

GENETIC PARAMETERS FOR MILK YIELD AND SOME REPRODUCTIVE TRAITS OF HOLSTEIN COWS USING REML AND GIBBS SAMPLING

U. M. El-Saied¹, E. Mousa² and S. Abou-Bakr³

1- Animal Production Research Institute, Ministry of Agriculture, Dokki, Giza, Egypt. 2- Animal Production Department, Faculty of Agriculture, Assiut University, Assiut, Egypt. 3- Animal Production Dept., Faculty of Agriculture, Cairo University, Giza, Egypt

SUMMARY

A total of 1391 lactation records were obtained from 726 Holstein cows raised at a commercial farm. Variance components were estimated using two procedures: REML and Gibbs sampling with a multiple-trait repeatability animal model. The model included year-season of calving (16 groups) and parity (first three lactations) as fixed effects and additive genetic and permanent environmental as random effects. Records were analyzed to compare covariance estimates for 305-day milk yield, days open and number of services per conception obtained by both procedures.

REML estimates of heritability for the three traits were 0.090, 0.045 and 0.003, respectively. The corresponding repeatability estimates were 0.386, 0.081 and 0.030. Gibbs sampling estimates of heritability for the same traits were 0.313, 0.024 and 0.022, respectively, where, the corresponding estimates for repeatability were 0.354, 0.056 and 0.045.

REML genetic correlations between 305-day milk yield and each of days open and number of services per conception were 0.605 and 0.974, respectively. The corresponding Gibbs sampling estimates were 0.684 and 0.601. These high and positive estimates of genetic correlations indicate that the nature of the relationship between milk yield and fertility traits may cause a problem in realizing rapid improvement for both of them simultaneously.

REML phenotypic correlations between 305-day milk yield and each of days open and number of services per conception were 0.131 and 0.091, respectively. The corresponding Gibbs sampling estimates were 0.121 and 0.085. Estimates from both procedures appeared to be similar.

REML genetic and phenotypic correlations between days open and number of services per conception were 0.706 and 0.703, respectively. The corresponding Gibbs sampling estimates were similar (0.655 and 0.702).

The results indicated that heritability estimate for 305-day milk yield was much higher using Gibbs sampling. Although heritability estimates for the reproductive traits were not similar from both procedures, they were all low indicating that the direct genetic selection to improve these traits would be ineffective. Running time for the multitrait analysis using REML was almost six hours and that needed using Gibbs sampling was almost two weeks.

Abbreviation key: 305-MY = 305-day milk yield, DO = Days Open, NSPC = Number of services per conception, DF-REML = Derivative Free-REML, GS = Gibbs Sampling, BLUP = Best Linear Unbiased Prediction, ML = Maximum Likelihood.

Keywords: Holstein-Friesian, genetic parameters, REML, Gibbs sampling, milk yield, fertility

INTRODUCTION

The most usual methods in analyzing animal breeding data have been BLUP, ML and REML. Recently, much attention has been paid to the Bayesian approach which presents some advantages over the frequentist approach in analyzing categorical traits (Mousa, 1999). Analysis of categorical traits by linear methodology violates several assumptions of the linear model and is not optimal (Gianola, 1982). Gibbs sampling incorporates Bayesian prior knowledge by weighting new information with old ones providing confidence ranges for estimating (co)variance components. This advantage allows larger multitrait analysis than REML. Solutions for variance component from both procedures are similar with flat priors (Van Tassell *et al.*, 1995 and Mousa, 1999). GS has been applied to Bayesian analysis for categorical traits (Sorensen *et al.*, 1995 and Wang *et al.*, 1997). However, REML has been extensively applied for normal distribution traits.

The objective of this study was to compare the frequentist and Bayesian approaches from the practical point of view. Heritability, repeatability and genetic and phenotypic correlations estimated by

REML and GS for 305-MY, DO and NSPC, as continuous traits, are compared using multiple lactation records of Holstein cows raised in a commercial farm in Egypt. Running time is also considered.

MATERIALS AND METHODS

Data

Data on milk yield and reproductive performance of 726 lactating Holstein cows in a single commercial herd (International Company For Animal Wealth), in Giza governorate (Egypt), were collected during the period from 1991 to 1998. Measures of reproductive performance included days open (DO) and number of services per conception (NSPC). Milk production was measured by actual 305-day milk yield (305-MY). Data included 1391 lactation records for 726 Holstein cows daughters of 220 sires and distributed over 16 year-season groups. Most of the cows were imported as pregnant heifers from U.S.A. Cows were artificially inseminated at the first observed estrus after parturition using frozen semen imported from U.S.A. Each year was divided into two seasons: warm (March to August) and cold (September to February).

Model

The following multiple-trait repeatability animal model was used to obtain (co)variance components for the three studied traits (305-MY, DO and NSPC) through REML and GS procedures:

$$y_{ijkl} = A_i + PE_i + ys_j + p_k + e_{ijkl}$$

where

y_{ijkl} = records of trait l ($l = 305\text{-MY, DO or NSPC}$) for the k^{th} parity of the j^{th} year-season of calving of the i^{th} animal;

A_i = the random effect of the additive genetic effect of the animal (726 levels);

PE_i = the random permanent environmental effect on the animal;

ys_j = the fixed effect of the j^{th} year-season of calving (16 levels);

p_k = the fixed effect of the k^{th} parity (3 levels representing the first three parities);

and

e_{ijkl} = the random residual effect associated with each observation.

The variance-covariance structure for the model was as follows:

$$V = \begin{bmatrix} a_1 \\ a_2 \\ a_3 \\ c_1 \\ c_2 \\ c_3 \\ e_1 \\ e_2 \\ e_3 \end{bmatrix} = \begin{bmatrix} A\sigma^2 a_1 & \sigma a_1 a_2 & \sigma a_1 a_3 & 0 & 0 & 0 & 0 & 0 & 0 \\ \sigma a_2 a_1 & A\sigma^2 a_2 & \sigma a_2 a_3 & 0 & 0 & 0 & 0 & 0 & 0 \\ \sigma a_3 a_1 & \sigma a_3 a_2 & A\sigma^2 a_3 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & I\sigma^2 c_1 & \sigma c_1 c_2 & \sigma c_1 c_3 & 0 & 0 & 0 \\ 0 & 0 & 0 & \sigma c_2 c_1 & I\sigma^2 c_2 & \sigma c_2 c_3 & 0 & 0 & 0 \\ 0 & 0 & 0 & \sigma c_3 c_1 & \sigma c_3 c_2 & I\sigma^2 c_3 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & I_1 \sigma^2 e_1 & \sigma e_1 e_2 & \sigma e_1 e_3 \\ 0 & 0 & 0 & 0 & 0 & 0 & \sigma e_2 e_1 & I_2 \sigma^2 e_2 & \sigma e_2 e_3 \\ 0 & 0 & 0 & 0 & 0 & 0 & \sigma e_3 e_1 & \sigma e_3 e_2 & I_3 \sigma^2 e_3 \end{bmatrix}$$

where,

A is the numerator relationship matrix,

$$\sigma^2 a_1, \sigma^2 a_2, \sigma^2 a_3$$

= the direct genetic variance for trait 1, 2 and 3,

$$\sigma^2 c_1, \sigma^2 c_2, \sigma^2 c_3$$

= the variance due to permanent environmental effects,

Each of I_1 , I_2 and I_3 is an identity matrix of order equal to the records of trait 1, 2 and 3,

$\sigma a_i a_j$

= all the direct genetic covariance items between any pair of the three traits,

 $\sigma e_i e_j$

= all the permanent environmental covariance items between any pair of the three traits and
 = all the error covariance items between any pair of the three traits.

Methods

Heritabilities, repeatabilities and genetic and phenotypic correlations were obtained employing the above mentioned multiple-trait repeatability animal model through two procedures: the Derivative-Free Restricted Maximum Likelihood (DF-REML) procedure of Thompson and Hill (1990) and the Gibbs sampling procedure presented by Van Tassell and Van Vleck (1996). The multiple-trait GS for animal model program has been developed to implement the GS algorithm for Bayesian analysis of a broad range of animal models. All known relationships among individuals were considered in the animal model. Initially, estimates for heritability and the proportion of permanent environmental variance were made through a single-trait analysis for each of the three variables studied following the REML procedure. These single-trait estimates were used as starting values for the multitrait analysis of both procedures. These initial estimates, at least, will help in facilitating convergence of the REML multitrait analysis.

Maximum of 25 convergence iterations with a minimum variance of function valued in simplex $< 10^{-3}$ were allowed for REML. This would insure a global maximum likelihood estimate with a reasonable degree of precision. Where a Gibbs chain of length 100,000 was run for each trait with burn in 5000 rounds and were considered to be an effective number of rounds (Mousa and Van Vleck, 1998).

RESULTS AND DISCUSSION

Preliminary least squares analysis using the PROC GLM option of SAS (1990) showed high significance for the effect of year-season of calving on all traits (305-MY, DO and NSPC). However, parity had a non-significant effect on NSPC and a significant effect on the rest of variables. The mean of 305-MY (7504 \pm 38.6) falls within the range reported in the international literature, while, means for DO (229 \pm 3.4 day) and NSPC (2.8 \pm 0.05 services) were clearly higher than the values frequently reported in the literature for the same breed. Detailed results are shown by Abou-Bakr *et al.* (2000).

REML and GS estimates of heritability and repeatability for 305-MY, DO and NSPC of Holstein cows are shown in table 1.

Table 1. REML and GS heritability (h^2) and repeatability (t) estimates for 305-day milk yield (305-MY), days open (DO) and number of services per conception (NSPC) of Holstein cows

Trait	REML		GS	
	h^2	t	h^2	t
305-MY	0.090	0.386	0.313	0.354
DO	0.045	0.081	0.024	0.056
NSPC	0.003	0.030	0.022	0.045

As shown in the table, GS heritability estimate for 305-MY was three times as much as the corresponding REML estimate. Although GS heritability estimates for DO and NSPC were not similar to their corresponding REML estimates, all these heritability estimates were low. Therefore, the direct genetic selection for these traits would be ineffective, regardless of the estimation procedure.

The difference in heritability between the two procedures for the studied traits is not very surprising. The frequentist school simply presents an estimate value to the heritability, with its confidence interval (depending on the employed software), where the Bayesian one presents the mean of the probability density distribution of the heritability, given a determinant sample. Moreover, the set of data used is relatively small which may cause non similar results. GS heritability estimate for 305-MY seems more reasonable than that obtained with REML.

Heritability estimate for 305-MY from GS of 0.313 is within the range frequently reported in the literature for this trait. However, REML estimate of 0.09 is lower than the range (from 0.135 to 0.310) found in the literature (Weller, 1989; Short and Lawlor, 1992; Marti and Funk, 1994 and Dematawewa and Berger, 1998). Differences in heritability estimates among the various studies for the same trait of

the same breed may be due to differences in the number of records used, the correction for non-genetic factors, the model used and the methodology employed. Badran and Shebl (1991) obtained very close estimate (0.10) to our result for heritability of milk yield using similar model for a similar data set size and employing the same methodology (REML).

Estimate of heritability for DO from REML (0.045) and GS (0.024) were low and comparable to others reported in the literature (Berger *et al.*, 1981; Hayes *et al.*, 1992; Marti and Funk, 1994; Rekaya, *et al.*, 1996 and Dematawewa and Berger, 1998). Although the adjustment to some environmental factors is expected to reduce some of the variation in production associated with DO, its heritability is still low suggesting that the trait is largely affected by the environmental conditions (Marti and Funk, 1994).

REML estimates from previous studies for heritability of NSPC were 0.008 (Moore *et al.*, 1990) and 0.06 (Berger *et al.*, 1981), i.e. very close to zero. Therefore, the direct genetic selection to improve this trait would be meaningless.

As shown in Table 1, repeatability estimates from both procedures were generally comparable. The obtained repeatability estimates are also comparable to those found in the literature for 305-MY (Dematawewa and Berger, 1998; Marti and Funk, 1994 and Welper and Freeman, 1992) and for DO and NSPC (Hayes *et al.*, 1992; Marti and Funk, 1994 and Dematawewa and Berger, 1998). Repeatability estimates for DO and NSPC were low indicating that cow's reproductive performance is of little use in predicting her performance in later lactations. Low estimates of repeatability obtained are in concordance with their low heritabilities. Factors other than genetic and permanent environmental effects (i.e., detection of estrus and managerial and nutritional factors) were main determinants of reproductive efficiency (Hayes *et al.*, 1992).

The direct genetic improvement for DO and NSPC traits is expected to be ineffective. Also, reproductive traits are very lowly repeatable. Therefore, poor fertility in cows appears to be largely a managerial problem. Improving management conditions that influence fertility is necessary.

Estimates of genetic and phenotypic correlations among the three studied traits from both REML and GS are shown in table 2.

Table 2. Genetic (r_g) and phenotypic (r_p) correlations for 305-day milk yield (305-MY), days open (DO) and number services per conception (NSPC) of Holstein cows estimated by REML and GS

Correlated Traits	REML		GS	
	r_g	r_p	r_g	r_p
305-MY & DO	0.605	0.131	0.684	0.121
305-MY & NSPC	0.974	0.091	0.601	0.085
DO & NSPC	0.706	0.703	0.655	0.702

The high and positive estimates of genetic correlations between 305-day milk yield and each of days open and number of services per conception indicate that the nature of the relationship between milk yield and fertility traits may cause a problem in realizing rapid improvement for both of them simultaneously. The results are in good agreement with those obtained by Dematawewa and Berger (1998). Genetic correlations of 305-MY with each of DO and NSPC are strong but undesirable. The results suggested that incorporating reproductive measures in bull indices could hinder the deterioration of reproductive performance in high yielding cows.

REML phenotypic correlations between 305-MY and each of DO and NSPC were very close to Gibbs sampling estimates. REML genetic and phenotypic correlations between DO and NSPC were also similar to Gibbs sampling estimates. More details of REML estimates are shown by Abou-Bakr *et al.* (2000).

Running time for the multitrait analysis using REML was almost six hours and that needed using GS was almost two weeks. The estimates obtained from both procedures, except for the heritability of 305-MY, in conjunction with the great difference between them in the running time suggested that, for the relatively small data sets of continuous traits, the use of REML appeared to be less time consuming. Mousa (1999) reported that variance components and heritability estimated using GS were similar to the estimates using REML for continuous traits in sheep. However, the heritability of 305-MY using GS was greater and seems more reasonable than that obtained with REML probably due to the influence of the prior distribution of the variance components on the posterior distribution (Van Tassell, 1994). More thorough studies with larger data sets for different types of variables through different assumptions are still needed to compare results from both procedures and recommend the best in each case.

CONCLUSION

The results indicated that estimates from REML and GS procedures lead to similar breeding decisions except the heritability estimate for 305-MY which was considerably greater, and more within the range of estimates reported in the literature, using GS than REML. This is probably due to the influence of the prior distribution of the variance components on the posterior distribution.

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THE SUBPOPULATIONS OF THE BONSMARA CATTLE BREED- THEIR PHYLOGENETIC RELATIONSHIPS AND THEIR CHARACTERIZATION IN TERMS OF GROWTH, CARCASS AND MEAT ATTRIBUTES

A. Kotzé

ARC Animal Improvement Institute, Private Bag X2, Irene, 0062, South Africa, PE Strydom, ARC Animal Nutrition and Animal Products Institute, Private Bag X2, Irene, 0062, South Africa

SUMMARY

Ninety bull calves of five Bonsmara strains, viz. Edelheer (E), T-49 (T), Wesselsvlei (W), Roodebos (R) and Belmont Red (BR) were fattened under intensive feeding conditions and serially slaughtered at four different slaughter weights. The phylogenetic relationships between the five strains were determined by means of blood typing. Growth performance, carcass characteristics and meat quality characteristics were compared between the subpopulations. The genetic distances between the animals confirmed the existence of five genetic subpopulations. Means for production and product characteristics were adjusted for mean overall subcutaneous fatness level (%) by means of analysis of covariance. T gained weight faster and more efficiently on a live and carcass weight basis than the other Bonsmara groups. Regarding carcass composition, T had proportionally more meat in the high-priced cuts of the carcass than W. Muscle of the W line had a significantly higher ageing potential (measured as myofibrillar fragmentation; MFI) than T, resulting in higher tenderness scores for W.

Keywords: Phylogenetic, subpopulation, meat, Bonsmara cattle

INTRODUCTION

The Bonsmara is an indigenous composite cattle breed which originated in the early 1940 s from a 5/8: 3/8 combination of the Afrikaner (indigenous Sanga or *Bos taurus africanus*) and Shorthorn/Hereford (*Bos taurus taurus*) through an initiative of the Department of Agriculture of South Africa (Bosma, 1980). By 1970, it was detected that the genetic structure of the breed had narrowed considerably due to over-exploitation of the Edelheer strain, which was the dominant breeding line in most Government stud herds. Consequently, it was decided to develop other subpopulations within the Government herds and certain private herds to re-establish genetic variation within the breed (Bosman, 1988). The Edelheer (E) breeding line (progenitor, the bull Edelheer) is still regarded as the main strain of the breed, since it dominated the artificial insemination industry of the Bonsmara prior to the introduction of the other subpopulations. The Wesselsvlei (W) strain, originated from the bull Spanner, a 5/8 Afrikaner x 3/8 Red Poll bull, instead of the normal Afrikaner/Hereford/Shorthorn combination, while the Roodebos (R) strain was developed from an unrelated group of animals in a specific Government herd. T-49 (T) is not a formal strain, but was regarded in this study as an independent strain due to the large number of animals within the E strain that were related to a certain bull, T-49. This bull achieved exceptional growth performance indices in the National Performance Testing Scheme (Bosman, D.J., 1996 - personal communication). The Belmont Red (BR) is an independent breed, developed in Australia from 1/2 Afrikaner, 1/4 Shorthorn and 1/4 Hereford. It was imported into South Africa and was further developed as an unrelated subpopulation within the Bonsmara breed.

In this study the phylogenetic relationships among the five Bonsmara strains were determined. Also, the strains were compared in terms of production and product characteristics. Such a data basis can serve as a marketing tool for producers. The Bonsmara, a popular local and now exported breed, is well known for its adaptability to harsh, extensive conditions combined with the anticipated favourable meat tenderness.

MATERIAL AND METHODS

Ninety Bonsmara weaner bulls (± 7 months) were selected from various herds over the country representing five different strains, viz. E (n=18), T (n=18), R (n=18), W (n=18), BR (n=18)

replicates per treatment). Animals were stratified into four groups according to live weight and slaughtered at the commencement of the trial (S0), slaughter weights of 75% (S1), 90% (S2) and 105% (S3). The animals were kept in single pens and fed a commercial pelleted diet (10.70 MJ ME/kg energy, 13.20% protein, 0.80% calcium, 0.47% phosphorus and 12.80% fibre) including *Eragrostis tef* hay at 1 kg per day. Feed conversion ratio (FCR) and average daily gain (ADG) for carcass and meat at all slaughter points were determined by using the carcass weights and carcass composition of S0 as the starting point.

Phylogenetic relationships

Blood samples were collected from each animal at the commencement of the trial. Phylogenetic relationships between the subpopulations were studied using the gene frequency values obtained from the electrophoretic analysis of eight structural gene loci that code for blood-soluble proteins, together with 23 blood group loci. In addition, the genetic differentiation within the subpopulations was studied. Values of the genetic distances between subpopulations, the phenograms and cladograms, as well as the goodness-of-fit statistics of those dendrograms were computed using the BIOSYS-1 program (Swofford and Selander, 1981).

Carcass measurement

Carcass and buttock length were determined to calculate the carcass compactness. The right sides were quartered between the 9th and 10th thoracic vertebrae where the eye muscle area was measured as the length x width of the *M. longissimus thoracis* (LT). The two quarters of the right sides were processed into 15 wholesale cuts according to the London and Home Counties cutting techniques (Gerrard and Mallion, 1977) and Bisschop (1946, as described by Naudé, 1974), which were dissected into meat (muscle + intermuscular fat), subcutaneous fat (SCF) and bone. The composition of each cut and the whole carcass side, as well as the distribution of bone, meat and subcutaneous fat in the carcass side were determined from the weights of the various tissues. The meat and subcutaneous fat of the prime rib cut (8th to 10th rib; Figure 1) were ground, mixed and proximate analyses were determined for percentage protein, moisture, ash and fat (A.O.A.C., 1985). The percentage yield of muscle and total fat was calculated from the chemical (fat, ash, protein, moisture) and physical composition of this cut (Naudé, 1972). The LT of the wing rib cut (11th to 13th rib) of the right side was retained after separating bone, fat and lean to determine the degree of intra-muscular fat (marbling) (A.O.A.C., 1985).

Muscle biochemistry and histology and meat quality measurements

The LT of the prime rib and the whole wing rib cut were analysed respectively for collagen content and solubility (Bergman and Loxley, 1963; Hill, 1966 and Weber, 1973), and sensory and physical parameters. Three samples (approx. 50g each) of the *M. longissimus lumborum* (LL; 1st lumbar vertebrae) of the right side were retained, vacuum-packed and aged between 3°C±3°C for 1, 7 and 14 days, respectively, for the determination of the myofibrillar fragmentation index (MFI) according to the method of Culler *et al.* (1978), as adapted by Heinzé and Bruggemann (1994).

For the histochemical demonstration of succine dehydrogenase the nitro-blue tetrazolium technique of Malaty and Bourne (1953) was used. Fibres were classified by means of a video image analysis (VIA: Kontron Germany) into red, intermediate and white according to the intensity of the staining reaction. Fibre cross-sectional areas were also determined by VIA. The sarcomere length was also determined by means of VIA (Kontron Germany).

Wing rib cuts were used for sensory analysis and sampled directly after cooking, while the other half was designated for shear force measurement. Aroma intensity, juiciness, overall tenderness, residual amount of connective tissue and overall flavour intensity were evaluated on an 8-point scale. The samples were also analysed for shear force using a Warner Bratzler shear device mounted on an Universal Instron apparatus (Instron Corporation, 1990). The reported value in Newton represented the average peak force measurement.

Statistical analysis

Sources of variation were investigated by analysis of variance (ANOVA) or analysis of covariance (ANCOVA). ANCOVAs were performed using the general linear model facility of the Genstat 5 statistical programme (Genstat 5 Committee, 1993). Means separation was achieved by application of the Bonferroni Multiple Comparison Method at the 5% test level. Pairwise correlations were determined within breed to describe the linear relationships between any two characteristics.

RESULTS AND DISCUSSION

Phylogenetic relationships

The phylogenetic study revealed heterozygosity levels varying between 31% and 43% for the Bonsmara. The lowest level was observed in T, which is in accordance with the development of this strain, being the most inbred. The highest heterozygosity levels were observed in E and R, which represent the largest section of the Bonsmara population. The formation of two clusters was observed, one by W and another formed by the rest of the population, except the BR which separated from the hypothetical trunk very early. Within the second cluster, E and T showed a higher relationship, differentiating from R. E and R were more related than E and W. The cladogram was topologically similar to the phenogram (dendrogram), which corroborates the stability of the classification. The rate of inbreeding relative to the other strains in the breed, F_{is} , confirmed that T had the highest level (25.0%), followed by BR, W, E and R with F_{is} values of 22.7%, 21.0%, 16.2% and 15.4% respectively. The relatively high F_{is} values for BR and W were also expected since these strains are fairly low in animal numbers and therefore more prone to inbreeding. The genetic distances among the subpopulations confirm the existence of five genetic subpopulations.

Growth and carcass characteristics

The W strain of the Bonsmara gained live weight significantly less efficiently and at a slower rate (non-significant) than the other strains but in particular T and R. Similar trends were found for carcass and meat gain, showing differences between T, R and W of more than 30% for carcass and meat growth rate and 20% for efficiency of carcass and meat gain. T and R also showed a tendency for higher total carcass fat yield and subsequent lower muscle yield compared to W (adjusted for carcass SCF), while T and E tended to yield more total carcass weight (2.3%) and meat (1.9%) in the high-priced cuts, compared to W and BR. BR, the most unrelated strain, had a significantly lower hindquarter compactness (conformation) than E and also tended to have the smallest eye muscle area of all the strains. In support of the differences in growth and carcass characteristics, Korver *et al.* (1987) reported carcass composition differences between animals, even after adjusting for maturity, while Kempster *et al.* (1982) found differences in muscle to bone ratios for Charolais and Devon breeds of similar maturity types.

Meat quality characteristics

Sensory panel scores and shear force values, showed a 17% advantage in meat tenderness and MFI for W compared to T for muscle aged for 7 days. MFI was used to measure the degree of fragmentation of the myofibrils caused by proteolyses (Olson and Parish, 1997). Although Olsson and Tornberg (1992) regarded fragmentation of myofibrils not as a crucial factor determining muscle tenderness, Culler *et al.* (1978) reported that MFI accounted for 50% of the variation in loin steak tenderness and regarded myofibril fragmentation as a more important effector of tenderness than sarcomere length or collagen solubility (similar age). In addition, Crouse *et al.* (1991) and Seideman *et al.* (1987) reported correlation coefficients of 0.53 and 0.60 between MFI and sensory tenderness for muscle aged over a period of one to seven days compared to 0.40 ($P < 0.001$) in the current study.

Muscle fibre type differences in size and ratio occurred among the Bonsmara groups. Intermediate muscle fibre area of E and white muscle fibre area of E and R were respectively 25% and 34% larger than that of BR, while the percentage white fibre of E tended to be higher than that of W. These differences did not seem to have any direct effect on the differences in muscle tenderness despite a correlation of -0.45 ($P < 0.001$) between white muscle fibre percentage and sensory tenderness. Calkins *et al.* (1981), who found a negative relationship between white fibre area and tenderness, but a positive relationship between red fibre area and tenderness, illustrated the effect of variation in muscle fibre characteristics. Calkins *et al.* (1981) and Dreyer *et al.* (1977) also reported that an increased percentage of white fibres could be associated with a decrease in sensory tenderness. The lack of fibre type related differences in muscle tenderness in the current trial could probably be attributed to the fact that a whole pattern of events takes place when muscle changes to meat. These events are influenced by a variety of physiological and physical interventions that have a major bearing on the ultimate meat quality (Devine and Chrystall, 1992). In this study it appeared as if the fragmentation of muscle independently had the largest effect in this process and probably masked the effect of other factors on meat tenderness. The significant negative correlations between MFI and white fibre percentage confirm the negative effect of white fibres on tenderness. With regard to MFI, Seideman *et al.* (1987), reported that myofibrillar fragmentation on its own explained more of the variation in tenderness than

any fibre type characteristic (size or ratio), while Crouse *et al.* (1991) showed that the effect of fibre type ratio and size on the variation in tenderness was limited to three days of ageing, whereupon the effect diminished and fragmentation of fibres took place independent of fibre type variation. Meat in the present study was aged for seven days.

Regarding the stromal protein properties (connective tissue), one aspect could not be satisfactorily clarified. E had a significantly higher collagen solubility than the other strains, while R was superior to T, W and BR. A significant interaction between strain and slaughter group was found, which indicated that the collagen solubility of E was very high at S1, but then declined sharply to levels closer to the other strains at S3. In contrast, W, BR and T did not show any variation in collagen solubility between slaughter groups, while R was intermediate to E and the other groups. T and W, being the most unlike strains with regard to sensory tenderness, were the most similar in collagen solubility. According to Crosley *et al.* (1994), such collagen solubility differences are expected among animals with large physiological age differences. However, the animals in this trial were all between nine and 12 months of age. Furthermore, Naudé and Bocard (1973) reported much less variation in collagen solubility among a number of breed crosses slaughtered within the same age class as the animals in the current trial. Their data showed values for collagen solubility ranging between 32% and 34%, which are much higher than the average value in the current trial.

No significant correlation between shear force measurement or sensory tenderness and collagen solubility was found in the current study, which is in contrast to the findings of Crouse *et al.* (1985). Once again, it can be assumed that other muscle properties had a greater influence on sensory tenderness than collagen alone. In support of this statement, Seideman *et al.* (1987) reported that MFI, as well as the percentage red muscle fibre, contributed significantly towards differences in sensory tenderness and shear force, while collagen content and solubility and sarcomere length had relatively insignificant effects on tenderness.

Relationships between growth performance and muscle characteristics

In the light of the differences found between T and W, and N and NB for growth performance and certain muscle/meat quality traits, relationships between production and product characteristics were investigated by means of simple correlation. In addition to the significant correlations between MFI and muscle tenderness, MFI for meat aged for 7 days, also had a negative relationship with average daily gain (Bo: $r=-0.44$) and a positive relationship with feed conversion ratio (Bo: $r=0.46$) measured on a carcass basis. The relationship between growth performance and sensory tenderness followed the same pattern, although the correlations were much lower for the Bonsmara, viz. $r=-0.23$ for ADG (carcass; $P>0.05$) and $r=0.25$ for FCR (carcass; $P<0.05$). Calkins *et al.* (1987) speculated that, if an increase in the concentration of catheptic enzymes occurs during rapid rates of growth due to increased protein turnover, enhanced muscle tenderness should result due to an increased stromal (connective tissue such as collagen) and contractile protein degradation. However, their study did not show any increase in enzyme or palatability traits as a result of higher growth rates, although it may be argued that higher growth rates were artificially induced by the feeding regime and were not due to the intrinsic genetic ability of the animals. On the other hand, an animal genetically superior in growth performance is expected to have a higher rate of protein synthesis, or a lower rate of protein breakdown, or both. These processes are controlled by various muscle enzyme systems, such as the calpain system (calpain enzymes and their inhibitor, calpastatin), which also plays a major role in meat tenderisation *post mortem* (Koochmarai, 1992). Although overemphasised, the action of growth promoting agents, such as β -agonists, is an example of the effect of this enzyme system. They are known for their enhancing effect on growth performance and detrimental effect on muscle tenderness, mainly through the retardation of myofibrillar protein breakdown by the proteolytic enzyme system, regulated by calpastatin (Koochmarai, 1992). It is, therefore, possible that such a system of net-protein gain in genetically fast-growing more efficient animals is coupled to a retardation in the protein breakdown process *post mortem* in these animals, resulting in less tender meat. However, although relatively high correlations were found between MFI and growth performance on the one hand and growth, muscle tenderness and MFI on the other, the direct relationship between tenderness and growth performance was relatively low. This could probably be attributed to the fact that sensory tenderness is a culmination of a number of aspects, besides MFI, that might have influenced the judgement of the sensory panellist, such as marbling, sarcomere length, connective tissue properties, muscle fibre traits, etc.

ADG was negatively correlated with red fibre percentage ($r = -0.52$; $P < 0.01$) and positively correlated with white fibre percentage ($r = 0.39$; $P < 0.05$). These relationships, to a certain extent, support the hypothesis that less tender meat may be associated with fast growers.

CONCLUSIONS

Despite very definite phylogenetic differentiation between the strains of the Bonsmara, the only consistent differences relating to production (growth performance), as well as product quality characteristics (carcass and meat quality) were found between T and W. The superior growth performance, higher IMF to SCF ratio and higher distribution of meat to the early developing high-priced cuts, could suggest that T should be later in carcass maturity than W. The differences that occurred between the strains, especially T and W, although slight, are simply the result of the intentions of the breeder society to broaden genetic diversity, and may be coupled to the specific origins of the different strains (Bosman, 1988). T, although not a formal strain, has T-49 as the dominant sire, which was favoured by many breeders as a result of its growth performance and was, therefore, expected to perform in that regard. On the other hand, the progenitor of W, the bull Spanner, introduced the characteristics of Red Poll, instead of Hereford/Shorthorn into the breed, probably with the resulting growth performance and meat quality as discussed. Therefore, the variation within the breed is probably higher than in other straight-bred groups of animals, with emphasis on the fact that this variation is to a certain extent captured within strains. This enables the breeder to utilise the variation efficiently through well-maintained breeding records which is standard procedure in the breed.

The contrast found between growth performance and meat quality for T and W may suggest that selection for fast growing, more efficient animals in a breed, which, in effect, is a selection for increased net-protein gain, may be confounded with a retardation in the protein breakdown process in the muscle *post mortem*, resulting in conflicting production and product quality. Further investigation, probably by means of the determination of proteolytic system activities in the muscle, is needed to verify these findings, since there is no direct relationship between tenderness and growth performance.

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ASSOCIATION BETWEEN MILK PRODUCTION TRAITS AND SOMATIC CELL SCORES OF HUNGARIAN HOLSTEIN-FRIESIAN CROSSBREDS USING MULTI-TRAIT ANIMAL MODEL

A.A. Amin

Department of Animal Production, Faculty of Agriculture, Suez Canal University, 41522, Ismailia, Egypt

SUMMARY

Genetic and phenotypic correlations were estimated for means of \log_2 SCC (somatic cell scores: SCS) with milk production traits of sample test-day. Data of SCS and milk production traits for six genetic groups, Holstein-Friesian (HF), Hungarian Native Breed (NHB) and four of their crossbreds were used. Multi trait animal model was used for the estimation of genetic and phenotypic (co)variances. All estimates of correlations, genetic (R_g) and phenotypic (R_p), between SCS and milk production traits were negative except with protein percentage. Sample test-day estimates (STD) of R_g between SCS and each of daily milk yield (DY), fat (F%), protein (P%) and lactose (Lc%) percentages were -0.13 ± 0.07 , -0.13 ± 0.08 , 0.11 ± 0.04 , -0.11 ± 0.08 , respectively. STD R_p estimates were higher than R_g 's for SCS with DY and P%. STD R_g with F% decreased with parity. The highest estimate of STD R_g between SCS and DY was -0.25 for HF in the 4th lactation. STD R_g of SCS with milk composition ranged from 0.08 to 0.20 and -0.10 to -0.25 for HF vs. 0.01 to 0.13 and -0.07 to -0.32 for NHB. It could be concluded that, relationship of SCS with milk production differs among purebreds and their crossbreds according to percentage of crossing.

Keywords: Somatic cell, correlations, milk, Hungarian-Holstein Friesian

INTRODUCTION

Despite a reduction in the incidence of clinical and subclinical mastitis over the past 25 years in some developed countries (Booth, 1995), mastitis remains one of the most costly health problems of dairy cattle and a major source of economic loss to dairy farms. Young *et al.* (1960) reported that an average value of 0.89 for the genetic correlation between SCC and clinical mastitis while a value of 0.83 was obtained by Afifi (1968). Therefore, developing efficient dairy cattle industry depends to a great extent on the evaluation of association between mastitis expressed as its correlated trait (SCC) and milk production traits. Phenotypic correlations between SCC and milk yield tended to be more negative in older lactations than in early lactations ranging from -0.12 to -0.24 (Banos and Shook, 1990).

The aim of the present study is to investigate the genetic association of test-day measures between SCS and milk production traits in six genetic groups of Holstein-Friesian (HF) and Native Hungarian Breed (NHB).

MATERIALS AND METHODS

A total of 458348 lactation records from 172065 cows daughters of 873 sires in the first four parities were used. Sample test-day somatic cell count (SCC) and milk production traits for 14329 Holstein Friesian (HF) cows, 13021 Native Hungarian Breeds (NHB) and 144715 of their crossbred cows calving between 1993 to 1997 were provided by the local associations in Hungary. Crossbred groups involved in the present study were classified according to percentage of HF inheritance into: $<25\%$ HF genes, $\geq 25\%$ $<50\%$ HF genes, $\geq 50\%$ $<75\%$ HF genes and $\geq 75\%$ HF genes. The data set involved measurements of at least 5 months and maximum observations were not more than 14 months for all studied traits. Traits involved in the data set were the actual test-day somatic cell score (SCS), daily milk yield (DY), fat (F%), protein (P%), and lactose (Lc%) percentages. Measurements of somatic cell count were adjusted for calendar month of test, stage of lactation and test day milk (Zhang *et al.*, 1994; Charfeddine *et al.*, 1997). Cows were not required to have a 2nd lactation to be included in the 1st lactation analysis. All cows included in the 2nd parity analysis might have not a usable first lactation data but calved successively in the 2nd parity at not more than 50 months of age. Genetic and phenotypic correlations among the various SCS means and milk production traits were estimated using an animal model of MTDFREML package (Boldman, 1997) that includes both animals with records and genetically related animals with no records, $y = XB + Zu + e$. Where y is an $n \times 1$ vector (augmented to $t \times 1$ with the additional of a $t-n$ null vector when evaluating animals without records) of observations on

the trait of interest; X is an $n \times p$ incidence matrix; Z is a $t \times t$ matrix equal to an $n \times n$ identity matrix relating observations to the animals that made them and augmented by null rows and vectors for animals that are to be evaluated but have no records; B is a $p \times 1$ vector of known fixed effects (farm, parity, age of calving within parity); u is a $t \times 1$ vector of random breeding values, which can be partitioned into u_1 , and $n \times 1$ vector representing animals having records and u_2 , a $(t-n) \times 1$ vector for related animals with no records; and e is an $n \times 1$ vector of random errors.

Thus,

$$E \begin{bmatrix} y \\ u \\ e \end{bmatrix} = \begin{bmatrix} XB \\ 0 \\ 0 \end{bmatrix}, \text{ and } V \begin{bmatrix} y \\ u \\ e \end{bmatrix} = \begin{bmatrix} V \dots \dots A\sigma^2_a \dots \dots I_n\sigma^2_e \\ A\sigma^2_a \dots \dots A\sigma^2_a \dots \dots 0 \\ I_n\sigma^2_e \dots \dots 0 \dots \dots I_n\sigma^2_e \end{bmatrix}$$

where $V=A^{-1}\sigma^2_a+I_n\sigma^2_e$, A = additive genetic relationship matrix, σ^2_a = additive genetic variance and σ^2_e = residual variance. SCC has been transformed to SCS with the base 2 log scale as $SCS=\log_2 [3+(SCC/100)]$ accepted by the National Co-operative Dairy Herd Improvement Program of the USA as a standard recording form for SCC (Rogers *et al.*, 1991).

RESULTS AND DISCUSSION

Table (1) shows estimates of R_g and R_p between all studied traits. R_g of SCS with milk traits were mostly negative. These results indicate that the increased somatic cells in milk yield are genetically associated with a slight decrease in milk yield, F% or Lc%. The highest relationships of SCS, either R_p or R_g , were obtained with DY. Results in Table (1) also show great differences between estimates of R_p and R_g of DY with F% and P%, while approximately similar values of R_p and R_g were obtained for the relationship of DY with SCS. Results of the present study were generally consistent with previous reports (Majjala and Hanna, 1974; Hargrove *et al.*, 1981; De Jager and Kennedy, 1987). R_p of SCS with Lc% was much lower than the corresponding R_g , which may indicate that lactose genetically decreased under mastitic conditions. R_g for Lc% with each of P% and F% were high, and ranged from 0.50 to 0.53 (Table 1).

Table 1. Sample test-day genetic (above) and phenotypic (below) correlations between different studied traits

	DY	F%	P%	Lc%	SCS
DY					
F%	-0.27±0.07				
P%	-0.33±0.18	0.38±0.14			
Lc%	-0.09±0.10	0.53±0.24	0.51±0.12		
SCS	-0.15±0.07	-0.09±0.11	0.12±0.07	-0.01±0.08	

DY: Daily milk yield, F%: Fat percentage, P%: Protein percentage, Lc%: Lactose percentage, SCS: Somatic cell score.

Correlations of SCS with milk traits within genetic groups

Phenotypic correlations (R_p) of SCS with milk traits are represented in Figure (1). R_p 's were high for crossbred of high HF inheritance than NHB and crossbred of low HF inheritance. Results in Figure (1), show that R_p of SCS with DY and F% changed across different genetic groups. Increasing R_p of SCS with F% was lower than of SCS with DY in HNB, <25%HF and ≥25-<50%HF. On the other hand, R_p 's of SCS with DY and F% were similar in HF. R_p estimates (Figure 1) of SCS with P% were positive and increased progressively with increasing HF inheritance, while this estimate for NHB was higher than for <25%HF. Results in Figure (1) show that STD may constitute a statistical model which reveal real association of SCS with each of F% and DY especially for HF and crossbreds with high HF inheritance. Genetic correlations (R_g) between SCS and milk traits in different genetic groups are shown in Figure (2). R_g estimates of SCS with P% were less than 0.05 for NHB and <25%HF. Moreover, no notable change in R_g of SCS with P% among NHB with <25%HF, ≥50-<75%HF and ≥75%HF was observed. Changing rate of R_g for SCS with P% from crossbred of low to medium HF inheritance crossbred (≥25-<50%, ≥50-<75%) was greater than the corresponding change rate from medium inheritance crossbreds to HF. Medium HF inheritance crossbreds had higher for only R_g estimate of SCS with F%. In general these results reflect the increasing trend of relationships with increasing HF inheritance. Estimates of R_g

for SCS with DY, F%, and Lc% declined with HF genes except in ≥ 50 -<75%HF, where positive R_g was observed for DY (0.1). Notable reduction of R_g for SCS with Lc% was shown in ≥ 25 -<50%HF.

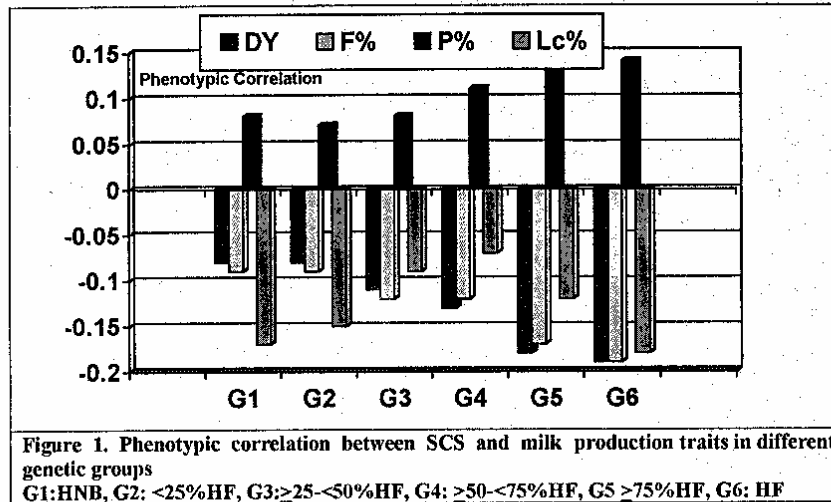


Figure 1. Phenotypic correlation between SCS and milk production traits in different genetic groups
G1:HNB, G2: <25%HF, G3:>25-<50%HF, G4: >50-<75%HF, G5 >75%HF, G6: HF

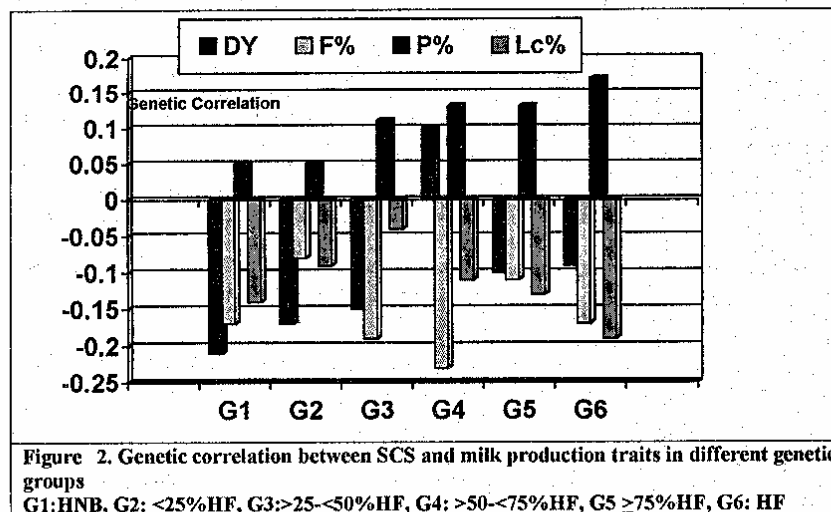


Figure 2. Genetic correlation between SCS and milk production traits in different genetic groups
G1:HNB, G2: <25%HF, G3:>25-<50%HF, G4: >50-<75%HF, G5 >75%HF, G6: HF

Correlations of SCS with milk traits within parity

Genetic and phenotypic correlations between milk traits and SCS in the first four parities are presented in Table (2). R_g 's for SCS with DY were negative and increased from 2nd to the 4th parity. R_g and R_p of SCS with F% decreased with parity. Downward trend was shown for R_p of SCS with DY. These results are in agreement with other reports (De Jager and Kennedy, 1987; Charfeddin, 1997). On the other hand, some studies indicated that the genetic correlations of MY with SCS within the early lactations were positive and ranged from 0.12 to 0.48 (Kennedy *et al.*, 1982; Monardes *et al.*, 1985; and Banos and Shook, 1990). The highest R_g estimates in the present study were -.16, -.14, .13 and -.13 in the 4th, 2nd, 2nd, 1st parities for DY, F%, P% and Lc%, respectively. These results indicate that, expected correlated response in milk production through selection against SCS will be more efficient if P% is genetically restricted in selection index. Schutz *et al.* (1990) found genetic correlations between SCS

and MY ranging from -0.15 to -0.28 in different lactation and suggested that mastitis, as indicated by SCS, is more common during early lactations of cows of sires that transmit higher milk yield, perhaps because of the stress from high productivity of milk. The highest R_p estimates were presented mainly in the 1st and 4th parities and differences between these estimates were very small.

Table 2. Sample test-day genetic and phenotypic correlations between somatic cell score and milk production traits per parity

Parity	R_g				R_p			
	DY	F%	P%	Lc%	DY	F%	P%	Lc%
1 st	.10±.11	.13±.04	.10±.04	-.13±.07	-.14±.07	-.11±.03	.07±.01	-.12±.09
2 nd	-.12±.07	-.14±.07	.13±.01	-.08±.01	-.11±.08	-.11±.07	.07±.05	-.08±.08
3 rd	-.14±.01	-.10±.03	.12±.09	-.12±.02	-.12±.01	-.09±.01	.11±.03	-.11±.07
4 th	-.16±.07	-.08±.11	.08±.11	-.04±.01	-.20±.11	-.07±.09	.12±.09	-.07±.04

DY: Daily milk yield, F%: Fat percentage, P%: Protein percentage, Lc%: Lactose percentage
 R_g : Genetic correlations, R_p : Phenotypic correlations

Correlations between SCS and milk traits within genetic groups within parities

Estimates of R_p and R_g of SCS with milk traits in different genetic groups within parities are presented in Table (3).

SCS with DY: Estimates were negative in all parities except in the 1st parity where positive. R_g 's in the 1st parity corresponded to negative R_p 's for each genetic group. The highest R_p (>0.20) was obtained for HF, <25%, and NHB in the 4th, (2nd & 3rd), and 1st parity, respectively. In General the highest genetic correlation estimates of SCS with milk yield were mostly obtained in the 4th parity for HF and NHB. While crossbreeds showed moderate estimates in deferent parities. This may suggest that SCS in the early and late parities may be genetically considered different traits, implying that selection in the early lactations could be more effective to reduce SCS and increase mastitis resistance. Estimates of R_p decreased with HF inheritance. Small differences among R_g 's within the 1st parity with advancing percentage of HF inheritance were observed compared with those in other parities. Differences between estimates among different genetic groups may reflect true genetic differences across all genetic groups used in the present study.

SCS with F%: R_g of SCS with F% within different parities in various genetic groups were mostly lower than the corresponding estimates with DY. However, this result is more obvious in the <25%HF genetic group. The highest R_g of SCS with F% was -0.27 found in the 3rd & 4th parity (Table 3). Differences between the highest R_g of SCS with DY and SCS with F% were small. Moderate values of genetic correlations among milk constituents may lead to the conclusion that measures of sample test day could be used as a reliable prediction indicator of the production in cases one or more component of milk production traits are missed in monthly observations.

SCS with P%: All estimates of phenotypic and genetic correlations were low to moderate and positive. Genetic correlations ranged from .01 to .20, while phenotypic correlations ranged from .02 to .22 and were nearly in agreement with previous works (Maijala and Hanna, 1974; Hargrove *et al.*, 1981; De Jager and Kennedy, 1987). R_g estimates of SCS with P% were very small (.01 to .09) across different genetic groups in the 1st parity. While R_p of SCS with P% in the 4th parity were very low except for HF and ≥75%HF. The highest R_p for medium HF inheritance crossbreeds (≥25-<50%, ≥50-<75%HF) ranged from 0.15 to 0.19 in the 2nd and 3rd parity. The highest R_p for NHB and <25%HF ranged from 0.10 to 0.13 in the 1st and 2nd parity. Estimates of R_p in HF and >75%HF increased with advancing order of lactation while changing rate was approximately similar across parities. Changes of R_p among various parities for HF were much greater than the corresponding changes across genetic groups in the 1st parity. Generally, negative relationship of SCS with F% and positive association of SCS with P% may suggest that sires that transmit higher SCS can also transmit the inheritance of milk with lower F% and higher P%.

SCS with Lc%: Estimates of correlations between Lc% and SCS were in general negative. Among all studied groups the highest R_g 's were -0.30, -0.27, and -0.21, obtained in the 3rd, 4th and 2nd parity for HF, respectively. These estimates were the highest correlations obtained for various relationships of SCS with milk production traits. This may indicate that a notable decline in Lc% in milk will occur under mastitic conditions in HF cows. R_g and R_p of SCS with Lc% were mostly higher than the corresponding estimates for SCS with F% of HF. These results may suggest that correlated responses to single trait selection against SCS might result in remarkable improvement in Lc%. Phenotypic