GENETIC AND ENVIRONMENTAL TRENDS IN MICHIGAN DAIRY CATTLE MILK PRODUCTION

Thesis for the Degree of Ph. D.
MICHIGAN STATE UNIVERSITY
Robert W. Everett
1966

ABSTRACT

GENETIC AND ENVIRONMENTAL TRENDS IN MICHIGAN DAIRY CATTLE MILK PRODUCTION

By Robert W. Everett

A method of separating genetic and environmental trends in dairy cattle production was applied to simulated production data to test the accuracy of the method. Results from the simulated data showed that the accuracy of the method of analysis is high and also indicated that the regression of daughters additive genetic value on dams additive genetic value within sires varied according to the method of pooling.

Application of the method of analysis of 65,560 two-year-old, 305-day, 2X, M.E. records of registered and grade Holstein cows recorded on Michigan D.H.I.A.--I.B.M. from 1953 to October, 1965, indicated a positive genetic trend and a negative environmental trend for both milk and fat production. Progeny produced by artificial insemination increased genetically 2.4 per cent per year in milk production and 2.6 per cent per year in fat production compared to 1.0 per cent and 0.8 per cent genetic increase per year in milk and fat production, respectively, in the naturally sired progeny.

The implications of managemental and nutritional trends are discussed. Estimates of the genetic correlation between daughter and dam and its influence on heritability estimation are given.

GENETIC AND ENVIRONMENTAL TRENDS IN MICHIGAN DAIRY CATTLE MILK PRODUCTION

By

Robert W. Everett

A THESIS

Submitted to the College of Agriculture
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Dairy

1966

ACKNOWLEDGMENTS

The author wishes to express his appreciation to Dr. Clinton E. Meadows for his patient guidance and constructive criticism during the investigation of the problem and writing of the thesis.

Thanks are also due to Dr. John L. Gill for his willing counsel, technical assistance, and interpretation of the results throughout the course of the study and in the analysis of the data.

The author is grateful to Dr. Lon D. McGilliard for the use of the simulated data.

TABLE OF CONTENTS

Page

ACKNOWLEDGMENTS ii

LIST OF TABLES iv

INTRODUCTION 1

REVIEW OF LITERATURE 3

Methods of Estimating Genetic and Environmental Trends 8
Adjustment of Data 18
Estimates of Genetic and Environmental Trends . 22

SOURCE OF DATA 35

METHODS. 38

RESULTS AND DISCUSSION. 46

SUMMARY. 80

LITERATURE CITED. 84

LIST OF TABLES

Table Page

1. The Variances Used in the Construction of the Simulated Dairy Herds. 35

2. Mortality Rates Used in the Simulated Herds 36

3. Averages of Characters in Simulated Herds . 46

4. Average Milk and Fat Production for the 13 Years Studied. 56

5. Parameters Used in Estimating Genetic and Environmental Trends in Milk Production . 58

6. Estimates of the Genetic and Environmental Trends in Milk Production Per Year. . . 62

7. Estimated Genetic Correlation Between Daughter and Dam. 62

8. Parameters Used in Estimating the Genetic and Environmental Trends in Fat Production. 69

9. Estimates of the Genetic and Environmental Trends in Fat Production Per Year . . . 70

10. Comparison of Artificially and Naturally Sired Progeny. 71

11. Heritability Estimates for Milk and Fat Production. 76

INTRODUCTION

The trend in dairy production has been an increased production per cow and a corresponding decrease in dairy cattle numbers. The trend in production per cow has two possible broad causes: an increase in genetic merit per cow and an increase in the level of management or environment. Environmental trends should exist because of the application of advances in husbandry, health and feed quality. However, seasonal or yearly fluctuations in the environment are not considered as permanent environmental influences since they can be adjusted statistically.

The estimation of genetic trend along with the selection practiced would yield an estimate of the effectiveness of selection for the production trait considered. This could also be a measure of the ability of the sire selection committees at the A.I. organizations to obtain superior sires with a high breeding value for yield. Such information derived from a large population of cows should be of interest to dairymen and owners of artificial insemination (A.I.) stud barns which furnish the genetic base for most dairy cattle.

The measurement of genetic and environmental trends may be more academic than practical. However, a positive genetic trend should verify the practical importance of selection since genetic gains can be attained at a low cost and are permanent in nature.

Accurate separation of genetic and environmental trends is difficult because the two are partially confounded. The purpose of this study is to test the accuracy of a method of separating genetic and environmental trends, and to apply the method of analysis to a large volume of data representative of the Michigan dairy cattle population.

REVIEW OF LITERATURE

The most serious difficulty in the estimation of selection response is the confounding of genetic with environmental changes. Thus, unsupported assumptions are needed to interpret trends. Selection in opposite directions can eliminate environmental bias, but does not permit estimates of selection response in one direction alone. Comparisons of several methods of selection in one direction still do not measure the absolute response; but the measurement of genetic divergence from a control may eliminate any systematic difference in environmental influences. In concept, the use of a control strain in which the genotypic mean would remain constant in successive generations would provide estimates of purely environmental changes. However, it is assumed that the effects of interaction of genotype and environment will be random over years, eliminating bias. Changes in gene frequency caused by random drift and natural selection and changes in gene expression caused by inbreeding and gradual disintegration of favorable espistatic gene combinations previously maintained by selection, are possible sources of change in genetic merit in control populations.

Maintenance of the largest possible effective size of the population minimizes inbreeding and random drift. Automatic selection can be avoided by using pedigreed matings which force equal reproductive contributions from each individual in each generation (Dickerson, 1960). Also, Wright (1938) has shown that this practice will approximately double the effective population size, relative to the practice of random mating.

If phenotypic response to continued selection has become neglibible relative to expectations based on selection differentials and heritabilities, something is inconsistent in the estimates of heritability or in their interpretation (Dickerson, 1955). An accurate comparison of the actual and expected response to selection depends upon valid separation of genetic and environmental trends.

Gowe *et al.* (1959) maintained that the function of control populations is to assess the magnitude of short-term fluctuations in environment, to maintain genetic consistency over a period of time and to serve as a gene pool with known genetic parameters for use as a base material in selection experiments. The control population has to be large enough to give a reasonably small standard error so that the mean is an efficient control. It should be representative and not react to specific environmental changes.

Genetic drift and natural selection should be eliminated as much as possible.

A simple genetic model may be adequate in the early stages of a selection program but genetic and environmental relationships become more complicated after prolonged selection. Possible causes are the loss of additive variance, increase in the proportion of non-additive variance, and negative genetic correlations between genotypes of the traits and components of fitness.

Dickerson and Hazel (1944) suggested that two factors which determine annual improvement from selection are the average genetic superiority of those animals selected to become parents and the average age at which parents bear offspring, the generation interval. Possible ways of obtaining more genetic improvement include increasing the genetic superiority of the potential parents, decreasing the generation interval, increasing the genetic superiority of the parents relatively more than the generation interval, and decreasing the genetic superiority of the potential parents relatively less than the generation interval.

Published reports of sluggish response to selection in animals are rare. Response to selection has been greater for traits that presumably had no history of continuous selection in one direction.

Response generally has been greater in the early generations of experiments and when the direction of selection has been reversed from that which previously was practiced.

Genetic-environmental interactions measure the extent that real shifts in genetic ranking do occur from one environment to another. Even a perfect knowledge of the ranking under one environment does not permit prediction of genetic ranking in another environment ($r_G < 1$). An appropriate measure of the degree of genetic-environmental interaction is the average genetic correlation (r_G) between performance of the same genotype in different environments. Theoretically, r_G may range from +1 to 0 and could go negative. As the genetic-environmental interaction goes from 0 to 1, the selective advantage of testing under a representative sample of field conditions rises sharply. Gains from increasing the number of locations falls off when the genetic-environmental interaction is unimportant (Dickerson, 1959).

Genetic-environmental interactions, measured by the genetic correlation between the same genotype in different environments (r_{ij}), may vary from $r_{ij} = 1$ to $r_{ij} = -1$. If $r_{ij} = 1$, genotypes would be ranked exactly the same in the different environments and there would be no loss of progress. If $r_{ij} = 0$, it is equivalent to the cyclic host-pathogen relationship which provides the net effect of a genetic change in the host population without appreciable gain in total performance on fitness. If one assumes a finite number of genes, each with pleiotropic effects on different components of fitness, then it follows that a given gene will have a selection advantage varying from one environment to another. Genes whose effects are rather consistently favorable or unfavorable in the whole range of environments will move toward fixation, leaving genetic variability in the population almost completely dependent upon genes having favorable effects in some environments and unfavorable effects in others. Genes whose unfavorable effects tend to be recessive and whose favorable effects show some degree of dominance will tend to be held at relatively high frequency. The degree of dominance may be low within any single environment, but high for the average over a series of different environments. Thus slippage between generations may occur simply because the genetic response under one environment is irrelevant in the environments into which the population subsequently moves (Dickerson, 1955).

It seems appropriate in light of the volume and complexity of the literature to present the remaining literature in three parts; methods of estimating genetic and environmental trends, adjustment of data, and estimates of genetic and environmental trends.

Methods of Estimating Genetic and Environmental Trends

Nelson (1943) used two methods to determine the amount of genetic change in a herd of cows. The first method involved computation of the average difference in production for all cows that had records in consecutive years and use of the result as an estimate of the environmental change between two years. All the differences were summed to estimate the average differences between non-consecutive years in environment. The second method is the least squares procedure, which does essentially the same thing, but yields a more conservative estimate of environmental change.

Dickerson and Hazel (1944) developed an equation for the average genetic gain from the superiority of the males and females retained for breeding. This involves both old and young sires and dams, and the superiority of the groups must be estimated previously.

Dickerson _et al_. (1954) evaluated the selection practiced in developing inbred lines of swine in a Mid-West Regional project.

Dickerson (1960) suggested the use of two methods of determining selection response. Measurement of genetic divergence as experimental mean minus control mean may eliminate any systematic difference in environmental influences. In concept, the use of a control strain would keep the genetic mean constant in successive generations and would provide estimates of purely environmental change.

Contemporary comparisons of progeny from sires of different birth years, by using frozen semen of earlier sires, could give an estimate of the average genetic change over a period of years, if there was no effect of semen storage or age of mates in future generations.

Formulas used by Flower *et al*. (1964) to estimate the selection differentials were essentially the same as those presented by Dickerson *et al*. (1954). Phenotypic trends were evaluated for the various traits by computing the regression on years. The regression estimates the average change per year for a particular trait. Environmental trends were obtained for birth and weaning weights through the use of repeat mating information obtained in two consecutive years; ΔE was the difference in average weights for calves from repeat matings in two consecutive years. Environmental trends were subtracted from phenotypic trends to obtain estimates of genetic progress.

Goodwin *et al*. (1955) presented a technique for measuring the genetic trend in poultry. The technique requires the use of identical matings during two breeding seasons. Comparisons are made between pairs of progenies descended from full-sister dams of the same age, both of the same generation in two successive years and of two successive generations reared in the same year, which measure the environmental and genetic trends, respectively. Separation of environmental trend from maternal changes with age is accomplished by adding to the repeated matings one-year old full sisters of the two-year old females in these matings.

Damon and Winters (1955) corrected for age and calculated the linear regression of performance on years within generations to obtain an estimate of the environmental trend. The regressions were averaged and the genetic gain was obtained as:

genetic gain = average annual performance increase
-average regression

Brinks *et al*. (1961) obtained a generation number for each calf by using the formula $G_o = \frac{Gs + Gd + 2}{2}$. Then a least squares analysis for generation and year effects was done. The data were adjusted for inbreeding of the calf and inbreeding of the dam.

Rendel and Robertson (1950) proposed a method to estimate the genetic gains directly from the selection applied. The genetic improvement per year is estimated from the selection differential and the additive genetic variance present in the population.

Clayton *et al*. (1957) checked genetic response with various types of individual and family selection in Drosophila according to the method proposed by Rendel and Robertson (1950). All responses and relaxed selection followed the theory very closely.

Searle (1961) developed equations for estimating herd improvement from three selection practices, culling low producing cows, selection of replacement heifers out of high yielding cows and obtaining replacements by proven sires. Upper limits to genetic improvement were calculated with the provision that there is no improvement in the superiority of the bulls, or $\Delta G_s = 0$. The equations become considerably more complicated when improvement in genetic ability of all animals is considered in the equations.

Henderson (1949) developed a method of analysis which utilizes maximum likelihood principles to account for incomplete repeatability and annual culling levels and utilizes all of the records to obtain the most precise estimates possible of the yearly environmental effects.

Robertson and Rendel (1954) compared A.I. sires with non-A.I. sires within herds and years. The difference between the average yield of n_a A.I. and n_n non-A.I. heifers was weighted by $n_a n_n/(n_a + n_n)$.

Tucker _et_ _al_. (1960) used the first-lactation contemporary herd-mate comparison within seasons to evaluate the influence of artificial insemination.

Each A.I.-non-A.I. progeny comparison was weighted as before, $n_a n_n/(n_a + n_n)$, and the weighted differences were tested by the "t" test. The variance of the difference is $\frac{S^2}{w} = \frac{N}{(N - 1)} w^2 [\Sigma(w_i d_i)^2 - \frac{(wD)^2}{N}]$ where $\sigma D^2 = \sigma^2/w$ and $w = \Sigma w_i$ and $D = \Sigma w_i d_i/\Sigma w_i = wD/w$ and d_i is the observed difference of an individual herd-year-season-sire contemporary comparison.

Van Vleck and Henderson, (1961b) developed a procedure which measures the change in merit of non-A.I. daughters, and allows measurement of the change in merit of the A.I. population according to the procedure of Robertson and Rendel (1954). The model was $Y_{ijkp} = u + h_i + S_j + m_k + e_{ijkp}$ where Y_{ijkp} is the record made in ith herd in the kth year-season of freshening by the pth first lactation cow sired by the jth sire, and u is a constant population parameter. The S_j are considered fixed effects and the h_j and m_k either fixed or random effects. Comparisons are made within herd-year-season groups.

The contemporary comparison ($d_{ijk} = Y_{1ijk.} - Y_{2ijk.}$) is between A.I. and non-A.I. daughter averages within a herd-year-season, where $Y_{1ijk.}$ is the mean of N_{1ijk} daughters of the jth A.I. sire in the ith herd and the kth year-season and $Y_{2ijk.}$ is the mean of n_{2ijk} non-A.I. daughters. Each comparison is weighted as by Robertson and Rendel (1954) and Tucker *et al.* (1960). All non-A.I.

sires were considered as one group and were used to estimate annual genetic change as a base for expected A.I. superiority, which is measured also. This method involves matrix algebra; there is an equation for every year-season and every A.I. sire used the comparisons. The advantage of this procedure over the method of Robertson and Rendel (1954) is that the non-A.I. genetic trend is estimated as well as the superiority of A.I. progeny over their non-A.I. contemporaries.

Henderson et al. (1959) presented an analysis that estimates environmental and genetic trends from repeated records subject to culling. This involves maximum likelihood estimation of the appropriate constants for cows, years, and groups. The procedure requires an equation for each constant, which makes the analysis acceptable only for a small population.

McDaniel et al. (1961) used first records of paternal half sisters in different years, adjusted for differences in the inheritance received from their dams by the regression in milk yield from dam to daughter. Adjustments also were applied to environmental causes of variation by the use of partial regression coefficients. The methods of fitting constants and maximum likelihood also were used.

The random-bred control (Gowe *et al.*, 1959) and the repeat mating technique (Goodwin *et al.*, 1955, 1960) use the principle:

	T_o	T_1
Control	0	t_1
Experimental group	0	$t_1 + g_1$

where T_i is time i and the *t*'s and *g*'s are the environmental and genetic trends, respectively.

Thus the *g*'s, *t*'s and *a*'s (age group constants) can be estimated. The change in performance over one year is $t + g$, and the change in performance over successive sire progeny groups is $t + g/2$, if one assumes that the mates are a random sample. If there are no effects of age or of culling dams, the change within sires provides an estimate of $t + g\ (\frac{1 - x}{2})$, where x is the regression of age of dam on age of sire. The genetic change (g) in any sire is assumed to be zero, so that the genetic change in his progeny is assumed to be g/2. The difference $(t + g) - (t + g/2)$ measures half the genetic change in that year. These techniques measure the genetic changes in the array of sires and assume that the same rate of change is occurring in both sexes. The assumption is essentially valid since dams are the daughters of sires of the previous generation.

Two estimates of change can be used, one derived from the regressions of performance on time, the other from differences in means with time. For example, $\Delta G = 2\ (b_{pt} - b_{st})$, where b_{pt} is the linear regression of population performance on time and b_{st} the regression of progeny performance on time pooled within sires. To avoid year to year fluctuations in environment, one may use $2b_{(P-S)T/S}$, twice regression of the difference between the population and individual sire means on time pooled within the sires. If one uses means rather than regressions, the genetic change over $\underline{Y}$ years is given by:

$$(2\ [(\overline{X}Ty - \overline{X}Sg) - (\overline{X}To - \overline{X}So)]\ )/y$$

where $\overline{X}T$ and $\overline{X}S$ are the population and repeated sire means.

The maximum variance of $2(b_{pt} - b_{st})$ is $4(Vb_{pt} + Vb_{st})$ if the regressions are positively correlated as one would expect. The variance of $2b_{(P-S)T/S}$ is simply $4Vb_{(P-S)T/S}$. The theoretical variance of $2(b_{pt} - b_{st})$ is approximately $4\sigma^2\ (\frac{1}{NT_Y} + \frac{1}{\Sigma_s n_s T_y})$, where $\underline{\sigma}$ is the standard deviation of the trait, $\underline{N}$ is the total number of records per year, $\underline{n_s}$ the number of records per year for the $\underline{S}$th sire, $\underline{Y}$ the total number of years and $\underline{y}$ the number of years in which the $\underline{S}$th sire is present. $T_Y = \frac{Y(Y^2 - 1)}{12}$ and $T_y = \frac{y(y^2 - 1)}{12}$.

This expression reduces to approximately $\frac{4\sigma^2}{\bar{n}\ \sum_s Ty}$ where $\bar{n}$ is the average number of records for each sire in any year.

The standard error of an estimate of genetic change derived by this method from a given body of data can be obtained from $\sqrt{\frac{4\sigma^2}{\bar{n}\ \sum_s Ty}}$ and will indicate whether an analysis is meaningful. If S = sires, $\bar{n}ST_y \approx \frac{16}{g^2}$.

The estimate of (t + g) can be adjusted according to the correlation between age of dam and years, and the estimate of (t + g/2) can be adjusted for the correlation between the ages of the sires and dams. If, for each year increase in the age of the sires, the age of the dams increased by six months, the pooled within sire regressions measure t + g/4, providing there are no effects of culling or age differences among dams. Once the genetic change is known, the effect of age of dam on the performance can be calculated. For example, pigs farrow at six month intervals so that the differences in any one year between progeny of second, third, fourth, etc., litter sows and of gilts measures respectively, $a_1 - g/4$, $a_2 - g/2$, $a_3 - 3g/4$, etc., where g is the annual genetic change and the a's are the age effects of the dams (Smith, 1962).

Smith (1963) used a method similar to the one presented earlier (Smith, 1962). Progeny groups were classified independently by age of sire and age of dam in terms of deviations from the herd-year average. Even with no genetic change, there would be a regression toward the mean in subsequent progeny performance of sires and dams. The extent of the regression on initial records can be estimated from heritability and the number of progeny tested per parent in the first year. The difference between the regressed performance in the first year and the observed performance in the second year will provide an estimate of the genetic change by the expression; $2(b_{2.1}\bar{X}_1 - \bar{X}_2) \cdot \frac{12}{M} \cdot \frac{12}{12 + N}$. The deviations from the herd-year average in the first year ($\bar{X}_1$) were regressed to the mean by $\underline{b_{2.1}}$ and compared with the observed deviation in the second year ($\bar{X}_2$). *M* is the average period in months between records and *N* is the average change in age (in months) of the mates of the sires or dams.

Burnside and Legates (1965) used a weighted regression of production on years with first lactations to estimate the annual change in production. Full sib families were used, and adjustment was made for the selection bias in production of the first full sib. The data were analyzed by least squares and weighted regression procedures to estimate the annual environmental trend through comparison with the annual production trend. Paternal half-sibs from dams of different ages were analyzed separately. This regression of production on years pooled within sires estimated one-half the genetic trend plus the environmental trend and was compared with the annual production trend to estimate the annual genetic trend.

Burnside and Legates (1965) concluded that the paternal half-sister approach (Smith, 1962) would be advantageous since it employed a larger volume of records and was apparently less biased by selection effects.

Adjustment of Data

Adjustments applied to data before the measurement of trends are important in yielding more accurate estimates. Robertson and Rendel (1954) concluded that the inclusion of mature cows in the calculations of "herd production levels" for yield led to absurd results, which apparently were due to the fact the effect of age on yield varied in herds at different levels.

Henderson (1958) found that a positive error of one pound fat induced in first lactation records by age correction factors resulted in the environmental trend being biased downward by 0.22 lb. of fat per cow per year. For a positive error of 0.01 in the estimate of ability, the downward bias is 0.08 lb. of fat per cow per year.

Lush _et_ _al_. (1941) suggested testing age correction factors by the regression of high M.E. records on their contemporaries and low M.E. records on their contemporaries. If the age correction factors were correct, the regressions would be similar in magnitude but opposite in direction. The regressions within sire and year computed by McDaniel _et_ _al_. (1961) were both positive and significant. The cows making the higher M.E. records should not have a positive regression, i.e. the age correction factors were too low for the young cows. Since the regressions were about 4 per cent of the mean, all first records were increased by 4 per cent. M.E. milk was also adjusted for estimated net energy consumed, season of calving, length of gestation, previous dry period and herd size by using partial regression coefficients.

Lush and Shrode (1950) concluded that two biases are present in age correction factors. First, if the regression of production on age is computed from the averages of all data available at each age, that curve will not show the effects of age alone but will show those effects combined with whatever effects culling actually had. Secondly, an opposite bias is introduced if the average inherent producing ability of the dairy population is increasing. If cows differ genuinely in their rate of maturity for milk production, then age correction factors, even though accurate for the average, will over-correct for some individuals and correspondingly will under-correct for others. They concluded that corrections for age will be more accurate if different age correction factors are used for cows differing in parity but of the same age. Their estimated correction factors accounted for 91 per cent of the age component of variance, which was 11 per cent of the total variance.

Miller (1964) indicated that the regression of production on age, computed by the paired comparison method, exceeds that computed by the gross comparison method, at ages less than maturity. For ages beyond maturity, the positions of the curves are reversed. Lush and Shrode (1950) pointed out that the difference in lb. between the paired and gross curves due to selection is expected to be: $\frac{n}{N}(\overline{Y}_1 - \overline{Y}_2)$, where n is the number of cows culled at age i, N is the total number of cows calving at age i, $\underline{Y}_1$ is the average of cows culled at age i and $\overline{Y}_2$ is the average of the cows calving at age i and kept for a later record. The ratio of the bias in the paired curve to the bias in the gross curve is, according to Lush and Shrode (1950), $-\frac{1 - t}{t}$, where t is the repeatability of individual records. Thus if $t = .5$, the biases cancel each other.

Lush and Shrode (1950) suggested that the practical importance of errors in age factors should be viewed in the light of normal variation in lactation records. They indicated that errors which amount to less than one quarter of the standard deviation of a cow's estimated producing ability generally can be ignored. This error is roughly 10 lb. of fat at the 500 lb. level, which means that age factor errors of 0.02 or less are not of practical significance for most purposes (Miller, 1964). However, maximum likelihood estimates of genetic trends require that accurate age factors be used. Miller (1964) concluded that the difference between gross and paired regressions of production on age, usually attributed to selection, is extreme only for the Western Midwest and Plains areas of the United States.

Arave *et al*. (1964) corrected all 2X, 305-day D.H.I.A. records for inbreeding by adding 50 lb. F.C.M. per unit of inbreeding. Intra-herd age-correction factors were calculated from a curvilinear regression of the form $Y = a + b_1X + b_2X^2$. These accounted for 91 per cent of the variance between lactations, but were biased due to culling. The age-correction factors and repeatability values differed considerably from herd to herd, indicating a source of downward bias in estimates of the environmental trend.

In swine, Dickerson *et al*. (1954) found that each increase of 10 per cent inbreeding of the dam and litter produced a highly significant decline of about .7 pigs per litter and of 3.4 lb. in weight per pig at 5 months of age.

Tucker *et al*. (1960) found that season of freshening was an important source of variation in first lactation contemporary comparisons. A tendency for a larger proportion of heifers to freshen in the fall months could be responsible for some of the differences in estimates of genetic ability of cows freshening in different seasons.

Estimates of Genetic and Environmental Trends

Friars *et al*. (1962) calculated estimates of heritability and genetic correlations within years from sire and dam components of variance in a population of chickens subjected to multiple objective selection. The slopes of the linear regressions of genetic parameters on years all were essentially negative. There was no indication of significant regression of heritability on years. One significant time trend in the environmental correlations was noted, and it was positive, in contrast to most of the trends in estimates of genetic and phenotypic correlations. In general, estimates of the genetic correlations were declining over the period of study.

Clayton and Robertson (1957) performed a selection experiment with Drosophila for 35 generations. After 24 generations the mean of the character had changed approximately 10 phenotypic standard deviations. In one line the response was linear from the 5th to the 30th generation. On the average, response to selection slowed at the 20th generation and in some lines ceased abruptly. In the lines selected downward there were sudden increases in variation followed by rapid responses. Genetic variation remained after response had ceased and the classical heritability approach to expected selection progress appeared to break down completely.

Robertson's (1955) selection for body size found immediate and sustained response in both directions in three stocks of Drosophila. In the first five generations response was twice as large in lines selected upward as in those selected downward. All three strains stabilized at about the same level, 8 to 10 units up and 14 to 17 units down. Reverse selection tended to return high and low stocks to the original level more quickly than they had moved away, but their means become equal below the level of the unselected stock. After progress from selection had ceased, selection of the large strains downward returned their size to the original level comparatively quickly, faster per generation than the earlier reverse selection. The failure to advance under selection was not due to loss of genetic variability since size was reduced easily under reverse selection. In the small strains reverse selection was ineffective and the strains behaved as if they were homozygous. Relaxation of selection in the large lines produced a moderate decline, but the small strains did not change under relaxed selection.

Lerner and Dempster (1951) selected for long shanks in a small population of Leghorns over an eleven year period. There was an increase or response during the first half of the experiment and an apparent cessation of gains during the latter half, even though there was no apparent decrease in phenotypic or genetic variability.

Dickerson _et_ _al_. (1954) studied the trends in size of litter and growth rate of 49 strains of inbred swine in nine seasons. On the average selection had produced no improvement in the size of litters weaned or in weight per pig at five months of age. The unadjusted linear regressions on time averaged -.21 pigs weaned per litter per year and -4.0 lb. per year in weight at five months of age. The regression of inbreeding on years ranged from 2.3 to 3.9 units per year. When the phenotypic time trend was adjusted for inbreeding there was no trend for size of litters, but a decrease of 2.9 lb. per pig per year for weight at five months of age. The selection practices were equivalent to automatic selection. For example, there is twice as much chance of saving an offspring from a litter of six as from a litter of three.

Damon and Winters (1955) estimated the genetic gain per year in size of litter to be .089. The annual increase in size of litter was .256 pigs per litter, but the linear regression coefficient within generation estimated the environmental trend to be 0.167 pigs per litter.

Brinks _et_ _al_. (1961) performed an analysis of least squares for effects of generations and years on performance of 2,027 Hereford calves over a 26 year period. After adjustments for inbreeding were made, birth weight, gain from birth to weaning and weaning weight showed a general upward trend.

Flowers _et_ _al_. (1964) estimated the phenotypic trends for birth weight and weaning weight in Hereford cattle by computing the regressions of the two traits on years, obtaining -1.00 and 5.00, respectively. Environmental trends were obtained for birth and weaning weights through the use of repeat mating information obtained in two consecutive years. The regressions of the annual environmental fluctuations indicate a negative environmental trend for both traits. The environmental regressions were subtracted from the phenotypic regressions to obtain an estimate of the average genetic changes per year. There appeared to be a positive genetic response to selection of approximately 1.0 lb. per year of birth weight and 4.56 lb. for weaning weight. Estimates of heritability from the genetic gain were .86 for birth weight and .77 for weaning weight. These estimates are high compared with others reported in the literature.

Brinks _et_ _al_. (1965) evaluated the response to selection in a closed line Hereford cattle. The average generation was 4.93 years. The expected genetic progress in the various traits was calculated from heritabilities, genetic correlations and relative weights in the selection index used. Estimates of the environmental and genetic changes were obtained from repeated mating information. Comparisons of expected and estimated genetic response for 26 years indicated that the genetic response obtained was approximately 20 per cent more than expected for the four traits measured. If adjustment for inbreeding had been made, considerably more genetic progress than expected would have been indicated.

Robertson and Rendel (1954) compared contemporary (within herds, years and seasons) A.I. and non-A.I. daughters with a weighting procedure described previously. They concluded that the bulls that have been used in A.I. stations have not been genetically superior for milk yield to the bulls that the owners would have used otherwise, although they have had significantly better genotypes for fat percentage.

Van Vleck and Henderson (1961a) used the contemporary comparison procedure of Robertson and Rendel (1954) to analyze first records of 24,995 A.I. and 32,831 non-A.I. progeny. The genetic merit of A.I. progeny for both milk and fat production was superior for all years. It was evident that the superiority in fat production was larger than for milk production, indicating stronger selection for fat production. The estimated gain in genetic merit was about one-half per cent per year, assuming the non-A.I. progeny remained constant.

Henderson (1958) used records from 1950-1954 in 11 New York Dairy herds to estimate the environmental trend in fat production. He used age factors for New York and a repeatability of 0.40. The environmental change was estimated to have caused an average decline per year of 3.0 lb. fat per cow.

Van Vleck and Henderson (1961b) used a procedure described previously (Van Vleck and Henderson, 1961a) to measure the change in merit of non-A.I. daughters, which then allows measurement of the change in merit of the A.I. population according to the method of Robertson and Rendel (1954). Contemporary comparisons of 236 Holstein A.I. sires by year and season of first freshening were obtained from 305-day, 2X, M.E. milk and fat records. The non-A.I. trend was +399.2 lb. of milk and 17.15 lb. of fat. The A.I. trend was 774.6 lb. of milk and 35.34 lb. of fat gain over the nine year period. The superiority of A.I., obtained by subtracting the former from the latter, was 375.4 lb. and 18.19 lb. for milk and fat, respectively.

Van Vleck and Henderson (1961c) analyzed the effect of genetic trend on sire evaluation on 235 A.I. Holstein sires which had contemporary comparisons within herds, years, and seasons. The comparisons were weighted by the method described by Tucker and Legates (1960). The contemporary comparisons also were regressed toward zero according to the regression of true breeding value on estimated breeding value, $\frac{W}{W + 17}$, where 17 is the ratio of the component of variance within sires to the component of variance among sires and $\underline{W}$ is the sum of the weights of all comparisons for a particular sire within herds, years and seasons. Their results indicate that the trend in genetic merit has little importance in evaluation of contemporary comparisons. The evaluation made with and without adjustment for genetic trend were highly correlated (r = .97 to 1.00). Genetic trend should be considered if the sires to be compared were used in widely different periods. The genetic trend of the natural service daughters has been about 0.5 per cent per year. If this were more rapid, adjustment for it should be made.

Gaalaas and Plowman (1961) also used Henderson's maximum likelihood procedure on 1,422 records by 369 cows over a period of 27 years. Constants for years ranged from -1.490 to +1,116 lb. of milk and -48 to +55 lb. of fat. Adjustment of the M.E. records for the effects of years reduced the range of yearly averages by more than 50 per cent for milk and fat, and reduced the mean square among years by 63 per cent. The regressions of milk on years were +6.63 and -17.68 lb. for M.E. records and those corrected for years, respectively. The corresponding regressions for fat were +1.071 and -1.069 lb.

Qureshi (1963) used first lactation milk and fat records of 3,771 and 2,557 Holsteins and Jerseys from 1951 to 1961 to obtain estimates of the average genetic merit of registered and grade progeny groups by the method of least squares. The average genetic merit in milk and milk fat yields tended upward in each progeny group, except in the progeny of registered Holstein sires. The rate of increase in average merit of progeny of grade sires invariably was higher throughout the study than that of progeny of registered sires, although the average production and genetic merit of the latter groups were at a higher level.

Dillon et al. (1955) used the maximum likelihood method developed by Henderson on 1,556 records by 578 cows. The regression estimate of environmental change was 53.54 ± 14.44 lb. of FCM per year. The regression of average real producing ability on years was 0.68 ± 14.00 lb. of FCM. The results indicate that the average real producing ability increased only 36.72 lb. of FCM during the 54 year period. The average absolute change in real producing ability between years was 706 lb. with extremes of +2,067 and -1,865 lb. of FCM.

Tucker and Farthing (1958) and Tucker et al. (1960) analyzed first lactations of Holsteins, Guernseys and Jerseys from North Carolina by using a weighted contemporary comparison between artificially and naturally sired herdmates within years and seasons. In the first analysis the daughters sired by A.I. were superior to their naturally sired herdmates by 15.7 lb. of fat and 366.0 lb. of milk. In the second analysis, records of first lactations initiated prior to 35 months of age were used. A contemporary comparison of the dams of the artificially and naturally sired progeny gave a weighted difference of 149 lb. of milk and 11.7 lb. of fat in favor of the dams served naturally. The superiority of the artificially sired progeny presumably is due to the genetic superiority of their sires. The comparisons of first lactations of daughters of A.I. sires with all available contemporary records of their naturally sired herdmates showed a difference of 276 lb. of milk and 13.3 lb. of fat for the artificially sired daughters. These comparisons are pertinent to the evaluation of young sires when only first lactation records are available. Restriction of the records of the artificially sired daughters to those made in first lactation diminished the advantage of the artificially sired daughters by 90 lb. of milk and 2.4 lb. of fat, because the older cows in the naturally sired group were selected on the basis of past performance. This bias due to selection is more evident where there are no first lactations of natural daughters contemporary to the first lactations of artificially sired daughters. The estimated bias was 120 lb. of milk and 3.1 lb. of fat.

McDaniel _et_ _al_. (1961) estimated general environmental changes by (a) the method of maximum likelihood developed by Henderson and (b) the differences between first records of paternal half-sibs in different years, adjusted for the regression of daughter on dam. They standardized 462 lactations, made from 1951 to 1958 by 230 cows at the USDA Experiment Station to 305-day, 2X, M.E. production. Maximum likelihood estimates indicated the environment deteriorated 1,363 lb. of M.E. milk in seven years. The paternal half-sib method yielded similar results.

Arave _et_ _al_. (1964) used the method described by Henderson _et_ _al_. (1959) to analyze 11,993 lactations of 3,900 Jersey cows in 12 cooperator herds in California. All records were corrected for age and were corrected for inbreeding by adding 50 lb. FCM per unit of inbreeding. Age-correction factors were calculated within herds by curvilinear regression. The maximum likelihood procedure estimated the yearly environmental effects. Estimates of the annual genetic increases ranged from -51 to +145 lb. of FCM, with an average increase of 74 lb. of FCM, or about 0.7 per cent of the mean annual yield. The pooled intrasire regression (Smith, 1962) of the progeny's most probable producing ability on generation number was 112 lb. FCM per generation. If one assumes that the average generation is four years, the estimated annual increase would be 28 lb. of FCM. Since analysis was made within sires, one-half the genetic change was measured, i.e. 56 lb. of FCM is the estimate of the true genetic gain.

Burnside and Legates (1965) analyzed the records of 34,840 Holsteins made from 1953 to 1961 in 335 herds. The weighted regression of production on years estimated the annual change in production to be 138 ± 23 lb. of milk and + .007 ± .001 per cent fat, when only first lactations were used. Full sib families comprised 14 per cent of the population; these records were analyzed by least squares and weighted regression procedures to estimate the annual environmental trend. Through comparison with the annual production trend, estimates of the annual genetic trend of + 99 ± 36 lb. of milk and + .018 ± .003 per cent fat were obtained. Records of paternal half-sisters out of dams that were two, three, or four-years-old at the time the half-sisters were born were analyzed separately. There was evidence that the mates of sires were more rigorously selected during the sire's latter years of service than during initial years; thus, only the lactations of the early progeny groups were analyzed. A pooled estimate of one-half the annual genetic trend plus the environmental trend was compared with the annual production trend and resulted in an estimate of the annual genetic trend of 122 ± 58 lb. of milk and .016 ± .005 per cent fat.

Methods of maximum likelihood with records subject to culling and to repeat mating systems have been used to estimate genetic trends. The most precise estimates of genetic trends are obtained from the utilization of the principle of maximum likelihood. The disadvantages of each method of analysis which utilizes matrix algebra is the genetic trend is estimated relative to another trend that is assumed to be constant, the analysis is too cumbersome to use on large amounts of data, or both. The simplest methods of estimation which utilize the calculation of generation intervals or repeat mating systems, invariably require unsupported assumptions in the interpretation of results.

The procedure of Van Vleck and Henderson (1961b), along with the method of Smith (1962), allows for the complete measurement of the genetic trend on a large volume of data with a minimum of unsupported assumptions. The utilization of matrix algebra in the procedure of Van Vleck and Henderson (1961b) limits the number of sires which can be studied, whereas the method of Smith (1962) has no mathematical limitations on the volume of data which can be easily analyzed. In consideration of the methods available, one can most efficiently analyze a large volume of data, with a slight loss in the precision of the estimates, by the use of the method of Smith (1962).

SOURCE OF DATA

The data obtained for this study came from two sources. For the preliminary investigation the data were obtained from simulated records of dairy herds which were used in an undergraduate course on dairy cattle breeding. The dummy herd records, where all parameters are known, were used to determine the accuracy of the methods of analysis. The parameters used in the dummy herds are listed in Table 1.

TABLE 1.--The variances used in the construction of the simulated dairy herds.

Source	Variance	Standard Deviation*
Total	684	-
Between herds (environmental)	225	15
Within herds	459	21
Genetic	121	11
Permanent environment	64	8
Between years	49	7
Residual	225	15

*Variances in 100 lb.^{2}, Standard Deviations in (100 lb.)^2.

The genetic ability of an offspring is obtained by averaging the genetic ability of both parents and adding a chance deviate. Mendelian segregation in the parents followed by recombination in the zygote results in half of the additive genetic variation in an offspring being accounted for by the parents and half being random. The random part has a standard deviation of approximately 8.0, i.e. $\sqrt{121/2}$. Therefore the variation due to chance is added to the genetic ability of each individual by multiplying a random normal deviate by 8.0.

There were 23 herds with 15 to 20 milking cows per herd per year. Each class meeting was considered a year and there were 19 years of data. Each student supposedly developed his own breeding plans and determined his own matings and cullings. The mortality rate due to disease, accidents, etc., was a constant; the computer randomly killed animals according to the probabilities listed in Table 2.

TABLE 2.--Mortality rates used in the simulated herds.

Age Group	Chance of Leaving the Herd
All bulls	0.167
Cows with $>$ 3 records	0.250
Cows with $\leq$ 3 records	0.100
Heifers	0.167

No animals were allowed to be sold to other herds so that the correct identification of animals was easily maintained. However, any bull of breeding age was allowed to be bred to cows of any herd. This simulation is not perfect because there were no genetic differences between the original herds, each cow had a calf every year, inbreeding was not built into the model, and no interactions were accounted for. However, these data are very useful because every parameter on every animal is known and recorded.

After the preliminary analysis of the simulated data was completed, all of the Michigan D.H.I.A. tabulated records were searched for available data. All first records of grade or registered Holstein cows that calved at less than 36 months of age and had identification for themselves and their sires were used. Since Michigan D.H.I.A. started their computer operation in 1953, records from 1953 thru October 1965 were available. All incomplete first lactation records were projected to 305-day, 2X, M.E. records according to factors pertinent to the reason for disposal. All 3X records and records with vital information missing, such as age at calving or lactation number, were eliminated from the study.

METHODS

To measure the genetic trend in production, one must separate the environment and genetic portions of the total trend. The confounding of these two portions has caused considerable problems in the past. The validity of estimates of genetic trends rests on the assumptions of random mating, no culling of dams, no differential mating of the dams according to age or genetic ability, and no maternal effects for milk or fat production. Each of these assumptions is invalid in certain cases. A perfect method of analysis would incorporate adjustments for deviations from the assumptions.

The total trend in milk and fat production in dairy cattle can be measured by the regression of production on time, $b_{P.T}$, which has expected value equal to

$$t + g \left(1 - \frac{\beta_{D_A \cdot T}}{2}\right)$$

and standard error of

$$\frac{1}{N - 2} \left(\frac{\sigma\hat{P}^2}{\sigma\hat{T}^2} - b_{P \cdot T2}\right)$$

where the true environmental trend is $\underline{t}$, the true additive genetic trend per year is $\underline{g}$, the regression of age of dam on time is $\beta_{D_A \cdot T}$, $\underline{N}$ is the number of cows in the regression, $\sigma\hat{P}^2$ is the variance of milk or fat production, and $\sigma\hat{T}^2$ is the variance of time. The expected value $b_{P.T}$ is equal to t + g when mating is random and there are no maternal effects or effects of culling or maternal age. The estimate of genetic trend is adjusted by $(b_{D_A \cdot T})$, the estimated regression of age of dam on time. If the regression $b_{D_A \cdot T}$ is not zero, it is an indication that the average age of the female genetic pool is not constant over time, or the average age of the females retained to produce calves has increased or decreased over the period of time studied. This regression is divided by two because the dam contributes half the genetic material which is measured in the trend. It is assumed that the regression of age of sire on time is zero. This may not be a valid assumption since the initiation of the young sire program in many A.I. studs. If one also accounts for the age of sire, the estimate of the regression with random mating, no maternal effects and no effects of culling would be:

$$b_{P.T} = \hat{t} + \hat{g}\,(1 - (\frac{b_{D_A \cdot T} + b_{S_A \cdot T}}{2}))$$

where $b_{S_A \cdot T}$ is the estimated regression of the age of sire on time.

The regression of daughter's production on time pooled within sires provides an estimate of the environmental trend plus half the genetic trend and is calculated by:

$$b_{P.T/S} = \sum_i w_i \, b_{P.T/S_i} / \sum_i w_i$$

$$= \hat{t} + \hat{g} \left(\frac{1 - b_{D_A.T/S}}{2} \right)$$

with standard error:

$$\sqrt{\frac{1}{\sum_i \left(\frac{1}{\frac{1}{N - 2} \left(\frac{\sigma\hat{P}^2}{\sigma\hat{T}^2} - b_{P.T}{}^2 \right)} \right)}}$$

where $b_{P.T/S}$ is the regression of daughter's production on time pooled within sires and $b_{D_A.T/S}$ is the regression of age of dam on time pooled within sires. This regression has an expectation of:

$$\beta_{P.T/S} = t + g/2$$

if mating is random and there is no effect of culling or maternal age. The $\underline{w}_i$ are the weights used to pool the individual regressions within sires; each weight is the inverse of the variance of the regression within a sire

$$\underline{w}_i = 1/V(b_{P.T}).$$

The regression of age of dam on time pooled within sires, ($b_{D_A.T/S}$) is different from $b_{D_A.T}$, since the former is obtained through use of the weighting factors (w_i) that were used to pool the regressions of production on time within sires. The quantity $(\frac{1 - b_{D_A.T/S}}{2})$ is equivalent to the regression of dam's birth year on years within sire. Each intra-sire regression has n daughters, and $\Sigma n_i = N$.

In addition to the regression of daughter's two-year-old production on years pooled within sires a regression of dam's two-year-old production on time within service sire should be calculated. This will yield an estimate of improvement over time in culling the dams of the daughters being analyzed. For example, if a sire is mated to cows with an average age of Z, and the regression of age of dam on time within sires is zero ($b_{D_A.T} = 0$), then an estimate of the regression of daughter's production on time within sires is:

$$b_{P.T/S} = \hat{t} + (1/2)\hat{g}.$$

The estimate is unbiased if the proportion of cows culled at age Z is constant over all the time measured. If there is a trend in culling, the regression of dam's production on time pooled within sires will estimate it.

The expectation of the regression of dam's production on time pooled within sires, with random mating and no maternal effects is

$$\beta_{P.T/S} = t + g$$

and is estimated by:

$$b_{P.T/S} = \Sigma w_i \, b_{D_P.T/Si} / \Sigma w_i$$
$$= \hat{t} + \hat{g}$$

The difference between the regression of daughter's production on time and the regression of dam's production on time pooled within sires is:

$$b_{P.T} - b_{D_P.T/S} = \Delta C$$

where ΔC is the additive genetic superiority over time associated with the culling methods used, or could measure a negative trend due to method of culling. The dams contribute one-half the genetic material of their offspring; therefore ΔC should be subtracted from the regression of daughter's production on time within sires to give an unbiased estimate of the genetic trend.

It is assumed that the correlation between ($b_{D_A \cdot T}$ and $b_{D_P \cdot T}$) the regression of age of dam on time and the regression of dam's production on time pooled within sires is zero. Inadequate age correction factors or environmental correlations would be possible causes of correlation.

The genetic trend or genetic improvement per year is measured by:

$$\Delta G = 2(\hat{t} + \hat{g}\ (1 - \frac{b_{D_A \cdot T}}{2}) - (\hat{t} + \hat{g}\ (\frac{1 - b_{D_A \circ T/S}}{2})))$$

$$= 2(\frac{\hat{g}}{2} - \frac{\hat{g}(b_{D_A \cdot T})}{2} + \frac{\hat{g}(b_{D_A \cdot T/S})}{2})$$

$$= \hat{g}(1 - b_{D_A \cdot T} + b_{D_A \cdot T/S})$$

with standard error

$$\pm \sqrt{4\ \{\left[\frac{1}{N - 2}\left(\frac{\sigma\hat{P}^2}{\sigma\hat{T}^2} - b_{P.T}{}^2\right)\right] + \left[\frac{1}{\Sigma\left[\frac{1}{\frac{1}{n - 2}\left(\frac{\sigma\hat{P}^2}{\sigma\hat{T}^2} - b_{(P.T)}{}^2\right)}\right]}\right]}$$

This estimate of the standard error is too large if the covariance of $b_{D_A \cdot T}$ and $b_{D_A \cdot T/S}$ is positive, the genetic correlation between daughter and dam is greater than .5, or both. The quantity:

$$\frac{1}{\underset{i}{\Sigma}\left(\frac{1}{\frac{1}{n - 2}\left[\frac{\sigma\hat{P}^2}{\sigma\hat{T}^2} - b_{P.T}\right]}\right)} = \frac{1}{\underset{i}{\Sigma}\left(\frac{1}{V(b_{P.T})}\right)}$$

$$= \frac{1}{\underset{i}{\Sigma}\ w_i}$$

The quantity $(1 - b_{D_A \cdot T} + b_{D_A \cdot T/S})$ is an estimate of the regression of daughter's additive genetic value on dam's additive genetic value, usually assumed to be 0.50.

These standard errors are valid only if the assumptions of random mating, homogeneous variances, independence of the estimates, regression of daughter's genetic ability on dam's genetic ability within sires equal to 0.5 are valid.

Weighting of the regressions within sires also was done by using their weighted mean, where the w_i are equal to $\frac{1}{n_i}$. The estimates of the regressions of production on time, pooled within sires, are then:

$$b_{P.T/S} = \Sigma(w_i\ b_{P.T/S_i})/\Sigma w_i$$

$$= \Sigma(\frac{1}{n_i}\ b_{P.T/S_i})/\Sigma\frac{1}{n_i}$$

where n_i is the number of observations for the ith sire. The variance of a regression, pooled within sires by the method of geometric means is:

$$V(b_{P.T/S}) = \Sigma[(\frac{1}{n_i})^2\ V(b_{P.T})]/[\Sigma\frac{1}{n_i}]^2$$

The estimate of ΔG is obtained after the regression of daughter's production on time pooled within sires, has been corrected for ΔC, the improvement in culling over time.

The environmental trend (Δe) is obtained by;

$$\Delta e = b_{P.T} - \Delta G$$

with approximate standard error;

$$\sqrt{V(b_{P.T}) + V(\Delta G)}$$

If the covariance of $b_{P.T}$ and ΔG is positive as one would expect, then this is a maximum estimate of the standard error, i.e. the true standard error may be much smaller.

The difference between the method of analysis presented and the method of Smith (1962) are the calculation and use of ΔC and $b_{D_A.T/S}$. Also, $b_{D_P.T/S}$ is calculated in order to estimate ΔC. Smith (1962) assumes there is no effect of culling dams or $\Delta C = 0$. In place of $\beta_{D_A.T/S}$ in the expectation of $\beta_{P.T/S}$ Smith (1962) uses $\beta_{D_A.T}$, thus after subtracting $\beta_{P.T/S}$ from $\beta_{P.T}$, the coefficient of $\hat{\underline{g}}$ is always 0.50 or half of the genetic trend is always estimated.

RESULTS AND DISCUSSION

There were 1,556 two-year-old daughters with dam information in the simulated herds. Of these, 1,008 were daughters of 128 bulls that sired daughters in two or more years, which allows one to calculate the regressions of production on years within sires. Also, 548 two-year-old daughters were by sires which had offspring in only one year. The averages of the characters measured are given in Table 3.

TABLE 3.--Averages of characters in simulated herds.

Character	Average*
Daughters' average production	12,559.
Dams' average production	12,763.
Daughters' superiority	-204.
Daughters' average additive genetic value	1,045.
Dams' average additive genetic value	825.
Daughters' superiority	+220.
Average age of the dams at the time of the daughter's birth	3.88 years

*Production and genetic values are in lb.

The averages in Table 3 indicate that cows which are retained in the herd and later produce calves have, on the average, a better environment (424. lb. of production) than the average of their daughters, if one compares first records only. There is an average difference of 3.88 years in the time between the measurements of a daughter and her dam. Either a genetic or phenotypic trend may account for some of the apparent difference of the daughters.

The analysis of the genetic and environmental trends in the simulated herds was done in two ways. First, the analysis (as described previously) was performed by weighting the regression of production on time within a sire by the inverse of the variance of the regression. In the second analysis, the regression of production on time within a sire was weighted by the number of observations in the regression, or the weighted mean of the regressions was obtained.

The regression of daughter's production on years ($b_{P.T}$) was 130.8, which is a measure of genetic and environmental trends and has an expectation of t + g $(1 - \frac{\beta_{D_A.T}}{2})$, where $\beta_{D_A.T}$ is the true regression of age of dam on years and was estimated to be 0.012. Therefore:

$$\hat{t} + .994\hat{g} = 130.8 \pm 18.2 \text{ lb.} \qquad (1)$$

In the first analysis, where the regressions of production on years within sires were pooled by weighting each by the inverse of its variance, the regression of daughter's production on years pooled within sires was -105.2. This has an expectation of $t + g (\frac{1 - \beta_{D_A.T/S}}{2})$, where $\beta_{D_A.T/S}$ is the true regression of age of dam on years pooled within sires, and $b_{D_A.T/S}$, its estimate, was 0.533. It follows that:

$$\hat{t} + \hat{g}(\frac{1 - 0.533}{2}) = -105.2 \pm 33.2$$

$$\hat{t} + .233\hat{g} = -105.2 \pm 33.2 \text{ lb.}$$

The figure .233 is equivalent to one-half the regression of dam's birth year on years pooled within sires. The calculated regression of dam's birth year on years pooled within sires was 0.467, thus yielding the correct 0.233, upon division by two.

If all the assumptions are valid the regression of dam's production on years pooled within sires has an expectation of t + g, and any bias is due to differential effects of culling over years. The regression of dam's production on years pooled within sires ($b_{D_P.T/S}$) was 375.3, thus yielding:

$$\begin{aligned} \Delta C &= (b_{P.T} - b_{D_P.T/S})/2 \\ &= (130.8 - 375.3)/2 \\ &= -122.3 \text{ lb.} \end{aligned}$$

where ΔC is an estimate of the bias due to culling of dams over years. The bias should be subtracted from the regression of daughter's production on years, pooled within sires, to obtain an unbiased estimate of g:

$$\begin{aligned} \hat{t} + .233\hat{g} - \Delta C &= -105.2 - (-122.3) \\ &= 17.1 \text{ lb.} \qquad (2) \end{aligned}$$

An estimate of the genetic trend per year can be obtained by subtracting equation 2 from equation 1, and solving for $\hat{g}$ as follows:

$$\begin{array}{rrcl} & \hat{t} + .994\hat{g} & = & 130.8 \\ - & \underline{(\hat{t} + .223\hat{g}} & \underline{=} & \underline{17.1)} \\ & .761\hat{g} & = & 113.7 \text{ lb.} \\ & \Delta G & = & 149.4 \text{ lb.} \end{array}$$

The quantity 0.761 is an estimate of the true regression of daughter's additive genetic value on dam's additive genetic value, pooled within sires ($\beta_{d_g . D_g / S}$). The estimate, $b_{d_g . D_g / S}$, is usually assumed to have an expected value of 0.50, but in these data the actual $\beta_{d_g . D_g / S}$ calculated from parameters was 0.816, quite different from the assumed relationship, but in line with the estimated relationship between daughter and dam. In simulated cases where all assumptions are strictly met, the $b_{d_g . D_g / S}$ is expected to be 0.50 and estimates from the difference between equations 1 and 2 would also be 0.50.

The estimate of the genetic trend was:

$$\Delta G = 149.4 \pm 75.8 \text{ lb.}$$

The environmental trend can be calculated by subtracting ΔG (the genetic trend) from the $b_{P.T}$ (the phenotypic trend).

$$\begin{aligned} \Delta\hat{e} &= b_{P.T} - \Delta G \\ &= 130.8 - 149.4 \\ &= -18.6 \pm 77.8 \text{ lb.} \end{aligned}$$

where the standard error is a maximum if $b_{P.T}$ and ΔG are positively correlated.

The true regression of daughter's genetic ability on years ($\beta_{d_g.T}$) was 134.9 lb. and the true environmental trend was -4.1 lb. per year. Theoretically, according to the model for the simulated herds, there should not have been any environmental trend, i.e. the total phenotypic trend should have been genetic. The environmental trend that occurred must be attributed to sampling from the distribution of the model of simulation.

If the assumptions of random mating, no maternal effects, and no effects of culling had been made, but no corrections were made for the effects of age and production of dams, the following estimates of the genetic and environmental trends would have been obtained.

$$
\begin{aligned}
\hat{t} + \hat{g} &= 130.8 \pm 18.2 \text{ lb.} \\
-\ \underline{(\hat{t} + \hat{g}/2} &\underline{= 105.2 + 33.2)} \\
\hat{g}/2 &= 236.0 \text{ lb.} \\
\Delta G &= 472.0 \pm 75.8 \text{ lb.} \\
\Delta e &= 130.8 - 472.0 \\
\Delta e &= -341.2 \pm 77.8 \text{ lb.}
\end{aligned}
$$

The corrections made for the age of dam and culling seem to be essential in obtaining a reasonably accurate estimate of the genetic trend. The most serious error in most procedures is assuming that the regression of daughter's genetic ability on dam's genetic ability is 0.50.

The second analysis was performed on the simulated herds. In this case the regression of production on years were pooled within sires by their weighted mean rather than by the inverses of their variances. The estimated regression of daughter's production on years ($b_{P.T}$), which measures the phenotypic trend, remains the same as in the first analysis:

$$
\begin{aligned}
b_{P.T} &= \hat{t} + \hat{g}\left(1 - \frac{b_{D_A.T}}{2}\right) \\
&= \hat{t} + .994\hat{g} \\
&= 130.8 \pm 18.2 \text{ lb.}
\end{aligned}
$$

Equation 2 has the same expectation as in the first analysis, but the numerical estimates vary considerably. The regression of daughter's production on time, within sires ($b_{P.T/S}$), was 56.1, the regression of age of dam on time within sires ($b_{D_A.T/S}$) was -0.117 and the regression of dam's production on time witin sires ($b_{D_P.T/S}$) was 161.5 lb. The result corresponding to equation 2 is:

$$\hat{t} + \hat{g}\left(\frac{1 - b_{D_A.T/S}}{2}\right) - \Delta C = b_{P.T/S} - \left[(b_{P.T} - b_{D_P.T/S})/2\right]$$

$$\hat{t} + \hat{g}\left(\frac{1 - (-.117)}{2}\right) - \Delta C = 56.1 - \left[(130.8 - 161.5)/2\right]$$

$$\hat{t} + .558\hat{g} = 71.5 \pm 138.0 \text{ lb.}$$

One-half the regression of dam's birth year on years pooled within sires equals 0.558, which is in close agreement with the calculated coefficient of $\hat{g}$. The estimates of the genetic and environmental trends were:

$$\begin{array}{rrcl} & \hat{t} + .994\hat{g} & = & 130.8 \pm 18.2 \text{ lb.} \\ - & \underline{(\hat{t} + .558\hat{g}} & \underline{=} & \underline{71.5} \pm 138.0) \text{ lb.} \\ & .436\hat{g} & = & 59.3 \text{ lb.} \\ & \Delta G & = & 136.0 \pm 278.0 \text{ lb.} \\ & \Delta e & = & -5.2 \pm 279.0 \text{ lb.} \end{array}$$

where the standard errors are probably biased upward.

The true regression of daughter's additive genetic value on dam's additive genetic value, pooled within sires, ($\beta_{d_g.D_g/S}$) as calculated from the parameters, was 0.466, which is only slightly less than the value expected under ideal conditions (0.50). The results of this second analysis agree very closely with the true genetic and environmental trends of 134.9 lb. and -4.1 lb., which were calculated from the known parameters of simulation.

In the second analysis, the measurement of the genetic and environmental trends under the assumptions of random mating and no culling, but without corrections for the effects of age and production of dams, would have yielded:

$$\hat{t} + \hat{g} = 130.8 \pm 18.2$$

$$- \underline{(\hat{t} + \hat{g}/2 = 56.1)}$$

$$\hat{g}/2 = 74.7 \text{ lb.}$$

$$\Delta G = 149.4 \pm 278.0 \text{ lb.}$$

$$\Delta e = -18.6 \pm 279.0 \text{ lb.}$$

The bias caused by failure to correct for non-random mating and culling is not as serious in these data, where the regressions of production on time within sires are pooled by their weighted mean as it is when the regressions are pooled by the inverses of their variances.

The method of pooling the regressions within sires in these data has a large effect on the values of the intermediate equations that are used to estimate the genetic trend. The method of pooling by the inverse of the variance of each regression should yield the most precise results. It is important that each sire be represented adequately in all years. A sire having a few daughters one year and then a few daughters five years later, will receive greater weight than he deserves because the variance of the regression of production on time will be relatively smaller than the variance for a sire whose daughters appear equally distributed over all years. If one takes a random sample of cows, it is expected that the estimates of the regressions within sires would be as follows, assuming the regression of production on years is 130.0 lb. of milk:

$b_{P.T}$ = 130.8 lb.
$b_{P.T/S}$ = 65.4 lb.
$b_{d_g.D_g/S}$ = 0.500
$b_{D_A.T}$ = 0.000
$b_{D_A.T/S}$ = 0.000

The total trend is genetic. Effective sire culling, non-representation of daughters in some years, and the method of pooling have caused the calculated value $b_{d_g.D_g/S}$ to differ from 0.50. Since only first records were used in the study, it may be of interest to observe the effect of using later records and the average of records on the values of the regressions pooled within sires.

There were 65,560 two-year-old Holstein cows on record at the Michigan D.H.I.A. computer laboratory which met the qualifications of being milked twice a day, having their first record at less than 36 months of age and having registration or ear tag identification recorded for the sire of the cow and the cow herself. Those cows calving for the first time after January 1953 or completing their first lactation before October 1965 were included in the study. Records of the 65,560 Holstein cows were sorted by dam identification number (file 1) and cow identification number (file 2). File 1 and file 2 were then matched to identify dams for as many of the cows as possible. There were 4,672 dams identified for the 65,560 cows. Table 4 lists the average milk and fat production of the cows and their dams over 13 years.

There was a linear increase in the number of observations per year. Until 1963 all cows on test were not recorded at the computer laboratory. In 1963, H.I.R. herds were forced to join D.H.I.R. recording and in 1959, all D.H.I.A. herds were forced to go on computer processing. Previous to that time, many records were processed by hand, and lactation cards were made and sent to U.S.D.A., but copies of the lactation cards were not maintained as a permanent file in Michigan. Bias could be involved if records of only the most progressive herds were processed by computer in the earlier years and the poorest managed herds on D.H.I.A. were forced to go to computer processing in 1959. There was a general increase in both milk and fat production of the cows and their dams over the period studied.

TABLE 4.--Average milk and fat production for the 13 years studied.

Year	Number of Cows	Average Milk	Average Fat	Number of Dams	Average Milk	Average Fat
1953	8	12,773 ± 1,031	461 ± 37			
1954	488	12,743 ± 133	459 ± 5	1	8,406 ± 2,894	374 ± 96
1955	1,727	12,543 ± 70	452 ± 3	4	12,246 ± 1,448	437 ± 48
1956	2,307	12,739 ± 61	460 ± 2	4	10,780 ± 1,448	394 ± 48
1957	2,837	12,647 ± 55	460 ± 2	49	12,878 ± 414	460 ± 14
1958	3,818	12,746 ± 47	463 ± 2	88	12,427 ± 308	458 ± 10
1959	5,400	13,097 ± 40	476 ± 1	160	13,048 ± 228	474 ± 8
1960	6,669	12,911 ± 36	470 ± 1	299	12,959 ± 167	469 ± 6
1961	7,635	12,848 ± 34	467 ± 1	498	13,088 ± 130	480 ± 4
1962	8,431	13,299 ± 32	483 ± 1	677	13,139 ± 111	482 ± 4
1963	9,075	13,742 ± 31	500 ± 1	913	13,209 ± 96	483 ± 3
1964	10,092	14,101 ± 29	513 ± 1	1,106	13,409 ± 87	491 ± 3
1965	7,072	13,785 ± 35	503 ± 1	873	13,652 ± 98	497 ± 3
	65,560	13,323 ± 12	484 ± 1	4,672	13,272 ± 42	488 ± 1

The analysis of genetic and environmental trends in milk and fat production was performed for four populations within the 65,560 cows used in the study. These were: (1) all cows, (2) all artificially sired cows, (3) all naturally sired cows and (4) only those cows whose dams had corresponding two-year-old production records.

The estimates of parameters and their standard errors that are needed to evaluate trends in milk production are given in Table 5.

There were 3,030 sires that had three or more daughters represented in the data. One must have information on at least three daughters of each bull to calculate standard errors. Also it is essential that not all daughters of each bull freshen in the same month so that the regression of production on time can be calculated. These mechanical restrictions eliminated 4,179 cows of the 65,560 available.

Only 4,672 of the 65,560 cows, or 7.1 per cent, had dams that also had an available first lactation record initiated at less than 36 months of age. Prior to 1961, D.H.I.A. was very lax in the enforcement of recording accurate information pertinent to the lactation records. Lack of identification of records, the first lactation or some other, eliminated many possible observations. Herds leaving and joining

TABLE 5.--Parameters used in estimating genetic and environmental trends in milk production.

	All Cows	A.I. Cows	Non-A.I. Cows	All Cows With Dams
No. of sires	3,030	1,076	2,337	247
No. of daughters	61,381	37,397	22,137	4,014
No. of dams	4,024	3,337	568	4,014
$b_{D_A.T}$	.174 ± .01	.198 ± .01	.138 ± .02	.365 ± .02
$b_{P.T}$	165 ± 4.1	201 ± 5.7	119 ± 6.2	200 ± 23
$b_{D_A.T/S}$*	.376 ± .03	.441 ± .03	.191 ± .19	.069 ± .01
$b_{P.T/S}$*	1,212 ± 3.3	341 ± 6.7	189 ± 8.1	-629 ± 18
$b_{D_P.T/S}$*	60 ± 12	34 ± 13	348 ± 50	760 ± 18
$b_{D_A.T/S}$†	.385 ± .06	.299 ± .06	1.07 ± .23	.512 ± .02
$b_{P.T/S}$†	41 ± 5.7	28 ± 7.2	-15 ± 9.4	56 ± 22
$b_{D_P.T/S}$†	129 ± 22	-2 ± 24	596 ± 59	96 ± 22

*Regressions within sires pooled by the inverses of their variances.

†Regressions within sires pooled by their weighted mean.

D.H.I.A. also reduced the possibility of obtaining matching daughters and dams. The age of calving more frequently was recorded correctly; probably fewer observations were lost due to improper recording of this than for lack of correct lactation number.

Of the sires used in Michigan in the last 13 years, 1,076 or 31.5 per cent were used artificially and 2,337 or 68.5 per cent were used naturally. Also, 383 or 11.2 per cent sired daughters both naturally and artificially.

Table 5 indicates that 62.8 per cent of the properly recorded two-year-old cows were sired artificially and 37.2 per cent were sired naturally. Of those sired artificially 8.9 per cent had matching dams with a recorded two-year-old record, but only 2.6 per cent of the naturally sired daughters had matching dams with a recorded two-year-old record.

The regression of age of dam on time indicates that the average age of dam increased 0.17 years per year of the study whereas one would expect this regression to be zero. This is an indication that the genetic pool of the females is not being replaced as rapidly as that of the males. Another possible cause of positive regression is the procedure of recording information. Upon joining D.H.I.A., a farmer may not have information on the proper age and lactation number of older cows and would record this information only for young animals, where it is available.

The regression of production on time indicates that there has been an average increase of 165 ± 4.1 lb. of milk per year over the 13 year period. This is a total increase of 2,145 lb., or an increase of 1.2 per cent of the mean per year. The artificially sired population increased 201 ± 5.7 lb. of milk per year for a total increase of 2,613 lb. or 1.5 per cent of the mean per year. The naturally sired population of cows increased only 119 ± 6.2 lb. of milk per year for a total increase of 1,547 lb. or a 0.9 per cent increase per year.

The estimates of the genetic and environmental trends were obtained as described previously, and the results are given in Table 6. As an example, the genetic and environmental trends for all cows (61,381), estimated by the use of the weighted mean of the regressions within sires, were obtained as follows:

$$
\begin{aligned}
b_{P.T} &= \hat{t} + \hat{g}\left(1 - \frac{b_{D_A.T}}{2}\right) \\
&= \hat{t} + \hat{g}\left(1 - \frac{.174}{2}\right) \\
&= \hat{t} + .913\hat{g} \\
&= 164.7 \pm 4.11 \text{ lb.} \\
b_{P.T/S} &= \hat{t} + \hat{g}\left(\frac{1 - b_{D_A.T/S}}{2}\right) \\
&= \hat{t} + \hat{g}\left(\frac{1 - .385}{2}\right)
\end{aligned}
$$

$$
\begin{aligned}
&= \hat{t} + .308\hat{g} \\
&= 40.9 \pm 5.66 \text{ lb.} \\
b_{D_P . T/S} &= \hat{t} + \hat{g} \\
\Delta C &= b_{P . T} - b_{D_P . T/S} \\
&= 164.7 - 128.9 \\
&= 35.8 \text{ lb.} \\
\Delta C/2 &= 17.9 \text{ lb.}
\end{aligned}
$$

Therefore, the genetic and environmental trends are:

$$
\begin{aligned}
\hat{t} + .308\hat{g} &= 40.9 - 17.9 \\
&= 23.0 \text{ lb.}
\end{aligned}
$$

$$
\begin{aligned}
\hat{t} + .913\hat{g} &= 164.7 \text{ lb.} \\
-\ \underline{(\hat{t} + .308\hat{g}} &\underline{= \ \ 23.0)} \\
.605\hat{g} &= 141.7 \text{ lb.} \\
\Delta G &= 234.2 \pm 14 \text{ lb.} \\
\Delta e &= -69.5 \pm 15 \text{ lb.}
\end{aligned}
$$

An estimate of the genetic correlation between the additive genetic values of a daughter and her dam is 0.605. This is considerably higher than the assumed 0.50. Table 7 provides the estimates of the genetic correlations between daughter and dam according to the method of pooling and the population of cows used, and indicates that the estimated relationship is considerably higher than the assumed 0.50. The reason for this discrepancy from the theoretical value probably is due to effective sire

TABLE 6.--Estimates of the genetic and environmental trends in milk production per year.

Method of Pooling	All Cows	A.I. Cows	Non-A.I. Cows	All Cows With Dams
Inverse of Variance				
$\Delta\hat{g}$	-1,652 ± 11	-92 ± 18	-351 ± 20	1,565 ± 58
$\Delta\hat{e}$	1,817 ± 12	293 ± 19	470 ± 21	-1,365 ± 62
Geometric Mean				
$\Delta\hat{g}$	234 ± 14	498 ± 18	-109 ± 23	343 ± 63
$\Delta\hat{e}$	-70 ± 15	-297 ± 19	227 ± 24	-143 ± 67
Smith's Method				
$\Delta\hat{g}$	205 ± 14	314 ± 18	138 ± 23	252 ± 63
$\Delta\hat{e}$	-40 ± 15	-113 ± 19	-19 ± 24	-52 ± 67

TABLE 7.--Estimated genetic correlation between daughter and dam.

Method of Pooling	All Cows	A.I. Cows	Non-A.I. Cows	All Cows With Dams
Inverse of Variance	.601	.621	.526	.351
Geometric Means	.605	.550	.968	.573

selection, non-uniform distribution of sire's daughters over time or the method of pooling, and is of considerable importance in estimating the correct genetic and environmental trends in production. The genetic trends would be considerably larger if the assumed value of 0.50 was used.

Examination of Table 6 indicates that the methods of pooling the regressions within sires yield diverse results. Previously, in the analysis of the simulated data, pooling by the inverses of the variances of regressions of production on time within sires produced intermediate results, which were beyond expectation. The exact reason for this is unknown, since these estimates should be the most efficient estimators of the parameters desired. A possible cause of the unexpected regression of production on time within sires is the selection of sires on preliminary proofs. If the best sires are retained for future service according to preliminary proofs, one would expect a regression of future daughters' superiority on present daughters to be less than 1.0 and greater than zero, depending on the number of daughters involved. This would tend to lower the regression of production on time within sires, but it still would be expected to be between zero and the regression of production on time ($b_{P.T}$). The regression of production on time within sires of all cows was 1,212 lb. and cannot be explained by the above. If, however, after the preliminary proof on a bull, farmers then mate their best cows to bulls with the best preliminary proofs, this would cause an inflation of the regression of production on time within sires. An indication of whether this occurs would be the magnitude of the regression of the dams production on time within service sires ($b_{D_p.T/S}$). This theory is immediately rejected since $b_{D_p.T/S}$ is quite low, indicating that the poorer cows are mated to the best bulls, if the bulls are randomly used in all herd levels. To carry the argument farther, suppose that in herds at lower levels of production the best cows are mated to the best preliminary proven bulls at a greater frequency than during the period when the preliminary proof was compiled. This would yield a reasonably low $b_{D_p.T/S}$, but also should yield a much lower regression of production on time within sires than the one obtained. Therefore, there seems to be no reasonable answer for the unrealistic intermediate results obtained by pooling the regressions within sires by the inverses of their variances. The unequal distribution of a sire's daughters over time would seem to be an unlikely answer for such a large volume of data because many sires would have to produce superior daughters as they grew older, to produce such a large deviation from expectation.

Smith's method (1962), with results seen in Table 6, uses the regression of production on time within sires, pooled by their weighted mean. The main difference between Smith's method and the method immediately above it in Table 6, is that the method of weighted mean utilizes ΔC, the calculated bias due to non-random mating of the dams over time according to production. Smith's method yields the more conservative estimates of the genetic trends in production, although both methods are in close agreement. Results for all cows from Smith's method (1962) indicate that a genetic gain in milk production per year of 1.54 per cent of the mean has occurred over the 13 year period. Results from the method of weighted mean indicate that a genetic gain of 1.76 per cent per year has occurred. According to Smith's method (1962), the A.I. Holstein population in Michigan has experienced a 2.36 per cent genetic gain per year in milk production compared to a 1.04 per cent genetic gain for the non-A.I. Holstein population. This shows a considerable advantage for genetic gains in milk production through artificial insemination. The corresponding figures using the weighted mean method are: a 3.74 per cent genetic gain per year in milk production for the A.I. population and a 0.82 per cent genetic decrease per year in milk production for the non-A.I. population.

The estimates of the environmental trends are, in general, slightly negative, with the most conservative estimates showing a reduction in environment of 40 lb.

of milk per year. The estimates of the yearly environmental trends from the regression within sires pooled by the inverse of the variance are inappropriate since they are estimated from phenotypic and genetic trends which seem to be unreasonable. From the other estimates of the environmental trend in Table 6, it can be seen that there is a larger negative trend in the artificially sired population than in the naturally sired cows.

A negative environmental trend is not necessarily an indication of a decrease in advancements in management and nutrition. Recent trends in management and nutrition have stressed more efficient labor utilization and maximizing the pounds of milk per labor unit. This has led to less individual care for each cow and an increased number of cows per farm. These management and feeding practices could very well be typical of a slight negative environmental trend, which could be economically, an advantage to the farmer.

Modern dairy farm management specialists have advocated more efficient use of labor by utilizing mechanical devices which enable efficient management of more animal units per man. A farmer cannot economically compete without these advances, which tend to force the loss of individuality of the cows. Modern dairy farm management advances tend to cause a negative environmental trend per cow, but probably a positive dollar trend per man hour worked.

In Michigan, since 1953 the grain consumed per cow per lactation has increased approximately 2,000 lb. per cow per lactation, from about 2,000 lb. in 1953 to 4,000 lb. in 1965. From research data, this would immediately indicate a large positive environmental trend in production per year. Previous to the recommendation of challenge grain feeding or high grain feeding, farmers were selecting cows which produced large amounts of milk on approximately 7.0 lb. of grain per day of lactation, with the remainder of the ration being a given number of pounds of hay and silage. In recent years, since high grain feeding has become popular, cows which produce best on 15.0 lb. of grain per day of lactation, consumed with a balanced amount of hay and silage, are selected to remain in the herd. A genetic-environmental interaction would cause a different ranking of cows exposed to the two environments. If this does occur, the effect on the measurement of genetic trends is not known. Since production of each cow is the observation measured, it may be that under high grain feeding, selection for production involves selecting for a slightly different cow genetically. Thus, the changes in feeding practices may be partially or totally reflected as genetic gains under the model used to analyze the data. If advances in management produce a rather large negative environmental trend, it is possible that advances in nutrition cannot compensate for it, resulting in a slightly negative total environmental trend.

In the simulated data, changes in the nutritional regime were not incorporated. Thus, the results were a lot easier to interpret.

Table 8 contains the parameters used to estimate the genetic and environmental trends in butterfat production. In the total population of cows there has been an estimated increase of 6.26 ± .15 lb. per year in butterfat over the 13 years studied. This is a 1.3 per cent increase per year. In milk production the 165 lb. increase per year is equivalent to a 1.2 per cent increase per year. Therefore, the percentage increase in fat production has been slightly greater than that for milk production. This is in line with the emphasis put on fat production in past years. The artificially sired population increased 7.37 ± .21 lb. of fat per year for a 15. per cent increase per year, which corresponds to a 1.5 per cent increase in milk production per year. In the naturally sired population of cows studied, the regression of production on time indicated there was an increase of 4.8 ± .23 lb. of fat per year or an increase of 1.0 per cent of the mean, which corresponds to a 0.9 per cent increase in milk production per year for the naturally sired cows.

TABLE 8.--Parameters used in estimating the genetic and environmental trends in fat production.

	All Cows	A.I. Cows	Non-A.I. Cows	All Cows With Dams
No. of sires	3,030	1,076	2,337	247
No. of daughters	61,381	37,397	22,137	4,014
No. of dams	4,024	3,337	568	4,014
$b_{D_A \cdot T}$	.174 ± .01	.198 ± .01	.138 ± .02	.365 ± .02
$b_{P \cdot T}$	6.3 ± .15	7.4 ± .21	4.8 ± .23	8.3 ± .83
$b_{D_A \cdot T/S}$*	.376 ± .03	.441 ± .03	.191 ± .19	.069 ± .01
$b_{P \cdot T/S}$*	68.4 ± .12	11.5 ± .24	30.1 ± .29	-13.7 ± .68
$b_{D_P \cdot T/S}$*	2.6 ± .43	1.7 ± .49	14.2 ± 1.8	14.8 ± .68
$b_{D_A \cdot t/S}$†	.385 ± .06	.299 ± .06	1.07 ± .23	.512 ± .02
$b_{P \cdot T/S}$†	1.4 ± .21	.4 ± .26	1.1 ± .34	4.6 ± .82
$b_{D_P \cdot T/S}$†	1.6 ± .80	1.1 ± .88	-5.9 ± 2.1	2.5 ± .82

*Regressions within sires pooled by the inverses of their variances.

†Regressions within sires pooled by their weighted mean.

The regressions of fat production on time within sires pooled by the inverse of their variances were abnormally high or low depending on the population analyzed. The exact reasons for this are unknown, but possible reasons were given earlier in the discussion of trends in milk production. The regressions of fat production on time within sires pooled by their weighted mean were very close to values one would expect. The estimates of the genetic and environmental trends are given in Table 9.

TABLE 9.--Estimates of the genetic and environmental trends in fat production per year.

Method of Pooling	All Cows	A.I. Cows	Non-A.I. Cows	All Cows With Dams
Inverse of variance				
ΔG	-100 ± .38	-2.2 ± .64	-57.0 ± .74	53.3 ± 2.2
Δe	106 ± .41	9.5 ± .67	61.8 ± .77	-45.0 ± 2.4
Geometric mean				
ΔG	11.9 ± .52	18.3 ± .67	9.3 ± .82	11.5 ± 2.3
Δe	-5.7 ± .54	-11.0 ± .70	-4.5 ± .84	-3.3 ± 2.4
Smith's method				
ΔG	8.1 ± .52	12.6 ± .67	3.8 ± .82	6.5 ± 2.3
Δe	-1.8 ± .54	-5.2 ± .70	1.0 ± .84	1.8 ± 2.4

The results in Table 9 show similarities to those in Table 6. If one uses most conservative estimates of Smith's method (1962), the results indicate a general negative trend in environment for both milk and fat production. For all cows, the genetic trends show increases of 1.5

per cent per year for milk production and 1.7 per cent per year in fat production. The artificially sired population of cows had estimated genetic increases of 2.4 per cent per year in milk production and 2.6 per cent per year in fat production. Naturally sired cows had estimated genetic increases of 1.0 per cent per year in milk production and 0.8 per cent per year in fat production. There seems to have been more selection pressure on fat yield in the A.I. population than in the natural population. A definite case can be made for the artificial breeding of cows to proven bulls, because these bulls created genetic trends in milk and fat production that were 1.4 per cent and 1.8 per cent greater than the respective trends created by bulls used in natural service.

TABLE 10.--Comparison of artificially and naturally sired progeny.

	Artificially Sired	Naturally Sired	Superiority of A.I.
Milk	13,401 ± 15	13,198 ± 19	203 ± 25
Fat	487 ± .55	479 ± .71	8 ± .90
	Superiority of daughters over their dams		
Milk	463 ± 69	-125 ± 197	588 ± 208
Fat	18 ± 2.51	-3 ± 6.01	21 ± 6.51

The results in Table 10 indicate that artificially sired progeny are phenotypically superior to their naturally sired counterparts by 203 ± 25 lb. of milk and 8 ± .9 lb. of fat. It is assumed that the artificially and naturally sired progeny are distributed proportionately over the years studied. The artificially sired progeny have a greater superiority over their dams than do the naturally sired progeny, which emphasizes the advantage of greater selection pressure on sires selected by the A.I. organizations compared to the farmer's less accurate evaluation of untested sires. Tucker et al. (1958) found that artificially sired progeny were superior to the naturally sired progeny by 15.7 and 366 lb. of fat and milk. The results in Table 10 do not provide a direct comparison with Tucker's work, since herd effects were not removed, but they indicate the superiority of artificially sired progeny over naturally sired cows in Michigan, if one assumes that artificially and naturally sired progeny are randomly distributed according to herd levels.

Specht and McGilliard (1960) studied the Michigan D.H.I.A. records made from 1945 to 1955. A phenotypic trend of 0.9 per cent of the annual average yield was calculated. The phenotypic trend per year has since increased to approximately 1.3 per cent of the average annual yield. In 1955 the artificially sired progeny were superior to the naturally sired progeny by 80 lb. of milk and 11 lb. of fat. They estimated that a genetic gain of 1.7 to 2.3 per cent of the average annual yield could be expected from progeny testing in a population of 10,000 tested cows. The average annual yield at that time was 12,237 lb. of milk and 435 lb. of fat. Their estimates of genetic progress were based on the records of 10,000 cows tested by D.H.I.A., or about 7 per cent of the dairy cattle in Michigan. As of September 1965, there were 123,000 cows tested by D.H.I.A. or Owner Sampler, which is about 23 per cent of the dairy cows in Michigan. The increased amount of information makes selection of sires more accurate. The genetic trends obtained from the Michigan data, in general, agreed quite closely with the theoretical estimates of genetic gains which can be obtained by progeny testing in a large population of cows (Specht and McGilliard, 1960). The genetic trends in the naturally sired population agreed very closely with the 1.0 per cent genetic gain per year with no progeny testing at all. In general, these results agree rather well with estimates of possible genetic gain obtained in other data from the Michigan dairy cattle population.

The results of the estimates of the genetic and environmental trends in Michigan do not agree, in general, with the published results of studies made in other states.

Van Vleck and Henderson (1961a) estimated a 0.5 per cent superiority in genetic gain of the artificially sired progeny over the naturally sired progeny. This would indicate an approximate genetic gain of 1.5 per cent of the average annual yield for artificially sired progeny in New York. The artificially sired progeny were superior in all years and in all respects to the naturally sired progeny. Michigan data indicate superiority of artificially sired progeny over naturally sired progeny of 1.4 per cent and 1.8 per cent for milk and fat, respectively. Burnside and Legates (1965) obtained a phenotypic trend of 138 ± 23 lb. of milk per year for North Carolina cows, which is in general agreement with the 1965 lb. per year increase found in these data. They used the method of Smith and estimated the genetic trend in milk production to be 122 ± 58 lb., which is considerably lower than the advance estimated from these data. Van Vleck and Henderson (1961b) obtained estimates of the genetic trends for milk and butterfat production for artificially and naturally sired progeny in New York. Genetic trends for milk production were 86 lb. and 44 lb. per year for artificially and naturally sired progeny respectively, and the corresponding values for fat production were 3.9 lb. and 1.9 lb. The estimates obtained from Michigan data are approximately twice as large as those found in New York, but the relative

superiority of artificially sired progeny over the naturally sired progeny is much the same. Henderson (1958) estimated the environmental trend to be -3.0 lb. per year for fat production in a sample of 11 herds. This estimate is in close agreement with the results obtained in this study using all cows. Arave et al. (1964) analyzed 12 Jersey herds in California for genetic trends in fat-corrected-milk using the maximum likelihood method of Henderson et al. (1959) and Smith's method (1962). The genetic trends ranged from -51 to +145 ± 21 lb. of FCM with an average of 74 lb. of FCM, or a 0.7 per cent increase per year when they used the method of Henderson et al. (1959). Smith's method (1962) yielded an estimate of the genetic trend of 56 lb. of FCM increase per year. These estimates are approximately half as large as the estimates obtained from the Michigan data, but the fact that Arave's data were from Jerseys and were expressed as FCM may account for most of the differences. Dillon et al. (1955) and Qureshi (1963) obtained estimates of the genetic trends from small amounts of data and found them to be very near zero.

Estimates of heritability obtained without removing the variation due to herds are summarized in Table 11. Herd variation adds considerably to the estimate of heritability; more accurate estimates should be calculated from records analyzed within sires and herds.

TABLE 11.--Heritability estimates for milk and fat production.

		Regression of Daughter on Dam		Correlation Between Daughter and Dam	
		Milk	Fat	Milk	Fat
Total Population	3	(.53 ± .03)	(.65 ± .02)	(.52 ± .03)	(.57 ± .03)
	3	.46	.57	.45	.50
Within Sire	1	-.47	-.58	-.92	-.60
Within Sire	2	.54	.49	.48	.48
A.I. Population	3	(.67 ± .03)	(.66 ± .03)	(.60 ± .03)	(.58 ± .03)
	3	.63	.63	.57	.55
Within Sire	1	2.02	1.46	1.89	1.50
Within Sire	2	.60	.58	.57	.56
Non-A.I. Population	3	(.25 ± .08)	(.52 ± .06)	(.31 ± .06)	(.48 ± .06)
	3	.13	.28	.17	.26
Within Sire	1	.26	-1.48	.26	-.97
Within Sire	2	.32	.16	.16	.19
Dummy Herds	3	(1.00)		(.93)	
	3	.61		.57	

1 = Regressions and correlations within sires pooled by the inverses of the variances.

2 = Regressions and correlations within sires pooled by their weighted mean.

3 = Linear regressions and correlations.

Table 11 is presented merely to illustrate the differences between estimates of heritability where the genetic correlation between daughter and dam within sires is assumed to be 0.50 and where estimates of the genetic correlations within sires are used (Table 7). The values in parentheses, e.g. (.53 ± .03), are estimates obtained by multiplying the regression of daughter on dam or the correlation between daughter and dam by the inverse of the assumed genetic correlation, 0.50. The other estimates of heritability are obtained by multiplying by the inverse of the estimated genetic correlations within sires, given in Table 7.

The heritability estimates obtained by doubling the linear regressions and correlations are consistently higher than those obtained by multiplying the correlations and regressions by the inverse of the estimates of the genetic correlation between daughter and dam. Comparison of the estimates obtained by the use of the estimated genetic correlation with those obtained by doubling the linear regressions and correlations give an indication of possible bias due to an invalid assumption. The estimates of heritability obtained from the regressions and correlations within sires pooled by the inverses of their variances are unrealistic and beyond the limits of the theoretical values of heritability. The estimates obtained from the regressions and correlations within sires pooled by their weighted mean are more reasonable, but it must be remembered that the variation due to herds is not removed and the estimates obtained from the total population and the artificially sired population are, therefore, inflated. A large proportion of the herd variation has been removed from the estimates obtained from the naturally sired population since the estimates were calculated within sires, and most naturally used sires are in single herds. It was not the purpose of this study to obtain accurate estimates of the additive genetic variance, but the results do indicate that the most accurate estimates of heritability may be obtained by pooling regressions within sires by their weighted mean in the naturally sired progeny.

The heritability estimates obtained from the simulated data are large, but since all the parameters used in constructing the data are known, components can be separated and the estimates can be interpreted. The true heritability of milk production in the simulated data is 0.18, and the heritability of milk production expressed as a deviation from the herd average is 0.26. When herd variation is not removed, the estimate of heritability obtained from the original parameters is 0.51. The corresponding estimates were 0.61 and 0.57 in the simulated data. When comparing the estimates of heritability obtained from the simulated data with

those obtained in the A.I. and total populations, it may be concluded that the heritability of production in Michigan Holsteins is nearly the same as that used in the simulated data, i.e. 0.18 for milk production and 0.26 for milk production expressed as deviations from the herd average. These values correspond quite closely with the estimates obtained in the naturally sired population of Michigan Holsteins. An important point here is that in the data used in this study, the estimated genetic correlation between daughter and dam was greater than the assumed 0.50.

Unanswered questions arising from this research are: Why are the results obtained by the pooling of regressions by the inverses of their variances unrealistic compared to those obtained by pooling by weighted mean? How can the environmental trend be separated into managemental and nutritional trends?

SUMMARY

In a preliminary analysis, 1,556 two-year-old cows from simulated dairy herd data were analyzed to determine the accuracy of the proposed modifications of the method of Smith (1962) for evaluating genetic and environmental trends in production data. The results indicate that first lactations of cows selected to produce offspring are superior to their daughter's first lactations, but are inferior genetically to their daughters. The analysis of trends indicated there was a 131 lb. increase per year in milk production; the estimated genetic and environmental components were 136 lb. and -4.1 lb., respectively. Pooling the regressions of production on time within sires by the inverses of their variances or by their weighted mean produced accurate estimates of the genetic and environmental trends. Pooling by the inverse of the variance yielded unreasonable intermediate results, but gave accurate estimates of the genetic and environmental trends.

Estimates of the regression and correlation of daughter's additive genetic value on dam's additive genetic value within sires differed from the assumed 0.50, the degree of difference depending on the method

of pooling. The known regression and correlation of daughter's additive genetic value on dam's additive genetic value within sires substantiated the results.

The modified analysis of Smith (1962) was then applied to the Michigan Holstein production records that were recorded by D.H.I.A. from 1953 through October 1965. There were 65,560 two-year-old registered and grade Holstein cows which had their first lactation at less than 36 months of age. Records of the dams of 7.1 per cent of these cows were in the data. All records were projected to a 305-day, 2X, M.E. basis. There was a linear increase in the number of observations of about 1,000 per year up to 1964, where 10,092 observations were available. The linear regression of production on time was 165 ± 4.1 lb. of milk and 6.3 ± .15 lb. of fat per year for all cows, and the mean production was 13,323 ± 12 lb. of milk and 484 ± 1 lb. of fat. The two-year-old cows calving in 1964 averaged 14,101 ± 29 lb. of milk and 513 ± 1 lb. of fat.

The most conservative estimates of the genetic and environmental trends were obtained by Smith's method (1962). A genetic trend of 205 lb. of milk per year or increase of 1.54 per cent of the mean was calculated, whereas the phenotypic trend was 1.2 per cent per year. The phenotypic trend in fat production per cow per year was 1.3 per cent and the estimate of the genetic trend

was 1.7 per cent per year. These indicate negative environmental trends in milk production of -40 lb. per year and in fat production of -1.8 lb. per year.

Genetic trends in the artificially and naturally sired progeny also were measured. The artificially sired population had phenotypic trends of 201 ± 5.7 lb. of milk and 7.4 ± .21 lb. of fat per year, compared to a 119 ± 6.2 lb. of milk per year and 4.8 ± .23 lb. of fat per year in the naturally sired population. This is equivalent to a 1.5 per cent increase in milk and fat per year in the artificially sired progeny and a 0.9 per cent increase in milk and 1.0 per cent increase in fat production per year for the naturally sired progeny. The artificially sired population of cows had genetic increases of 2.4 per cent per year in milk production (314 lb.) and a 2.6 per cent per year in fat production (12.6 lb.). Naturally sired cows had genetic increases of 1.0 per cent per year in milk production (138 lb.) and a 0.8 per cent per year in fat production (3.8 lb.). Estimates of environmental trends were negative in all cases except the fat production of the naturally sired progeny.

Estimates of the genetic correlation between daughter and dam averaged approximately 0.60, considerably higher then the assumed 0.50. Estimates of heritability were obtained by multiplying the inverse of the genetic correlation by the phenotypic relationship between daughter and

dam. Both the calculated genetic correlations and assumed genetic correlations (0.50) were used. The parameters estimated indicate that the heritability of milk production is approximately 0.16 and fat production approximately 0.18. The heritability of deviations of first records from their herd average would be approximately 0.26 for milk production and 0.29 for fat production.

LITERATURE CITED

Arave, C. W., Laben, R. C., and Mead, S. W. 1964. Measurement of genetic change in twelve California dairy herds. J. Dairy Sci., 47:278-283.

Brinks, J. S., Clark, R. T., and Rice, F. J. 1961. Estimation of genetic trends in beef cattle. J. Animal Sci., 20:903 (abstr.).

Burnside, E. B. and Legates, J. E. 1965. Estimation of genetic trend for production in a dairy cattle population. J. Dairy Sci., 48:804 (abstr.).

Clayton, G. A., Morris, J. A., and Robertson, A. 1957. An experimental check on quantitative genetical theory I. Short term response to selection. Journ. of Genetics, 55:131-151.

Clayton, G. A., and Robertson, A. 1957. An experimental check on quantatitive genetical theory II. The long term effects of selection. Journ. of Genetics, 55:152-170.

Damon, R. A., Jr., and L. M. Winters. 1955. Selection for factors of performance in the swine herds of the Hormel Foundation. J. Animal Sci., 14:94-104.

Dickerson, G. E. 1955. Genetic slippage in response to selection for multiple objectives. Cold Spring Harbor Symposium on Quantitative Biol., 20:213-224.

Dickerson, G. E. and Hazel, L. N. 1944. Effectiveness of selection on progeny performance as a supplement to early culling in livestock. J. Agr. Research, 69:459-476.

Dillon, W. M., Jr., Yapp, W. W., and Touchberry, R. W. 1955. Estimated changes in the environment and average real producing ability in a Holstein herd from 1901 through 1954. J. Dairy Sci., 38:616. (abstr.).

Flower, A. E., Brinks, J. S., Urick, J. J., and Willson, F. S. 1964. Selection intensities and time trends for performance traits in range Hereford cattle under mass and recurrent selection. J. Animal Sci., 23:189-195.

Friars, G. W., Bohren, B. B., and McKean, H. E. 1962. Time trends in estimates of genetic parameters in a population of checks subjected to multiple objective selection. Poultry Sci., 41:1773-1784.

Gaalaas, R. F., and Plowman, R. D. 1961. Effectiveness of statistical adjustments for yearly fluctuations in production. J. Dairy Sci., 44:1188 (abstr.).

Goodwin, K., Dickerson, G. E., and Lamoureux, W. F. 1955. A technique for measuring genetic progress in poultry breeding experiments. Poultry Sci., 34:1197 (abstr.).

Gowe, R. S., Robertson, A., and Latter, B. D. H. 1959. Environment and poultry breeding problems. 5. The design of poultry control strains. Poultry Sci., 38:462.

Henderson, C. R. 1949. Estimation of changes in herd environment. J. Dairy Sci., 32:706 (abstr.).

Henderson, C. R. 1958. Estimation of environmental trends and biases from errors in age factors and repeatability. J. Dairy Sci., 41:747 (abstr.).

Henderson, C. R., Kempthorne, O., Searle, S. R., and Von Krosigk, C. M. 1959. The estimation of environmental and genetic trends from records subject to culling. Biometrics 15:192-218.

Lerner, I. M., and Dempster, E. R. 1951. Attenuation of genetic progress under continued selection in poultry. Heredity 5:75-94.

Lush, J. L. and Schrode, R. R. 1950. Changes in milk production with age and milking frequency. J. Dairy Sci., 33:338-357.

Lush, J. L., Norton, H. W., III, and Arnold, Lloyd. 1941. Effects which selection of dams may have on sire indexes. J. Dairy Sci., 24:695-721.

McDaniel, B. T., Plowman, R. D., and Davis, R. F. 1961. Causes and estimation of environmental changes in a dairy herd. J. Dairy Sci., 44:699.

Miller, R. H. 1964. Biases in the estimation of the regression of milk production on age. J. Dairy Sci., 47:855-860.

Miller, R. H., Legates, J. E., and Cockerham, C. C. 1963. Estimation of non-additive hereditary variance in traits of mice. Genetics 48:177-188.

Nelson, R. H. 1943. Measuring the amount of genetic changes in a herd average. J. Animal Sci., 2:358 (abstr.).

Qureshi, A. W. 1963. Genetic trends in milk and milk fat production of Texas Dairy Herd Improvement Association cows. J. Dairy Sci., 46:629 (abstr.).

Rendel, J. M. and Robertson, A. 1950. Estimation of genetic gain in milk yield by selection in a closed herd of dairy cattle. J. Genetics 50:1.

Robertson, A. and Rendel, J. M. 1954. The performance of heifers got by artificial insemination. J. Agr. Sci., 44:184.

Robertson, F. W. 1955. Selection response and the properties of genetic variation. Cold Spring Harbor Symposium on Quantatitive Biol., 20:166-177.

Searle, S. R. 1961. Estimating herd improvement from selection programs. J. Dairy Sci., 44:1103.

Smith, C. 1962. Estimation of genetic change in farm livestock using field records. Animal Prod. 4:239-251.

Smith, Charles. 1963. Genetic change of backfat thickness in the Danish Landrace breed of pigs from 1952 to 1960. Animal Prod. 5:259-268.

Specht, L. W., and McGilliard, L. D. 1960. Rates of improvement by progeny testing in dairy herds of various sizes. J. Dairy Sci., 43:63.

Tucker, W. L., and Farthing, B. R. 1958. Genetic improvement in dairy cattle attributable to sires used in artificial insemination in North Carolina. J. Dairy Sci., 41:740.

Tucker, W. L., Legates, J. E., and Farthing, B. R. 1960. Genetic improvement in production attributable to sires used in artificial insemination in North Carolina. J. Dairy Sci., 43:982.

Van Vleck, L. D., and Henderson, C. R. 1961a. Improvement in production of New York Holsteins due to artificial insemination. J. Dairy Sci., 44:1328.

Van Vleck, L. D., and Henderson, C. R. 1961b. Measurement of genetic trend. J. Dairy Sci., 44:1705.

Van Vleck, L. D., and Henderson, C. R. 1961c. Effect of genetic trend on sire evaluation. J. Dairy Sci., 44:1877.

Wright, S. 1938. Size of population and breeding structure in relation to evolution. Science 87: 430.