GENETIC AND ENVIRONMENTAL PARAMETERS
OF MILK PROTEIN YIELDS IN HOLSTEINS

by

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ABSTRACT

Milk, fat and protein first lactation records of 27,137 British Columbia Dairy Herd Improvement cows were analysed for gross genetic and environmental influences. The average production was 5,663 kg of milk containing 3.59% fat and 3.23% protein. Age at freshening accounted for 3.0, 3.7, 3.7, 0.28 and 0.15% of the variance in milk, fat, protein, percent fat and percent protein respectively. Cows freshening in the winter had higher average milk, fat and protein yields than those freshening in summer; however, the percentage constituents of both fat and protein were higher for the summer cows than for the winter cows.

Heritability of each characteristic and the phenotypic and genetic correlations between different characteristics were derived from paternal half-sib analyses with 100 sire groups. Heritability values were: milk 0.18; fat 0.24; protein 0.21; % fat 0.38, and % protein 0.47. Within herd-year-season phenotypic correlations between milk yield and the percentages were both negative, whereas the correlation between the constituent percentages was positive. Genetic trends in the cow population averaged 51.5 kg, 2.77 kg, 1.87 kg, 0.015% and -0.049% for milk, fat and protein yields and fat and protein percentages respectively.

The dollar returns from incorporating milk, fat and protein yields and/or the constituent fractions in various selection indices were estimated for different levels of protein payment. Higher dollar returns will be expected from selection based on total yields than from selection based on either fat or protein percentage. Measuring protein for a genetic

program will be feasible only when unrealistically high prices are paid
for protein.

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INTRODUCTION

Many investigations have been carried out on the more important parameters of dairy records. Most authors have, however, confined their work to the estimation of genotypic and environmental parameters of milk and milk fat. The estimates obtained exhibit a rather wide range and suggest that the parameters may vary considerably from one population to another.

Latest trends in consumption patterns and the high prices currently obtainable for non-fat milk products have caused attention to be directed towards the non-fat solids (SNF) of milk. There seems to be adequate justification for this due to apparent consumer interest in the protein content of dairy products. Sales of low fat and fat-free dairy products have increased, indicating a decline in the importance of butterfat. Shute and Yankowsky (1973) estimated that per capita consumption of dairy products in Canada dropped from 207 kg in 1949 to 162 kg in 1971. Particularly notable was the 20% drop in fluid milk consumption from 1960 to 1972. It was suggested that this decline may have been due in part to the apparent concern with cholesterol and saturated fat content in human diets. Consumption of skim milk rose by 11% between 1972 and 1973 while whole milk dropped 2%. Consumption of cheese, yoghurt and ice milk has been increasing.

Milk protein is a high quality protein containing an excellent balance of amino acids for human nutrition. In 1971, about 22% of the protein in diets of the average American came from milk (Graf, 1971). Milk protein is also relatively inexpensive under current marketing practices. Based

on 1973 retail prices in Canada, McFarlane and Fisher (1974) stated that protein in skim milk powder, on a unit weight basis, was cheaper than all other protein sources evaluated in the study. Dry beans, cheddar cheese, egg, fresh milk and meat were all found to be more expensive sources of protein than powdered skim milk. A kilogram of protein from steak was found to be several times more expensive than the same quantity of protein from any of the dairy products. Thus, from a nutritional viewpoint, the decreasing demand for milk fat and increased emphasis on the non-fat fraction suggests that the pricing structure of milk should no longer be based on fat ignoring other constituents such as protein.

Multiple Component Testing and Pricing (MCTP) of milk is now being strongly considered in many dairying countries. Testing for milk protein content started on a large scale in the Netherlands in 1957 (Politiek, 1968) and by 1972 as many as 10,000 protein determinations per day were being made to provide a broader basis of payment (Anonymous, 1972). Since then, Denmark, Poland and Switzerland have followed the Dutch example by paying for both protein and fat content in milk supplied to the cheese industry (Cerbulis and Farrel, 1975). These economic trends and the world protein shortages suggest that future selection goals for dairy cows should include milk protein.

In Finland, the breeding value of bulls for protein content is currently being evaluated through progeny testing. The importance of milk protein has made it necessary to investigate the alternatives of breeding for protein content or protein yields in general (Maijala, 1974). In the United States, Graf (1974) observed that several dairy cooperatives and farm organizations have recently adopted protein pricing while more are

ready to do so. Leuenberger (1976) reported that a protein payment
program has been so successful for Mississippi Valley members that
Scott County Dairy Herd Improvement Association in southeastern Iowa
has started testing for protein in member herds. California already
includes protein in their pricing method.

Protein payment of raw milk is particularly justified from an economic
point of view in cheese and fresh cheese manufacture where the direct
relationship of milk protein content to the conversion rate to cheese is
readily apparent. Compositional quality can have a direct bearing on
price paid by manufacturers, and this is becoming more important as the
proportion of milk used in manufacturing tends to increase. Payment for
milk on the basis of fat content alone would only be satisfactory in a
diversified industry if there were a perfect relationship between fat and
non-fat yields and industrial requirements.

The first decision to be made in devising a scheme for payment is
selection of the milk constituent or constituents on which it is to be
based. In practice, the choice lies between fat, protein, lactose, SNF
and total solids, singly or in combination. Such considerations should be
made from the point of view of market requirements, consumer protection,
animal breeding, economics of production and ease of testing at acceptable
cost. A protein price differential is preferred for a number of reasons.
An abbreviated comparison may be as follows:

1. Protein is the most variable part of the SNF and is the most
valuable nutritionally and industrially. In addition, reliable protein
tests are now available at a relatively low cost.

2. Protein content of milk can be changed more by breeding and

selection programs than other SNF components.

The analysis described in this thesis will document some of the variability associated with protein, as well as fat and milk yields of first lactation Holstein cows.

The protein content of milk will change little unless the price differential offered for increased protein content is large enough to make it profitable. As shown by Tabler and Touchberry (1959) and subsequently verified by other workers (Gaunt, 1973; Van Vleck, 1977), the dairyman benefits more by selecting for increased milk yield than for milk containing a higher percentage of protein. To develop breeding plans to change the composition of milk requires a knowledge of heredity and environmental components of these constituents. To gain information on the effectiveness of selecting for one trait and the concurrent change in other traits, the correlations among traits must be known. Estimates of these parameters will influence to a great extent the choice of future breeding plans.

The purpose of this work is to estimate from field data the genetic and environmental parameters of milk constituents and to determine the probable consequence of selecting for total yields of milk, fat and protein individually or in combined indices.

LITERATURE REVIEW

The sources of variation which affect protein and solid-non-fat (SNF) yields in the milk of normal lactating cows have been established and include breed, stage of lactation, climatic environment and level of nutrition. Protein and SNF, as well as fats, are under genetic control and can be changed through breeding practices. Far more information, however, exists on the fat content than on the SNF content of milk produced by commercial cattle. This may be due to the ease of technology of fat determination and pricing scheme of fluid milk. Selection for compositional quality has thus mainly been based on fat percentage.

Of the two fractions making up the total solid content (SNF and fat), fat is much more variable and under payment systems based on total solids selection for fat content would give greater economic gain than selection for any non-fat constituent. Protein is generally accepted as being the most variable of the SNF components. This has been shown in a recently published study by Herrington et al (1973). Earlier studies with limited data, gave some indications of the genetic variations in the protein content of cows milk (Pontous, 1964; Robertson et al., 1956; Von Krosigh et al., 1960, and Wunder and McGilliard, 1964), and heritability estimates from these studies ranged from .08 to .48. More recently, Armstrong et al (1971), obtained monthly samples over 2 years for SNF and protein content of herds in Canada. The averages and standard deviations were 8.733 ± .336 for SNF and 3.428 ± .247 for protein content. Results of a comparable New York study by Herrington et al (1973) were 12.018 ± .626 for total

solids, 3.530 ± .250 for fat and 3.127 ± .143 for protein. Butcher et al (1967) obtained means and standard deviations of 3.67 ± .29, 3.16 ± .19 and 12.23 ± .45 for percents fat, protein and total solids, respectively.

The possibility of increasing the protein content of milk by breeding requires a knowledge of both gentic and environmental influences on the trait. To increase milk yield or to change milk composition, selection for genetically superior sires and dams must be practiced. Accuracy of genetic selection is improved by adjusting for the environmental factors affecting lactation records. Since total milk yields and total solids percentages are inversely related, improvement in yield is difficult to achieve when the concentration of the solids has to be maintained or improved and since correlations are negative between these, improvement of both yields and percentages cannot be obtained (Barnard et al., 1970).

The nutrition of the cow has been shown to have markedly affected the milk composition. In many areas, cows placed on lush pasture in the spring exhibited increases in SNF content mainly due to increases in the protein percentages (Politiek, 1957) which were attributable to an increase in the plane of nutrition (Rook et al., 1960). Some studies have shown that the forage quality and quantity may affect SNF. The study by Murdrock and Hodgson (1967) showed that high intake of grass silage was associated with a fall in milk yields and SNF. These decreases were largely due to a reduction in energy intake on a high silage ration since when equal dry matter of silage or hay from the same field were fed, reductions in yields and SNF did not occur.

It has been well documented that very little change in milk protein or SNF

can be expected from increasing dietary protein to levels considerably above recommended standards. Typical of such studies was that of Rook and Line (1962) who varied ration protein from 70 to 160% of standard and observed no differences in the SNF or true protein. Alterations of the physical form of the rations have had variable effects on milk SNF. Cornell workers (Bishop et al., 1963, and Loosli et al., 1963) have investigated the effect of pelleting concentrates on milk composition. Their results indicated that pelleting caused little change in milk SNF or protein but may cause a decrease in milk fat at low forage intake.

Seasonal influences on lactation percent fat were reported by Blanchard et al (1966), Gacula et al (1968) and Waite et al (1956). Late summer calving cows had higher lactational average fat tests. Environmental temperature ranges of 10-30°C tended to cause decreases in fat percentage but beyond this range sharp decreases can be expected not only in fat percentage but also in SNF and protein percentages as well.

Age had a significant effect on milk composition with a gradual reduction in percentages as the total yields increased with age (Waite et al., 1956). The effect became more pronounced as cows exceeded their third lactation with SNF decreasing more than fat (Gacula et al., 1968; Sargent et al., 1967). First lactation yield increased with age at calving but within the limits normally encountered in practice (20-36 months), age at first calving did not have a marked effect on either yields of milk, fat or protein or the composition of the milk produced in the first lactation. Such evidence as exists (Barnard et al., 1970) suggests that heifers reared on a very high level of feeding and calving very young may produce appreciably lower total yields in the early lactations compared with their

counterparts calving for the first time at a later age.

The expected genetic gain per generation resulting from selection for a single trait lactation yield of milk is given by the equation

$$\Delta G = i \; h^2_m \; \sigma_m$$

where h^2_m is the heritability of the lactational yield, σ_m is the phenotypic standard deviation and i is the intensity of selection. To make significant genetic changes in future generations, heritabilities of the milk constituent fractions must be considerably above zero and show some variation. Many studies have documented high heritability and repeatability values for milk constituent fractions. However, variances associated with protein yields and percentages are smaller compared with corresponding fat and percent fat values. It is therefore less efficient to select for protein through breeding than in the case of fat, and the progress in breeding for protein percent will be slower than in breeding for total protein yields (Gaunt, 1973).

It is therefore important that Artificial Insemination (A.I.) bulls, which potentially are used as service sires on a large number of cows, be superior for fat and protein potential. Contrary to what would be the ideal situation, Van Vleck (1977) contended that there were not enough bulls high for both milk predicted difference (P.D.) and SNF percentage to make selection effective for both simultaneously. He estimated that about twice as many bulls would have to be sampled to find as many high for both milk and SNF percentages as can be found for milk alone or for SNF alone.

The important question to breeders then is how much emphasis, if any, should be put on selection for protein or SNF percentages. Van Vleck

(1977) suggested that under the current pricing system the answer would be to ignore the percentage values and if the price of protein or SNF became great enough, then selection should be for dollar value and not for direct protein or SNF percentages.

The phenotypic and genetic correlations between milk yield, fat yield and fat percentage have been studied by several workers. The genetic correlation between milk and fat yield has in most cases been found to be close to .7 whereas estimates of the genetic correlation between milk yield and fat percent varied from practically zero (Robertson et al., 1956) to -0.77 (Farthing and Legates, 1957). Systrad (1971) estimated the correlated response of milk yield from selection on fat yield to be about 10 kg per generation for Danish data. Other studies on protein by Barnum et al.(1969), Butcher et al (1967) and Wilcox et al (1971) also suggested that attempts to increase the protein percentage would be an effective method but not as effective as increasing total protein yield.

As observed by Blanchard et al (1966), selection for any of the percentage traits would be expected to decrease milk yield and have comparatively little effect on total yields of SNF, although the percentage composition would be expected to change. Sargent (1970) asserted that selection for SNF percent would inevitably necessitate some sacrifice in total SNF yield and a larger sacrifice in milk yields. Gacula et al (1968) found that selection for milk yield alone generally had a lowering effect on the percentages of milk constituents. Further, it was concluded that if breeding programs were desired for increasing one or more constituents, an index was needed that would not cause depression in yield as a correlated consequence of selecting for constituent percentages.

If selection were based on protein percent alone, there would be a decrease in amount of milk, but fat percent would increase, and vice versa. However, it has to be pointed out that Gacula et al (1968) and other workers, primarily discussed the improvement in the percent of milk constituents while Venge and Christensen (1969) showed that better economic returns may be achieved by using the total amount of milk, fat and/or amount of protein as a criterion for selection. This study will seek to document such findings.

Using their parameter estimates in Holsteins, Butcher et al (1967) examined the direct and correlated responses to selection for milk constituents and concluded that due to the high genetic correlation between milk fat and protein (r = 0.77) and the greater genetic variance of fat percent, larger increases would be obtained by selecting for fat. Von Krosigh (1960) indicated similar results. It appears, therefore, that breeding for fat yields hitherto has also served to increase protein yield, and correspondingly the transition to selection for protein yield would mean no essential alteration in the progress of fat yields. Nevertheless, progress for protein yields will be greater (about 20% more) if selection is directly for it, but the difference is not so large as many would be inclined to believe (Maijala and Vilva, 1976). In fact, selection for milk yield alone would generally result in a correlated increase in protein and SNF yields which are about 90-100% as effective as direct selection for protein.

Indeed, the majority of recent studies concerning protein selection have been based on comparisons between selection for the single milk traits (eg. Bergman, 1971; Systrad, 1971; Wilcox et al., 1971). The results in

general showed that direct selection gave the greatest improvement for the trait in question. However, selection for fat or protein percent would not be profitable, because the indirect improvement in fat and protein quantity would only be relatively small. Furthermore, the cost of demanding replacement of a butterfat test plus selection by a corresponding protein test, seems to be unprofitable because of the high correlation between these two traits and the fact that butterfat will continue to be a valuable product. The most realistic alternative to a single trait selection seems to be a combined selection for milk, butterfat and protein yield. A study by Brascamp and Minkema (1972) cited by Petersen (1975) indicated that extensive selection and testing for protein as a basis for an index selection would not be profitable.

Economic conditions, however, change quite often in cattle breeding and in addition the change in response to selection of individual traits may be unknown. Therefore, it seems better, from time to time, to re-examine the relationship between the important characteristics in order to plan the breeding policy for the coming few generations. There is already an increasing interest on the part of dairy cattle breeders in some countries for specific information on the non-fat components of milk (Rennie, 1974). Such information is being requested in order that effective breeding and management programs can be developed. There will likely be an increasing demand in Canada for recorded information on bulls and cows with respect to non-fat components, particularly protein, in order to compete in world markets in cattle and semen.

The desirability of maintaining high levels of quality protein in the diet of our human populations is so important that it would seem wise

to emphasize protein percent sufficiently to prevent decreases below market standards and possibly in the future to increase both protein content of milk and total protein yield.

SOURCE OF DATA

Data used in this investigation were obtained from British Columbia Dairy Herd Improvement Association (B.C.D.H.I.A.) milk production records and were made available for research through the courtesy of the Dairy Herd Improvement Division of the B.C. Ministry of Agriculture.

Data accumulated during the period of April 1970 to March 1976 form the basis of this study. The data base included 88,000 lactations from 58,000 Holstein cows in 630 herds with lactation totals for milk, fat and protein. Since incomplete records were not identified, all records less than 275 days in length were excluded from the analyses. Records from 275 days to 305 days were considered as 305-day lactation but no adjustments were made for records less than actual 305-day lactation. Records with age to lactation start from 20-36 months with no recorded dry period, were considered as first lactations since lactation number was not reliable.

Transfer of records from the old testing scheme to the current D.H.I. program took place prior to July 1971 during which period herds were transferred from the Babcock testing to the Infra Red Milk Analyser (IRMA). Records made before July 1971, therefore, had complete lactation information on milk and fat yields but not necessarily complete protein tests. The mean lactational yield for milk, fat and protein percentages from reliable sources (Wilcox et al., 1971) for Holsteins were 7073 kg, 3.70% and 3.11% with standard deviations of 1425 kg, 0.39% and 0.25% respectively. A minimum level of acceptance of a record for inclusion in

the analyses was therefore set at overall fat and protein content of 2.0% for each constituent while the upper limits were correspondingly 6.0% and 5.0% in a lactational yield of 3636 kg to 12,273 kg of milk. These limits were well outside ± 2 standard deviations and therefore permitted more than 95% of the total records for each trait to be included in the analyses.

PART 1: ANALYSIS OF ENVIRONMENTAL PARAMETERS

MATERIALS AND METHODS

The first analysis of 27,137 first lactations gave estimates of yearly trends and seasonal effects for milk, fat, protein lactational yields and percent fat and percent protein. A year-season was defined as the year and season of a lactation based on date of lactation start. Months were thus grouped into 12 year-seasons with 2 seasons of six months each year. Season 1 included April through September and Season 2, October through March. These periods were chosen rather than the conventional Record of Performance (R.O.P.) classification of March through August and September through February, because they agree more closely with summer pasture grazing and winter feeding in the Lower Fraser Valley of B.C. which included the bulk of the data.

Further restrictions were imposed by eliminating records from those herds with less than six complete lactations in three consecutive seasons. These restrictions left lactations from 584 herds out of an initial 630 herds for the analyses.

The fixed effects model assumed for all measures of lactational yield was as follows:

$$X_{ijkl} = U + H_i + Y_j + S_k + YS_{jk} + A_{ykl} + e_{ijkl} \tag{1}$$

where X_{ijkl} = the actual lactational yield for milk, fat, protein, percent fat or percent protein.

U   = the population mean for the trait under study.

H_i = a constant common to all cows in the ith herd.

Y_j = the effect of the jth year of freshening.

S_k = the effect of the kth season of freshening.

YS_{jk} = the joint effect of the kth season in the jth year when the effect of season and year are held constant.

A_{ijkl} = the age in months at parturition of the lth cows of the ith herd freshening in the jth year and in the kth season.

e_{ijkl} = a random effect associated with the lth cow of the ith herd herd freshening in the jth year and in the kth season, which is assumed to be independent and normally distributed with mean equal to zero and variance $\sigma^2 e$.

All effects in the model except e_{ijkl} were regarded as fixed. Since the number of herds (584) was too large for existing programs at the University of B.C. Computing Centre, a least squares technique for absorbing one main effect with a large number of levels was employed. This technique depends on sorting data and absorption in a sequential manner. The reduced model was as follows:

$$X_{ijkl} = U + Y_j + S_k + YS_{jk} + A_{jkl} + e_{ijkl} \qquad (2)$$

The sum of squares for the herd effects was obtained from the difference $R(U,h,y,S,Y S,A) - R(U,y,S,YS,A)$ where $R(U,h,y,S,YS,A)$ and $R(U,y,S,YS,A)$ indicate the reduction in sums of squares due to fitting constants for the effects included in the parentheses.

RESULTS AND DISCUSSION

A summary of the results of the least squares analysis of variance
for milk, fat, protein yields and % fat and % protein are presented in
Table 1. This table also shows the value of R^2 for the statistical model
1, that is the proportion of the total variation in each trait that was
accounted for by fitting the full model 1. Partial R^2 values are also
shown for the individual effects in the model.

For lactation yields and composition, the statistical model accounted
for 32, 32, 36, 19 and 16 percent of the total variation for milk yield,
fat yield, protein yield, % fat and % protein respectively; all effects,
except the year by season interaction, were significant for all traits.
Year by season interactions were significant for protein, % fat and %
protein but not for milk and fat yields.

Year

The overall least squares means and least squares standard errors
for the yields and composition are reported in Table 2. Figures 1 and 2
show the yearly trends in yields and percentages of the constituents.
The graphs were made by plotting the least squares constants of each
dependent variable associated with years against year of lactation start.
They are, therefore, estimates of year effects removing the other effects
in the model.

Over this comparatively short period of time, there was an increasing
trend in all the three yield traits studied. This may in part be due to

Table 1. Summary of the Analysis of Variance: Lactation Yields (kg)
and Composition

Trait	Total Fitted[a]	Total CSS[b]	Categories[c]				
			Herd	Year	Season	Year x Season	Age
Milk	.323	2.7396 X 10^8	0.2770*	.0081*	.0077*	.0002	.03*
Fat	.323	0.40186 X 10^8	0.2663*	.0154*	.0030*	.00038	.0374*
Protein	.364	0.29566 X 10^8	0.3078*	.0127*	.0062*	.0009*	.0369*
% Fat	.194	995.84	0.1799*	.0082*	.0017*	.0012*	.0028*
% Protein	.164	350.795	0.1246*	.0316*	.0004*	.0060*	.0015*
D.f.	26542	26541	582	5	1	5	1

a. Fraction of the total sums of squares accounted for by
fitting the effects in the statistical model equation (2).

b. Total corrected sums of squares (kg^2).

c. Fraction of the total sums of squares accounted for by
each effect in the statistical model.

* Significant source of variation ($P \leq .05$).

Table 2. Least Squares Means ($\bar{X}$) and Standard Errors (SE) for Lactational Yields (kg) and Composition for Different Years

Years	Number of Observations	Milk $\bar{X} \pm SE$	Fat $\bar{X} \pm SE$	Protein $\bar{X} \pm SE$	% Fat $\bar{X} \pm SE$	% Protein $\bar{X} \pm SE$
1970-71	2504	5572±20	202.1±0.8	174.4±0.7	3.64±0.01	3.13±0.01
1971-72	4313	5548±15	197.3±0.6	182.1±0.5	3.57±0.01	3.29±0.00
1972-73	4633	5627±15	197.7±0.6	182.3±0.5	3.53±0.01	3.25±0.00
1973-74	5631	5675±14	201.7±0.5	182.4±0.4	3.57±0.01	3.22±0.00
1974-75	6136	5699±13	205.2±0.5	183.8±0.4	3.62±0.01	3.23±0.00
1975-76	3930	5852±17	211.1±0.6	188.7±0.5	3.63±0.01	3.23±0.00
OVERALL	27137	5663.2	202.5	182.3	3.59	3.23

FIG.1.   YEARLY   TRENDS   FOR   LACTATIONAL YIELDS
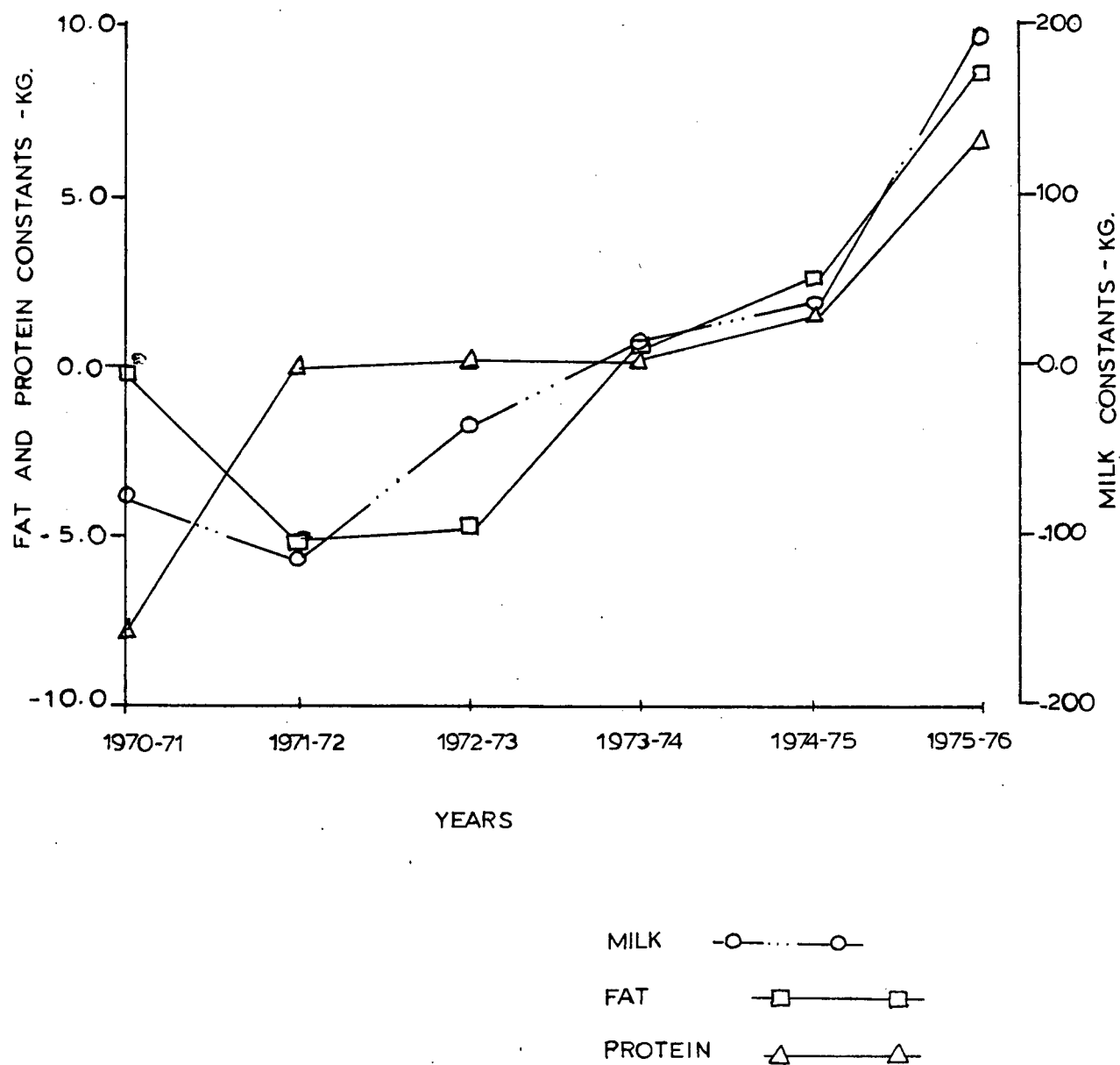
FIG.2.   YEARLY TRENDS OF MILK CONSTITUENTS:
(% fat and % protein)
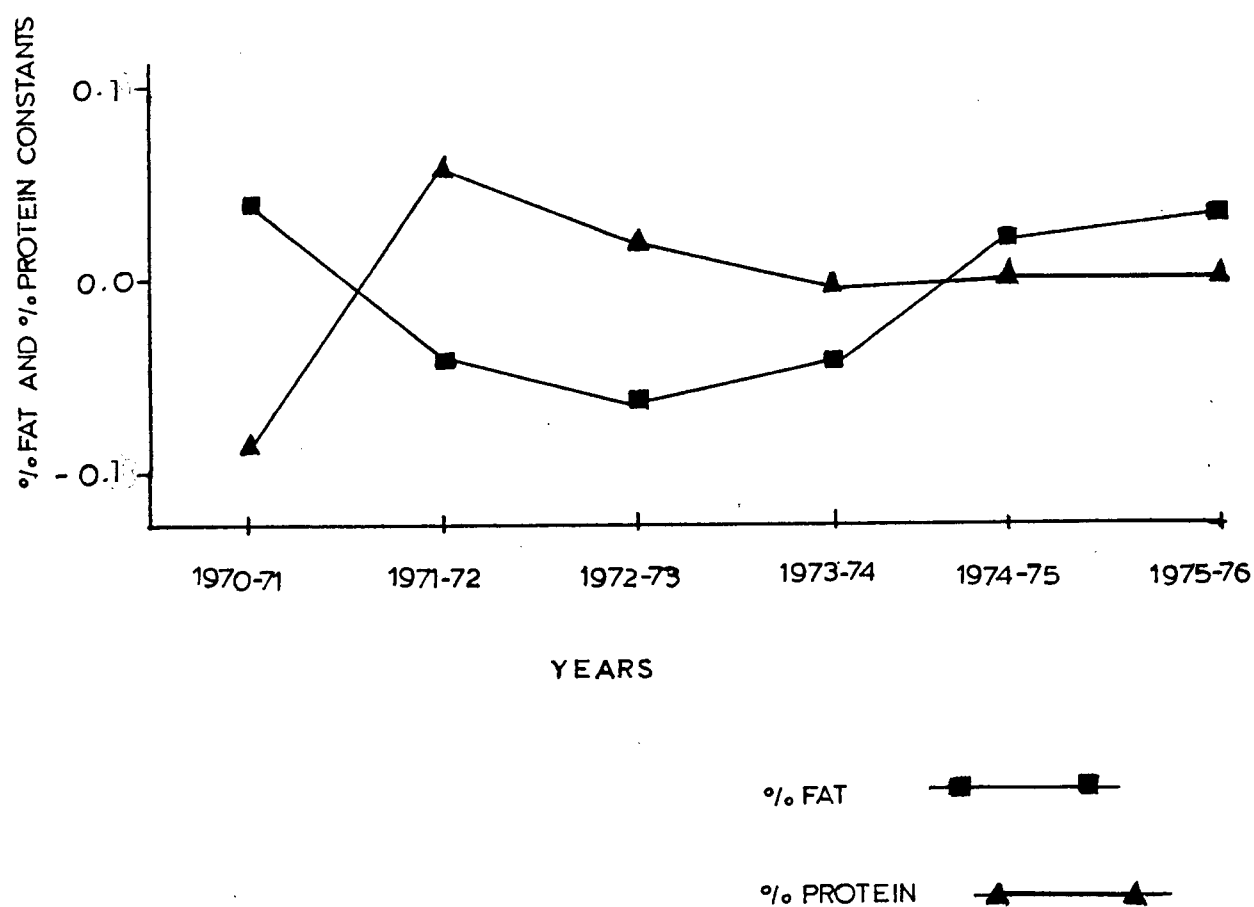
genetic improvement and partly to improved feeding and management.
No attempt is made here to differentiate between these two sources of
improvement. Burnside and Legates (1965), working with first lactation
records of Holstein-friesian heifers, reported a mean milk production
of 5635 kg in 1954 and 6660 kg in 1962, thus giving an annual trend of
128 kg milk. Similarly, Gacula et al (1968) recorded 5955 kg milk in
1960 and 6452 kg in 1962 which gave an annual trend of 124 kg milk. In
the present study, the least squares subclass mean $(u + \hat{y}i)$ in 1970 was
5575 kg and 5852 kg in 1975. The annual trend was 55 kg milk. Van Vleck
(1966) and Gacula et al (1968) used different lactation records, while
the present study limits itself to first lactation records only.

Trends for fat, protein, % fat and % protein were 2.25 kg, 3.5 kg,
-.0025% and -.025% respectively. Results of more recent workers using
first lactation records were as follows: Halgrave and Legates (1971)
showed 53 kg milk per year and Hintz et al (1978) had 36 kg milk per year,
while Kennedy and Moxley (1975) obtained 57 kg milk, 1.9 kg fat, 1.1 kg
protein, -.003% fat and -.014% protein per year. Verde et al (1972)
also reported annual trends of 90 kg milk, 1.1 kg fat and -.052% fat.

Complete transfer of herds from the Babcock test was not completed
before July 1971. Records made before this time therefore may contain
incomplete protein tests. Even though screening was employed to remove
suspicious data, it appeared that not all of such data were
effectively removed. This explains the unusually low protein yields
and percentages for the first year (1970), otherwise a downward trend was
observed for % protein which could be explained by selection for increased
milk yield while ignoring protein. There was no apparent trend in % fat.

Table 3. Least Square Means ($\bar{X}$) and Standard Errors (SE) for Lactational Yields (kg) and Composition for Different Seasons

Seasons	Number of Observations	Milk $\bar{X} \pm$SE	Fat $\bar{X} \pm$SE	Protein $\bar{X} \pm$SE	% Fat $\bar{X} \pm$SE	% Protein $\bar{X} \pm$SE
1	13343	5592±9	201±0.4	180±.3	3.60±.004	3.23±.002
2	13794	5735±9	204±0.3	184±.3	3.56±.004	3.22±.002
TOTAL	27137	5663	202.5	182.3	3.59	3.22

Using the year constants in Figure 2, downward trends over the period were from +.065 to -.093 for % protein and .046 to -.065 for % fat. Gacula et al (1968) over a five-year period, reported downwards of 0.08 to -.10 for % fat and .07 to -.04% for % protein.

Season

Season of calving was a significant source of variation for all the traits under study. The season of calving least square means and standard errors are reported in Table 3. Season of calving accounted for 7.7, 3.0, 6.2, 1.7 and 0.04 of the variation of lactation averages for milk fat and protein yields and % fat and % protein respectively. In terms of percentage of total variation, season effects estimates for the constituent percentages were small. Cows freshening in the winter had higher average milk, fat and protein yields than those freshening in summer; however, the constituent percentages were higher for the summer cows than

for the winter cows.

Year by Season Interaction

Year by season interaction was not significant for milk and fat yields but was significant for protein yield and the constituent percentages. The variances accounted for by the interaction effects were, however, minimal. The year-season subclass means are graphed in Figures 3 and 4. The results indicate that spring grazing tends to decrease fat and protein constituents while increasing milk yield as reported by Waite et al (1956). The results of year, season and year-season effects are in general agreement with the findings of other workers (Bereskin and Freeman, 1965; Gacula et al., 1968; and Van Vleck, 1966).

Herd

Herd effects were highly significant for all traits. In terms of percentage of total variance, herd was the most important of the effects fitted in the statistical model. Herd estimates accounted for 27.77, 26.6, 30.8, 18.0 and 12.45 percent of the total variances for milk, fat yield, protein, % fat and % protein respectively.

Age

Age effects were significant for all traits under study. The R^2 values were 3.0, 3.7, 3.7, 0.28 and 0.15 percent for milk, fat, protein, % fat and % protein respectively. The partial regression coefficients from least squares regression analyses were 0.102, 0.117, 0.117, 0.037 and 0.033 for milk, fat, protein, % fat and % protein respectively.

Table 4. Least Square Means ($\bar{X}$) and Standard Errors (SE) for Lactational Yields (kg) and Composition for Each Year-Season

Year Season	Number of Observations	Milk $\bar{X}\pm SE$	Fat $\bar{X}\pm SE$	Protein $\bar{X}\pm SE$	% Fat $\bar{X}\pm SE$	% Protein $\bar{X}\pm SE$
Summer 70	942	5516±32	201±1.2	171±1.06	3.66±.014	3.10±.008
Winter 70-71	1562	5635±25	203±.96	178±.86	3.62±.011	3.17±.006
Summer 71	1994	5481±22	197±.85	181±.73	3.61±.009	3.30±.006
Winter 71-72	2319	5615±20	198±.77	184±.68	3.51±.009	3.28±.005
Summer 72	2298	5527±21	195±.79	180±.68	3.55±.009	3.27±.005
Winter 72-73	2335	5729±21	200±.78	184±.68	3.50±.009	3.22±.005
Summer 73	2552	5628±20	200±.75	180±.64	3.57±.008	3.21±.005
Winter 73-74	3079	5723±18	203±.68	184±.60	3.57±.008	3.23±.004
Summer 74	3043	5624±18	203±.68	183±.60	3.63±.008	3.25±.005
Winter 74-75	3093	5775±18	207±.68	185±.60	3.61±.008	3.21±.004
Summer 75	2514	5773±20	207±.76	187±.65	3.61±.008	3.25±.005
Winter 75-76	1406	5931±26	215±1.01	190±.87	3.61±.0112	3.21±.007
TOTAL	27137	5663	203	182	3.59	3.23

Summer = Freshening from April through September

Winter = Freshening from October through March

FIG.3. YEAR SEASON TRENDS FOR LACTATIONAL YIELDS

YEAR-SEASONS

MILK   —o————o—

FAT   —□————□—
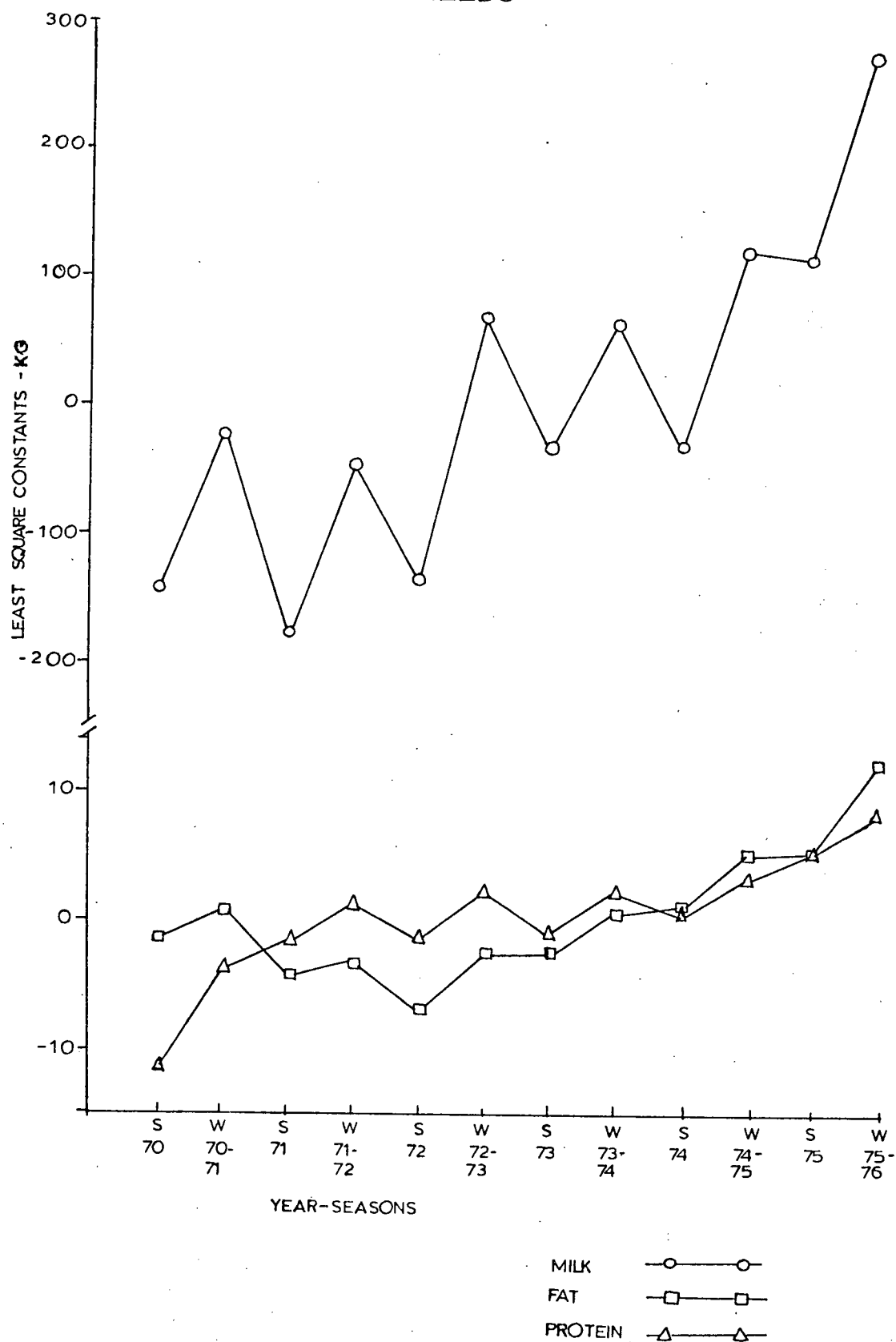
PROTEIN   —△————△—

FIG. 4. YEAR SEASON TRENDS FOR LACTATIONAL COMPOSITION
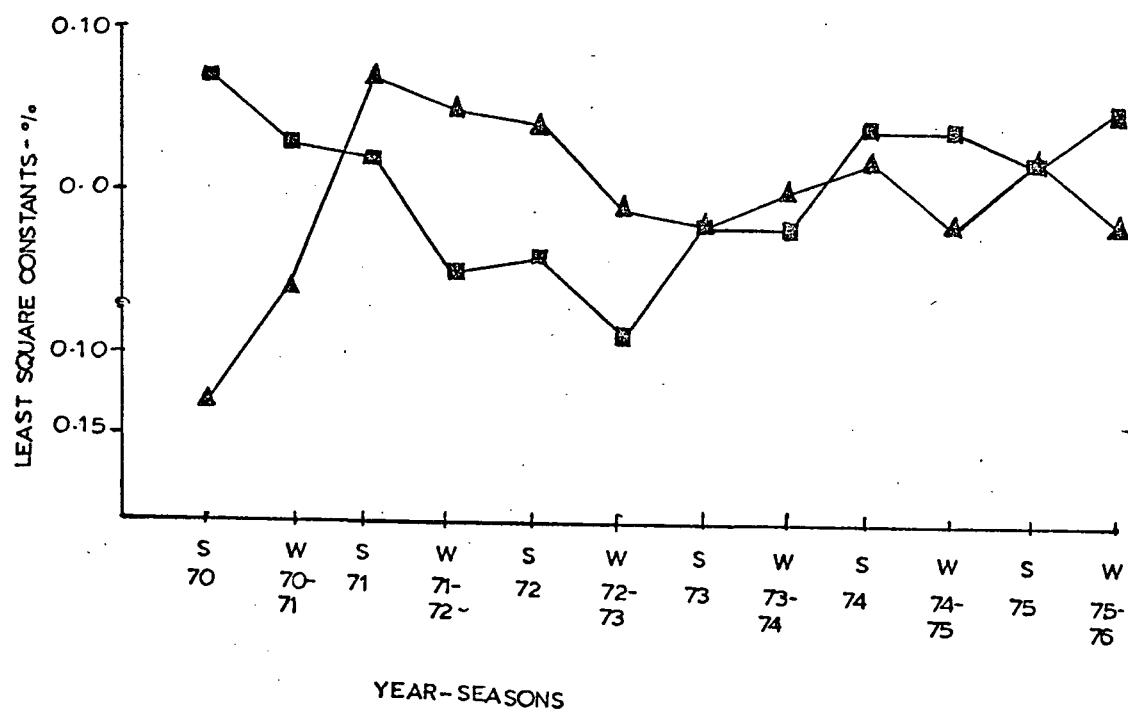
This is an indication that cows calving late produce higher milk, fat
and protein yields and also higher fat and protein fractions than
their counterparts calving for the first time at a younger age.

Summary

Herds, years, seasons and age were significant sources of variation
for all the traits studied. Year-season interaction was a significant
source of variation for protein yields, % fat and % protein but not for
total milk and fat yields. Differences in lactational averages and com-
position were related to the season in which lactation started. In
general, it appeared that cows freshening in a season resulting in
depression of lactation milk yield had above-average lactation percentages
of fat and protein. Over the six-year period, total milk production
increased with a corresponding lowering in the protein content while the
fat content remained fairly constant. Environmental variance is a source
of error that reduces precision in genetical studies and if these are
not removed, smaller genetic estimates are obtained. This is a result
of an increase in the environmental variance not accompanied by a
proportionate increase in genetic variance.

PART II: ESTIMATION OF GENETIC PARAMETERS

MATERIALS AND METHODS

The second analysés were based on a subset of the previous data.
It had been determined from the analyses in Part I that the protein levels
recorded for the first year 1970 were low due to incomplete protein tests.
It was therefore decided to exclude records from the first year and thus
eliminate the first two year-seasons as well as records with no sire
identification.

A total of 19,213 275-305 day first lactation records for cows with
identifiable sires who calved during 1971-76 were obtained from the 27,137
original records. This new data represented records involving 100 sires.
The following restrictions were imposed to isolate the new data from the
bulk of the data base.

   i) Cows were milked for 275 days and up to 305 days.

   ii) Age at first calving was between 20 and 36 months.

   iii) Only sires with 10 or more daughters distributed among 5 or more
herds were used.

   iv) Only herds with 20 or more first lactation records representing
three or more sires with at least six records in a year-season were
included.

These restrictions were designed to limit records to sires widely
and extensively used in Artificial Insemination (A.I.) and to eliminate
confounding sire with herd and/or season effects. A total of 4182

herd-year-seasons (HYS) for 547 herds were formed. A herd-year-season
was defined as a year or season within a herd. For example, two cows
occurring in the same herd but freshening in different years or seasons
were classified into different HYS. Similarly, two cows in different
herds but freshening in the same year or season were also separated
into different HYS.

Sires were grouped according to the year in which their first
daughter's record appeared. A group was defined as a set of sires entering
service during the same period of time. For example, sire group 1 (G1)
included all sires which had their daughters calving for the first time
prior to September 1972, while sire group 2 (G2) represented sires which
had their daughters calving for the first time between October 1972 and
September 1973. Table 6 shows the complete classification of the sire
grouping.

The reason for grouping was to define populations with different
means around which sire genetic values were distributed. According to
Schaeffer et al (1975), year groupings are logical since sires selected
for A.I. in 1971 were conceptually drawn from a population of all possible
zygotes from matings made in that time, while sires selected in 1976 were
drawn from a population of all possible zygotes from more recent matings.
Since genetic trend has been upward with milk production (Miller et al.,
1969), the average merit of sires sampled in 1976 should be greater than
that of sires sampled in 1971.

The grouping procedure was also important in removing bias (Henderson,
1975) because evaluation of sires that continue in service over a long
period of time after being returned to service generally tended to decline

and also sires of later generations appeared to be under-evaluated relative to older sires.

The model assumed to describe the 305-day first lactation record was:

$$Y_{ijkl} = HYS_i + G_j + S/G_{jk} + e_{ijkl}$$

where Y_{ijkl} = the actual 305-day lactation yield or composition.

HYS_i = the effect due to the ith herd-year-season of calving, considered fixed and common to all records in the ith HYS.

G_j = a constant common to all records of daughters in the jth genetic group (year) in which a sire's first daughter calved, considered as fixed.

S/G_{jk} = a random sire effect common to daughters of the kth sire in the jth group. The breeding values of sires in the same group are regarded as a random sample from the same population.

and e_{ijkl} = a random variable mutually uncorrelated with any other variable in the model.

In sex-limited inheritance such as milk production, breeding values of sires are based on the performance of their offspring. If the records of progeny of sires are made on a comparable basis, the genetic covariance between members of a sire's progeny is primarily a function of the additive genetic variance: $\sigma^2_{A/4}$. Therefore, σ^2_s is an estimate of $\sigma^2_{A/4}$. This is because sire effects are the only genetic effects common to a daughter of a sire and another daughter of the same sire.

Heritabilities, genetic and phenotypic correlations, were calculated using the paternal half-sib intra-class correlation method. The sire

component of variation, σ^2_s for each dependent variable was calculated

by the formula:

$$\sigma^2_s = \frac{MS_{sires} - MS_{error}}{K_1}$$

K_1 is the weighted number of progeny per sire. The value of K_1 was calcu-

lated to be 186.76 by the method described by Becker (1975) for unequal

number per subclass (unbalanced design).

That is:

$$K_1 = \left[n.. - \frac{\sum_i \sum_j n_{ij}^2}{n..} \right] / df \text{ (sires per group)}$$

Heritability was then estimated as:

$$h^2 = 4\sigma^2_s / (\sigma^2_s + \sigma^2_e)$$

where h^2 is an estimate of heritability in the narrow sense,

σ^2_e = the error component of variance and contains both environmental

variance and genetic variance

and σ^2_s = the component of variance for sires.

The standard error of the heritability estimates were obtained by

the approximate method of Swiger et al (1964) when normality of the intra-

class correlation t is assumed.

$$S.E. (h^2) = 4 \sqrt{\frac{2(n-1)(1-t)^2 \left[1+(K_1-1)\ t\right]^2}{K_1^2 (n-s)(s-1)}}$$

where t is the intra-class correlation calculated as

$$t = \sigma^2_s / (\sigma^2_s + \sigma^2_e)$$

and n = the number of observations

s = the number of sires involved

and K_1 = a coefficient determined as already noted.

Traits are influenced by both genotype and environmental factors. The relation can be expressed simply as:

P = G + E

where P is the observed phenotype of an individual, G denotes the mean value for that genotype over the environment typical of the population and E is the deviation from G of the actual phenotype of the individual. The statistical model assumes that the correlation between the genotype and the environment are zero.

Genetic correlations were estimated by the formula

$$rg = \frac{Cov\ X,Y}{\sqrt{\sigma^2_x \cdot \sigma^2_y}}$$

where σ^2_x and σ^2_y are the sire components for traits X and Y respectively and Cov X,Y is the covariance of traits X and Y. The covariance (Cov X,Y) was arrived at by the expression $\sigma^2(x+y) = \sigma^2 x + \sigma^2 y + 2\ Cov\ X,Y$ where $\sigma^2(x+y)$ is the sire component of the sum of traits x and y. Phenotypic correlations were obtained directly from the LSA8 computer program output (Peterson, 1965).

RESULTS AND DISCUSSION

Classification of the season of calving is shown in Table 5.
Grouping of sires, the number of sires represented in each group and
the total number of records analysed for the various groups are entered
in Table 6. A summary of the analysis of variance of yields of milk, fat,
and protein and the fractional constituents of fat and protein is presen-
ted in Table 7. The table shows the R^2 values for the statistical model,
that is, the proportion of the total variation in each trait that was
accounted for by fitting the effects of herd-year-season, sire group,
sires and age (as a covariable). For lactation yields of milk, fat and
protein, percent fat and percent protein, the statistical model accounted
for 46, 44, 50, 36 and 31 percent respectively of the total variation.
All effects were significant (P $\leq$ .05) except the effect of sire groups
in the percent protein analysis.

Table 8 shows the least squares means of yields and fractional com-
ponents with their standard errors. Lactation production and constituents
are represented graphically in Figures 5 and 6. Very few records (only 58)
were represented for the two sires in group 5 out of the total data of
19,213. This small number of observations was reflected by the consid-
erably larger standard errors associated with the group for all the traits
analysed. Weighted regression analysis based on the number of sires
in sire groupings gave increasing trends for milk, fat and protein
yields and fat percent but a negative trend for percent protein. The

Table 5. Classification of Season of Calving

Subclass	Season of Calving
1	April to September
2	October to March

Table 6. Number of Sires in Each Group

Sire Group	Year in Which First Daughter Calved	Number of Sires Represented	Number of Lactations
G1	Prior to September 1972	64	15,031
G2	October 1972-September 1973	14	2,518
G3	October 1973-September 1974	8	718
G4	October 1974-September 1975	12	825
G5	October 1975-September 1976	2	58
TOTAL		100	19,213

Table 7. Summary of the Analysis of Variance: R^2 Values for Lactation Average Yields and Composition

Component	Total Fitted	HYS	Groups	Sires/Groups	Age
d.f.	1912	4181	4	95	1
Milk	.553	.458*	.0019*	.056*	.037*
Fat	.562	.444*	.0035*	.071*	.046*
Protein	.617	.503*	.0020*	.063*	.049*
% Fat	.475	.357*	.0010*	.114*	.003*
% Protein	.453	.310*	.0004	.140*	.0021*

* Source of variation significant ($P \leq .05$)

Table 8. Least Square Means ($\bar{X}$) and Standard Errors (SE) of Lactation Yields (kg) and Composition (%) for Different Sire Groups

Group	Milk (kg) $\bar{X} \pm SE$	Fat (kg) $\bar{X} \pm SE$	Protein (kg) $\bar{X} \pm SE$	% Fat $\bar{X} \pm SE$	% Protein $\bar{X} \pm SE$
1	5716.7±33.6	205.85±1.29	183.88±1.03	3.62±.007	3.23±.004
2	5676.7±31.1	204.97±1.46	183.26±1.17	3.63±.008	3.24±.004
3	5913.1±49.7	216.12±1.96	188.71±1.66	3.68±.010	3.20±.005
4	5920.2±46.2	217.16±1.77	191.61±1.42	3.69±.009	3.24±.005
5	5626.2±99.9	199.21±3.82	182.34±3.07	3.53±.020	3.24±.011
OVERALL MEANS	5770.6	208.66	185.96	3.63	3.23

FIG. 5.   SIRE GROUP TRENDS OF LACTATIONAL YIELDS
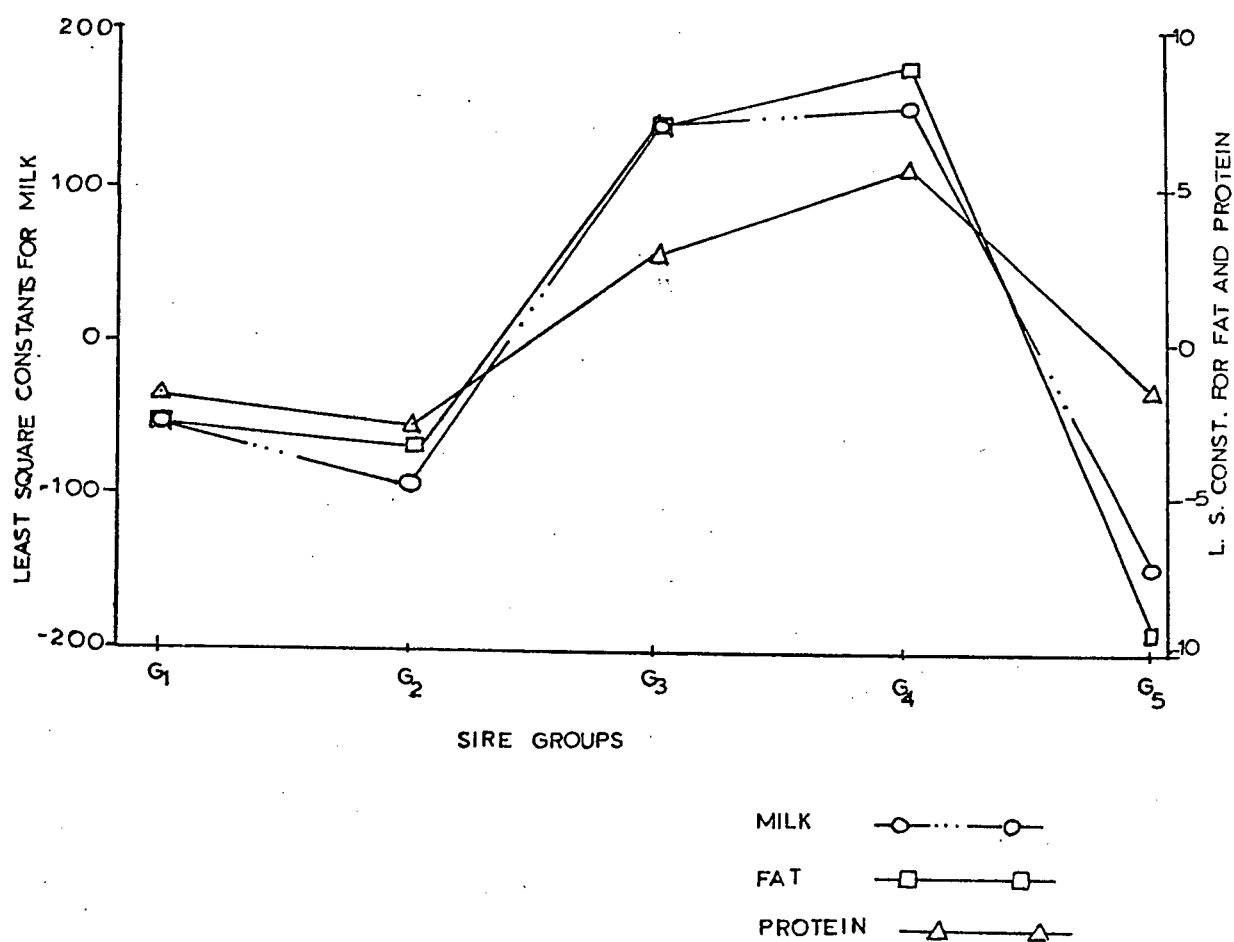
FIG.6. SIRE GROUP TRENDS OF LACTATIONAL
CONSTITUENTS (%fat and %protein)
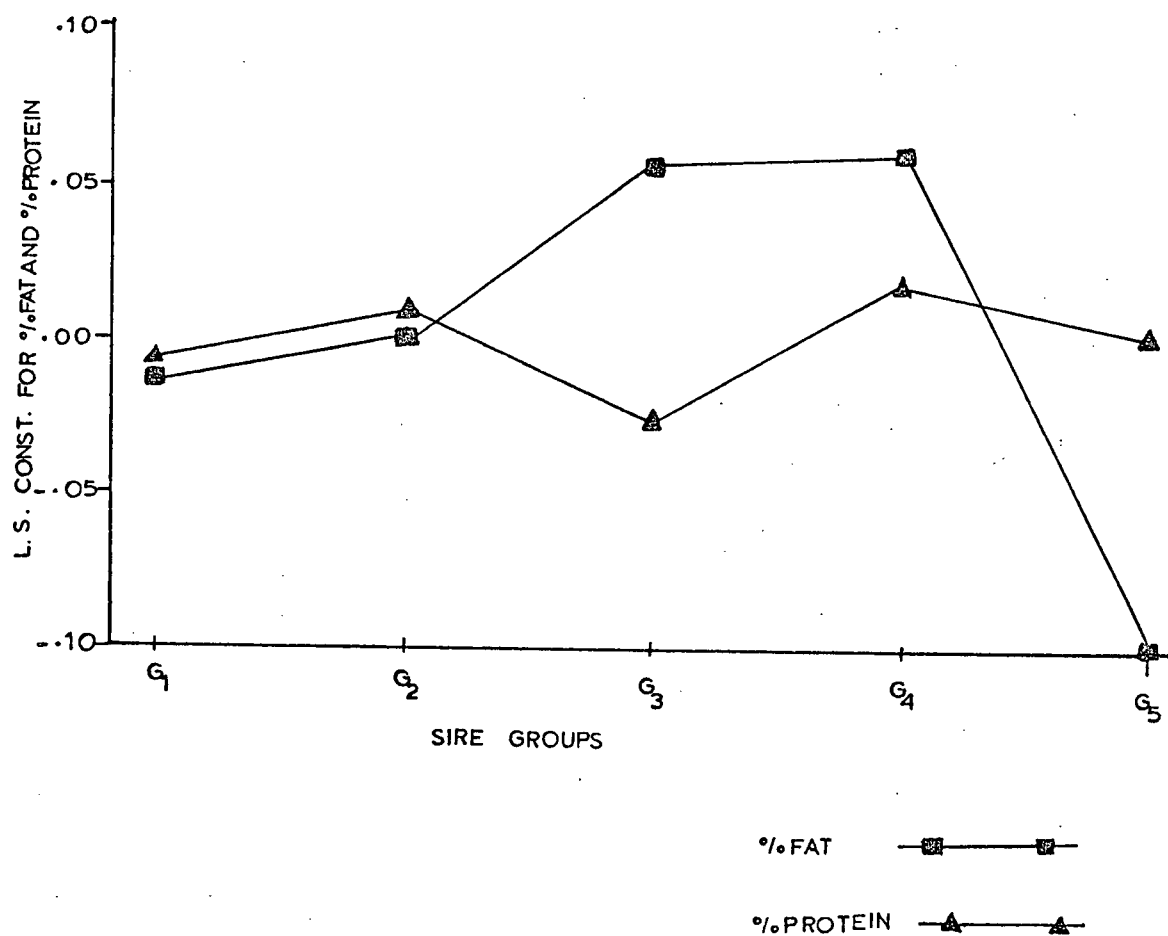
annual genetic trends were 51.53 kg milk, 2.77 kg fat, 1.87 kg

protein, 0.015% percent fat and -0.049% for percent protein.

Results of most authors (Gacula et al. 1968; Kennedy and Moxley

1975, and Verde et al. 1972), however, showed negative genetic trends

in both percent fat and percent protein. The results from this study

showed, therefore, that fat percent has increased while protein per-

cent decreased.

Estimates of heritabilities, genetic and phenotypic correlations,

have been reported in Table 9.

Phenotypic Correlations

Phenotypic correlations among the traits ranged from -.24 to +.86

(Table 9). Milk yield was negatively correlated with the two constituent

fractions and the values are in close agreement with the comprehensive

studies of Wilcox et al (1971) whose values have been reported in Table

10. Gaunt et al (1966) reported correlation values of -.28 and -.27

for milk with % fat and milk and milk with % protein, respectively, while

Thompson and Loganathan (1968) had -.26 for milk with % fat and -.11

for milk with % SNF. Blanchard et al (1966) also obtained -.25 and -.16

for milk with % fat and milk with % SNF respectively. Thus, a negative

phenotypic correlation between lactation milk yield and fat percentage of

approximately -.20 is rather generally accepted (Legates, 1960). A

negative relationship of about the same magnitude appears to exist for

the SNF constituents. The value for the current study (-.24) was similar

to the accepted values. Robertson (1956), however, obtained a very low

correlation of only -.14 between milk and % fat. Since the phenotypic correlation between SNF or protein and milk yield is negative and ranges from -.08 to -.26, a tendency for high yielding cows to produce milk which is slightly lower in the fractional constituents would be expected.

The correlation between fat and protein percentages was .54 in data of Gaunt et al (1966) and for Robertson et al (1956), the figure was .40, and a value of .52 from Politiek (1957). These are much lower than the value reported by Von Krosigh et al (1960) of nearly .70. The correlation found in this study was .56 for % fat ⇌% protein.

In summary, the phenotypic correlation between the percentage contents of fat and protein was positive and of the order of magnitude similar to other workers. Yields were highly correlated with each other, the values ranging from .73 to .86 (Table 9). This underlines the great opportunity for improvement by direct selection. Other workers (Thompson and Loganathan, 1956) reported slightly higher phenotypic correlations for corresponding yields. Their values ranged from .75 to .97.

Genetic Correlations

Genetic correlations (rg) among yields (Table 9) were not only high and positive but also similar to the phenotypic values. The remaining genetic correlations were considerably larger in absolute values than the corresponding phenotypic correlations. The values for genetic correlations that could be compared were similar to those reported by other workers. By way of comparison, the genetic correlations between milk constituentswhich were recorded by Wilcox et al (1971) in their comprehensive study, have been reproduced in Table 10. The genetic correlation

Table 9. Phenotypic Correlations, Genetic Correlations and Estimates of Heritability for Milk Yields and Composition

	Milk	Fat	Protein	% Fat	% Protein	h^2
Milk		.73[a]	.86	-.24	-.31	.18±.03
Fat	.60[b]		.80	.48	.09	.24±.04
Protein	.75	.82		.04	.18	.21±.03
% Fat	-.26	.62	.27		.56	.38±.05
% Protein	-.33	.34	.37	.74		.47±.06

a. Elements above the main diagonal are phenotypic correlations.
b. Elements below the main diagonal are genetic correlations.

Table 10. Genetic Correlations and Heritability Estimates: Holsteins from Wilcox et al (1971)

	Milk	Fat	Protein	% Fat	% Protein	h^2
Milk						.23
Fat	.70					.25
Protein	.82	.81				.21
% Fat	-.30	.46	.13			.57
% Protein	-.30	.17	.28	.54		.37

between milk yield and constituent factors were both negative; -.26 and -.33 for milk-% fat and milk-% protein respectively. Corresponding figures obtained by Gaunt et al (1966) were -.28 and -.27. These negative values would be expected since high milk production has been associated with low percentage of the constituents, both within and between breeds by several workers.

It appeared, however, that genetic correlations obtained for the percentage composition in this study were slightly larger than those reported by Wilcox et al (1971). In particular, r_g (% fat and % protein) of .62 for this study and that of .46 by Wilcox and coworkers. Nevertheless, the observed r_g value of .62 was still smaller than that reported by Johnson (1957) who estimated a value of .69 for Holstein. The correlation between % fat and % protein was positive and large. A breeder selecting for a higher percentage for one of the constituents would thus automatically be selecting for a higher percentage composition in the other constituent.

Heritability

Reliable estimates of heritability require the use of a large number of records. In general, milk constituent fractions have high heritabilities. Table 11 is a summary of the heritability estimates by various workers on Holstein populations. The heritabilities from this study using paternal half-sib analysis were slightly lower than most of the results reported by other workers, most of whom used daughter-dam regression analysis for their estimates. Studies by Van Vleck and Bradford (1965) have shown that genetic estimates from daughter-dam

Table 11. Heritability Estimates of Milk, Fat and Protein Yields and Milk Constituents for Holsteins from Various Sources

	Milk	Fat	Protein	% Fat	% Protein
Gacula et al. 1968	.37	.45	.30	.45	.75
Blanchard et al. 1966	.29	.29		.68	
Gaunt et al. 1968	.24	.24	.20	.57	.45
Wilcox et al. 1971	.23	.25	.17	.57	.37
Van Krosigh et al. 1960				.44	.37
Thompson & Loganathan 1968	.23	.09		.45	

regressions were larger than estimates obtained from paternal half-sib analysis on the same set of data. However, the values from this study are similar to those obtained by Wilcox et al (1971) in their comprehensive study. Heritability for milk seemed low, (.18), but Wunder and McGilliard (1964) had earlier reported a heritability value of only .17. One reason for this low estimate could be due to the removal of genetic trends which parallel increasing mean production (Van Vleck, 1966).

PART III: APPLICATIONS

DIRECT AND CORRELATED SELECTION

Genetic progress is expressed as:

$$\Delta G = i_x \; \sigma_{p_x} \; h^2_x$$

where i_x is the intensity of selection. This is the difference between the average value of a quantitative character in the whole population and the average value of those selected to be parents of the next generation expressed in standard deviation units. σ_{p_x} is the phenotypic standard deviation and h^2_x is the heritability of the trait.

Correlated response arises from the fact that traits may be genetically correlated. A change in a trait y due to selection for trait x can be predicted from the expression:

$$CR_y = i_x h_x h_y r_{g_{xy}} \sigma_{p_y}$$

where CR_y is the correlated response in trait y when selection pressure has been placed on trait x, h_x and h_y are the square roots of the respective heritabilities, $r_{g_{xy}}$ is the genetic correlation between the traits and σ_{p_y} is the phenotypic standard deviation of the trait y.

If it is assumed that only 5% of the sires and 80% of the dams are used, the intensity of selection (i_x) after Pirchner (1969) would be 1.205. For comparative purposes, it is convenient to express the responses anticipated from selection as the change in yield for a selection differential on a single lactation basis. This eliminates the need for

specifying the selection intensity in illustrating the comparative

magnitude of the response to alternative selection models. With a

selection differential of one standard deviation, the expected genetic

change may thus be expressed as:

$$\Delta G_x = h^2 \, \sigma p_x$$

and the expected correlated change in trait y may be expressed as:

$$\Delta GC_y = h_x h_y r_{g_{xy}} \sigma p_y$$

Estimates of expected genetic changes from single trait selection

and expected genetic changes are presented in Table 12. These expected

values are based on estimates of genetic correlations and heritability

values from Part II analysis. In Table 13, the expected genetic changes

have been expressed as percentages of direct single trait selection.

Table 12, for example, shows that an increase of 305 kg in milk yield

could be expected in one generation of selection for milk yield alone

while correlated responses in milk yield from selection for fat and protein

yields would be 211 kg and 247 kg respectively. These correlated responses

in yields of milk represent 69% and 81% of the expected yield in milk

from direct selection for milk. On the other hand, decreases of 115 kg

(-38%) and 162 kg (-53%) in milk yield would be expected from selection

for percent fat and percent protein.

Direct selection for fat was expected to give the highest response

in fat yields. Expected correlated responses from the other traits were

all positive and were 8.1 kg, 11.9 kg, 12.2 kg, and 7.4 kg respectively

for correlated responses from selection for milk, protein, percent fat

and percent protein. The results indicate that selection for protein

Table 12. Direct and Correlated Responses from Single Trait Selection (kg)

	Response to Selection				
Trait Under Selection	Milk	Fat	Protein	% Fat	% Protein
Milk	305*	8.1	7.6	-.023	-.018
Fat	211	15.6	9.6	.063	.021
Protein	247	11.9	10.9	.026	.023
% Fat	-115	12.2	4.0	.130	.058
% Protein	-162	7.4	6.0	.105	.081

*Direct responses are shown on the main diagonal and are underlined.

Table 13. Correlated Responses Expressed as Percent of Direct Selection
Response

	Response to Selection				
Trait Under Selection	Milk	Fat	Protein	% Fat	% Protein
Milk	100*	52	68	-18	-22
Fat	69	100	88	48	26
Protein	81	76	100	20	28
% Fat	-38	78	37	100	72
% Protein	-53	47	55	81	100

*Direct selection on the main diagonal (underlined).

yield and % fat are nearly as effective in increasing fat yields as direct selection for fat yield. Direct selection in fat yield was also expected to give correlated responses of 211 kg in milk yield (69%), 9.6 kg (88%) in protein yield and slight increases (48% and 26%) in fat and protein percentages as direct selection for the individual traits would give.

Direct selection for protein showed that this would be effective but the variability in protein is much less than that for fat. Therefore, the potential for genetic progress in increasing protein content is much less in absolute terms than it is for fat. For example, direct selection for protein was expected to give 10.9 kg which in absolute terms was only 70% of the value of direct selection for fat (15.6 kg) even though the heritability values for fat and protein yields are essentially the same. Correlated responses in protein yield from selection for milk, fat, percent fat and percent protein were 7.6 kg, 9.6 kg, 4.0 kg and 6.0 kg which are correspondingly 68%, 88%, 37% and 50% of direct selection for protein. Direct selection for protein was also expected to give increases of 81% (247 kg) in milk yield, 76% (11.9 kg) of fat yield and 20% and 28% for the percentages relative to direct selection of the individual traits.

Direct selection for percent fat and percent protein gave the greatest responses in the constituent fractions in each case. Correlated responses from selection for milk were both negative. Also, correlated responses in milk yield when selection was for percent fat and percent protein were negative. This means that selection for percent composition would decrease milk yield and vice versa. However, selection for percent

fat and percent protein would give slight correlated increases in fat and protein yields.

The expected genetic gain in milk yield per cow per year is 45 kg if selection is for milk alone (Anderson et al. 1978). This corresponds to a selection intensity of 0.148. Using quota milk prices in British Columbia ($33.39 per 100 kg milk and 28¢ differential for a point of fat above 3.5%), gross dollar gain or loss following one generation of selection were calculated for varying prices for a point of protein above 3.2% at $.00 to $.42. The results are reported in Table 14.

The results show that selection for the yield traits resulted in positive dollar returns with selection for milk yield returning the highest. Gross dollar returns from selection for milk decreased as the price for protein payment increased. This is due to the negative correlation between milk yield and % protein. On the other hand, the gross dollar returns from selection for fat and protein yields increased with increasing payment for protein.

Selection involving percent fat and percent protein resulted in negative dollar returns, the magnitude decreasing with increasing payment for protein. This means that even though selection for percent fat and percent protein increase fat and protein percentages in the milk, the dollar returns for the increased percentages are not enough to make up for the correlated decreases in milk yield.

Table 14. Dollar Gain or Loss for Different Protein Differential Prices Following one Generation of Direct and Correlated Selection

Trait Under Selection	Protein Differential						
	$.00	$.07	$.14	$.21	$.28	$.35	$.42
Milk	14.73	14.62	14.50	14.38	14.27	14.15	14.03
Fat	12.03	12.16	12.29	12.42	12.55	12.68	12.81
Protein	13.09	12.18	13.40	13.48	13.62	13.75	13.88
% Fat	-3.16	-2.35	-2.00	-1.65	-1.31	-0.96	-0.61
% Protein	-5.54	-5.08	-4.62	-4.15	-3.70	-3.24	-2.78

SELECTION INDICES

Selection indices are the optimal methods of selection for an aggregate of several traits. Such an index combines the different traits in a way that maximizes the probability of progress in the aggregate economic value. In general, the index is defined as:

$$I_i = b_1 X_1 + b_2 X_2 + \ldots + b_n X_n$$

where the b_i's are the derived optimum weighting coefficients for the ith trait.

Hazel (1943) defined the genetic-economic value of an index as:

$$H = a_1 g_1 + a_2 g_2 + \ldots a_{igi} \ldots + a_n g_n$$

where the a_i's are the economic values corresponding to one unit of X_i. Subsequently, Henderson (1963) showed that an estimate of b_i is given by:

$$\hat{b} = P^{-1} G A$$

where P is a phenotypic variance-covariance matrix of the traits involved in the payment scheme, G is a genotypic variance-covariance matrix of all the traits under selection and A is a column vector of relative economic weights.

Genetic changes for the individual traits may not necessarily be continually in the direction considered desirable. Greater utility of the selection index would appear possible if in the derivation of the coefficient b_i's, restrictions might be imposed which would ensure that certain specified traits are not changed in the wrong direction. The derivation of the solution to this problem was given by Kempthorne and

Nordskog (1959). The desired set of b_i's is obtained from the following matrix equations:

$$b = [I* - P^{-1}G*^1(GP^{-1}G*^1)G*]p^{-1} GA$$

where $I*$ is the identity matrix with ones on the diagonals and zero elsewhere, $G*$ is the rows of G for which the traits are not to change, $G*^1$ is the transpose of G and p^{-1}, G, and A are the same matrices previously defined.

Using current Quota Milk prices in British Columbia ($33.39 per 100 kg milk and $.28 differential for a point of fat above 3.5%), gross monetary benefits or Dollar Returns (DR) of milk and its constituent yields and fractions were estimated for various selection indices. With the b's computed, an estimate of DR through an index I_1 is

$$DR_i = \gamma(\hat{b}_i^1 P_i b_i)^{.5}$$

where γ is a factor of selection intensity. γ was set equal to 0.148 which corresponds to a genetic gain of milk yield of 46 kg per cow per year when selection is for that trait alone.

In the analysis, whole milk (WM) was differentiated from base milk (BM). Base milk is the product obtained after fat and protein have been removed from whole milk. Since whole milk contains fat and protein, the price per kilogram will be different at any given fat and protein percentage. Base milk will, however, maintain a constant price per kilogram and would only change in like manner as fat and protein when the differentials of payment for fat and protein change. This was important in selecting economic weights for the analysis. A variance-covariance matrix of the relationships between whole milk, fat and protein was used to derive the variance-covariance matrix of base milk, fat and protein. The procedure is outlined in Appendix 1. The

Table 15. Phenotypic (Above Diagonal) and Genotypic (Below Diagonal) Correlations and Heritability Estimates for Base Milk, Fat and Protein Yields

Trait	Base Milk	Fat	Protein	h^2
Base Milk		.74	.89	.19
Fat	.56		.80	.24
Protein	.72	.82		.21

phenotypic and genotypic correlations of base milk, fat and protein yields and the corresponding heritabilities are presented above in Table 15.

Six selection indices were considered.

Index 1 = $b_{1m} X_m + b_{1f} X_f + b_{1p} X_p$

Index 2 = $b_{2m} X_m + b_{2f} X_f$

Index 3 = $b_{3m} X_m + b_{3p} X_p$

Index 4 = $b_{4f} X_f + b_{4p} X_p$

Index 5 = $b_{5wm} X_{wm} + b_{5\%f} X_{\%f} + b_{5\%p} X_{\%p}$

Index 6 = $b_{6wm}^* X_{wm} + b_{6\%f}^* X_{\%f} + b_{6\%p}^* X_{\%p}$

where the b_i's are row vectors of selection index weights pertaining to the traits base milk (m), fat (f), protein (p), percent fat (%f), percent protein (%p) and whole milk (wm). Payment was always based on all three traits but may have a value of zero for an individual component. The

selection indices are interpreted as follows: Index 1 is an index based on selection for base milk, fat and protein yields; Index 2 is based on selection for base milk and fat; Index 3 is selection for base milk and protein while Index 4 is selection for fat and protein yields. These first four indices were constructed based on relative economic weights for one kilogram of each trait entered in the analysis. The relative economic weights are reported in Appendix 2.

Index 5 is a selection index based on selection for whole milk yield, percent fat and percent protein. Index 6 is selection for whole milk yield while keeping percent fat and percent protein constant. Indices 5 and 6 were constructed based on relative economic weights for one kilogram of whole milk, 0.1% fat and 0.1% protein increases. The coefficients of the various indices for different protein differential prices are reported in Table 16. Relative economic weights for comparisons between the different Dollar Return (DR) values were calculated for varying protein prices with quota milk price and fat differential at current British Columbia levels and for a point for protein above and below 3.2% protein content at $.00 to $.42. In Table 18, the gross dollar differences in selection for base milk, fat and protein yields (Index 1) have been converted to percent dollar advantage relative to selection for base milk and fat (Index 2), base milk and protein (Index 3), and fat and protein (Index 4), by the formula $(\frac{I_1}{I_i} - 1)$ x 100%, where I_i is the corresponding dollar return for indices 2 through 4. In the last row of Table 18, dollar differences have been contrasted for Index 5 vs. Index 6. Thus, in Table 18, for example, a value of 0.0 means no selection advantage, while a value of 5.1 means a selection advantage of 5.1% in the appropriate contrast.

Table 16. Coefficients of Selection Indices for Different Levels of Protein Differential Payment[a]

Index		Protein Differential						
		$.00	$.07	$.14	$.21	$.28	$.35	$.42
I_1	BM)	.047	.034	.022	.011	-.001	-.012	-.023
	F)	1.085	1.085	1.040	1.020	1.000	.979	.959
	P)	-.678	-.200	.176	.551	.927	1.302	1.677
I_2	BM)	.035	.030	.026	.021	.016	.011	.006
	F)	.830	.986	1.107	1.227	1.348	1.469	1.590
I_3	BM)	.040	.027	.015	.004	-.007	-.019	-.030
	P)	.706	1.154	1.503	1.852	2.202	2.551	2.901
I_4	F)	.916	.939	.960	.981	1.001	1.022	1.043
	P)	.791	.856	.875	.893	.911	.928	.946
I_5	WM)	.048	.043	.038	.034	.029	.029	.020
	%FAT)	15.140	13.852	12.564	11.276	9.988	9.828	7.412
	%PRO)	57.341	51.557	45.773	39.989	34.205	32.859	22.637
I_6	WM)	.036	.033	.029	.026	.023	.022	.016
	%FAT*)	255.071	236.866	206.662	182.457	158.253	153.526	109.844
	%PRO*)	-555.748	-502.926	-450.105	-397.283	-344.462	-334.099	-238.819

[a]Relative economic weights for the traits considered are reported in Appendices 2 and 3.

Table 17. Gross Dollar Returns per Generation of Selection for the Indices
Considered for Various Protein Differential Prices*

	Price for Protein Differential						
Index	$.00	$.07	$.14	$.21	$.28	$.35	$.42
Index 1 (I_1)	15.30	15.58	15.67	15.86	16.15	16.52	16.98
Index 2 (I_2)	15.20	15.58	15.67	15.80	15.98	16.19	16.44
Index 3 (I_3)	14.44	14.78	14.91	15.14	15.46	15.88	16.39
Index 4 (I_4)	14.46	15.16	15.49	15.82	16.15	16.47	16.80
Index 5 (I_5)	13.55	12.27	10.98	9.69	8.40	8.15	5.83
Index 6 (I_6)	11.45	10.36	9.27	8.18	7.10	6.88	4.92

* Relative economic weights for the traits considered are
reported in Appendices 2 and 3.

Table 18. Gross Dollar Returns of Indices 2 Through Index 4 Relative to
Index 1 and Index 5 Relative to Index 6. Units are Expressed as
Percentages

	Price for Protein Differential						
Contrast	$.00	$.07	$.14	$.21	$.28	$.35	$.42
I_1 vs I_2	0.66	0.0	0.0	0.38	1.06	2.05	3.28
I_1 vs I_3	5.96	5.40	5.10	4.76	4.46	4.03	3.60
I_1 vs I_4	5.81	2.77	1.16	0.25	0.0	0.30	1.07
I_5 vs I_6	18.34	18.43	18.45	18.46	18.31	18.46	18.50

RESULTS AND DISCUSSION

In all cases when protein was included in the index, the coefficient associated with protein increased as the price differential increased. The relative value of the coefficients for other traits in the indices decreased progressively as expected.

Individual animal selection for milk and fat produced a gross progress of $15.20 per generation in the absence of protein payment. By selecting for milk, fat and protein but without protein payment, a gross progress of $15.30 per generation resulted. The difference of $.10 per generation was due to the correlated responses in milk and fat yields by including protein in the selection index. As the relative economic value of protein was increased, the differences between selection for base milk, fat and protein (Index 1) and selection based on only base milk and fat (Index 2) narrowed until these two indices were equal at protein differentials of $.07 and $.14 and then increased, thus describing a curvilinear relationship. These observations parallel the results of Anderson et al (1978).

A general pattern of gradual decrease and an eventual increase in the differences between dollar return for Index 1 on one hand and dollar returns from Indices 2, 3 and 4 on the other hand, with increased payment of protein, was apparent from the results. Selection for base milk, fat and protein (Index 1) was equal or superior to all the other forms of selection in gross dollar return at all levels of protein differential. The Dollar Return values also show that measuring protein has its greatest

advantage in selection for base milk and protein (Index 3) and selection for fat and protein (Index 4) at unrealistically high prices for protein as in the case of selection for base milk and fat (Index 2). There did not seem to be any advantage, therefore, of including protein in a selection index except when the price differential was equal to or greater than that of the fat differential.

Dollar Returns for selection involving whole milk and the constituent fractions (Indices 5 and 6) continued to decrease with increased protein payment. The gross dollar returns were considerably smaller at all levels of protein differential. This means that gross dollar return, from selection based on total yields of milk, fat and protein is expected to be greater than income from selection based on milk yield and fat and protein percentages. Comparison between Index 5 and Index 6 showed that a selection advantage of 18% for Dollar Return from the unrestricted selection (Index 5) over the restricted selection (Index 6) existed.

SUMMARY AND CONCLUSIONS

The analyses in part I showed that cows freshening in the winter season had above average lactational yield but below average lactational values for the constituent fractions. Differences in lactational averages and composition can therefore be related to the season in which lactation started. Annual trends from part I analyses included both environmental and genetic components. Trends from part II analyses based on sire groupings gave estimates of genetic trends to be 51.5 kg milk, 2.77 kg fat, 1.87 kg protein, 0.015% percent fat and -0.049% percent protein, thus indicating a genetic improvement in all traits except protein percentage. This can be explained by selection for milk and fat content ignoring protein.

Heritability estimates and genetic and phenotypic correlations from part II analyses agreed with the literature. Genetic and phenotypic correlations among the yields of milk, fat and protein were all strongly positive. The size of these genetic correlations attest to the importance of milk in determining the yield of fat and protein. The values further indicate that yield of the components such as fat is rather closely tied genetically to the yield of protein. It can therefore be said that genes affecting one trait were also responsible for positive changes in the other traits. The breeder selecting for any of the yield traits would automatically be selecting for the other two traits, though with less pressure. It is anticipated, however, that attempts to increase protein percentage by selection on fat content would not be efficient even with the high genetic correlation of 0.74. The reason being that in the Netherlands there has been indirect

selection for protein percentage through selection for fat percentage but the responses obtained have fallen far below expectations from the regression of fat on protein (Politiek 1957, 1968). The impression is that protein percent hardly increased with fat content. The Dutch experience in commercial breeding suggests that if an increase in protein content is wanted, it may only be obtained by direct selection for this trait.

The expected selection responses in the yield traits would be about 5.4% to 8.0% of the lactational yield per generation. Selection for milk yield, however, would result in decreases in the functional composition but selection for fat and protein yields would result in slight to moderate elevation in the fractional composition. The small variation in percent fat and percent protein reflect the futility of attempting to change the relative amounts of fat or protein content in milk. In general, the heritabilities for the percentages are approximately twice that of the lactation yield traits. This is evidence that environment has less effect on the percentages of fat and protein content of milk than on the lactational yields of milk, fat and protein. Despite the high heritabilities, however, single trait selection to increase the percentage constituents would result in a significant reduction in the yield traits while leading to very little change or improvement in actual milk composition.

The parameter estimates from part II analyses were used in the computations for direct and correlated selection responses in part III. The results suggest that selecting for milk alone is a relatively efficient means for improving yield of fat and protein. Joint selection for yield of milk, fat and protein would result in more yield of fat and protein than selection for milk alone and would subsequently result in more farm income.

If the desired result is for higher yields of fat and protein, then selection should be based on those traits. Current pricing systems give a relatively high value to the base milk fraction which dictates its inclusion in any practical selection program. Selection should not be directed toward increased percent fat or percent protein since such a program would cause a decrease in milk yield resulting in lower dollar returns. Even when selection indices are used, milk yield is still the most important trait with regard to dollar returns.

There was, as expected, an economic advantage of programs employing measurements on milk, fat and protein over programs employing only partial measurements. Based on the British Columbia pricing system, the value of base milk was $.236 per kilogram and $3.036 per kilogram of fat with no payment for protein. When payment for protein was imposed with various differentials of $.00 to $.42 per point of protein above 3.2%, the price per kilogram of base milk dropped progressively. There was, therefore, a decreased advantage of a three trait selection over base milk and fat or base milk and protein or an index with fat and protein yields, as the price of protein increased. Selection for total yields of base milk, fat and protein resulted in higher dollar returns than selection for whole milk and composition.

Despite the decreasing demand for milk fat and the increased demand for cheese and milk protein products, dairymen should select for total milk yield and ignore both fat and protein yields as the additional dollar returns for multiple trait selection are minimal under current pricing schemes. From a nutritional point of view, the goal could as well be to increase the total yields of fat and protein rather than just their percentage fractions or proportionality in milk. Standardization of these

constituents during processing could be used to attain the most desirable composition of the final product to enhance flavour and marketability. However, such a selection program would require changes in the pricing scheme for milk in order to give a financial incentive to the breeder.

The analyses discussed in this thesis were empirical derivations and did not consider costs of measurements of fat or protein testing program. Economic justification could be reached only when costs of measurement and testing have been entered into the genetic program and found feasible for implementation.

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APPENDIX 1

Derivation of variance-covariances of base milk (BM) from whole milk (WM) variance-covariance.

Whole milk = BM + Fat + Protein

$$= BM + F + P$$

$$\therefore V_{WM} = V_{BM} + V_F + V_P + 2\ Cov_{BM,F} + 2\ Cov_{BM,P} + 2\ Cov\ FP \qquad (1)$$

Now

$$Cov_{(WM,F)} = Cov_{(BM,F)} + Cov\ F,P + V_F$$

and

$$Cov_{(WM,P)} = Cov_{(BM,P)} + Cov\ P,F + V_P$$

$$\therefore \quad Cov_{(BM,F)} = Cov_{(WM,F)} - Cov_{(P,F)} - V_F$$

and

$$Cov_{(BM,P)} = Cov_{(WM,P)} - Cov_{(P,F)} - V_P$$

From (1)

$$V_{BM} = V_{WM} - V_F - V_P - 2\ Cov_{(BM,F)} - 2\ Cov_{(BM,P)} - 2\ Cov_{F,P}$$

$$= V_{WM} - V_F - V_P - 2\left[Cov_{(WM,F)} - Cov_{P,F} - V_F\right] -$$

$$2\left[Cov_{(WM,P)} - Cov_{F,P} - V_P\right] - 2\ Cov\ F,P$$

$$= V_{WM} + V_F + V_P - 2\ Cov_{(WM,F)} - 2\ Cov_{(WM,P)} + 2\ Cov\ P,F$$

APPENDIX 2

Relative Economic Weights ($)[1] at Various Protein Differential Prices for 1 kg each of Base Milk[2], Fat and Protein

Trait	Protein Differential						
	$.00	$.07	$.14	$.21	$.28	$.35	$.42
Base Milk	0.2359	0.2135	0.1911	0.1689	0.1463	0.1239	0.1015
Fat	3.0359	3.0359	3.0359	3.0359	3.0359	3.0359	3.0359
Protein	0.0	0.8890	1.5421	2.1952	2.8483	3.5014	4.1545

[1]Economic weights based on $33.39/100 kg milk and 28¢ fat differential.

[2]Base milk = Whole milk - (Fat + Protein).

APPENDIX 3

Relative Economic Weights ($)[1] at Various Protein Differentials for 1 kg of Whole Milk, and 0.1% each of Fat and Protein Content

Trait	Protein Differential						
	$.00	$.07	$.14	$.21	$.28	$.35	$.42
Whole Milk	0.2359	0.2135	0.1911	0.1689	0.1463	0.1239	0.1015
% Fat	0.28	0.28	0.28	0.28	0.28	0.28	0.28
% Protein	0.0	0.07	0.14	0.21	0.28	0.35	0.42

[1]Economic weights based on $33.39/100 kg milk and 28¢ fat differential.

APPENDIX 4

Genotypic and Phenotypic Variances of Traits Analysed (kg^2)

Trait	Genetic	Phenotypic
Milk	524.00	2883782
Fat	1062.24	4231.22
Protein	589.12	2725.42
% Fat	.04749	.11394
% Protein	.018148	.03426

APPENDIX 5

Genetic Correlations with Standard Errors

	Milk	Fat	Protein	% Fat
Fat	.60 ± .075			
Protein	.75 ± .048	.82 ± .036		
% Fat	-.26 ± .107	.62 ± .065	.27 ± .090	
% Protein	-.33 ± .092	.34 ± .091	.37 ± .082	.74 ± .041