ESTIMATES OF GENETIC PROGRESS IN THE DEVELOPMENT OF THE AMERICAN RED DANISH CATTLE

By

Norman Ray Thompson

AN ABSTRACT

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NORMAN RAY THOMPSON ABSTRACT

Milk and butterfat yields and related information were collected on the foundation generation and on successive back-crosses to Red Danish sires. The relation of certain environmental factors to butterfat production was investigated by a least squares procedure. Butterfat yield did not vary significantly with month of calving, but did vary significantly ($P < .01$) with age at calving, previous calving interval, and length of lactation period. The regression of butterfat yield on age at calving was curvilinear and of the form $Y = \bar{Y} + 10.012(X-\bar{X}) - 0.067(X^2-\bar{X}^2)$, where X is age in months and Y represents butterfat. Yield of butterfat increased at a rate of 1.96 pounds for each additional month of previous calving interval, and 0.99 pound for each additional day of lactation period. Also, butterfat yield exhibited an upward environmental trend of 6.49 pounds per year ($P < .05$).

Additive correction factors were developed from the least squares estimates, and used to adjust the original butterfat records. The foundation generation, using fully adjusted records, averaged 351 pounds butterfat; the first-cross generation, 379; the second, 377; and the third, 389. The increase of 28 pounds from foundation to first-cross generation was very highly significant ($P < .001$), the 2-pound decrease to the next generation was not significant, while the gain of 12 pounds by the third-cross generation was very highly significant ($P < .001$).

Selection in the foundation groups, based on comparison of all cows with those having daughters in the first-cross generation gave estimated additively genetic superiorities (for those having daughters) of zero to

+13.4 pounds butterfat per lactation period. Selection in the first- and second-cross generations gave estimated additively genetic superiorities of zero to +5.1 pounds butterfat. These latter values are based on the amount of selection practiced from lactation to lactation.

The effect of age at calving on butterfat production was investigated in some detail, and tentative age correction factors were developed for the American Red Danish breed. Factors based on fitting an intra-cow quadratic regression to the data were the most efficient of any developed here, both in making use of more records than in the paired method and in accounting for a larger proportion of the variance than did any other method. Based on comparison of sets of regression factors, the second-cross generation reached peak production at an earlier age than did the first cross. Preliminary evidence was found that the presently recommended Bureau of Dairy Industry factors are too low for the 2- and 3-year age brackets.

Heritability of butterfat yield, using the method of intra-sire regression of daughter on dam, was estimated as 0.39 ± 0.11 on a single record basis. Repeatability of butterfat production was estimated as 0.43. The intra-cow correlation of age at calving with previous calving interval was 0.07 ($P < .05$). Other intra-cow correlations among age at calving, month of calving, and previous calving interval were numerically small and not significant statistically. Repeatabilities of calving interval, month of calving, and length of lactation period were estimated as 0.04, 0.37, and 0.18, respectively. The first and third values suggest rather low genetic determination.

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INTRODUCTION

The development of populations of domestic animals which have useful or desirable traits has been marked by several means and procedures. Among these are inbreeding, selection, and migration. Inbreeding accompanied by selection has been used in the development of relatively uniform populations termed breeds. Migration, accomplished by man, has introduced new genes to populations and, through crossing and up-grading, has led to shifts in gene frequencies within these populations. Selection, of course, has been an ever-present tool, ready for use in each generation so long as rates of reproduction remained normal.

The development of the American Red Danish breed of dairy cattle (Cranek, 1952) is an excellent example of the effects of migration on gene frequency. Although the foundation stocks were highly diverse genetically, repeated back-crossing to Red Danish sires soon led to much less diversity as evidenced by phenotypic characters. In addition, the frequency of genes which affect economic traits favorably appears to have been increased. Cranek reported gains in milk and butterfat production from the foundation groups to the successive generations.

In making his investigation, Cranek corrected milk and butterfat records only for age at calving and number of days milked. The correction values used were based on information from the literature, rather than from the experimental data. He investigated the relation of month of calving and previous calving interval to milk and butterfat yields, but did not make use of the findings. In view of these facts, it appeared desirable to make further investigation of the data, particularly with regard to factors other than changes in gene frequency which might have affected phenotypic performance.

Accordingly, the writer set up several investigational objectives. These were:

1. Obtain joint estimates of the effects of month of calving, previous calving interval, age at calving, year of calving, and length of lactation period on butterfat production.
2. "Correct" the raw data for these effects, and make further evaluation of the changes in butterfat production from repeated back-crossing to Red Danish sires.
3. Construct a set of age correction factors for the American Red Danish breed.
4. Estimate the repeatability of month of calving, length of lactation period, and length of calving interval.
5. Estimate heritability and repeatability of butterfat production, based on records that had been corrected for the environmental effects listed in the first objective.
6. Investigate rates and effectiveness of selection within each generation.

The fourth, fifth, and sixth objectives were not anticipated at the beginning. However, it soon became evident that estimates of heritability and repeatability would be needed in the estimation of genetic progress from generation to generation. Further, estimates of heritability and repeatability have some general application, in that they indicate the relative roles of heredity and environment in determining the characters considered. Information on the status of selection can be used to help determine the possibilities for both further and more effective selection. Therefore the second three objectives were included.

REVIEW OF LITERATURE

This review will cover the most pertinent reports in the following subject areas:

1. Genetic progress.
2. Repeatability and heritability.
3. Selection in dairy herds.
4. Environmental factors.
5. Age correction factors.
6. Mathematical bases and procedures.

In some instances, most of the available information will be cited; in others, only a single report by way of example.

A. Genetic Progress

General

The concept of genetic progress in the breeding of domestic animals probably appeared, in some crude form, at a very early time. Selection of breeding animals was practiced long before anything was known about the science of genetics. Thus at the beginning of the twentieth century a number of domesticated breeds of birds and mammals had been developed that far surpassed their more distant ancestors with respect to characters of economic value.

Basis

The basis for genetic progress is the shifting of gene frequencies so that the genes which favor expression of desirable attributes or characters are more numerous in the population than their alleles.

The demonstration of such shift is relatively simple when only a single pair of genes is concerned, since genotypic and phenotypic classes are discrete and in many cases can be identified. In the absence of dominance, each of the three genotypes coincides with the corresponding phenotype, and each phenotype and genotype can be identified. With complete or partial dominance, identification of certain genotypes becomes difficult to impossible, however. The effects of a single pair of genes, in numerous cases, are not noticeably modified by environmental forces. However, the demonstration becomes somewhat more difficult with characters of economic value because (1) such characters appear to be determined by many gene pairs, (2) the sum of gene effects includes both individual additive effects and those due to interactions among genes, and (3) non-genetic forces exert large and variable effects on the final expression of the character.

Definitions

Definitions of genetic progress can range from the rough estimates secured from early grading up experiments to the somewhat more precise estimates of recent years. Several early grading up experiments (Olson and Biggar, 1922; Cunningham, 1926; Fairchild, 1926; Weaver *et al.*, 1928) demonstrated the substantial improvement that could result when mediocre females were bred to superior males. The composition of this improvement was not separated into genetic and non-genetic portions, although the effects of environment were recognized in two experiments and demonstrated in one.

Improved definitions of genetic progress became possible after methods for separating genetic and non-genetic effects were elucidated

(Fisher, 1918; Wright, 1935) and applied to particular problems (Lush, 1940). Perhaps the most conservative definition of genetic progress which we can state today is "that improvement in economic value or performance which is due to increases in frequencies of desirable genes and to their individual roles in producing a superior phenotype". The phenomena of heterosis, hybrid vigor, "nicking", etc., are not included in this strict definition of genetic progress, even though they may be of great economic importance.

Estimation and Estimates

A more exact estimation of genetic progress has been evolved only as new techniques have been developed to estimate additive genetic effects separately from other genetic effects, and to evaluate the non-genetic effects that commonly are grouped and termed environmental. Wright (1939) recognized that environmental effects were large and that they might interfere in the estimation of genetic effects. Dickerson and Hazel (1944) used the heritability ratio (additively genetic variance/total phenotypic variance) to estimate the additively genetic superiority of a selected group of parents, from which the additively genetic superiority of their unselected offspring in turn could be predicted. Their method has been used by many recent workers to estimate genetic gains.

Nelson (1943) indicated a procedure somewhat different from that of Dickerson and Hazel, in that comparisons were to be made over entire herds or flocks from year to year, rather than from generation to generation. The use of this latter procedure requires preliminary estimation of non-genetic year-to-year deviations in animal performance.

(These deviations should be considered regardless of method, if performances of any group are measured over more than a single year.)

Numerical estimates of potential genetic progress in dairy cattle include those by Lush (1949), and Rendel and Robertson (1950). Estimates of actual genetic progress have been reported by Rendel and Robertson (1950), Laben and Herman (1950), Mahadevan (1951a,b), the Iowa Station (1952), Harvey (1953a), and Stonaker (1953). In general, neither the theoretical nor the actual increases have been large; an approximate figure would be one per cent a year. Similarly, neither have the increases been large under conditions of artificial insemination with the use of a few carefully selected sires (Robertson and Rendel, 1950, 1954).

B. Repeatability and Heritability

Cranek (1952) reviewed the literature on repeatability and heritability of milk and butterfat yield, and discussed methods of estimation. He obtained values for heritability, using data on various groups of American Red Danish cows, which ranged from 0.38 ± 0.08 to 0.66 ± 0.20 for milk yield, and 0.42 ± 0.10 to 0.67 ± 0.19 for butterfat yield. Corresponding values for repeatability were 0.49 to 0.53 for milk yield, and 0.61 to 0.74 for butterfat yield.

The environmental factors discussed in preceding paragraphs are not all necessarily non-genetic in an absolute sense. Some of them may be determined in part genetically. Repeatability of length of calving interval has been estimated variously at 0.133 (Legates, 1954) and 0.184 (Rennie, 1954), although heritability appears to be essentially zero for this trait. Tandon (1953) observed a repeatability of 0.8 for length of dry period in Indian cattle. Although very little is actually known, it is likely that length of lactation is determined in part genetically.

C. Selection in Dairy Herds

Only a few reports are available on this subject. Seath (1940) found culling rates of 28.6 per cent and 30.9 per cent per year, respectively, for Iowa and Kansas herds. Asdell (1951) reported an average removal rate of 21.9 per cent annually among herds in 17 states. The rate varied with age of cow, being as low as 6.0 per cent for ages 2-3 years and up to 35.2 per cent for ages 7-8 years. Since much of the culling ordinarily is for dairy purposes, disease, etc., the opportunity for making selections for breeding purposes is reduced accordingly.

D. Environmental Factors

General

The term *environmental* is used here in a broad sense, in that it pertains to all factors nearly or completely of a nongenetic origin and which may affect quantity or quality of milk produced. These non-genetic or environmental factors for the most part exert temporary effects, although a few (injuries, disease, malnutrition, etc.) may affect the subject individual permanently. Non-additively genetic effects, resulting from genic interactions and commonly termed epistasis and dominance, similarly affect the individuals throughout life, but these effects are determined at fertilization rather than during the subject's lifetime.

The effects of environmental factors on production have been recognized for many years (Pearl and Miner, 1919; Norton, 1932; Wright, 1939), and numerous investigations of them have been made. Nutrition, time of calving, climate, dry period, calving interval, gestation, and age at first calving all have been shown to affect production.

Nutrition

Nutrition was shown at an early time to have major effects on yields of milk and butterfat (Roberts, 1892; Doane, 1900; Wing and Foord, 1904), although the butterfat percentage apparently could not be altered appreciably except in an indirect manner (Eckles, 1912). The effects of successive increments of feed are curvilinear over more than a limited range of nutritional levels (Jensen *et al.*, 1942). The effects of nutrition are not limited to those of a direct and immediate nature. Optimal nutrition during growth may improve performance after reaching maturity (Weaver *et al.*, 1928).

Time of Calving

The effect of month or season of calving has been investigated by a number of workers. In general, under temperate zone conditions, cows calving in the fall and early winter months yield more milk than those calving at other times of the year (McDowell, 1922; Hammond and Sanders, 1923, Turner, 1923; Wylie, 1925; Sanders, 1927-28; Headley, 1933; Frick *et al.*, 1947; Cranek, 1952). However, Oloufa and Jones (1948) found no significant differences that could be attributed to month of calving under the mild climatic conditions prevalent in western Oregon. Several workers (Hammond and Sanders, 1923; Sanders, 1927-28; Cannon, 1933; Cranek, 1952) have constructed correction factors for month of calving. Differences in quantity and quality of feed available from month to month appear to be a causative factor (Bettenay, 1949; Cullity, 1949; Scott and Wilson, 1952). Jordão and Assiz (1948-49) observed both higher milk yield and lower rate of decline among cows calving in May-August (winter) than in November-February (summer). Their observations were made on cows kept in the Southern Hemisphere.

Climate

The effect of season (apart from time of calving) has been the subject of several reports. Butterfat percentage tends to be low in summer and high in winter (Ragsdale and Turner, 1922; Headley, 1933; Becker and Arnold, 1935). Conversely, milk yield tends to be higher in summer than in winter (Arnold and Becker, 1935; Erb and Shaw, 1953). The recent review by Hancock (1954) strongly suggests that extremes of climate (and more specifically of temperature) affect not only butterfat percentage and milk yield but also solids-not-fat content. Specifically, moderately high temperatures favor low fat percentage, high milk yield, and low SNF, and moderately low temperatures the opposite. Erb and Shaw (1953) have devised sets of correction factors for adjusting monthly milk and butterfat yields according to calendar month in which secured.

Dry Period

The reports of investigations on length of dry period preceding the lactation (Carroll, 1913; Hammond and Sanders, 1923; Sanders, 1927-28; Dickerson and Chapman, 1939; Dickerson, 1940; Klein and

Woodward, 1943; Erb and Shaw, 1953) indicate the desirability of 1 to 2 months duration. While extremely short periods are detrimental, those longer than 2 months seem to offer no advantage in terms of increased yields. In fact, Dickerson (1940) found that dry periods longer than 2 months were accompanied by relatively low production. He observed that such low production was related to low persistency and producing ability, hence probably was of genetic rather than environmental origin. Correction factors for length of dry period have been proposed (Hammond and Sanders, 1923; Sanders, 1927-28; Klein and Woodward, 1943; Erb and Shaw, 1953).

Calving Interval

Length of time interval between calvings can affect yields both in the current lactation and in that which follows (Tyler and Hyatt, 1950). Production appears to increase with longer calving interval, in a linear fashion up to about 12 months (Gaines and Palfrey, 1931; Erb and Shaw, 1953) but at a lesser rate for longer periods (Cranek, 1952; Erb and Shaw, 1953).

Gestation

The effects of advancing gestation on milk yields have been investigated both from the standpoint of days of gestation while milking (Erb and Shaw, 1953) and of service period (days from calving to next conception) (Hammond and Sanders, 1923; Sanders, 1927-28; Jordão and Assiz, 1948-49). Production tends to decrease as service period decreases and as days of gestation increase. Correction factors for days of gestation have been prepared by Erb and Shaw (1953), and for service period by Hammond and Sanders (1923) and by Sanders (1927-28).

It should be noted that dry period, days of gestation, and service period all are components of calving interval.

Age at First Calving

Age at first calving depends partly on management. Davis (1953) reported that age at first calving was significantly correlated ($r = 0.409$, $P < 0.01$) with butterfat yield in first lactation but not with productive life. Adjustment for this variable ordinarily coincides with correction for age at calving.

Miscellaneous

The number of times milked per day usually is assumed to affect production (Norton, 1932; Lush and Shrode, 1950). The effect appears not to be constant from lactation to lactation, at least not for the first 2 or 3, and provision is made for such inconstancy in adjusting records of cows milked 3 or 4 times daily when such records are used in proving sires (Kendrick, 1953).

Pathological factors, including chronic disease, can take a heavy toll of milk production. Records made under these handicaps may deviate excessively from the normal, and perhaps should be excluded altogether when making comparisons. Psychological factors such as association with numerous other individuals (Schein et al., 1955) may affect cows adversely, although a certain amount of competition among animals has been thought beneficial (Maynard, 1947).

Problems

The magnitude and nature of environmental effects give rise to numerous problems in connection with evaluation of animal performance on a genetic basis. The problems become especially critical in evaluating dairy sires (Laben, 1954). Korkman (1953) has noted the problem of non-genetic differences between herds that are due partly to unequal levels of nutrition, and has made comparisons among daughters of A.I. (artificial insemination) sires within similar planes of nutrition. McGilliard (1954) and Henderson et al. (1954) have considered use of the contemporary herd average to circumvent differences of an environmental nature between herds. Robertson and Rendel (1954) compared progenies of A.I. and non-A.I. sires on an intra-herd basis for the same reason. Year-to-year variations have been observed by Libizov (1933), Plum (1933), and Laben and Herman (1950). Their existence tends to reduce the value of daughter-dam comparisons (Laben, 1954) and has led to the use (Robertson and Rendel, 1954) of daughter averages alone. Methods to separate yearly environmental effects have been reported by Henderson (1948, 1949) and extended to IBM computation by Harvey (1953b).

Numerical Estimates

The magnitude of various environmental effects may be expressed either as plus or minus deviations (percentages or constants) from the mean or as proportions of the total variance among records. Examples of the former (Hammond and Sanders, 1923; Sanders, 1927-28; Cranek, 1952; Erb and Shaw, 1953) generally have been computed from simple one-way tabulations or at best with only partial adjustment for correlations among the several effects. In general, recommended correction values for any single variable (except for age at calving) have not been greater than plus or minus 10 per cent at the most. Erb and Shaw (1953) indicated that previous dry period and days calf was carried, however, can influence records more than 25 per cent when acting together.

Year to year deviations and environmental trends have been estimated by Laben and Herman (1950), workers at the Iowa Station (1952), Harvey (1953a), and Dillon et al. (1955). Legates (1949) found the variance component for year to year changes in herd average to be only about 5 per cent of the total variance, and further that almost nine-tenths of this component was due to changes in individual herd averages from year to year. Bayley (1950) found that 9 environmental factors accounted for approximately 50 per cent of the variation in yields of milk and butterfat. The total size of all temporary environmental or genetic effects may be expressed as the total variance minus that due to repeatability of individual production records. On such a basis, temporary environment accounts for more than half of all variance in milk and butterfat records.

Correction Factors

Although correction factors for environmental effects have been developed by a number of workers, their use in practice has been limited chiefly to correcting records for age at calving and number of times milked daily. Length of lactation commonly is standardized to 305 days, at which length the effect of calving interval appears to be minimized (Dickerson, 1940) but not entirely eliminated (Erb and Shaw, 1953). Bayley (1950) devised an index, based on a multiple regression analysis, to adjust records for 6 environmental factors (selection rating, age at calving, TDN feeding rate, days carried calf, herd size, and condition of cow at time of calving), but no wide or general use appears to have been made of this index.

The applicability to data of corrections for environmental effects depends on (1) the reliability of the initial estimates of such effects, i.e., whether based on simple one-way tabulations or on appropriate least squares or maximum likelihood estimates, (2) the standard errors of such initial estimates and the limits of error when used to "correct" small samples of data, (3) the actual reduction in total variance from making corrections to data, and (4) the fraction of the variance due to a given effect that is removed by making corrections. Individual estimates of environmental effects, unless the various effects are not correlated, may be biased; joint estimates should avoid this pitfall. Further, the use of correction factors may not be justified if the limits of error in application are very large and/or only a small amount of variance is removed.

E. Age Correction Factors

One of the major environmental factors, age at calving, will be treated separately. Much work has been done on this factor, and some of the findings will be presented.

Historical

The increase in milk yield of cows from lactation to lactation, up to maturity, is a readily recognized phenomenon and was noticed at an early date (Hills, 1908). Early age correction factors arose partly from the need for making comparisons among A.R. (Advanced Registry) records of the several dairy breeds. A number of the earlier reports were based on such records (Holdaway, 1916; Pearl and Patterson, 1917; Gowen, 1920a, b, c; Hooper, 1921; Gowen and Gowen, 1922; McCandlish, 1922; Ragsdale et al., 1924; Norton, 1932). With the growth of Cow Testing Associations (now Dairy Herd Improvement Associations) the need arose for factors appropriate for records made under other than A.R. conditions. Clark (1924), using data from 11 Land Grant College herds, prepared age correction factors for the Holstein, Jersey, Guernsey, and Ayrshire breeds. A decade later the Bureau of Dairy Industry, U.S.D.A., developed a set of "all-breed" age conversion factors from D.H.I.A. records available at that time, and put them to use in the proved sire program which began in 1935 (Kendrick, 1953). Factors for the various breed groups were developed and released by the Bureau of Dairy Industry in 1941, and subsequently individual sets were made available for most dairy breeds (Kendrick, 1953). To date (June, 1955) no separate set of factors has been reported for the American Red Danish breed.

Age and Production

Pearl (1914) found the increase in milk and butterfat production with advance in age to be curvilinear, first rising rapidly, then more slowly to a peak, then declining gradually. He postulated a curve of the form $Y = A + bX + cX^2 + d \log X$ to describe the variation. Pearl and Miner (1919), using Scottish Ayrshire records, obtained the curve $Y = 12.4766 + 0.6146\,X - 0.0366\,X^2 + 3.6641 \log X$, with the highest point occurring at $10\frac{1}{2}$ years of age. Dickerson and Chapman (1939) found the increase "essentially linear up to about five years of age, when maximum production was reached". Other workers have found, in general, that the increase is curvilinear, with the highest yearly milk production somewhere between the fifth and eighth years.

The increase in milk yield from lactation to lactation appears to be associated in part with gains in live weight up to maturity (Illinois Sta. Rpt., 1934-35), and in part with the rise and decline of physiological processes that relate to milk secretion. Genetic differences in the rate of increase exist, not only between breeds of dairy cows but also within breeds (Libizov, 1933; Dickerson and Chapman, 1939). Non-genetic factors such as level of nutrition may affect the increase one way or another.

Methods for Computing

At least three methods for computing age correction factors are available. In the first, all records at each age of calving are averaged, a smooth curve is fitted through the means, the high point of the curve is determined, and the multiplicative factors are developed from this curve to correct records in the various age classes to the production level of the highest class. This first method is termed the gross method by the writer, and is identical with the "lumped" lactation method noted by Hammond and Sanders (1923). In the second method, first and second records of the same cows are compared and a segment of the curve is established, then second and third records of the same cows are compared, *et seq*. In the third method the form of the curve is anticipated in advance and appropriate intra-cow sums of squares and cross products and terms of higher orders are computed, a set of equations set up and solved, and the resulting values used to establish the curve.

The first method is simple, easy to understand, and the calculations are straightforward. However, any appreciable and effective culling of low-producing cows between first and second lactations (or later) will tend to throw bias into the age curve, both in elevating the portions representing second and later lactations (Hammond and Sanders, 1923) and in transferring the high point of the curve to an unduly late age. The second method, while somewhat more tedious to compute, avoids the bias inherent in the first method, but may introduce a bias in the opposite direction (Lush and Shrode, 1950). The third method is superior to the second in that it utilizes a maximum of information and the computations are not unduly involved, but the bias of the second method may be present here also. Stonaker (1953) tried to avoid the second bias (as well as the first) by regressing the first records of each group of pairs back to the mean for all first records (paired and unpaired together) according to a repeatability value of 0.5.

Efficiency

The obvious purpose of age correction factors is to minimize an otherwise large source of non-genetic variability and thus increase the accuracy of comparisons among individuals whose records were made at different ages. Lush and Shrode (1950) estimated that age of calving accounted for only about 14 to 16 per cent of the total variance among records of dairy cows. They further estimated that the B.D.I. factors (Kendrick, 1941) took out 91 per cent of the age variance. It is obvious, however, that even the most efficient age correction factors cannot remove more than about one-sixth of the total variance among records. The remaining variance still may be expected to contain substantial components due to other non-genetic effects such as level of nutrition. Further, the application of age correction factors to small groups may be hazardous (Anthony, 1932), since the limits of error in the use of such standard values tend to vary inversely with the number of individuals concerned.

Problems

The problems attendant to the development and application of age conversion factors to dairy records have continued to be investigated in recent years. Ward and Campbell (1938), from results with New Zealand Herd Test data, suggest that neither percentage addition (multiplicative) factors nor those in which constant amounts are added to the original records are correct, but that a regression formula is preferable. Dickerson and Chapman (1939) found evidence that the increase in yield with age was related to initial level of production. Lush and Shrode (1950) showed that a bias opposite to that discussed earlier under the "first" method could occur when age curves were developed by the use of paired records, i.e., the higher portions of the curve would be depressed. However, they did not make any estimate of such bias from their data.

F. Mathematical Bases and Procedures

Biological processes, in general, are concerned with many variables. The effects of these variables seldom follow any simple law or pattern. The measurement of biological variables may vary from highly objective to highly subjective, or be well nigh impossible to specify at all. The measurements may give anything from discrete classes to (for all practical purposes) continuous variation. Further, numerous interactions may take place among the variables. Therefore, a simple situation seldom if ever exists, and adequate analyses tend to become complex. At best, much variability remains unattributed and unexplained; thus the "error" variance is large. Multivariate analyses generally are necessary and *a priori* knowledge of the subject matter is highly desirable.

Methods

The methods for analysis of biological data began perhaps with calculation of what we now consider phenotypic correlations among various classes of genetically related individuals. Rietz (1909) appears to have pioneered such correlations, and Gowen and associates at the Maine Station made numerous contributions between the years 1915 and 1925. Fisher (1918) showed that, under certain assumptions, the parent-offspring correlation would include one-half of the additive genetic variance, and the full-sib correlation one-half of the additive and one-fourth of the dominance variance. Wright (1935) extended the procedure to include epistatic variance. Bywaters (1937) and Jafar *et al.* (1950) have made estimates of both linear and non-linear genetic variances, and estimates of the linear or additive portion have been made for a number of traits by numerous workers. Estimates of the heritability ratio (additive genetic variance/total phenotypic variance) have become fairly common in the literature.

Kempthorne and Tandon (1953) have investigated the problem of variable numbers of offspring per parent when heritability is estimated from regression of offspring on parent. Lush (1953) has discussed the hazards and pitfalls in estimating heritabilities. These hazards and pitfalls include sampling errors, biases due to selection of data, discontinuous phenotypic variation, non-linear scales of measurement, highly correlated environments for classes of relatives compared, and non-randomness in the mating systems used.

The early development of practical methods of statistical analysis was characterized, among other things, by the use of planned experiments with a state of complete orthogonality throughout. The methods of analysis of data from such experiments are relatively simple. However, much of the data in animal science, particularly field data, lacks the orthogonality of a planned experiment, and such procedures as the conventional analysis of variance are not adequate. In some cases "missing plot" techniques may suffice. In others, it is necessary to go back to the more general procedures involving least squares and maximum likelihood. Yates (1934) and Hazel (1946) attacked the problems in the analysis of data with different numbers in the subclasses. Henderson (1948, 1949) developed specific methods and computational procedures, and applied them to a particular problem. Harvey (1953b) extended the procedures to include IBM operations on the data wherever feasible.

A number of workers (Dickerson, 1942; Baker _et al._, 1943; Hetzer _et al._, 1944; Knapp _et al._, 1951; Touchberry, 1951) have used variance components to derive genetic variances and covariances, and to estimate heritabilities and genetic correlations. Estimates derived from least squares analyses of data can be used to "correct" the raw data for the effects concerned (Price _et al._, 1953). It should be recognized that such correction of data does not remove _all_ of the variance for a given effect. For example, variance due to linear regression does not account for all of the variability in a factor, and the remaining variance (deviations from regression) stays in the error term in the analysis.

Transformations apparently have not been used widely on animal data, although such use might be appropriate in certain instances. Cummings et al. (1947) used an arc-sine transformation on swine data.

In closing, two aspects of the present status of mathematical procedures should merit comment. First, the increasing availability of high speed computers has lessened the computational burden of multivariate analyses (though not the planning). Second, the status of variance components as a genetic tool is far from static. Lowry (1955) has reviewed the use of variance components rather carefully.

PROCEDURES

A. Preliminary

Collection of Data

The major portion of the data used (3,270 lactation records) was collected earlier by Cranek (1952). In addition, 981 more lactation records were obtained from herd owners early in 1953. Milk and butterfat production, sire, dam, age and date of calving, days milked, etc., for each lactation period were obtained from the herd owner. The data was key punched into standard 80-column IBM cards (one card for each lactation period of each cow). These IBM cards (appropriately designated as "detail" cards) were used in subsequent operations with the data. Although both milk and butterfat production were reported, only the butterfat data were used in analyses by the writer.

Planning the Investigation

Preliminary analyses of a small sample of data suggested that the effects of age, season of calving, and previous calving interval on butterfat production might be correlated. Cranek (1952) found both month of calving and previous calving interval to affect milk and butterfat production. His analyses were based on simple one-way classifications, which ignored the possibilites of correlations among these and other factors affecting production. He made no attempt to correct records for these two factors.

Cranek had used mixed breed age conversion factors on the records of the Red Danish crosses, and there was a possibility that such factors were not entirely appropriate for the breed. Also, a need had arisen for a set of age factors that (1) were based on actual performance of Red Danish cattle at successive ages and (2) could be used to adjust the rapidly accumulating production records on immature cows to "mature equivalents".

There was a possibility that year to year deviations and trends in production had occurred, due to factors such as changes in feeding and management. These deviations and trends, if they existed, could have thrown both random errors and biases into the comparisons between foundation generations and the successive crosses to Red Danish bulls. Further, there was a possibility that more precise comparisons between generations than those made by Cranek could be obtained. Cranek, after correcting the records for age at calving and length of lactation, used the entire remaining error variance to test significance of differences among generation groups. It was possible that the remaining error variance could be reduced still further by correcting the records for effects related to year of calving, month of calving, and previous calving interval. In addition, the error variance after such reduction still would include both additively genetic, non-additively genetic, and environmental components, and only the latter two should be included in the appropriate error term for testing additively genetic differences among generation groups.

In view of the preceding observations (possible correlations among variables, need for age conversion factors, possible yearly trends, and potential increase in precision of the comparisons among the generations), it was decided finally to (a) derive least squares estimates of several non-genetic effects on butterfat production, and (b) make corrections accordingly to the individual lactation records.

The variables included in the least squares analysis were year of calving, month of calving, age at calving, previous calving interval, and length of lactation period. Real producing ability of cows was considered, also, but not included in the least squares equations as solved. Inbreeding was excluded, since the analysis was on an intra-cow basis and the effect of inbreeding therefore should be the same (and hence variance zero) among successive records of the same cow. Year effects were not expected to follow any particular pattern, and so one constant was allowed for each year. The effect of month of calving was expected (based on results in the literature) to be curvilinear, and a quadratic curve of the form $Y = A - bX + cX^2$ was postulated. The effect of age at calving was shown by the earlier workers to be curvilinear. Preliminary investigations by the writer on the data used here indicated that a curve of the form $Y = A + bX - cX^2$ would account for most of the variability due to age. The effects of previous calving interval and of length of lactation both were assumed to be linear. The resulting mathematical model thus contained 12 constants for years (1941 to 1952, inclusive), 2 quadratic regressions (four terms), and 2 linear regressions, and necessitated a set of 18 equations in 18 unknowns.

The mathematical model assumed was:

$$Y_{ij} = \mu + a_i + b_j + d_1M + d_2M^2 + d_3A + d_4A^2 + d_5K + d_6L + e,$$

in which Y_{ij} is the record of the <u>ith</u> cow calving in month <u>M</u> of the <u>jth</u> year, at age <u>A</u> (in months), with previous calving interval <u>K</u> (in months) and length of lactation period <u>L</u> (in days). The a_i stand for deviations (from the population mean) of real producing ability of individual cows, the b_j for deviations associated with year of calving (and presumably due to causative factors present and operating during these years), and the d's symbolize regression of butterfat yield on the respective variables. μ is the population mean, and *e* is the error or random deviation from this mean.

Preliminary Operations on the Data

Of the 9,572 IBM detail cards originally at hand, only 4,251 were suitable for the analysis. The rest were set aside because of no milk or butterfat data, records shorter than 200 or longer than 365 days, obviously incomplete or sub-normal lactations, and miscellaneous discrepancies. Further, 881 single-record cards (cows with only single records available) among the 4,251 were not used in the least squares analysis, since they would drop out automatically in the process of obtaining the 18 intra-cow equations. Similarly, 1,069 of the 3,370 cards (4,251 minus 881) had no previous calving interval. Therefore only 2,301 detail (or individual lactation) cards were used in the least squares analysis.

B. Least Squares Solution for Non-genetic Effects

Nature and Properties of Least Squares Estimates

The nature of least squares procedure is such that the error or residual sum of squares (that which remains after removing the sums of squares due to the specified parameters from the total sum of squares) is minimized. The formal procedure is to (1) develop the error equation from the mathematical model, (2) take a partial derivative of the error equation with respect to each variable in turn, (3) set all partial derivatives equal to zero, and (4) solve the resulting set of equations simultaneously for the unknown parameters.

The properties of least squares estimates are such that (Henderson, 1948):

1. Estimates of the parameters are unbiased.
2. Sampling errors for the several parameters are (in effect) minimized.
3. Estimates of the parameters are independent of the distribution of the errors.
4. If the errors are assumed to be distributed normally, tests of hypotheses can be made.
5. Computations are always possible (barring cases of inconsistency and dependency, e.g., denominator of the determinant not equal to zero).
6. Maximum information is obtained from the data. This is a consequence of minimizing the sampling and other experimental errors, the amount of information obtained being inversely proportional to the size of these errors.

If the several parameters in a least squares estimate are correlated, the components of variance due to their interactions should be estimated, since otherwise the error term may be improperly increased in size. However, the above-mentioned properties will be true, regardless, and failure to estimate interaction effects will only render tests of significance less sensitive than they should have been.

Calculation of Terms for the Equations

In practice, the formal derivation of the least squares equations is not actually done. Instead, the appropriate equations are set up directly, and the needed sums of squares and cross products are computed from the raw data. The procedure used in this investigation follows the example by Harvey (1953b) and the methods developed by Henderson (1948). Table 1 shows coefficients for the original equations, i.e., the overall sums, sums of squares, and sums of cross products, uncorrected for the mean. Since the matrix is symmetrical, the coefficients below the diagonal will be correspondingly the same as those above. For instance, $L_{i.}$ will be the term for the lower left hand corner as well as the upper right hand corner. The zeros in cells containing the diagonal terms denote that all coefficients off the principal diagonal within these cells are zero. Symbolically, $b_j b_{j'} = 0$ when $j \neq j'$. Note that the numbers of equations are very large for $\mu + a_i$, several for b_j, and only one for each regression coefficient. A dot in a subscript denotes summation over that factor.

These original equations actually were never set up, since more than 1,100 equations would have been necessary and the resulting computational load would have been truly formidable. Instead, a reduced set of equations (Table 2) was computed by the use of reduction formulas. (See examples immediately below.) These formulas actually obtain an intra-cow matrix, and the second terms of the right-hand members will be recognized as correction factors for obtaining intra-cow sums of squares and cross products. For example,

Table 1. Coefficients in the original equations.

Equations	$\mu + a_i$	b_j	d_1	d_2	d_3	d_4	d_5	d_6	Sums
$\mu + a_i$	${}_0 n_{i\cdot}{}^0$	n_{ij}	$M_{i\cdot}$	$M_{i\cdot}^2$	$A_{i\cdot}$	$A_{i\cdot}^2$	$K_{i\cdot}$	$L_{i\cdot}$	$Y_{i\cdot}$
b_j		${}_0 n_{\cdot j}{}^0$	$M_{\cdot j}$	$M_{\cdot j}^2$	$A_{\cdot j}$	$A_{\cdot j}^2$	$K_{\cdot j}$	$L_{\cdot j}$	$Y_{\cdot j}$
d_1			$\sum_{ij} M_{ij}^2$	$\sum_{ij} M_{ij}^3$	$\sum_{ij} (MA)_{ij}$	$\sum_{ij} (MA^2)_{ij}$	$\sum_{ij} (MK)_{ij}$	$\sum_{ij} (ML)_{ij}$	$\sum_{ij} (MY)_{ij}$
d_2				$\sum_{ij} M_{ij}^4$	$\sum_{ij} (M^2A)_{ij}$	$\sum_{ij} (M^2A^2)_{ij}$	$\sum_{ij} (M^2K)_{ij}$	$\sum_{ij} (M^2L)_{ij}$	$\sum_{ij} (M^2Y)_{ij}$
d_3					$\sum_{ij} A_{ij}^2$	$\sum_{ij} A_{ij}^3$	$\sum_{ij} (AK)_{ij}$	$\sum_{ij} (AL)_{ij}$	$\sum_{ij} (AY)_{ij}$
d_4						$\sum_{ij} A_{ij}^4$	$\sum_{ij} (A^2K)_{ij}$	$\sum_{ij} (A^2L)_{ij}$	$\sum_{ij} (A^2Y)_{ij}$
d_5							$\sum_{ij} K_{ij}^2$	$\sum_{ij} (KL)_{ij}$	$\sum_{ij} (KY)_{ij}$
d_6								$\sum_{ij} L_{ij}^2$	$\sum_{ij} (LY)_{ij}$

Note: A pair of zeros in corners of a cell indicates that all elements off the diagonal in that cell are zero.

Table 2. Coefficients in the reduced equations ($\mu + a_i$ eliminated).

Equations	b_j	d_1	d_2	d_3	d_4	d_5	d_6	Sums
b_j	$C(b_jb_j)$	$C(b_jd_1)$	$C(b_jd_2)$	$C(b_jd_3)$	$C(b_jd_4)$	$C(b_jd_5)$	$C(b_jd_6)$	$S(b_j)$
d_1		$C(d_1)$	$C(d_1d_2)$	$C(d_1d_3)$	$C(d_1d_4)$	$C(d_1d_5)$	$C(d_1d_6)$	$S(d_1)$
d_2			$C(d_2)$	$C(d_2d_3)$	$C(d_2d_4)$	$C(d_2d_5)$	$C(d_2d_6)$	$S(d_2)$
d_3				$C(d_3)$	$C(d_3d_4)$	$C(d_3d_5)$	$C(d_3d_6)$	$S(d_3)$
d_4					$C(d_4)$	$C(d_4d_5)$	$C(d_4d_6)$	$S(d_4)$
d_5						$C(d_5)$	$C(d_5d_6)$	$S(d_5)$
d_6							$C(d_6)$	$S(d_6)$

$$
\begin{aligned}
C(b_j b_j) &= n_{.j} - \sum_i n_{ij}^2 / n_{i.} \quad , \\
C(b_j b_{j'})_{j \neq j'} &= \phantom{n_{.j}} - \sum_i n_{ij} n_{ij'} / n_{i.} \quad , \\
C(b_j d_1) &= M_{.j} - \sum_i n_{ij} M_{i.} / n_{i.} \quad , \\
C(b_j d_2) &= M_{.j}^2 - \sum_i n_{ij} M_{i.}^2 / n_{i.} \quad , \\
S(b_j) &= Y_{.j} - \sum_i n_{ij} Y_{i.} / n_{i.} \quad , \\
C(d_1) &= \sum_{ij} M_{ij}^2 - \sum_i (M_{i.})^2 / n_{i.} \quad , \\
C(d_1 d_2) &= \sum_{ij} M_{ij}^3 - \sum_i (M_{i.} M_{i.}^2) / n_{i.} \quad , \\
S(d_1) &= \sum_{ij} M_{ij} Y_{ij} - \sum_i (M_{i.} Y_{i.}) / n_{i.} \quad .
\end{aligned}
$$

In the first equation, $C(b_j b_j)$ is the reduced term (or equivalent to an intra-cow sum of squares), $n_{.j}$ is the original term (analogous to an uncorrected sum of squares), and $\sum_i n_{ij}^2 / n_{i.}$ is the correction factor. Equations for the remaining coefficients of the reduced equations are similar to these examples.

By the use of the reduced equations, not only were μ and the a_i eliminated, but also the number of equations was reduced to 18. Since the b_j equations were not independent, it was necessary to assume $\sum_j b_j = 0$ and subtract the coefficient of b_{12} in each equation from the coefficient of each of the other b_j terms, after which both the b_{12} row and column of the matrix were deleted. Thus only a 17 x 17 matrix was left to solve.

It may be well to note carefully the broader significance and import of the method described above. While the primary objective was to reduce the number of equations so that a solution would be feasible, the procedure actually led to an intra-cow matrix of variances and covariances. It is possible, in like manner, to compute other reduced matrices, e.g., intra-sire, and from their solutions to secure estimates of genetic variances and covariances.

Solution of the Equations

Numerous procedures for solving equations are described in the literature. The abbreviated Doolittle method (Doolittle, 1878; Dwyer, 1941) was selected for this particular problem, since the inverse matrix which appears during the solution was needed to calculate appropriate error terms for testing significance of the estimated parameters.

The error mean square (Table 4) was obtained by subtracting from the total sum of squares (corrected for the mean) the sums of squares due to fitting constants for years and regression coefficients for the other variables, and dividing the remainder by 2,283 degrees of freedom. The square root of the product of the error mean square and the appropriate diagonal elements of the inverse matrix gave standard errors for the various constants and regression coefficients.

C. Correcting the Data for Non-genetic Effects

Development of Correction Factors

Estimates of the various parameters obtained in the least squares solution (Table 3) were used to develop additive correction factors for adjusting the original butterfat records. The general procedure was to (a) find the mean for a given variable, (b) calculate the expected average deviation in butterfat yield for each class or level of the variable, and (c) reverse the sign of the deviation. Correction factors developed and used on the butterfat data are shown in Tables 5, 6, 7, and 8.

Table 3. Estimates of parameters obtained from least squares analysis.

Parameter	Numerical value	Standard error	t-ratio
Year of calving:			
Linear (all years)	6.49	2.35	2.76**
1941	15.576	14.971	1.040
1942	-5.041	13.044	0.386
1943	18.434	11.146	1.654
1944	30.577	10.210	2.995**
1945	-0.096	8.889	0.0108
1946	4.303	7.403	0.581
1947	-3.927	5.752	0.683
1948	10.545	4.266	2.472*
1949	41.024	3.385	12.119**
1950	75.881	3.302	22.980**
1951	85.323	3.440	24.803**
Month of calving:			
Linear	-0.770	2.917	0.264
Quadratic	0.009	0.220	0.0004
Age at calving:			
Linear	10.012	0.341	29.361**
Quadratic	-0.067	0.0022	30.455*
Previous calving interval:			
Linear	1.955	0.383	5.104**
Length of lactation:			
Linear	0.994	0.0374	26.578**

*Significant at 5 per cent probability level.
**Significant at 1 per cent probability level.

Table 4. Mean squares for parameters included in least squares analysis.

Parameter	Degrees of freedom	Mean square
Years	11	5,384
Month of calving (linear & quadratic)	2	1,217
Age at calving (linear & quadratic)	2	406,390
Previous calving interval (linear)	1	14,039
Length of lactation period (linear)	1	520,408
Residual or error term	2,283	757

Table 5. Correction factors for year of calving.

Year of calving	Correction to butterfat lactation record of individual cow (lb.)
1941	32
1942	26
1943	19
1944	13
1945	6
1946	0
1947	- 6
1948	-13
1949	-19
1950	-26
1951	-32
1952	-39

Table 6. Correction factors for butterfat yield according to age at calving, based on the equation $\hat{Y} = \bar{Y} + 10.012(X - \bar{X}) - 0.067(X^2 - \bar{X}^2)$.

Age	Corr.	Age	Corr.	Age	Corr.
mo.	lb.	mo.	lb.	mo.	lb.
18	208	48	40	78	-7
19	200	49	37	79	-6
20	193	50	33	80	-6
21	186	51	30	81	-5
22	178	52	27	82	-4
23	171	53	24	83	-3
24	165	54	21	84	-2
25	158	55	18	85	0
26	151	56	16	86	1
27	145	57	13	87	2
28	139	58	11	88	4
29	132	59	9	89	6
30	126	60	7	90	8
31	120	61	5	91	10
32	114	62	3	92	12
33	109	63	2	93	15
34	103	64	0	94	17
35	98	65	-2	95	20
36	93	66	-3	96	23
37	88	67	-4		
38	82	68	-5		
39	76	69	-5		
40	73	70	-6		
41	68	71	-7		
42	64	72	-7		
43	59	73	-7		
44	55	74	-8		
45	51	75	-8		
46	48	76	-8		
47	44	77	-7		

Note: For ages past 96 months, add 3 pounds for each additional month.

Table 7. Correction factors for butterfat yield for length of lactation period (number of days milked).

Number of days milked	Correction (lb.)
200	92
.	.
.	.
.	.
250	42
.	.
.	.
.	.
291	1
292	0
293	-1
.	.
.	.
.	.
300	-8
.	.
.	.
.	.
365	-73

Note: Intermediate values (indicated by dots) varied by 0.994 pounds of butterfat for each day of difference in length of lactation period. Actual values used in correcting records were taken to the nearest whole pound.

Table 8. Correction factors for butterfat yield for length of previous calving interval.

Previous calving interval	Predicted deviation in butterfat production	Correction to butterfat lactation record of individual cow
mo.	lb.	lb.
9	-3.634	4
10	-2.640	3
11	-1.646	2
12	-0.652	1
12.7	0	0
13	0.342	0
14	1.336	-1
15	2.330	-2
16	3.324	-3
17	4.318	-4
18	5.312	-5

Note: For calving intervals longer than 18 months, a correction factor of -5 pounds was used uniformly.

Only the linear trend for year of calving (Table 3) was used. The estimate of the effect of month of calving on butterfat yield was not significant (Table 3) and consequently no correction factors were developed for this variable. The corrections for age at calving, unlike those commonly used, were additive rather than multiplicative and further based on mean age at calving (64 months) rather than the age (74 months) at which production reached a peak.

A convenient example of the computations is afforded by the factors for previous calving interval (Table 8). The mean interval was 12.7 months. The regression of butterfat yield on previous calving interval was 1.955 pounds per month. Therefore the correction factor (to the nearest whole pound) for 12 months was +1 pound, for 13 months 0, for 14 months -1 pound, etc.

Procedure for Correcting the Butterfat Data

The detail cards were sorted into classes for one variable at a time, and the appropriate correction factors for that variable were gang punched into the detail cards. Then the original butterfat values were corrected by adding algebraically the correction factors punched in each card. An intermediate value, corrected only for year of calving, previous calving interval, and length of lactation, was punched in each detail card. These intermediate values were used in calculating age correction factors. The final fully corrected value punched in each card was used variously, as will be seen later.

Estimated Producing Ability of Each Cow

The mean or average of all fully corrected butterfat records of each cow was taken as the best estimate of her producing ability. A summary card was punched for each cow (Table 25, Appendix). This card showed number of lactation records, and both total and average butterfat yield. The average butterfat record of each cow was used in calculating heritability and in making comparisons among generation groups. Individual lactation records were used in calculating repeatability of butterfat production and in the development of age correction factors.

D. Heritability and Repeatability of Butterfat Production

An estimate of the heritability of butterfat production (Table 10) was needed in connection with comparisons among generations and estimates of genetic progress. The method chosen was that of intra-sire regression of daughter on dam (Lush, 1940). This method was used because (a) no bias should result from selection among dams (Eisenhart, 1939), (b) the errors inherent in this method are probably smaller than in the half-sib correlation method, and (c) an appropriate standard error of the regression is not difficult to calculate. The average butterfat records of 413 daughter-dam pairs, in the first-cross and foundation generations respectively, were used to estimate heritability of butterfat production. The initial estimate of 0.56, based on cow averages, was reduced to a single-record basis and a value of 0.39 by use of the formula reported by Laben and Herman (1950).

An estimate of the repeatability of butterfat production was needed in adjusting the heritability value to a single-record basis. This was obtained by use of 744 records on 237 cows in the first-cross generation. The computational procedure should be evident from Table 9.

Table 9. Estimation of repeatability of butterfat yield.

Source of variation	Degrees of freedom	Mean square	Expectation of mean square
Total	743		
Between cows	236	1,026	$\sigma^2 + 3.72\ \sigma_c^2$
Within cows	507	272	σ^2

$$\sigma_c^2 = (1{,}026 - 272)/\ 3.72 = 203$$

$$\text{Repeatability} = \frac{203}{203 + 272} = 0.4274$$

Table 10. Estimation of heritability of butterfat yield.

Item	Daughters[a]	Dams	Covariance
Overall uncorrected S. S. & S. C. P.	62,171,123	58,314,428	58,911,145
Correction factors	60,730,749	56,263,076	58,333,750
Intra-sire corrected S. S. & S. C. P.	1,440,374	2,051,352	577,395

$$\bar{H} = 2\left(\frac{577{,}395}{2{,}051{,}352}\right) = 0.56294 = \text{heritability based on average records.}$$

Applying the formula by Laben and Herman (1950):

$$H = \bar{H}\left(r + \frac{1 - r}{\bar{d}}\right) = 0.56294\left(0.4274 + \frac{1 - 0.4274}{2.1036}\right)$$

$$= 0.3938 \pm 0.1129$$

H = single-record heritability.

r = repeatability.

$\bar{d}$ = average number of records for the dams.

[a] Daughters by 31 sires.

E. Comparisons of Foundation Generations with Successive Crosses to Red Danish Sires

Methods and Assumptions

The method of Dickerson and Hazel (1944) for estimating genetic shifts from generation to generation (and hence genetic progress) requires that the selection differential, in terms of phenotypic superiority, be known for both sexes in each parental generation. Since this information for the Red Danish bulls was not known, the method could not be used here. Instead, direct comparisons were made between foundation groups and the first-, second-, and third-cross generations of Red Danish females, both between groups as a whole and between daughters and dams.

In making these comparisons between generations, it was assumed that:

1. The phenotypic mean of each group is an unbiased estimate of the genetic mean. (This assumption implies the absence of bias due to selection.)
2. The errors e_{ij} are normally distributed with mean zero and variance σ_e^2.
3. The variance σ_e^2 is divisible into an additively genetic portion σ_G^2, a portion σ_c^2 containing non-additively genetic and permanent environmental effects, and a temporary environmental portion σ_E^2.
4. The variance σ_e^2 is equivalent (for all practical purposes) to the phenotypic variance σ_p^2.
5. The major part of the variation in temporary environmental factors was removed by corrections to the data, and the remainder

affects the data randomly.

If the phenotypic mean of several performances of the same individual is considered to be the best estimate of its genetic merit, and if the error variance of a single performance is equal to σ_P^2 minus σ_G^2 (Robertson, 1955), the error variance of the mean of several performances becomes some specific function of σ_P^2 minus σ_G^2. The appropriate error variance for the mean performance of a group of individuals may be expressed in similar manner, with due consideration for the average number of phenotypic performances per individual and the number of individuals in the group. Thus it is feasible to compute a genetic standard error for each group mean, and also for the difference between any two group means. The latter standard error may be used, as in the present instance, for testing the genetic significance of differences between average butterfat yields in successive generations of cows.

The actual procedure used in this investigation for derivation of a genetic standard error for a group mean may be shown by an example. Assume that we have a group of 25 cows with an average of 2 butterfat records apiece. The error variance of 757 (Table 4) obtained in the least squares analysis represents the intra-cow portion of the total variance of a single record. It also corresponds to the term E in the repeatability ratio C/(C + E), in which C represents the variance <u>between</u> cows and E the variance <u>within</u> cows. Since a numerical value of 0.43 for repeatability of butterfat production already has been calculated (Table 9), we can divide 757 by (1 - 0.43) and obtain 1,323 as an estimate of C + E. The latter value is an estimate, also, of the phenotypic variance of a single record which remains after making corrections for year of calving, age at calving, length of previous calving interval, and length of lactation. Multiplying 1,323 by the heritability estimate of 0.39, we obtain 521 as an estimate of σ_G^2. The proper error variance of a single record by one cow thus becomes 1,323 minus 521 or 802. This error variance is assumed to include both the temporary environmental component σ_E^2 and the component which contains the nonadditively genetic and permanent environmental variance σ_C^2. The latter may be considered equal to 802 minus 757 or 45, the former to the within-cow variance of 757.

If a cow has two or more records, the σ_E^2 component (757) is reduced accordingly (Lush, 1945), whereas σ_C^2 remains unchanged. Therefore the error variance for the average butterfat yield of a cow with two records becomes $\sigma_C^2 + \frac{1}{2}\sigma_E^2$, or 423. For 25 cows with 2 records apiece, both terms are reduced, and the error variance for the group mean becomes $1/25\,\sigma_C^2 + 1/50\,\sigma_E^2$, or 18. Finally, the standard error for testing the difference between the average butterfat yields of two 25-cow groups with 2 records per cow will be the square root of 36, or 6 pounds. The usual t-test, of course, is applicable here.

The same standard errors, as outlined above, are applicable to both related and unrelated groups. The additively genetic variance among daughter-dam pairs, for example, is reduced to $3/4\,\sigma_G^2$, but the non-additively genetic variance remains the same (or very nearly so) and the environmental variance may be expected not to differ. Since the additively genetic variance was excluded from the error variance, the appropriate error terms were presumed (for practical purposes) to be the same for daughter-dam comparisons as for unrelated groups. Thus only one set of standard errors was used (in this investigation) for testing group differences.

F. Calculation of Age Correction Factors

Gross Factors

Total butterfat yields were listed for each age group (by years and months of age), without regard to individual cows but with the number of lactation records that fell in each age group. Mean butterfat yield was calculated for each age group, and a smooth curve was fitted to the array of means (Table 11). Then, taking the high point of the curve as 100, relative production at each age interval was calculated. Finally, the reciprocals of the relative production values were obtained (Table 12). These reciprocals were the multiplicative age correction factors desired.

Paired Factors

These were derived in much the same manner as the gross factors, except that comparisons were made between first and second, second and third, etc., lactations of the same cows. The increments were used to set up a series of mean butterfat yields for different ages, and from these mean values appropriate curves were derived (Tables 11, 12).

Regression Factors

Intra-cow sums of squares, cross products, and terms of higher orders were computed, much as in setting up the least squares equations, except that records corrected for every variable except age at calving were used. The pairs of equations which resulted were easily solved. (In this particular problem, the means of both the dependent and

Table 11. Changes in butterfat yield with relation to age at calving.

Generation	No. of records	Formula for curve ($\hat{Y} =$)	Method of calculation
First cross	1,730	$261 + 3.12\ A - 0.0225\ A^2$	Gross
First cross	838	$293 + 2.65\ A - 0.0255\ A^2$	Paired lactations
First cross	1,253	$319 + 3.85(A-\bar{A}) - 0.0238(A^2-\bar{A}^2)$	Regression, intra-cow
Second cross	368	$308 + 4.18\ A - 0.0903\ A^2 + 0.0008350\ A^3$	Paired lactations
Second cross	643	$315 + 6.40(A-\bar{A}) - 0.0438(A^2-\bar{A}^2)$	Regression, intra-cow

Table 12. Multiplicative age correction factors, based on formulas in Table 11.

	First-cross generation			Second-cross gen.		
Age mo.	Gross	Paired	Regression	Paired	Regression	B. D. I.[a]
24	1.37	1.28	1.31	1.44	1.43	1.31
36	1.22	1.16	1.16	1.22	1.21	1.18
48	1.12	1.08	1.08	1.12	1.08	1.08
60	1.06	1.03	1.03	1.07	1.02	1.02
72	1.02	1.00	1.01	1.04	1.00	1.00
84	1.00	1.00	1.00	1.00	1.01	1.00
96	1.00	1.02	1.01	b	b	1.00

[a]Bureau of Dairy Industry factors (Kendrick, 1953) for Holstein and Red Dane.

[b]No records available (from data used in investigation) for this age.

Table 13. Analysis of variance of changes in butterfat yield with relation to age at calving.

Generation and method	Source of variation	Degrees of freedom	Mean square
First cross:			
Gross	Linear	1	1,609,070**
	Quadratic	1	193,346
	Residual	1,727	108,050
Paired	Linear	1	465,699**
	Quadratic	1	7,097
	Residual	835	5,988
Regression	Linear	1	336,277**
	Quadratic	1	157,650**
	Residual	845	2,212
Second cross:			
Paired	Linear	1	238,125**
	Quadratic	1	12,926
	Cubic	1	979
	Residual	364	3,683
Regression	Linear	1	351,779**
	Quadratic	1	87,990**
	Residual	405	2,366

**Significant at 1 per cent probability level.

independent variables were used as origins, and therefore only two equations were needed to solve for two unknowns, namely the linear and quadratic coefficients.) The construction of curves (Table 11) and the development of the correction factors (Table 12) were similar to procedures for the gross and paired factors.

G. Repeatability of Environmental Factors; Correlations among Factors

Incidental to the setting up of an intra-cow matrix for the least squares analysis, opportunity was afforded to estimate repeatabilities of month of calving (Table 14), length of calving interval (Table 15), and length of lactation (Table 16), and to develop simple correlations among these variables and age at calving (Table 17). Repeatabilities were estimated by the same method used for butterfat production. The correlations were estimated on an intra-cow basis.

H. Selection in the Various Generations

The comparison of cows in succeeding generations made possible certain estimates of selection (Table 18), since not all dams in a given generation had daughters. The phenotypic difference between mean butterfat yields for all dams and those dams having daughters can be interpreted as a selection differential. Such a differential, when multiplied by the heritability ratio, gives an estimate of the additively genetic superiority of the selected dams.

The calculation of paired age correction factors gave opportunity for estimates of selection, within generations, from lactation to lactation (Table 19). Not all the cows completing first lactations

Table 14. Repeatability of month of calving.

Source of variation	Degrees of freedom	Mean square	Expectation of mean square
Total	2,300		
Between cows	1,117	20.642	$\sigma^2 + 2.806\,\sigma_c^2$
Within cows	1,183	7.740	σ^2

$$\sigma_c^2 = (20.642 - 7.740)/\ 2.806 = 4.598$$

$$\text{Repeatability} = \frac{4.598}{4.598 + 7.740} = 0.3727$$

Table 15. Repeatability of length of calving interval.

Source of variation	Degrees of freedom	Mean square	Expectation of mean square
Total	2,300		
Between cows	1,117	5.707	$\sigma^2 + 2.806\,\sigma_c^2$
Within cows	1,183	4.517	σ^2

$$\sigma_c^2 = (5.707 - 4.517)/\ 2.806 = 0.424$$

$$\text{Repeatability} = \frac{0.424}{0.424 + 4.517} = 0.0858$$

Table 16. Repeatability of length of lactation.

Source of variation	Degrees of freedom	Mean square	Expectation of mean square
Total	2,300		
Between cows	1,117	777.864	$\sigma^2 + 2.806\,\sigma_c^2$
Within cows	1,183	484.991	σ^2

$$\sigma_c^2 = (777.864 - 484.991)/\ 2.806 = 104.376$$

$$\text{Repeatability} = \frac{104.376}{104.376 + 484.991} = 0.1771$$

Table 17. Simple intra-cow correlations among month of calving, age at calving, previous calving interval, and length of lactation.

	Age at calving	Previous calving interval	Length of lactation
Month of calving	0.0143	-0.0034	0.0567
Age at calving		0.0685*	0.0618
Previous calving interval			-0.0332

*Significant at 5 per cent probability level.

Table 18. Overall selection[a] in each generation, based on fully corrected butterfat records.

Generation	Selection differential[b]	Estimated additively genetic superiority[c]
	lb.	lb.
Guernsey foundation	+ 20	+ 7.9
Holstein foundation	+ 9	+ 3.5
Milking Shorthorn foundation	+ 13	+ 5.1
Jersey foundation	0	0
Brown Swiss foundation	+ 11	+ 4.3
Mixed breed foundation	+ 34	+13.4
All foundation groups	+ 16	+ 6.3
First cross	- 1	- 0.4

[a]Based on comparison of all cows with cows having daughters in next generation.

[b]Difference between mean of cows having daughters in next generation and all cows in the generation considered.

[c]Selection differential times heritability ratio (0.39).

Table 19. Selection from lactation to lactation, based on actual uncorrected butterfat records.

Lactation	Per cent culled[a]	Selection differential[b]	Estimated additively genetic superiority[c]
		lb.	lb.
A. First-cross generation			
First	39	+ 4	+ 1.6
Second	22	0	0
Third	12	+ 1	+ 0.4
Fourth	10	+ 5	+ 2.0
Fifth	8	+ 1	+ 0.4
Sixth	3	0	0
Seventh	4	+10	+ 3.9
Eighth	1	0	0
B. Second-cross generation			
First	37	+ 10	+ 3.9
Second	32	+ 3	+ 5.1
Third	17	+10	+ 3.9
Fourth	9	- 8	- 3.2
Fifth	3	- 9	- 3.5

[a]Percentages based on original number completing first lactation.

[b]Difference between mean of cows retained for following lactation and mean of all cows completing current lactation.

[c]Selection differential times heritability ratio (0.39).

remained for seconds, and similarly for second and later lactations. Thus rates and differentials of selection could be estimated.

RESULTS AND DISCUSSION

A. Effects of Environmental Factors on Butterfat Production

Estimates from Least Squares Analysis

The various constants and regression coefficients are shown in Table 3. The rather large deviations of the constants for years are similar in magnitude to those observed by Harvey (1953a), Dillon et al. (1955), and the Iowa workers (1952). The linear environmental trend of +6.5 pounds of butterfat per year (equal to 162 pounds FCM) is much greater than the 53 pounds FCM reported from the Illinois investigation (Dillon et al., 1955). Cranek (1952) observed a small phenotypic increase in butterfat production (about 2 pounds a year) but did not attempt to evaluate environmental and genetic trends.

The non-significance of effect of month of calving on butterfat production is not surprising. Cranek observed that month of calving accounted for only 1.9 per cent and 2.4 per cent of the variances in milk and butterfat yields, respectively. Although the overall differences (in his results) were highly significant, he found that differences between some consecutive months were not significant. Note that the analysis by Cranek was made on a single-classification basis, whereas that by the writer was made jointly with other variables by least squares procedure. This difference in procedure may account in some part for the discrepancies in results, both here and elsewhere.

Age at calving was included as a variable in the least squares analysis only for the purpose of obtaining factors to use in correcting the raw data (Table 6). Since the factors represent mean values over several breeds, they are not closely comparable to those derived from records of first- and second-cross generations. Further, the additive nature of the factors rather limits their applicability to the data from which derived.

The effect of previous calving interval on butterfat production (b = 1.955 pounds a month) is much less than the value of approximately 10 pounds a month observed by Cranek (1952) and of 0.23 pound a day by Rennie (1954). Erb and Shaw (1953), using D.H.I.A. records adjusted for previous dry period and days carried calf, reported effects roughly on the order of those by Cranek.

The significant effect of length of lactation (b = 0.994 pounds butterfat per day) was expected. The early production testing practice of milking cows 365 days was popular at one time, the object being to obtain the most milk possible. The relation of 365-day yield to 305-day yield was investigated by Norton (1932), who found the former to be 20 per cent more than the latter. Dickerson (1940) furthered the cause of the 305-day record by reporting that such records were practically independent of the effects of current calving interval. By that time (1940) the "farmer's class" of record was widely used. Only production for the first 305 days of the longer records was reported, while those shorter than 305 days were considered complete lactations and reported for actual number of days milked. The error in thus handling short records becomes apparent when it is noted that the intra-cow (and hence largely environmental) effect is nearly one pound per day of lactation. An unduly short calving interval, for example, could lead to a lactation period of less than 305 days, with correspondingly lowered production.

Interrelations of Environmental Factors; Genetic Aspects

Functionally, the effects of the environmental factors discussed above can be due to a variety of causes. Feeding probably is an important cause of both yearly and seasonal deviations. Management can alter month of calving to some extent, as well as calving interval and length of lactation period. Certain factors may be significantly interrelated in their effects, although only one such case appeared in this investigation (Table 17).

The repeatability value of 0.1771 for length of lactation (Table 16) suggests (but does not establish definitely) a rather low heritability. The repeatability of 0.3727 for month of calving (Table 14) probably does not imply any reasonable degree of heritability, since much managerial control is exerted here. The repeatability of 0.0858 for calving interval (Table 15) is somewhat less than the value of 0.133 found by Legates (1954), and about equal to 0.084 reported by Bettini and Peretti (1954).

Relative Importance of Effects

Mean squares due to fitting constants and regressions for the factors investigated are shown in Table 4. The relatively great effects of age at calving and length of lactation are obvious, and lend ample justification to the use of 305-day age-corrected records. The effect due to previous calving interval, while much smaller, may well be worthy of consideration in some instances. Likewise, the yearly deviations either should be evaluated (as by a linear regression) or bypassed by such devices as intra-year comparisons. In such problems as evaluation of sires by daughter-dam comparison, the year effects deserve ample consideration.

Correction Factors for Environmental Effects

Attention was called earlier to the factors developed and used in this investigation (Tables 5, 6, 7, 8). It is well to note that such factors make effective correction to the raw data for only predicted average effects. It follows that only a major part of the variability due to a given factor is removed; the rest remains in the error term in the analysis of variance.

In some cases it would be preferable to use a within-group analysis rather than over all classifications present. Such a case would exist when (a) inclusion of the additional variable would complicate the analysis greatly and/or (b) the correction factor would be relatively ineffective in reducing variance.

B. Heritability and Repeatability of Butterfat Production

Estimates of these factors are shown in Tables 9 and 10. The value for heritability of 0.39 ± 0.11 is not far from Cranek's estimate of 0.42 ± 0.10. Both estimates are based on daughter-dam pairs from foundation and first-cross generations. Note that the heritability was calculated from cow averages, then reduced to a single-record basis. The final value of 0.39 may be biased upward slightly, since the method of calculation included repeating the dam's record with each daughter's record. Kempthorne and Tandon (1953) have shown an example in which such bias existed.

C. Estimates of Genetic Progress

Assumptions

Six assumptions basic to the comparison of successive generations were made in the section on procedure. One of these specified no bias from selection. The full extent of selection in the foundation generations is unknown, although some effective selection did occur (Table 18). Selection in the first-cross generation did occur, both with respect to dams of second-cross individuals (Table 18) and from lactation to lactation (Table 19), but apparently with little or no effect on phenotypic or genotypic level. The selection among first- and second-cross individuals apparently was aimed at reducing the generation interval and securing third-cross and later individuals as soon as possible, since culling percentages in the early lactations were rather high (Table 19). Asdell (1951) reported culling rates of less than 15 per cent after first lactations, although Seath (1940) noted rates of 35.0 per cent and 37.1 per cent in Iowa and Kansas D.H.I.A. herds, respectively.

Differences among Generations

The average butterfat production of each generation group is shown in Tables 20 and 21. Using records on all individuals, there was a very highly significant increase ($P < .001$) (Table 22) from the foundation groups as a whole to the first-cross generation. The same was true for the Guernsey, Milking Shorthorn, Brown Swiss, and mixed breed groups, but not for the Jerseys. The gain from the Holstein foundation group to first cross was significant ($P < .05$). No gain was apparent from first-cross generation to second-cross, but the increase from

Table 20. Average butterfat production in each generation group.
I. Foundation breed groups.

Generation	No. cows	No. rec. per cow	Average butterfat	Standard error
			lb.	lb.
Guernsey foundation				
All cows	236	2.22	339	1.28
Cows with daughters in first cross	107	2.68	359	1.75
Holstein foundation				
All cows	163	2.01	375	1.61
Cows with daughters in first cross	67	2.58	384	2.25
Milking Shorthorn found.				
All cows	178	2.02	333	1.54
Cows with daughters in first cross	65	2.35	346	2.38
Jersey foundation				
All cows	67	2.52	382	2.27
Cows with daughters in first cross	31	3.29	382	2.98
Brown Swiss foundation				
All cows	32	2.50	365	3.30
Cows with daughters in first cross	11	2.82	376	5.33
Mixed breed foundation				
All cows	125	1.79	349	1.93
Cows with daughters in first cross	27	2.07	383	3.90
All foundation cows	801	2.10	351	0.74

Table 21. Average butterfat production in each generation group. II. Crosses to Red Danish bulls.

Generation	No. cows	No. rec. per cow	Average butterfat	Standard error
			lb.	lb.
First cross				
All cows	703	2.22	379	0.74
Cows with Guernsey dams	139	2.17	389	1.68
Cows with Holstein dams	100	2.11	380	2.01
Cows with Milking Shorthorn dams	83	2.19	367	2.17
Cows with Jersey dams	50	2.60	401	2.59
Cows with Brown Swiss dams	13	2.46	358	5.21
Cows with mixed breed dams	32	2.22	390	3.47
Cows with daughters in second cross	212	3.19	378	1.15
Second cross				
All cows	411	1.99	377	1.02
Cows with dams in first cross	308	2.03	378	1.16
Third cross				
All cows	123	1.60	389	2.05

Table 22. Comparison of average butterfat production among generation groups.

Generations compared	Ave. gain or loss	Standard error of difference
	lb.	lb.
Gross basis (over all cows):		
All foundation vs. 1st cross	+ 28	1.03 (P < .001)
Guernsey vs. 1st cross	+ 40	1.48 (P < .001)
Holstein vs. 1st cross	+ 4	1.77 (P < .05)
Milking Shorthorn vs. 1st cross	+ 46	1.70 (P < .001)
Jersey vs. 1st cross	- 3	2.39 (P < .3)
Brown Swiss vs. 1st cross	+ 14	3.38 (P < .001)
Mixed breed vs. 1st cross	+ 30	2.07 (P < .001)
First cross vs. 2nd cross	- 2	1.26 (P < .2)
Second cross vs. 3rd cross	+ 12	2.29 (P < .001)
Daughter-dam basis:		
Guernsey vs. 1st cross	+ 30	2.43 (P < .001)
Holstein vs. 1st cross	- 4	3.01 (P < .2)
Milking Shorthorn vs. 1st cross	+ 21	3.22 (P < .001)
Jersey vs. 1st cross	+ 19	3.95 (P < .001)
Brown Swiss vs. 1st cross	-18	7.45 (P < .02)
Mixed breed vs. 1st cross	+ 7	5.22 (P < .2)
First cross vs. 2nd cross	0	----

second to third cross was very highly significant ($P < .001$).

On a daughter-dam basis, very highly significant increases ($P < .001$) occurred from Guernsey, Milking Shorthorn, and Jersey groups to first cross, and no apparent change from Holstein or mixed breed groups. The first-cross daughters of Brown Swiss foundation dams showed a significant decrease ($P < .02$). No change at all was evident from first- to second-cross generations.

In general, the increases were large from foundation generations to first cross, virtually zero to second cross, and moderately small to third cross. The latter increase (to third cross) may be poorly estimated, since only 123 third-cross females were considered. The nature of these increases cannot be delineated precisely, but may include:

1. Heterosis or hybrid vigor in the first cross.
2. Additive genetic gain over the successive generations, due to superiority of sires used.
3. Small additive genetic gains due to selection among foundation dams (Table 18).

The large increases from foundation generations to first cross are comparable to those secured by Fohrman _et al_. (1954) in the first crossbred generation.

D. Age Correction Factors

Age at calving was shown earlier (Table 4) to be a major source of variability in butterfat production. Therefore, it seemed appropriate to investigate this source of variability in some detail. Accordingly, curves were fitted to the partially corrected data (corrected for year of calving, previous calving interval, and length of lactation). Only records for the first- and second-cross generations were utilized. An attempt was made to fit curves to data from sub-groups of the first-cross generation based on breed of dam, but numbers were too few to give consistent results. Similarly, numbers were too few to fit a reliable curve to data from the third-cross generation.

The formulas for the curves fitted (Table 11) should be self explanatory. The constants (319 and 315) for the regression formulas represent sample means or averages, while the linear and quadratic terms stand for functions of deviations from the means. Constants in the other formulas came from solution of simultaneous equations, as did the numerical coefficients of the regression terms in all formulas. Analyses of variance of the several curves are presented in Table 13, and the final age correction factors in Table 12.

The gross age correction factors probably are biased upward (due to selection from lactation to lactation), and the error or residual mean square is very large. The paired factors probably are biased downward (due to regression of selected individuals back toward the group average in following lactions), but the error mean square is reduced greatly. (Note the very small mean square for the cubic term.) The regression factors also may be expected to be biased downward, but the error mean square is reduced still more and the quadratic term has become highly significant. In addition, the regression factors utilized at least 50 per cent more records (Table 11), and hence more information, than did the paired factors.

Both the paired and regression factors for the first-cross generation agree closely with the B.D.I. factors recommended for Holstein and Red Dane (Kendrick, 1953). However, both the paired and regression factors for the second-cross generation are somewhat higher, especially in the 2- and 3-year age brackets. It is recommended that larger samples (e.g., 1,000 to 2,000 records) be taken for second-cross and later generations, and curves fitted on an intra-cow basis. A regression on year of calving might well be included also, and some correction should be attempted for the expected downward bias due to selection. From the resulting curves it should be possible to construct a satisfactory set of age correction factors for the American Red Danish breed.

E. General

Substantial overall gains resulted from the program of grading up diverse foundation stocks with Red Danish sires. These include (a) genetic gains, (b) increases in production due to improvement in environmental factors, and (c) a unified breed program. The first is evidenced by the increases in production from generation to generation, the second by the upward environmental trend of 6.5 pounds of butterfat a year, and the third by the existence of an active breed association. Possibilities for future gain and improvement include (a) improvement of selection among females and (b) selection and sampling of sires with fullest use of newer knowledge. As shown earlier, selection among females in the first- and second-cross generations was neither uniformly nor always highly effective. This possibly can be improved through increased attention to environmental effects, close relatives, and estimated real producing ability. Selection of sires should be capable of similar improvement.

SUMMARY

Milk and butterfat yields and related information were collected on the foundation generation and on successive back-crosses to Red Danish sires. The relation of certain environmental factors to butterfat production was investigated by a least squares procedure. Butterfat yield did not vary significantly with month of calving, but did vary significantly ($P < .01$) with age at calving, previous calving interval, and length of lactation period. The regression of butterfat yield on age at calving was curvilinear and of the form $Y = \bar{Y} + 10.012(X-\bar{X}) - 0.067(X^2-\bar{X}^2)$, where X is age in months and Y represents butterfat. Yield of butterfat increased at a rate of 1.96 pounds for each additional month of previous calving interval, and 0.99 pound for each additional day of lactation period. Also, butterfat yield exhibited an upward environmental trend of 6.49 pounds per year ($P < .05$).

Additive correction factors were developed from the least squares estimates, and used to adjust the original butterfat records. The foundation generation, using fully adjusted records, averaged 351 pounds butterfat; the first-cross generation, 379; the second, 377; and the third, 389. The increase of 28 pounds from foundation to first-cross generation was very highly significant ($P < .001$), the 2-pound decrease to the next generation was not significant, while the gain of 12 pounds by the third-cross generation was very highly significant ($P < .001$).

Selection in the foundation groups, based on comparison of all cows with those having daughters in the first-cross generation, gave estimated additively genetic superiorities (for those having daughters) of zero to

+13.4 pounds butterfat per lactation period. Selection in the first- and second-cross generations gave estimated additively genetic superiorities of zero to +5.1 pounds butterfat. These latter values are based on the amount of selection practiced from lactation to lactation.

The effect of age at calving on butterfat production was investigated in some detail, and tentative age correction factors were developed for the American Red Danish breed. Factors based on fitting an intra-cow quadratic regression to the data were the most efficient of any developed here, both in making use of more records than in the paired method and in accounting for a larger proportion of the variance than did any other method. Based on comparison of sets of regression factors, the second-cross generation reached peak production at an earlier age than did the first cross. Preliminary evidence was found that the presently recommended Bureau of Dairy Industry factors are too low for the 2- and 3-year age brackets.

Heritability of butterfat yield, using the method of intra-sire regression of daughter on dam, was estimated as 0.39 ± 0.11 on a single record basis. Repeatability of butterfat production was estimated as 0.43. The intra-cow correlation of age at calving with previous calving interval was 0.07 ($P < .05$). Other intra-cow correlations among age at calving, month of calving, and previous calving interval were numerically small and not significant statistically. Repeatabilities of calving interval, month of calving, and length of lactation period were estimated as 0.09, 0.37, and 0.18, respectively. The first and third values suggest rather low genetic determination.

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APPENDIX

IBM Procedures and Operations

Five card layouts were used (Tables 23, 24, 25, 26, and 27). In addition, trailer cards were used to take answers from group and single card operations. Data for the original card layout (Table 23) was key punched from mimeographed forms which had been filled in previously by the owners of the Red Danish cattle. Sources of the data on the remaining cards should be apparent from an examination of Tables 24, 25, 26, and 27.

Machines used include key punch, verifier, sorter, collator, reproducer, multiplier, and tabulator. The availability of a high speed electronic calculator (IBM # 604) greatly facilitated later stages of the investigation.

The procedures used were mostly if not entirely standard. It was found preferable, in obtaining sums of products with the #602A multiplier, to punch individual products in a trailer card after each detail card, then total the answer cards on the tabulator. Machine time was saved by this procedure, as compared to multiplication with summary punching.

Table 23. Original layout of IBM detail or individual lactation cards.

ITEM	COLUMNS (inclusive)
Generation	1-2
Cow number	3-6
Color	7
Inbreeding coefficient of cow	8-10
Herd owner code	11-13
Sire of cow	14-17
Inbreeding coefficient of sire	18-20
Dam of cow	21-24
Inbreeding coefficient of dam	25-27
Lactation number of cow	28-29
Calving date (year, month)	30-33
Age at calving (years, months)	34-37
Previous calving interval (months)	38-39
Times milked daily	40
Length of lactation (days)	41-43
Milk (pounds)	44-48
Butterfat (pounds)	49-51
Conversion factor (age, days milked)	52-54
Mature equivalent milk (pounds)	55-59
Mature equivalent butterfat (pounds)	60-62
Percentage of butterfat	63-64
Disposal of cow	65-66
Remarks each lactation	67-68
Sex of calf	69
Calf born alive or dead	70
Defect (of calf)	71-72
Color of calf	73
Sire of calf	74-77

Table 24. Revised layout of IBM detail or individual lactation cards (blue-edged).

ITEM	COLUMNS (inclusive)	SOURCE
Generation	1-2	(1)
Cow number	3-6	(1)
Inbreeding coefficient	7-9	(1)
Herd owner code	10-12	(1)
Sire of cow	13-16	(1)
Dam of cow	17-20	(1)
Lactation number	21-22	(1)
Year of calving	23-24	(1)
Month of calving	25-26	(1)
Age at calving (years, months)	27-30	(1)
Age at calving (months)	31-33	(2)
Previous calving interval (months)	34-35	(1)
Length of lactation (days)	36-38	(1)
Milk (pounds)	39-43	(1)
Butterfat (pounds)	44-46	(1)
(25-26) squared	47-49	(2)
(31-33) squared	50-54	(2)
Correction for year of calving	55-56	(3)
Correction for previous calving int.	57	(3)
Correction for length of lactation	58-59	(3)
Correction for age at calving	60-62	(3)
(44-46) (55-56 (57) (58-59)	63-65	(4)
(63-65) (60-62)	66-68	(4)

(1) Reproduced from original detail cards (Table 23).
(2) Calculated by #602A IBM multiplier.
(3) Gang punched from master cards. Negative values were indicated by X-punching.
(4) Calculated by #604 IBM multiplier, with sign control for positive and negative correction values.

Table 25. Layout of IBM cow summary cards (green-edged) used in least squares analysis.

ITEM		COLUMNS (inclusive)	SOURCE
Generation		1-2	(1)
Cow number		3-6	(1)
Card count (number of records)		7-8	(2)
Number of calvings per year:			
	1941	9	
	1942	10	
	.	.	(3)
	.	.	
	.	.	
	1952	20	
Sum of (Month of calving)		21-23	(4)
Sum of (Month of calving)^2		24-27	(4)
Sum of (Age at calving)		28-31	(4)
Sum of (Age at calving)^2		32-37	(4)
Sum of previous calving interval		38-40	(4)
Sum of length of lactation		41-44	(4)
Sum of butterfat		45-48	(4)

(1) Reproduced from detail cards.
(2) Count of detail cards.
(3) Selectively punched from detail cards.
(4) Accumulated from corresponding columns in detail cards.

Table 26. Layout of IBM cow summary cards used in comparing generations and in estimating heritability and repeatability of butterfat production.

ITEM	COLUMNS (inclusive)	SOURCE
Generation of cow	1-2	(1)
Cow number	3-6	(1)
Inbreeding coefficient of cow	7-9	(1)
Herd owner	10-12	(1)
Sire of cow	13-16	(1)
Dam of cow	17-20	(1)
Card count (number of records)	21-22	(2)
Sum of butterfat (corrected)	23-26	(4)
Average butterfat of cow	27-29	(3)
Dam's average butterfat	30-32	(5)
$(27-29)^2$	33-38	(3)
$(30-32)^2$	39-44	(3)
(27-29) x (30-32)	45-50	(3)
Generation of dam	51-52	(6)

(1) Reproduced from detail card.
(2) Count of detail cards.
(3) Calculated by #604 IBM multiplier.
(4) Accumulated from columns 66-68 of detail cards.
(5) Reproduced from columns 27-29 of dam's summary card.
(6) Reproduced from columns 1-2 of dam's summary card.

Table 27. Layout of IBM detail cards used in calculating age correction factors.

ITEM	COLUMNS (inclusive)	SOURCE
Generation of cow	1-2	(1)
Cow number	3-6	(1)
Generation of dam	7-8	(2)
Age at calving (months)	12-14	(3)
Butterfat (corrected except for age)	16-18	(4)
$(12\text{-}14)^2$	19-25	(5)
$(12\text{-}14) \times (12\text{-}14)^2$	26-35	(5)
$(12\text{-}14)^2 \times (12\text{-}14)^2$	37-49	(5)
$(12\text{-}14) \times (16\text{-}18)$	50-55	(5)
$(19\text{-}25) \times (16\text{-}18)$	56-65	(5)
$(16\text{-}18)^2$	66-75	(5)

(1) Reproduced from detail cards.
(2) Gang punched from col. 51-52 of cow summary cards used to compare generations, etc. Punched only for cows in first-cross generation.
(3) Reproduced from col. 31-33 of detail cards (Table 24).
(4) Reproduced from col. 63-65 of detail cards (Table 24).
(5) Calculated by #604 IBM multiplier.

Note: Cow summary cards similar to these were summary punched, with with totals for age at calving, (age at calving)^2, and butterfat. Squares and cross products then were obtained as for the detail cards.