists the total number of observations and the number of herds and sires within herds for each breed.

TABLE 9

NUMBER OF OBSERVATIONS

Breed	Total	Herds	Sires Within Herds
Holstein	4677	651	2451
Guernsey	1001	163	500
Jersey	501	82	243

Henderson (26) has described a method of obtaining components of variance and covariance necessary for estimates of genetic parameters in non-orthogonal systems (method 1). Except for the constant μ, all elements in the model are uncorrelated variables with zero means and variances H, HS, and P. The results of the variance and covariance component analyses are presented in Tables 10 and 11, respectively.

TABLE 10

COMPONENTS OF VARIANCE FOR AGE, WEIGHT, MILK, AND FAT*

Breed	Component	Age		Weight		Milk		Fat	
		Comp.	%	Comp.	%	Comp.	%	Comp.	%
Holstein	H	7.1	33	59.6	31	144.6	35	21.6	39
	HS	2.1	10	22.4	12	33.7	8	3.3	6
	P	12.4	57	110.8	57	236.6	57	30.3	55
	Total	21.6		192.8		414.9		55.2	
Guernsey	H	12.1	47	34.0	25	100.0	39	24.7	43
	HS	- 3.4**	0	9.3	7	12.5	5	2.8	5
	P	13.5	53	91.9	68	144.9	56	30.6	52
	Total	22.2		135.2		257.4		58.1	
Jersey	H	4.3	24	50.7	35	61.1	33	16.6	35
	HS	.9	5	18.8	13	15.4	8	4.9	10
	P	12.9	71	75.9	52	107.5	59	26.0	55
	Total	18.1		145.4		184.0		47.5	

* Weight, Milk, and Fat in coded units.
** Negative HS component considered zero.

The estimation of the components of variance is a means of apportioning the total variance among a group of contributing elements. The H component represents the variance due to differences between herds. These variations are thought to be principally environmental in nature (28). The HS component can be interpreted as portraying the variation between sets of daughters by different sires in the same herd; this would appear to be largely genetic, unless progeny groups within a herd were treated differently. The P component is an estimate of the variation between daughters of the same sire within the herd.

TABLE 11

COMPONENTS OF COVARIANCE BETWEEN AGE, WEIGHT, AND MILK AND FAT*

Breed	Component	Age-Weight	Weight-Milk	Age-Milk	Weight-Fat	Age-Fat
Holstein	Cov_h	5.4	47.0	0.0	17.4	0.3
	Cov_{hs}	5.1	9.1	2.7	3.0	0.3
	Cov_p	11.4	31.7	11.9	11.4	5.0
	Total	21.9	87.8	14.6	31.8	5.6
Guernsey	Cov_h	- 0.4	24.6	- 6.7	19.8	- 2.7
	Cov_{hs}	5.2	2.1	4.9	-22.9	2.5
	Cov_p	10.2	29.2	8.9	31.5	4.2
	Total	15.0	55.9	7.1	28.4	4.0
Jersey	Cov_h	-25.1	39.3	-29.1	4.2	- 3.5
	Cov_{hs}	93.1	-51.8	79.2	- 0.6	0.2
	Cov_p	-55.1	59.0	-45.6	11.0	4.6
	Total	12.9	46.5	4.5	14.6	1.3

* Weight, Milk, and Fat in coded units.

Age Components. Considerable between-breed variation is observed in the components of age variation. The differences between herds contribute only 24% in Jerseys but account for 47% in Guernseys. Although the HS is small, this component is a larger part of the variance in age than was expected. One might suppose that differences in age at first calving would vary little from a group of daughters by one sire to a group by another sire in the same herd. However, the results estimate HS to be 0-10% of the total variation. To the extent that level of development of the heifers is a consideration in the age at which heifers are bred, this phenomenon may reflect genetic differences in rate of growth. Nevertheless, environmental differences undoubtedly are of principal importance in determining the age at first calving. The size of HS may indicate that breeders are more interested in the daughters of one sire than those of another and are breeding them at different times. Another possibility is that breeders may be using different sires at different times of the year. Breeding for fall freshening is a common practice and may cause sire progenies to differ in age at first calving.

Weight Components. Differences among herds again are quite important contributors to the variation in weight at first calving, the proportion of H ranging from 25-35%. Genetic differences as portrayed by HS are also large enough to merit consideration (see heritability estimates).

Milk and Fat Components. The H component indicates that differences between herds account for 33-43% of the variation in production. The contribution from differences between sires within herds is rather stable, ranging from 5-8% of the total variation in milk and 5-10% of the total variance in fat. The total variation in milk for Holsteins is much greater than that of the other breeds, yet there is little breed difference in the total variation in fat. The larger average milk production for Holsteins may be associated with this phenomenon.

HERITABILITIES

Estimates of the heritability of the measurements of weight and production are useful to evaluate the genotypic contribution to observed differences. These values may be obtained by the following ratio from Table 10: $\frac{4HS}{H + HS + P}$. The heritabilities are presented in Table 12.

TABLE 12

HERITABILITIES

Breed	Weight	Milk	Fat
Holstein	.46	.32	.24
Guernsey	.28	.20	.19
Jersey	.52	.34	.41

The estimates of the heritability of weight at first calving range from .28 to .52, i.e. differences in this measurement appear to be transmitted to a relatively high degree. Most of the previous estimates of the heritability of weight, while they were estimated for various stages of development, fall within the range of the present estimates. Johansson (29)

reported a heritability of weight at first calving of .34 for Red Dane heifers tested in special progeny testing stations. Mason et al. (40) reported heritabilities of weight in Red Dane heifers at two different stages of development. The heritability of September weight (prior to parturition) was .41, while the heritability of March weight (after five months' lactation) was .37. Touchberry (48) found a heritability of .37 for weight in 187 Holstein daughter-dam comparisons, where the measurements were obtained at the calving date nearest the animal's third birthday. Turner (50) reported an intra-sire regression of daughter's body weight on dam's body weight of .28 in Jerseys. Turner's weight data were obtained from animals of various ages but were corrected to a "mature-equivalent" weight basis.

Most heritability estimates for milk and fat production have been on the order of .2 to .3 (47). The range in the present study is from .2 to .4. However, most previous estimates were based on lactations at various stages of life, whereas these estimates apply specifically to first lactations. Although the data are usually corrected for age differences, such estimates need not correspond precisely to those obtained in the present example.

Johansson (30) reported a heritability of 300-day first lactation fat yield of .33 for Swedish Red and White cattle. In an analysis of the records of Red Dane heifers tested in progeny stations in Denmark, Johansson (29) found heritabilities of 250-day first lactation milk and fat yield of .58 and .56, respectively. Mason et al. (40), in a similar analysis of progeny test station records, reported a heritability of first lactation milk yield of .57. The heritability of fat of .33 found by Johansson agrees generally with the present results, but the values reported from progeny testing station analyses are larger than the present findings. However, the phenotypic variation seems to be reduced when animals are tested under similar environmental conditions, as in the Danish testing stations. The ratio between the genetic variance and the total variance would be increased, thus yielding estimates of heritability larger than estimates based upon records made under field conditions (29).

CORRELATION ANALYSIS

The extent of the association between two measurements in the same animal is given by the phenotypic correlation. Table 13 presents the overall phenotypic correlations found in the present study.

TABLE 13

OVERALL PHENOTYPIC CORRELATIONS BETWEEN AGE, WEIGHT, MILK, AND FAT

	Holstein			Guernsey			Jersey		
Trait	Weight	Milk	Fat	Weight	Milk	Fat	Weight	Milk	Fat
Age	.34	.15	.16	.28	.10	.11	.25	.08	.04
Weight	---	.31	.31	---	.30	.32	---	.28	.18

The phenotypic correlations between weight and production are all of the order of .3, except for the correlation of fat and weight in Jerseys. Previous estimates by various workers have ranged widely, but most seem to have been of the order of .4 (see previous discussion). The correlation between age and weight appears to be about .3, while the correlation of age and production appears to be around .1. The extent of the correlation between age and weight demonstrates that, had the production data been corrected for age differences, the variation in production due to age and weight jointly would also have been removed.

The within-herd phenotypic correlation measures the degree of association present in the herd group. Any association due to herd differences is removed, thus permitting a clearer view of the fundamental relationships (see Table 14).

TABLE 14

PHENOTYPIC CORRELATIONS

BETWEEN AGE, WEIGHT, MILK, AND FAT WITHIN HERDS

	Holstein			Guernsey			Jersey		
Trait	Weight	Milk	Fat	Weight	Milk	Fat	Weight	Milk	Fat
Age	.36	.23	.24	.43	.30	.32	.28	.24	.24
Weight	---	.21	.21	---	.25	.26	---	.22	.21

The phenotypic correlation between age and weight appears to be slightly larger within the herd group than over a group of many herds. On the other hand, the correlation between weight and production within the herd is less than on an overall basis, the association within herds being on the order of .2. The correlation of age and production is distinctly larger when the differences between herds are removed. The intra-herd correlation is of the order of .2 to .3, whereas the correlation between age and production is only .1 on an over-all basis.

In view of the effects apparently being exerted by herd differences, an estimate of the correlation between weight and production due to these effects is needed. Since the principal differences between herds are thought to be environmental (28), this correlation might be termed the "environmental" correlation. Estimates of this association may be obtained by employing the between-herd components of variance and co-variance previously obtained (see Tables 10 and 11). Table 15 presents the estimates of the association due to the influence of herd differences.

TABLE 15

CORRELATIONS BETWEEN WEIGHT AND PRODUCTION OF HERDS

Breed	Milk	Fat
Holstein	.51	.48
Guernsey	.42	.68
Jersey	.71	.14

Except for the correlation between weight and fat production in Jerseys, the correlations between weight and production due to herd differences are quite large--of the order of .5. Thus, it appear that there are factors peculiar to different herds which influence weight and production in a positive direction.

The importance of herd differences in the relationship between weight and production has been investigated by Hofmeyr (27). In a study of Red Dane heifers from 748 different herds, Hofmeyr classified the herds from which the animals came into low, medium, and high groups, according to the contemporary herd average production. He found that the phenotypic correlation between weight at calving and first lactation yield of 4% FCM declined from the low to high herd levels. The correlation between weight and yield was .33 for low herds, .27 for medium herds, and .17 for high herds. He concluded that weight at calving in relation to age is especially important in regard to heifers from low-yielding herds and that the level of nutrition prior to calving has a pronounced influence on lactation yield.

The preceding measures of correlation have ignored the common effects of age and weight upon production. The partial correlation coefficients listed in Table 16 are estimates of the association between weight and production independent of age, and of age and production independent of weight. The correlations are presented on overall and intraherd bases.

TABLE 16

PARTIAL CORRELATIONS BETWEEN AGE, WEIGHT, MILK, AND FAT

	$r_{13.2}$		$r_{14.2}$		$r_{23.1}$		$r_{24.1}$	
Breed	T	H	T	H	T	H	T	H
Holstein	.05	.17	.06	.18	.28	.14	.27	.14
Guernsey	.01	.22	.05	.24	.29	.14	.30	.14
Jersey	.01	.19	.00	.19	.27	.17	.17	.15

1 = age, 2 = weight, 3 = milk, 4 = fat; T = overall basis, H = intraherd.

When many herds are considered, the correlation of age with production is close to zero when weight is held constant. Thus, on the aggregate basis, age has little or no relationship to production independent of weight. The correlation of weight and production with constant age appears to be of the order of .3. Comparison of the overall partial correlations with the phenotypic correlations in Table 13 reveals that the partial correlations of weight and production are about the same as the overall phenotypic correlations. Thus, when differences between a large number of herds are ignored, the association between weight and production is largely independent of age.

The overall partial correlations are similar to those of earlier studies of records from many different herds. Gowen (21), in a study of Jersey ROM 365-day records of cows of various ages, reported partial correlations of .23 and .22 for weight with milk and fat, respectively. Turner (49) found a correlation of .25 between age and fat production when weight was held constant in an analysis of 2700 AR Guernsey records of animals three to four years of age. In addition, Turner reported a partial correlation of .25 between weight and fat production. Hofmeyr (27) computed partial correlations of age and weight with production at three different levels of herd production averages, as well as on an overall basis, in a study of the records of 934 Red Dane heifers from 748 herds. The partial correlations between age and yield of 4% FCM were .12, .08, .01, and .08, for low, medium, and high herds, and the total basis, respectively. Thus, the association of age and production adjusted for weight was small in any case, but especially so where the herd conditions were relatively superior. The association of weight with production adjusted for age also declined with increasing level of herd environment. Weight was only one-half as closely associated with production in the highest herds as for the lowest group of herds. The findings of the above workers agree well with the present results, with the exception of Turner's estimate of .25 for the partial correlation of age and fat production. The two results need not correspond due to differences in the data employed, but this may not explain all of the disagreement.

The intraherd partial correlations in Table 16 indicate that age is slightly more closely associated with production than is weight. A comparison of overall and intraherd partial correlations shows that the association between age and production is much larger when herd differences are removed. The association between weight and production appears to be only about one-half as large within the herd as in a group of many herds. A comparison of the intraherd partial correlations with the within-herds phenotypic correlations (Table 14) indicates that the correlations of age and weight with production are reduced by a similar amount by holding the remaining factor constant.

The preceding discussions have contained estimates of the phenotypic, partial, and "environmental" correlations of weight and production. The role of genotypic differences as a common source of variation in weight and production is as yet undetermined in these data. Hazel et al. (25) have advanced a method of obtaining estimates of this relationship. According to these authors, the genetic correlation between traits 1 and 2 is $r_{G_1G_2} = \frac{Cov\ G_1G_2}{S_{G_1}S_{G_2}}$, where Cov G_1G_2, S_{G_1}, and S_{G_2} are the genetic covariance and standard deviations, respectively. Lush (37) has discussed the interpretation of genetic correlations. Such a correlation may be thought of as measuring the degree to which genes controlling one trait also contribute to the expression of the other measurement in question. The most important cause of genic associations between traits is pleiotropy, i.e. genes which influence one trait also influence the other. Linkage (39) and variable selection pressure in isolated sub-groups may account for minor genetic associations between traits. Lush concluded that negative pleiotropic effects are expected to be much more frequent than positive ones.

As an estimate of genetic variance and covariance, the components between sires within herds may be employed. The genetic variance and covariance are 4 HS and 4 Cov_{hs}. Table 17 presents the genetic correlations between weight and production.

TABLE 17

GENETIC CORRELATIONS BETWEEN WEIGHT AND PRODUCTION

Breed	Milk	Fat
Holstein	.33	.35
Guernsey	.19	-4.49
Jersey	-3.05	-0.20

Estimates outside normal limits are obtained for weight and milk in Jerseys and for weight and fat in Guernseys ($-1 \leq r \leq +1$). Reference to Table 11 shows that the estimates of Cov_{hs} in Jerseys, and to a lesser extent in Guernseys, are rather erratic, with large positive and negative values occurring. This is the source of the aberrant behavior of the genetic correlations. Since the covariance estimates are more stable the larger the number in the breed sample, small numbers may be a source of inaccuracy. The results may reflect a lack of resolving power in the method of estimation of the variance and covariance components where the numbers involved are comparatively small (the summed components agree closely with the computed total variances and covariances).

Little can be said of the other Guernsey and Jersey estimates which are not invalid by inspection, in view of the accompanying disturbances. How much confidence can be placed upon the estimates of genetic correlation for Holsteins is questionable. The degrees of freedom for Holsteins exceed those for Jerseys and Guernseys by factors of 9 and 4, respectively, so the Holstein estimates should at least provide a general picture of the parameters involved. As expected, the correlations for milk and fat agree rather closely.

TABLE 18

A COMPARISON OF VARIOUS ESTIMATES OF THE GENETIC CORRELATION BETWEEN WEIGHT AND PRODUCTION

Source	Breed	Milk	Fat
Touchberry (48)	Holstein	-.53	.24
Mason *et al.* (40)			
a. Initial weight	Red Dane	.25	---
b. March weight	Red Dane	.02	---
Blackmore (4)	Holstein	-.02	---
Present Study	Holstein	.33	.35

The present results for Holsteins are compared with those of other workers in Table 18. The estimate for milk agrees generally with that of Mason *et al.* for initial weight (weight prior to first calving), while that for fat is of the general order of Touchberry's result. The data used by Touchberry and Blackmore were corrected for age differences. Touchberry used the lactation record nearest the third birthday, while Blackmore employed the lifetime record of 3.5% FCM. The data employed by Mason *et al.* were obtained from first lactation records, so this study is more comparable to the present analysis than those of Touchberry and Blackmore.

The positive results of Touchberry and Mason *et al.*, coupled with the present findings, point to a positive genetic relationship between weight and production, at least for the first lactation. How may such results be interpreted? As mentioned previously, most of any observed genetic correlation must be the product of the manifold effects of genes. Where phenotypic differences in two traits are markedly controlled by genotypic differences and the number of genes affecting each trait is large, some pleiotropy may well exist. Milk production and body weight apparently fit these requirements. Intraherd heritabilities of production and weight have been found to be on the order of .2 to .3 and .5, respectively (see previous discussion). Though the evidence is scant, both production (47) and weight (42) appear to be controlled by a large number of genetic factors. However, a factor affecting two different traits might well have opposite effects on the two scales of measurement. Lush (37) believes that this is the more common association.

If the genetic correlation between weight and production is as large as .3 and if the heritabilities of production and weight are as large as have been estimated, it would seem that selection for one would achieve visible gain in the other as well. Concurrent selection for milk production and size (as reflected by beef characteristics) is an important feature of improvement programs in the dual-purpose breeds of cattle. Blackmore (4) concluded that simultaneous selection for milk production and meat-type characteristics would be impractical.

Information concerning the amount of genetic progress made by simultaneous selection for weight and milk production would be of value in further study of the problem. On the commercial basis, it is doubtful if size has received consistent degrees of emphasis in selection programs, (with the possible exception of the dual-purpose breeds). Vacillating degrees of importance attached to weight, therefore, would appear to preclude obtaining much useful information on the degree of progress which has been made by simultaneous selection for the two traits among commercial dairy herds.

MULTIPLE REGRESSION ANALYSIS

The method of multiple linear regression has been employed in previous efforts to determine how production changes with weight, independent of age.

The exponential relationship, $Y = a\,W^b$, suggested by Brody to be more appropriate than a linear relationship, has been tested by Gaines (15) and by Bailey and Broster (2). From data on 11 Holstein cows Gaines reported regression coefficients of production on weight on the logarithmic grid ranging from .28 to 1.49, depending on the stage of lactation at which weight was measured. Bailey and Broster found an exponential value of .82 ± .22 in data from 99 first lactations of Dairy Shorthorn cattle. They concluded that the deviation from unity was not serious and that a linear function could adequately express the relationship. Turner (50) tested the linearity of the regression of fat production on weight in Guernsey cattle of three to four years of age by a test involving the correlation ratio (η). He concluded that the departure from linearity was not great. These results indicate that there is some basis for the assumption of a linear relationship.

Multiple regression equations were calculated for both milk and fat. Partial regression coefficients (b) of production on age and weight, standard partial regression coefficients (b'), standard errors of the partial regression coefficients, and standard errors of estimate are presented in Table 19 for the overall basis.

Age and weight appear to be rather poor predictors of production. In milk for Holsteins, for example, the standard error of estimate is almost 2000 pounds, while the standard deviation of milk production is only slightly more than 2000 pounds. Age appears to be a rather unimportant source of variation in production, since the age coefficients are not significantly different from zero for Jerseys and Guernseys.

TABLE 19

PARTIAL REGRESSIONS OF MILK AND FAT PRODUCTION ON AGE AND WEIGHT

Breed	Constant (a)	SEE	Partial Coefficients				Stan. Part. Coeff.	
			$b_{y1.2}$	SE	$b_{y2.1}$	SE	$b'_{y1.2}$	$b'_{y2.1}$
A. Milk								
Holstein	44.65	19.36	.24	.06	.43	.02	.06	.29
Guernsey	31.81	15.25	.05	.11	.41	.04	.01	.29
Jersey	35.96	12.98	.03	.14	.32	.05	.01	.28
B. Fat								
Holstein	15.70	7.05	.10	.02	.15	.01	.06	.29
Guernsey	13.55	7.22	.04	.05	.20	.02	.03	.31
Jersey	24.27	7.24	.00	.08	.10	.02	.00	.18

1 = age, 2 = weight, y = production, SEE = standard error of estimate, SE = standard error of regression coefficient.

In every case the weight coefficient is much larger than the age coefficient. The standard partial regression coefficients give a better comparison of the importance of age and weight since these coefficients measure the part of the standard deviation of the dependent variable contributed by the independent variable in question. From these entries in Table 19, weight is seen to be a more important influence on individual production records over a group of many herds than is age.

The variation upon which the estimates above are based contains a large amount of herd differences. Although no practical method of analyzing these herd variations is available, environmental characteristics peculiar to individual herds may be expected to be the chief components. To obtain a clearer picture of any existing relationships between weight and production, these environmental fluctuations were eliminated by computing regressions within herds. Most practical applications are made within herds.

Within herds the relative contributions of age and weight are virtually the reverse of the overall situation. Age is now a slightly more important factor in production than is weight. A comparison of the overall and intraherd partial coefficients shows that weight is a smaller source of variation in production within herds than of overall variation. Two observations may be made from these results: (1) the removal of differences between herds (chiefly environmental) also removes much of the variation in production associated with weight, and (2) variation in production due to differences

TABLE 20

WITHIN-HERDS PARTIAL AND STANDARD PARTIAL REGRESSIONS OF PRODUCTION ON AGE AND WEIGHT

Predicted Quantity	Breed	Part. Coeff. $b_{y1.2}$	Part. Coeff. $b_{y2.1}$	Stan. Part. Coeff. $b'_{y1.2}$	Stan. Part. Coeff. $b'_{y2.1}$
Milk	Holstein	.76	.21	.18	.15
"	Guernsey	.90	.18	.24	.15
"	Jersey	.57	.20	.19	.17
Fat	Holstein	.30	.07	.19	.14
"	Guernsey	.45	.08	.26	.14
"	Jersey	.29	.09	.20	.15

1 = age, 2 = weight, y = production.

in age at first calving is much more important relative to weight within herds than on an overall basis. The latter observation is due in part to a decrease in the total variation, however, all of the increase cannot be attributed to this reduction. There is apparently a tendency for variation due to age to cancel out when the influence of differences between herds (probably largely environmental) is included.

Several previous studies in multiple regression are available. Bailey and Broster (2), in an intraherd study of 99 first lactation records of Dairy Shorthorns, found partial regressions of 4% FCM (tens of pounds) on weight (pounds) and age of .51 and -.11, respectively. Gaines _et al._ (17), in an investigation of 231 lactations of 57 Holstein cows, reported a within-herd, within-cow partial regression of .04, where the dependent variable was FCM in pounds and weight (pounds) was recorded within the first month following parturition. In earlier work, Gaines <u>et al</u>. (18) analyzed 199 Holstein and 140 Jersey eight-month lactation records made in Illinois DHIA herds, for which age and estimated body weights were available (weight was estimated by taped chest girth measurements). The regressions of FCM in pounds on weight in thousands of pounds were 13 and 26 for Holsteins and Jerseys, respectively. The corresponding age partial regressions were .96 and .37. Johansson (29) found partial regressions of first lactation butterfat yield (kg.) on weight (kg.) and age at calving (days) of .14 and .13, respectively, in an analysis of records of Red Dane heifers in Danish progeny stations.

The work of Bailey and Broster is most comparable to the present study. A comparison shows that their regression of milk on weight is more than twice as large as the present intraherd regressions. However, their data were in terms of FCM and were collected over a longer time interval than in the present case.

Tests of the significance of the reduction in within-herd variation due to fitting regression coefficients for age and weight are presented in Table 21. The reductions in residual variation due to fitting age and weight simultaneously, due to fitting weight alone, and due to fitting both age and weight as compared to weight alone, are shown. It is evident that the fitting of partial regression coefficients for age in addition to weight reduces the within-herd variation to a significant degree, as compared to fitting weight alone. Again, this is in contrast to the overall situation where the fitting of partial regression coefficients to age was of little value.

TABLE 21

ANALYSIS OF VARIANCE OF REGRESSION WITHIN HERDS

Breed	Source	DF	Milk Mean Square	Fat Mean Square
Holstein	Due To Fitting Age & Weight	2	37502**	5016**
	Due To Fitting Weight	1	46391**	5807**
	Due To Fitting Age After Weight	1	28614**	4226**
	Residual	4023	243	30
Guernsey	Due To Fitting Age & Weight	2	7117**	1642**
	Due To Fitting Weight	1	8008**	1783**
	Due To Fitting Age After Weight	1	6226**	1500**
	Residual	835	138	29
Jersey	Due To Fitting Age And Weight	2	2082**	480**
	Due To Fitting Weight	1	2462**	528**
	Due To Fitting Age After Weight	1	1703**	432**
	Residual	416	109	27

** P<.01.

DISCUSSION AND CONCLUSIONS

The influence of weight upon production, the factors controlling such influences, and the importance which should be attached to body weight in the management and selection of dairy cattle can be evaluated partially from the information obtained in previous sections.

IMPLICATIONS IN DAIRY CATTLE MANAGEMENT

We have two pictures of the quantitative influence of weight on production in the first lactation. First, partial regressions and phenotypic correlations indicated that the influence of weight on first lactation records over the many herds studied is much larger than that of age. Weight accounted for approximately 8% of the variation between first lactation production records, while age was not a measurable source of variation. Partial correlations indicated that age was not important in the influence of weight on production when differences between herds were ignored. Secondly, the importance of age and weight to intraherd production estimated by least squares and partial regression indicated that larger heifers had little or no economic advantage in the first lactation. Weight apparently should receive only 50% as much emphasis in predicting intraherd production as for predicting production in a group of many herds. Only 2% of the intraherd variation in production was directly attributable to weight.

In practice, the separate pictures of the importance of age and weight must be integrated since they are entangled in nature. In application, when we consider age, we are also considering weight to some extent, and vice versa.

The quantitative influence of weight upon first lactation production is not large enough to show economic advantage when contrasted to the feed cost of obtaining the weight gain and the additional cost of maintaining the heavier animal. There is an additional point to be considered in that larger animals may have more economy of scale, i.e. fewer animals required to produce a given amount of milk, fewer replacements needed, etc.

The primary consideration of body weight in management would seem to be to develop dairy heifers as rapidly as possible to calve them at least at an earlier age than is the case in the sample studied. Since these samples have been taken from the more progressive herds in Michigan, there well may have been a tendency to withhold breeding in order to obtain larger first lactation records. In such situations, the marginal value of the increased milk production obtained is greater than has been shown here due to the increased value placed on breeding stock by higher production. Nevertheless, it seems that commercial dairymen need to reconsider the level of development at which heifers are commonly bred.

The results indicate that a dairy heifer should be bred as soon as sufficient body development is reached that birth complications, interference with growth, and unfavorable effects on later lactations will be precluded. There may be some need to place more emphasis on size rather than on age, since the latter appears to decrease the economy of first lactation production.

The early entrance of heifers into productive life is justifiable on grounds other than the economy of production. One of the chief obstacles to rapid genetic improvement of dairy cattle is the length of the generation interval. The earlier animals are production tested, the more rapidly their genetic worth can be ascertained, as well as that of their parents. For example, the average age at calving in the Holstein sample was 29 months. This would mean that the worth of a sire could not be evaluated until the youngest member of the progeny group was 39 months of age if completed records are used and the average conditions hold. If the average age at calving were 23 months, the sire proof could be obtained 6 months earlier. It seems reasonable to assume that some time gain can be made in progeny testing through earlier calving of heifers without hindering the economy of first lactation production.

The conclusion reached in the preceding discussion finds support in earlier work. Turner (49) concluded that early breeding and a rapid succession of pregnancies are necessary for the most rapid gland development and the most economical production, since the greater production of large cows only slightly exceeds the cost of obtaining the additional product. He further concluded that the sires whose daughters are above the average for the breed in fat production without exceeding the average in body weight are especially desirable because their daughters are increasing the economy of fat production in the breed.

The work of Reid et al. (46) with different levels of nutrition in heifers adds further strength to the conclusions of the present study. In a lifetime experiment three groups of Holstein heifers were raised from birth to first calving on low, medium, and high planes of nutrition. After the date of first calving, they were placed on comparable normal rations. The low-plane group averaged over 200 pounds smaller at first calving than either of the better-fed groups. However, the low-nutrition group produced only slightly less than the other groups during the first lactation. Moreover, in later lactations, the low-plane heifers equalled and then excelled the production of the larger, better-fed heifers. Thus, there is an indication that heifers calving at comparatively low levels of development produce just as well as those calving at high levels of development.

Gethin (19) has reviewed the relation of age at first calving to later production. He concluded that earlier first calvers are more economical producers than later calvers. Gethin further concluded that 24 months is the minimum age at first calving to avoid growth complications.

The effect of earlier breeding and lower levels of development at the time of breeding upon the length of the productive life is an area where future study is needed. No final conclusions on standards for the proper level of development at which heifers should be bred can be made until the effect upon longevity is ascertained. However, from the standpoint of production in the first lactation, the breeding of heifers at slightly younger ages and lower levels of development than is the common practice appears justifiable.

IMPLICATIONS IN DAIRY CATTLE SELECTION

Comparison of overall and intraherd regressions and correlations indicated that differences between herds made significant contributions to the association of weight and production. Conversely, differences between herds appeared to neutralize the influence of age on production since age was far more important within the herd than on an aggregate basis.

The role of differences between herds in the overall contribution of weight to production was measured by the "environmental" correlation between weight and production. With the single exception of the association between weight and fat production in Jerseys, these correlations were all of the order of .5. This indicated that herd differences, which are presumably chiefly environmental in nature, are the most important causes of the association of weight and production. Hofmeyr's work (27) indicates that the nature of differences between herds may be such that smaller heifers have a much better opportunity to reach their productive potential in the higher producing herds, as compared to the poorer herds.

To ascertain the role of the genotype in the relationship between weight and production, genetic correlations were computed. Although irregular results were obtained for Jerseys and Guernseys, probably because of small numbers, the correlations for Holsteins of .3 for both milk and fat indicate that the genotype may make an important contribution to correlated changes in weight and milk production.

Some of the difficulty in evaluating the nature of the factors controlling the association between weight and production lies in how we choose to view the mechanisms through which the association is brought about. Speaking of weight as a "source" of variation in production may be improper as the word source may be a misnomer. Milk production is usually pictured as a result of the forces of heredity and environment and the interplay between the two. Thus it would seem more nearly correct to view associations of weight with production as being an expression of some function of heredity and environment. Weight, as such, may have little to do with milk production. However, an association between weight and production may be produced by environmental and hereditary factors which are reflected by both measurements. Thus, to learn the nature of the relationship, a partition of the weight-production association between hereditary and environmental sources seems to be necessary.

The most important factors affecting the relationship between weight and production appear to be those which are expressed through differences among herds. These are thought to be chiefly environmental in nature, such as herd to herd variations in level of nutrition. The work of Reid et al. (46) indicates that these differences act upon both weight and production in a similar manner, rather than on production through weight. Reid's experiment also suggests that the plane of nutrition of growing heifers may not be as important to later production as has been believed. His results indicate that the plane of nutrition during the lactation period is more important than that prior to the productive period. In the present data the plane of nutrition would probably be little changed over the period of life studied, whereas the three groups of animals in Reid's experiment were treated differently prior to first freshening but similarly thereafter. Ideally, one would like a mass of field data similar to Reid's experimental data, so that the environmental differences prior to first calving could be evaluated. The present study provides no clue as to whether the plane of nutrition in the growing period or plane of nutrition in the lactation period is more important.

The genetic correlations obtained, while they are not conclusive, in view of previous results, give further indication that genes which cause the heifer to grow well also cause her to produce well. Previous estimates may have been smaller due to consideration of several lactations simultaneously.

What does the presence or absence of a genetic correlation mean in practice? If there is a marked degree of positive correlation between the genotypes for weight and production, selection for one characteristic would achieve some gain in the other measurement, even without paying attention to the second at all. If there is no correlation, selection for one alone would achieve no genetic gain for the other except by chance. Gain in both traits could be achieved by concurrent selection, but the amount of gain possible for each would be less than if selection were solely for one or the other. If there is a significant negative correlation, selection for one would result in a net genetic loss in the other.

Further light might be shed on the subject if we could learn whether there has been a consistent trend in size in connection with prolonged selection for milk production. If the correlation is as high as .3, we should be increasing the size of our animals when we select for greater milk production.

Mason _et_ _al_. (40), in a study of the relationship of body size and first lactation production in Red Dane cattle, concluded that selection for milk yield alone would produce a taller cow with less fleshing and a tendency to convert flesh into milk during lactation. The bases for this conclusion were genetic correlations of -.45 between milk production and weight gain during the lactation and .31 between wither height and production.

Until the existence of a genetic correlation between weight and production is further substantiated, no final disposition of the role of weight in estimating breeding value for milk production can be made. In the meantime, it would be unwise to give much consideration to weight in choosing the parents of the future generation. Should there be no genetic correlation, in fact, the amount of genetic improvement possible in milk production would be decreased by paying attention to weight. Should a negative genetic correlation exist, actual losses in the ability for milk production might result from strong emphasis upon weight.

Even if a genetic correlation is established with some degree of certainty, the course of action to be taken is in doubt. The present results indicate that the larger heifer is not a more economical producer than the smaller heifer (in the first lactation). If such a situation prevails throughout productive life, it is questionable whether body size should be emphasized any more than is absolutely necessary to prevent deleterious effects on the length of productive life. If the genetic correlation is large (.3 or greater), increasing the size of dairy cattle would be concomitant with increasing their ability for production. To select for both traits would be to accentuate increases in size.

In conclusion, weight at first calving does not appear to be a factor of economic importance in first lactation production. The primary consideration of weight in the first lactation lies in evaluating the level of development at which heifers should be bred. This stage of development should be established in such a way that growth is not hindered materially and the length of productive life is not decreased.

The principal causes of the association between weight and production appear to be environmental differences such as those which are manifested between herds. In the present example, the principal factor is probably herd to herd differences in the level of nutrition.

The investigation indicates that the genetic association between weight and production merits further study. The results suggest that the selection for milk production may also indirectly be selection for size.

IMPLICATIONS IN STATISTICAL ANALYSIS OF PRODUCTION DATA

Several authors (5,50) have suggested that production data be corrected for differences in weight. The present results indicate that the intraherd direct influence of weight on production is only about 2% of the total variation in production. If this association is proven to be entirely environmental, correction for weight differences may be worthwhile. If a marked genetic correlation exists, some of the variation "due" to weight is heritable. Under this condition, corrections for weight differences would remove some of the genetic variation in production.

The present results seem to contradict Gaines' conclusions that age has no effect on production independent of weight and that age correction is unsound. Gaines' premise appears to be correct for a group of many herds, but not entirely sound on an intraherd scale. Age appears to account for 4-5% of the intraherd variation in first lactation production, independent of weight. Age corrections of high precision would remove this fraction plus most of the joint variation due to age and weight.

IMPLICATIONS IN FUTURE INVESTIGATION

There are many aspects of the weight-production association which require further attention if we are to accurately assess the importance of weight in dairy cattle. Of course, the present type of analysis needs to be repeated with larger numbers of observations and for later lactations.

However, the following topics, which for one reason or another could not be examined in the present analysis, appear to offer promise of yielding useful information:

(1) Interaction between age and weight

(2) Analyses of variance in production due to independent effects of age and weight

(3) Effect of calving at younger ages and smaller size on longevity

(4) Independent influence of weight on production at very low and very high levels of weight

(5) Heritable variation in production associated with weight (estimation of heritability independent of weight)

(6) Linearity of relationship between weight and production (application of curvilinear regression)

(7) Estimation of simultaneous genetic gains for weight and production in dual-purpose breeds of cattle

(8) Apparent canceling of intraherd production variation due to age differences by differences between herds.

SUMMARY

First lactation milk and fat production records (including age and weight at calving) for 4677 Holsteins, 1001 Guernseys, and 501 Jerseys compiled in the Michigan DHIA-IBM program over a three and one-half year period were analyzed to ascertain the relation between weight and level of production.

Least squares estimates of the independent influences of age and weight at calving on first lactation production were presented in Tables 4 and 6. Maturity, as measured by age, was negatively related to the economy of first lactation production. The expected change in production associated with a change in weight at first calving was dependent upon the level at which the change in weight occurred. In all three breeds, there were instances where a decrease in production was associated with increased weight. The production response to level of development appeared to reach a maximum at weights 300-400 pounds above the breed average for the age. When the value of added production accompanying increased weight was contrasted to the added expense involved, heavier heifers had little or no advantage in the first lactation.

Partial regressions of production on age and weight were computed on overall and intraherd bases. When many herds were considered, weight was more important to production than age. The intraherd regressions of milk production on age and weight at calving were on the order of 75 pounds per month and 200 pounds per 100 pounds, respectively. Weight was only about

one-half as important in predicting production records within the herd as compared to production records among many herds.

Large between-herd correlations of weight and production indicated that differences between herds contributed significantly to the association.

Estimates of the genetic correlation between weight and production were on the order of .3, indicating significant genetic contribution to the association between weight and production. Irregular results were obtained for Jerseys and Guernseys.

Individual differences in weight at first calving were found to be heritable to the extent of .3 to .5. Heritabilities of first lactation milk and fat production ranged from .2 to .3 and .2 to .4, respectively.

It was concluded that dairy heifers should be bred as soon as sufficient size is attained to minimize harmful effects on the length of productive life.

The results indicated that selection for increased milk production may indirectly result in increased body size in dairy cattle.

It was further concluded that correction for weight differences may remove a fraction of the genetic variation in production.

REFERENCES

(1) Agricultural Economics Department, Michigan State University. Compilation of Average Prices of Farm Commodities. Mimeo. 1957.

(2) Bailey, G. L., and Broster, W. H. The Influence of Live Weight on Milk Production During the First Lactation. J. Dairy Research, 21: 5. 1954.

(3) Beck, G. H., and Turk, K. L. Size and Its Influence on Milk Production. Purebred Dairy Cattle Association Mimeo. 1948.

(4) Blackmore, D. Phenotypic and Genetic Relationships Between Body Measurements and Milk Production in Holstein Cattle. Unpublished Manuscript. 1958.

(5) Branton, C., and Stone, E. J. Interrelationships of Age, Body Weight, and Milk Production of Holstein-Friesian Cows in Louisiana. J. Animal Sci., 16: 1068. 1957.

(6) Brody, S. B. Growth and Development With Special Reference to Domestic Animals. X. The Relation Between the Course of Growth and the Course of Senescence With Special Reference to Age Changes in Milk Secretion. Missouri Agr. Expt. Sta., Research Bull. 105. 1927.

(7) Brody, S. B. Factors Influencing the Apparent Energetic Efficiency of Productive Processes in Farm Animals. J. Nutrition, 17: 235. 1939.

(8) Brody, S. B. Lactational Performance and Body Weight. Science, 95: 485. 1942.

(9) Brody, S. B., and Procter, R. C. Growth and Development With Special Reference to Domestic Animals. XXXV. Energetic Efficiency of Milk Production and the Influence of Body Weight Thereon. Missouri Agr. Expt. Sta., Research Bull. 222. 1935.

(10) Brody, S. B., Ragsdale, A. C., and Turner, C. W. The Rate of Growth of the Dairy Cow. III. The Relation Between Growth in Weight and Increase of Milk Secretion With Age. J. Gen. Physiol., 6: 21. 1924.

(11) Davis, H. P., Morgan, R. F., Brody, S. B., and Ragsdale, A. C. Relation of Height at Withers and Chest Girth to Live Weight of Dairy Cattle of Different Breeds and Ages. Nebraska Agr. Expt. Sta., Research Bull. 91. 1937.

(12) Davis, H. P., Morgan, R. F., and Gaines, W. L. Live Weight and Milk Energy Yield in the Nebraska Station Dairy Herd. J. Dairy Sci., 26: 625. 1943.

(13) Davis, H. P., and Willett, E. L. Relation Between Rate of Growth and Milk and Fat Production. J. Dairy Sci., 21: 637. 1938.

(14) Edwards, J. Effect of Breed, Size of Cow, Yield of Milk, and Stage of Lactation Upon Efficiency of Milk Production. J. Dairy Research, 7: 211. 1936.

(15) Gaines, W. L. Live Weight of Cow at Various Stages of Lactation in Relation to Milk-Energy Yield. J. Dairy Sci., 24: 795. 1941.

(16) Gaines, W. L. Live Weight Versus Metabolic Body Size in Dairy Cows and Goats. J. Dairy Sci., 29: 259. 1946.

(17) Gaines, W. L., Davis, H. P., and Morgan, R. F. Within-Cow Regression of Milk-Energy Yield on Age and Live Weight. J. Dairy Sci., 30: 273. 1947.

(18) Gaines, W. L., Rhode, C. S., and Cash, J. G. Age, Live Weight, and Milk-Energy Yield in Illinois Cows. J. Dairy Sci., 23: 1031. 1940.

(19) Gethin, R. H. The Age at First Calving of Dairy Cattle in Relation to Subsequent Performance. Animal Breeding Abstracts, 18: 133. 1950.

(20) Gowen, J. W. Studies on Conformation in Relation to Producing Ability in Cattle. IV. The Size of the Cow in Relation to the Size of Her Milk Production. J. Agr. Research, 30: 865. 1925.

(21) Gowen, J. W. Conformation of the Cow as Related to Milk Secretion, Jersey Registry of Merit. J. Agr. Sci., 23: 485. 1933.

(22) Gowen, J. W. The Conformation of the Parents as Related to the Milk Secretion of the Daughter, Jersey Record of Merit. J. Agr. Sci., 23: 514. 1933.

(23) Gowen, J. W. On the Genetic Constitution of Jersey Cattle, As Influenced by Inheritance and Environment. Genetics, 18: 415. 1933.

(24) Harvey, W. R. The Analysis of Non-Orthogonal Data With IBM. Mimeo., Proc. Am. Soc. Animal Production. 1953.

(25) Hazel, L. N., Baker, M. L., and Reinmuller, C. F. Genetic and Environmental Correlations Between Growth Rates of Pigs at Different Ages. J. Animal Sci., 2: 118. 1943.

(26) Henderson, C. R. Estimation of Variance and Covariance Components. Biometrics, 9: 226. 1953.

(27) Hofmeyr, Jan. A Study of Danish and Swedish Progeny Testing Methods for Dairy Bulls. Kungl. Lantbrukshogskolans Annaler, 22: 425. 1955.

(28) Johansson, I. The Heritability of Milk and Butterfat Yield. Animal Breeding Abstracts, 18: 1. 1950.

(29) Johansson, I. An Analysis of Data From the Danish Bull Progeny Testing Stations. Z. f. Tierzuchtg. u. Zuchtungsbiol., 63: 105. 1954.

(30) Johansson, I. The First Lactation Yield as a Basis of Selection Compared to the Second and Third Lactations. Proc. Brit. Soc. Animal Prod., 79. 1955.

(31) Johansson, I., and Hildiman, S. E. The Relationship Between Certain Body Measurements and Live and Slaughter Weight in Cattle. Animal Breeding Abstracts, 22: 1. 1954.

(32) Kendrick, J. F. Estimating the Weights of Dairy Cows From Heart Girth Measurements. USDA BDIM, 695. 1936.

(33) Kleiber, M. Body Size and Metabolic Rate. Physiol. Revs., 27: 4. 1947.

(34) Kleiber, M., and Mead, S. W. Body Size and Milk Production. J. Dairy Sci., 28: 49. 1945.

(35) Kleiber, M., and Mead, S. W. Body Size and Lactation Rate. J. Dairy Sci., 28: 49. 1945.

(36) Knott, J. C., Hodgson, R. E., and Ellington, E. V. Methods of Measuring Pasture Yields With Dairy Cattle. Wash. Agr. Expt. Sta., Bull. 295. 1934.

(37) Lush, J. L. The Genetics of Populations. Unpublished Lecture Notes. 1948.

(38) Lush, J. L., Christensen, F. W., Wilson, C. V., and Black, W. H. The Accuracy of Cattle Weights. J. Agr. Research, 36: 551. 1928.

(39) MacArthur, J. W. Selection for Small and Large Body Size in the House Mouse. Genetics, 34: 194. 1949.

(40) Mason, I. L., Robertson, A., and Gjelstad, B. The Genetic Connexion Between Body Size, Milk Production, and Efficiency in Dairy Cattle. J. Dairy Research, 24: 135. 1957.

(41) Morrison, F. B. Feeds and Feeding. 22nd ed. Morrison Publ. Co., Ithaca, N. Y. 1956.

(42) Pease, M. S. Experiments on the Inheritance of Weight in Rabbits. J. Genetics, 20: 261. 1928.

(43) Pfau, K. O., and Bartlett, J. W. The Relationship of Body Size to Milk Production in Dairy Cattle. Purebred Dairy Cattle Association Mimeo. 1954.

(44) Purebred Dairy Cattle Association Type Committee. Unified Score Card. Purebred Dairy Cattle Association. 1943.

(45) Ragsdale, A. C., and Brody, S. B. Estimating Live Weights of Dairy Cattle. Missouri Agr. Expt. Sta., Bull. 354. 1935.

(46) Reid, J. T., Loosli, J. K., Turk, K. L., Asdell, S. A., and Smith, S. E. Progress Report on a Study of the Effect of Plane of Early Nutrition Upon Reproductive and Productive Performance of Holstein Cattle. J. Dairy Sci., 40: 610. 1957.

(47) Shrode, R. R., and Lush, J. L. The Genetics of Cattle. Advances in Genetics, 1: 209. 1947.

(48) Touchberry, R. W. Genetic Correlation Between Five Body Measurements, Weight, Type, and Production in the Same Individual Among Holstein Cows. J. Dairy Sci., 34: 242. 1951.

(49) Turner, C. W. The Relation Between Weight and Fat Production of Guernsey Cattle. J. Dairy Sci., 12: 60. 1929.

(50) Turner, C. W. The Inheritance of Body Weight in Relation to Milk Secretion. Missouri Agr. Expt. Sta., Research Bull. 147. 1930.

(51) Turner, C. W., Ragsdale, A. C., and Brody, S. B. The Relation Between Age, Weight, and Fat Production in Dairy Cows. Missouri Agr. Expt. Sta., Bull. 221. 1924.