HETEROGENEITY OF WITHIN-HERD VARIANCES FOR CONFORMATION AND ITS RELATIONSHIP TO VARIOUS HERD PARAMETERS IN THE U.S. HOLSTEIN POPULATION

by

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Dissertation submitted to the Faculty of the
Virginia Polytechnic Institute and State University
in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

in

Animal Sciences (Dairy)

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March 1989

Blacksburg, Virginia

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ABSTRACT

Two data sets of first-parity classification records were analyzed to examine heterogeneity of variances for conformation in the U. S. Holstein population. Data set I included records for final score and linear descriptive traits on cows scored from 1983 through 1986. Results indicated a strong negative correlation ($r = -.59$) between within-herd standard deviation for final score and herd-mean final score.

Regression analysis suggested a curvilinear decrease (concave up) in within-herd standard deviation for final score with increasing herd-mean final score. Within-herd standard deviations for linear descriptive traits demonstrated a linear decline with increases in herd-mean final score.

Daughter contemporary deviation for final score was regressed on her sire's Predicted Difference type within 25 mean/standard deviation subclasses. Response to selection was greatest in high-mean/variance herds and least in low-mean/variance herds.

Restricted maximum likelihood estimates of sire and error variance were approximated within each of 5 herd-mean subclasses of the data. Regressions revealed environmental variance for final score decreased curvilinearly (concave up) with increasing herd-mean final score. Genetic variance declined linearly. Heritability demonstrated no significant trend. For most linear traits, environmental variance decreased linearly with increasing herd-mean final score. Linear decreases in genetic variance were noted for foot angle, udder depth and rump angle. Heritability had positive trends for body depth, angularity, rear udder height, udder support, and teat placement.

Data set II included first-parity final scores on cows classified from 1967 to 1986. Relationships estimated between herd mean and within-herd variance for final score on recent data were confirmed. Positive trends over time were noted for: within-herd standard deviation for final score, the antagonistic relationship between herd mean and within-herd variance, the antagonistic relationship between average Predicted Difference type and within-herd variance, and average herd-mean Predicted Difference type.

Results indicate selection for final score was occurring in the population. Differences in within-herd selection differentials accounted for 24% of the differences in within-herd variance for final score.

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INTRODUCTION

Genetic evaluations for production or type traits assume within-herd variances are homogeneous throughout the population. Violation of this assumption could result in erroneous estimates of transmitting ability and mask true selection differentials. Thus, candidates for selection might not be truly elite with regard to genetic potential. If one considers additive relationships between individuals in estimating transmitting abilities, the problem magnifies. Improper evaluations for individuals contribute to erroneous evaluations of their relatives, and the problem perpetuates itself through generations.

With regard to selection differentials, heterogeneous variances result in more individuals being selected from more variable populations. This may or may not be advantageous, depending on heritability of the trait in the population of interest. However, heterogeneity of within-herd variance for any quantitative character should be considered in breeding strategies aimed at maximizing genetic progress. For production traits, the problem of heterogeneous within-herd variances is well-documented. Relationships between within-herd variance and herd mean for production have been estimated for the U. S. Holstein population. Relationships among within-herd variability and other herd parameters have also been established. Those investigations were the first steps toward developing methods to correct the problem. They provided insight into grouping strategies and other methodologies as potential solutions.

The extent of heterogeneous within-herd variances for conformation traits is not well known in the U. S. Holstein population. Relationships between within-herd variance and various herd parameters have not been established. The effect of

herd-level for type on both genetic and environmental variance should be considered. Heterogeneous variances and selection response in different herds are also a matter of importance. Work is needed to examine factors influencing within-herd variability and its stability over time. Answers to these questions would provide a knowledge base for developing solutions to the problem. Our objectives in the following manuscripts were: (1) to determine the existence of heterogeneity and quantitate relationships between phenotypic, genetic, and environmental estimates of within-herd variance for final score and linear descriptive traits and herd-mean final score, (2) to examine associations between other herd parameters and within-herd variability for conformation, (3) to estimate response to selection for Predicted Difference type in herds differing in mean and variance for final score, (4) to estimate trends for within-herd parameters over time, (5) to determine if selection for type influences differences in within-herd variance for final score.

REVIEW OF LITERATURE

Genetic and Environmental Differences Among Herds

In 1935, Plum (44) investigated causes of variability in butterfat production for cows in Iowa testing stations. Breed differences accounted for only 2% of the total variation. Herd had a much larger effect accounting for 33% of the variance. These differences were mostly managerial but did include some genetic variability. Differences among cows within herd were considered mostly genetic. However, permanent environmental effects also contributed to among cow variability. This component comprised 26% of total variance. Within-cow differences were considered as: feeding variations within the herd, other year-to-year differences, length of dry period, and season of calving. These effects accounted for 6%, 1%, 1%, and 3% of the total variation, respectively. This study suggested, even after accounting for age, feeding, dry period, season of calving and general level of management, a considerable portion of the variance in butterfat production was still unexplained.

Johnson (28) utilized records collected up to 1938 by the Holstein-Friesian Association of America to determine importance of progeny uniformity in sire evaluation. Sires' first ten daughters were used in assessing differences in uniformity of progeny for butter fat production. This study represented a total of 256 progenies. For daughter groups, a range of 95 pounds characterized the least variable group, while a range of 728 pounds was seen in the most variable group. These data indicated some progeny groups were definitely more uniform than others. Differences in uniformity of sires' progeny were also supported by later work (10,61,69). The author noted many factors, other than sire, could contribute to

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these differences. Management practices, such as feeding according to production as opposed to group feeding or differential culling criteria, were considered major influences. The effect of sire on daughter uniformity was estimated at .16 and deemed small. Thus, management played the major role. This was supported by Robertson and Rendel (49) who analyzed records from 1400 heifers obtained through artificial insemination. Evidence suggested only 10% of the differences in yield among herds was genetic in origin. Genetic influence on fat percentage seemed more substantial. However, evidence was not very conclusive.

Robertson and McArthur (48) used data from a small group of herds, important in producing bulls for the British-Friesian breed, to investigate herd differences. They chose samples of bulls from dominant herds. Bulls were categorized into different studs which consisted of herds under similar breeding regimes. Weighted differences between yield of a bull's daughters and contemporary herd mates were computed with no attention given to the level of herds where daughter's performed. Thus, they assumed no bias in favor of bulls from one stud over another when they were used in genetically dissimilar herds. As with other studies (9,28,49) only a small portion (12%) of the among stud variability was genetic. Authors cited similar work (9) with Jerseys. Although the study was lacking in statistical analysis of data, Robertson and McArthur (48) applied their methods and estimated among stud differences at 20%.

Pirchner and Lush (43) used two methodologies in estimating fraction of additive differences among herds. In method one, within-sire regression of heifer production on herd average was determined. If among herd differences were entirely environmental, this regression would approach unity. If inter-herd differences were entirely genetic, the regression should approach a theoretical limit

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of .5. In method two, the variance component for herd differences for half-sibs in different herds was compared to that of unrelated individuals in different herds. In this analysis, the herd component between unrelated cows in different herds would be expected to represent all differences in average breeding value and average environment of the herds. For paternal half-sibs in different herds, the herd component should contain all environmental and one quarter of the additive genetic differences. Assuming dominance and epistatic influences were nearly random between herdmates, the difference in the two herd components should have contained three quarters of the additive differences among herds. This estimate was used to determine total genetic differences between herds.

Method one was applied to records on 1,072 Jerseys and 880 Holsteins. Results indicated that 14% of the differences among Jersey herds was heritable, where for Holsteins, the estimate was 10%. Method two was used on records of 2903 artifically sired Holstein heifers and 735 of their dams. This method estimated the heritability of herd differences at 6.5%. These estimates were supportive of estimates given in other work (44,48,49). Since much of the data came from herds which had previously used natural service heavily, the authors postulated that expanded use of artificial insemination techniques would eventually minimize all genetic differences among herds.

Freeman and Henderson (16) analyzed records on 1210 Holsteins in 11 commercial herds to characterize additive and dominance relationships among individuals within herds. Results indicated dominance relationships were practically nil. The average additive relationship among individuals within a herd was .07 and the heritability of herd differences was approximately 5%. However, they noted that differences in selection goals and selection intensities were not considered in the

study. These factors could increase heritability for among-herd differences.

Wiener (72) used twin data to investigate genetic differences among herds. Sixty-five sets of twins were split at birth and placed into high and low yielding herds. Regressions of individual performance on herdmate average were not significantly different from unity implying differences were mostly environmental in nature.

Brumby (5) also used twins in the second part of a two-part study. Initially, young calves (240) were taken from 40 herds of different production levels, and raised and milked under identical management conditions. Additionally, 120 sets of identical twins were divided among the 40 high and low producing herds. This study indicated an important genotype by environmental interaction for milk production. Although marked differences in production per cow were noted for different herds, genetics played a minor role. In general, genetic differences for milk production between high and low producing herds were very small. Thus, similar genotypes performed differently under varying management situations. However, approximately 50% of herd differences were genetic for butterfat and protein percentages. This percentage was estimated at 25% for solids-not-fat.

In 1970, Miller (38) examined intra-sire regression of daughters on herdmate average to determine regional and breed differences in the regression coefficient. Data included 418,139 mature-equivalent lactation records representing five breeds across various regions of the country. Results suggested heritability of herdmate averages did vary among breds. For milk yield, Guernseys (.91) and Holsteins (.90) had the largest regression suggesting the smallest degree of genetic variation among herds. Jerseys (.85) and Brown Swiss (.84) had the lowest regression coefficients while Ayrshires (.87) were intermediate. The variability of genetic differences among herds between Jerseys and Friesians were reflective of that found in other

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studies (43,48).

For fat percent, Holsteins (.73) and Ayrshires (.74) demonstrated the least inter-herd genetic differences. Regional differences in coefficients for fat percent and milk yield were evident with the South (.79) and California (.85) having the largest coefficients for fat percent. For milk yield, New England (.91), the South (.93), and California (.95) had the least amount of genetic variability among herds.

Potential regional differences in genetic variability among herds was illustrated by McDaniel et al. (36). This potential was reflected in differences among herdmates' sires average transmitting ability for milk. In Holsteins, average predicted difference milk of herdmates' sires varied by as much as 134 kilograms between regions. This difference was 174 kilograms among the averages for the lowest and highest stud.

With regard to breed differences in the regression coefficient, Miller (38) suggested two sources of variability. The first was basic differences among breeds in the heritability of individual records. The second was variation among breeds in the average genetic relationship among cows within a herd relative to relationships between random members of the population.

Some work (10,61) suggested the effect of sire on progeny variability might be larger than first reported (28). VanVleck (61) suggested that 40-60% of differences in intrasire daughter variances were attributable to the sire. Repeatabilities of within-sire variance from year to year were calculated to give some indication of the degree to which sires contributed to heterogeneity of variance for production.

Clay et al. (10) found significant differences among sires for variability in daughters' milk records. Upon analysis of sire by herd subclasses, they cautiously

inferred that sires and herds contributed almost equally to differences in daughter variance. Although standard errors were somewhat large, these results suggested that daughter variability was under at least partial genetic control.

In 1972, Mao et al. (33) analyzed 900,000 milk records from New York Holsteins. They reported a declining trend over time in estimates of genetic variation among herds relative to total variation among herds. They suggested this result could be attributable to herds becoming more homogeneous genetically and/or more heterogeneous environmentally. The relative decline in genetic variability among herds could be expected if one assumed genetics and environment were independent. The use of artificial insemination through the 1950's may have greatly influenced genetic diversity. Gradual adoption of artificial insemination had produced a peak in relative genetic heterogeneity between herds around 1959, followed by a decline in relative additive genetic variability among herds of about 1% per year. As did Pirchner and Lush (43) and Mao et al. (33) foresaw almost all variability among herds as environmental in a few decades.

The limited role of genetics in defining differences among herds was also demonstrated in later studies (40,52,56). Using Canadian data, Schaefer et al. (52) determined herd genetic differences accounted for only 2.05% of herd phenotypic variance for milk yield and 12.74% for fat percentage. Thus generally, herd genetic differences appeared small. Morillo and Legates (40) suggested genetic differences among Holstein herds were small but real. They estimated genetic differences contributed about 10% to variance among herd averages for milk. This estimate was very similar to that given by Spike and Freeman (56) using 693 herds in Iowa, Kansas, and Missouri.

The concept that differences among herds for various traits are real has been

well documented. Generally, it has been illustrated that environmental factors are mostly responsible. Degree of genetic influence varies by trait, stud, geographic region, and other factors. Although genetic differences are considered small relative to environmental differences, they should be taken into account to obtain higher accuracy in genetic evaluations (55).

Conditions Affecting the Magnitude of Heritability

Genetic and environmental differences, among herds and management levels, sparked interest in investigating variability in the heritable fraction of certain quantitative traits. Not all research has demonstrated the same results. In 1953, Johansson (27) studied 29 herds of Swedish Red and Whites to investigate phenotypic levels and heritability of butterfat production under differing environmental conditions. Twelve herds, categorized as low level, were averaging less than 124 kg butterfat per cow per lactation. Seventeen high level herds were averaging greater than 145 kg butterfat per cow. Results indicated heritability for butterfat production was only slightly less in the low level herds. This work suggested genetic differences were not necessarily more obvious in better environments.

In 1956, Mason and Robertson (34) reported an increase in heritability with increased production levels based on results from 13,000 artificial insemination cows from Denmark. Herds were divided into three production levels. With increased production level, phenotypic variance increased while the coefficient of variation declined slightly. However, genetic variance demonstrated a substantial increase with increased level of production. Thus, estimates of heritability were higher.

Burnside and Rennie (6) analyzed 40,374 records to determine the heritability of milk yield at different production levels. Estimates were by the paternal-half sib

method and calculated at seven levels of production. Estimates were higher for intermediate levels and less at either extreme. Plotting estimates against levels (low to high) yielded significant ($P \leq .07$) quadratic response. Some differences could have been due to sire selection at different levels. A check of 9 sires did reveal similar rankings at all levels.

Legates (29) used intra-herd-sire estimates of heritability for fat yield to examine their relationship with herd level. Data contained 1825 Guernsey, 5458 Holstein, and 3,465 Jersey daughter-dam pairs. Results indicated no significant relationship between herd level and heritability estimate for any of the breeds. Definite increases in phenotypic and genetic variance accompanied increases in herd production. However, the coefficient of variation declined. This work suggested using different heritability estimates for herds at different production levels would not aid in developing selection procedures.

Touchberry (57) investigated heritabilities of milk yield, fat yield, and fat percent at different milk production levels using records from 20,024 Holstein daughter-dam pairs. Pairs were placed in 20 categories of production level each with a range of 400 pounds of milk. Estimates of heritability averaged .251, .251, and .571 across classes for each trait, respectively. For milk production, heritability estimates did not vary across production levels. Estimates for fat percent increased significantly while estimates for fat yield decreased as production level increased.

VanVleck and Bradford (62) analyzed 5,740 Holstein-Friesian daughter-dam pairs to examine heritability of milk yield at different environmental levels. Estimates were obtained at ten environmental levels. Results indicated daughter-dam estimates of heritability were essentially constant at all levels. This study also utilized a smaller data set of 2,568 records to estimate heritabilities by

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paternal half-sib correlations. Although the analysis only used four environmental levels, heritability did increase with improved herd production level. These conflicting results raised questions regarding estimation procedures. In another article, Bradford and VanVleck (3) noted potential problems with the parent-offspring method of estimating heritability. These included environmental correlations or large epistatic components of variance. In later work, VanVleck (58) stated that daughter-dam estimates of heritability could be highly susceptible to bias from changes in variance from time of dam's generation to time of daughter's generation.

More recently, Hill et al. (24) obtained records on daughters of British Friesian sires. Herds were split into high and low categories in three separate analyses. In the first analysis, grouping was on mean milk production while in subsequent analyses, grouping was on within-herd variance and coefficient of variation, respectively. Heritabilities for milk production were estimated within each level using untransformed and log transformed data. When data were split on mean production, estimates using untransformed data were .24 and .30 for low and high levels, respectively, and .25 and .35. for log transformed data, estimates were Correspondingly, for low and high levels of within herd variance, estimates were .24 and .30 for untransformed data and .27 and .36 were transformed data. When coefficient of variation was used to group herds, estimates were .22, .26, .26, and .32, respectively. The differences in heritability estimates for milk yield seen here were similar to those reported by Danell (11). Heritability estimates were .21, .25, and .28 at low, medium, and high levels of production.

Powell and Norman (45) classed lactation records by ranges of herd-average yield in 1979. Classes were less than 6000 kg, 6000 to 6999 kg, 7000 to 7999 kg, 8000

to 8999 kg, and 9000 kg or greater. Heritabilities were estimated within sire by twice the regression of Modified Contemporary Deviations of Holstein dams on those of their first daughters. Results demonstrated higher estimates of heritability in higher yielding herds.

Lofgren et al. (31) estimated heritabilities of milk yield at three levels of herd mean and variance. Data included lactation records on all Jerseys and 10% of Holsteins born after 1963. Records were grouped separately by mean and standard deviation for Modified Contemporary Average (MCA). When records were grouped on mean, results differed between Holstein and Jersey populations. In Holsteins, estimates were higher in low and high groups. Heritability was lowest in the middle group. This differed from other studies (6,11,24,35,45) where estimates increased with increases in herd mean. In Jersey data, heritability estimates increased with increasing levels of herd production. When herds were grouped by standard deviation for MCA, Holsteins did have slight increases in heritability estimates with increasing herd variance. However, these increases were near nil given standard errors of estimates. Again, Jerseys showed marked increases in heritability for milk yield as herd variance increased.

Boldman and Freeman (41) estimated heritabilities within three production levels by Restricted Maximum Likelihood, using an animal model. Production levels were determined on the basis of the average mature-equivalent milk yield of all cows freshening in the same herd-year. Results indicated heritability did increase with increasing production levels. The largest increase came between the low and medium production levels. They concluded using common heritabilities for all levels of production could result in incorrect rankings of elite cows.

Generally, most research in this area has reported increases in phenotypic

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and genetic variance with increased levels of milk production. However, not all work has indicated increases in heritability estimates. Results from various studies have suggested the potential for varying heritabilities at different production levels was real. Thus, the consequences, relative to selection and genetic evaluations, could be of significant importance.

Impact of Heterogeneous Variance on Genetic Evaluation and Selection Differential

Hammond (20) noted gene action was limited to only those manifestations which are physiologically possible. Certain environments, which affect animal physiology, have selective influential effects on genes contributing to phenotypic expression of a trait. He suggested selection be pursued in the most advantageous environment.

Falconer (15) explained that a character, measured in two different environments, was like different characters. Environments were regarded as differing treatments applied in order to measure the characters. His approach was analogous to dealing with correlated characters under selection. An optimum selection environment was established by using a ratio of indirect to direct selection response. He concluded only large increases in heritability could justify selection in an environment other than where the breed of interest exists.

Dickerson (13) stated that: "in the broad sense, there are no independent genetic and environmental variations in animal performance." He presented evidence suggesting poultry-farm environments in California were variable. This variability spurred important but unpredictable changes in rankings of genetic stock for egg production. This knowledge implied genetic evaluations should represent

animals tested over a wide range of environments.

The effect of differing herd environments on genetic evaluation and selection in cattle was investigated in the early 1960's. Robertson et al. (50) estimated transmitting abilities for 57 Friesians, 8 English and 11 Scottish Ayrshires, within three herd management levels. Correlations between breeding value estimates at each level were near unity. They concluded daughter records, regardless of management level, could be used with confidence in sire evaluations. VanVleck (59) added support to this argument. He noted correlations between sire breeding values estimated in different environments minimized the influence of a genotype by environment interaction in the usual sense.

In later work (35), McDaniel and Corley examined relationships among breeding values of 40 Holstein sires calculated at different levels of herd production. Progeny of sires were stratified in four groups according to milk yield of herdmates. Predicted Difference for sires had an average decrease of 289 kg from low to high herdmate groups. However, correlations between progeny means were high across herdmate groups. Authors suggested that sires ranked about the same at different herdmate levels.

Vinson (68) characterized the potential effect of heterogeneous within-herd variance on sire evaluation. If heterogeneity were ignored, progeny performance of a sire would be weighted relative to within-herd variance where progeny performed. Progeny performing in highly variable herds would have the greatest influence on the evaluation. Influence of progeny in less variable herds would be less. With equal distribution of a sire's progeny across herds, sire evaluations would not be greatly affected. VanVleck (66) supported this conclusion.

Very recently, Winkelman and Schaeffer (70) studied the effects of

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heterogeneous within-herd variances on genetic evaluation of dairy sires in Canada. Results indicated that accounting for heterogeneous within-herd variances did not improve the accuracy of sire evaluation. A comparison of four models revealed ignoring heterogeneity of within-herd variances, as opposed to accounting for it, gave the largest correlation of sire transmitting abilities between two data sets formed by randomly splitting sire progeny groups.

Selection of dams of sires had much greater potential to be influenced by heterogeneous within-herd variances than selection of sires (66,68). Vinson (68) maintained that high performing cows would be over-evaluated in high-variance relative to low-variance herds. This effect could mask true selection differentials in bull dams. VanVleck (66) also suggested all herds did not have an equal chance to produce dams of sires.

With regard to cow evaluation, Everett et al. (14) utilized herds of equal genetic merit to demonstrate elite status was more probable for cows in herds with large residual variance. Additionally, Powel et al. (46) reported more elite cows in herds at higher production levels, even when sire merit was similar. This was attributed to higher standard deviations, of cows deviated production records, in higher producing herds. They suggested that cow deviation in highly variable herds might receive undue weight in estimating cow transmitting abilities. However, they contended that higher heritability estimates in high producing herds partially justifies the bias. This was supported by Garrick and VanVleck (18) who argued that selection, assuming homogeneous within-herd variances, can be very efficient when heritability is higher in more variable herds.

Lofgren (30) noted erroneous estimates of a cow's transmitting ability can be carried over into the next generation through the pedigree portion of the Cow Index

formula (25). Use of an animal model to estimate transmitting abilities could be even more susceptible to this problem since it would include more relatives.

Within-Herd Variance and Herd Mean for Yield

Some evidence indicating a positive relationship between mean yield and variance was obtained as early as 1945. Johnson (28) found a slight tendency for high herd average fat production to accompany increased variation in Holstein data collected prior to 1939. The correlation coefficient for herd-mean yield and variability was estimated at .21. Similarly, Everett et al. (14) estimated the correlation between within-herd error standard deviation and mature equivalent herd average at .24.

In 1963, VanVleck (58,59) considered genotype by environment interaction in sire evaluation. New York data indicated both genetic and non-genetic variability for milk yield was greater in more optimum environments. This work demonstrated high correlations among breeding values estimated in different environments and downplayed genotype by environment interaction in the usual sense. However, the positive relationship between herd mean and variance indicated a need for transformation. VanVleck noted this unusual genotype by environment interaction could lead to more pronounced traditional genotype by environmental effects.

In subsequent work, VanVleck (58) noted increases with time in within herd-sire and total variance of milk records. This trend was seen for both mature equivalent and deviated from herdmate lactation data. Increases were attributed to increases in mean milk production. Additional evidence, given by Mirande (39), suggested residual variation for milk had increased with time. Larger standard deviations were also associated with high herd production.

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Danell (11) also found a positive relationship between herd mean and variance for milk production. Data were grouped into either low, medium, or high production categories with phenotypic variance was greatest in the high group and least in the low group. An increase in genetic variance was even more pronounced than for environmental variance.

Additional evidence was presented by Brotherstone and Hill (4) whose analyses indicated considerable heterogeneity of variance for milk yield. However, results indicated that heterogeneity was not simply a matter of scaling since they also found inter-herd heterogeneity in the coefficients of variation. These differences were presumed to be the effects of various management alternatives and preferential treatment of certain animals.

Pearson et al. (42) estimated the correlation between herd mean and within-herd variance for milk and fat yield at .4. This estimate was the result of work by Meinert et al. (37) who regressed Modified Contemporary Deviations (MCD) on sire's Predicted Difference for milk (PDM). Regression coefficients increased from lowest to highest mean and variance herds which suggested change in the covariance structure between PDM's and MCD's across different levels in within-herd variance.

Some of the most recent work considering within-herd variance and herd level for production was by Boldman and Freeman (41). They obtained estimates of additive genetic, residual, and permanent environmental variance under a sire-dam model. Using low, medium, and high production categories assigned according to mean mature-equivalent yield, estimates were obtained within each group. With untransformed data, genetic, permanent environmental, and residual variance all increased with increased production level. Genetic variances had the largest relative increase. Estimates of genetic variance doubled from lowest to highest production

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level. This supported other results (11,31,34,45) with regard to increases in genetic variance.

Results from this and previously mentioned studies have indicated a moderately strong positive association between the level of milk production and within-herd genetic and environmental variation. Research involving traits other than production is less extensive. With regard to conformation, some work (1,54) has suggested the relationship was opposite of that for milk.

Potential Adjustments for Heterogeneous Within-Herd Variance

Hill (23) examined methods of adjusting for non-homogeneous within-herd variances. Selection was on individual performance and differences in genetic mean among groups were nil. One alternative was adjusting observations according to an intra-group estimate of the standard deviation. A disadvantage was that this adjustment could alter selection differentials relative to normal data when selection was on small groups. In such cases, estimates of within-group variability were greatly influenced by the magnitude of extreme values. For large groups, this problem was trivial.

Hill (23) also suggested that, given equal heritabilities, many times scaling by estimated standard deviation yielded improved accuracy over disregarding heterogeneous variance. Transformation was also considered a possibility in many practical situations. Even if accounting for heterogeneity did not greatly affect accuracy, selection on performance was deemed "unfair" unless heterogeneous within-group variance was considered. In general, scaling by the estimated within-group standard deviation, seemed to work well even when group numbers were low.

In the case of heterogeneous heritabilities, the complexion of the problem was different. For milk production, some studies (11,12,24,30,34,39,46,58,64) revealed increases in within-herd variability were accompanied by increased heritability estimates. Thus, Hill (23) noted differential heritabilities would help the problem. In this case, non-linearity between breeding value and phenotype would be less than with equal heritabilities. Powell et al. (46) suggested higher heritabilities, in higher producing more variable herds, would indicate giving additional weight to herdmate deviation. They maintained adjustments for phenotypic heterogeneous variances and heritabilities would partially offset each other under this situation. If selection was for bull dams, VanVleck (63) proposed higher heritabilities, in more variable herds, would increase accuracy and possibly optimize the proportion of cows taken from differing herd levels. However, the opposite effect would occur if heritabilities were higher in less variable herds (18).

Lofgren (30) investigated differential within-herd variation as it relates to Cow Index (CI) for milk. Eight adjustments were considered for CI. Two alternatives used variable heritability estimates to adjust for differences in additive genotypes. One method applied a log transformation to the data while another standardized records to a common within-herd variance. Four other methods were combinations involving the original four adjustments. Although there were no large differences in apparent effectiveness of different adjustments, standardizing records to a common phenotypic within-herd variance seemed "best" for Jerseys and Holsteins. Given this result, large inter-breed differences were considered unlikely.

Lofgren (30) suggested that the "best" adjustment procedure was certainly not as well suited for implementation as some others. It required an estimate of within-herd variance and would have to be updated each year. Generally, it was

concluded that the cost for implementing most changes was unjustifiable relative to improving the current methodology.

Brotherstone and Hill (4) noted even after adjustments, some differential herd variability was still unaccountable. They reported evidence of differences among herds in coefficient of variation for milk yield, indicating that simple log transformation might not provide the solution. Scaling records to a constant coefficient of variation was proposed. Additionally, Garrick and VanVleck (18) warned that if transformation were used to adjust for heterogeneity when heritabilities were larger in more variable environments, selection efficiency could be compromised. They concluded sampling bulls should have progeny in a variety of differing herd environments.

Weller et al. (71) used the herd-year-parity mean of the ratio of milk production per day at five months post-partum and at peak-production post-partum as an indicator of herd stress level. Previous work had demonstrated heritabilities and sire components of variance for milk and fat yields were greater in high stress herds. They presented an algorithm to compute BLUP estimates of transmitting ability using variance components estimated as functions of an environmental gradient. Genetic correlation between various environmental levels was assumed 1.0. Prior to building mixed model equations, the square of sire variance was computed for each group as a function of the mean group ratio. Records were adjusted to obtain an equal sire component of variance. Residual variances were estimated for each group as a function of group stress level. The contribution of each record was weighted in the mixed model equations. Although the correlation between genetic evaluations which assumed homogeneity and the method presented was near one, repeatability was 2% higher when records were weighted.

With regard to heterogeneous variance in Best Linear Unbiased Prediction (BLUP) of sire transmitting abilities, Gianola (19) noted that records were automatically scaled, BLUP accounts for heterogeneous variance provided the covariance structure is known and that assumptions regarding the model hold. In the class of translation invariant linear functions of the records, BLUP actually maximizes expected genetic progress under the assumption of multivariate normality. Implementation of BLUP methodology depends on knowledge of the needed variances and covariances. In many practical situations, the only information available would be data used to predict transmitting abilities. In such cases, variance parameters should be estimated simultaneously by Restricted Maximum Likelihood procedures. Size of the matrices needed would prohibit application to the national sire evaluation program. If herds were the origin of heterogeneity, large numbers of variances would have to have been estimated. Additionally, individual parameter estimates would be highly variable due to limited information on each of them. Gianola (19) suggested a shortcut of stratifying herds into groups, similar to Hill et al. (25). His procedures could then be applied with some feasibility.

VanVleck (63,65) utilized Falconer's concept (15), that performance in a different environment was a new but correlated trait, to investigate response in one environment when selection was carried out in another. He (65) conceeded that dairy environments could not be separated into two distinct classes. However, this study focused on selection in two environments to illustrate potential problems with differing within-herd variance and their effect on genetic progress.

VanVleck (65) noted that response in environment one and correlated response in environment two depend on heritability and phenotypic variance in environment one, genetic covariance of the genotypes in different environments, and

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the fraction of selected individuals. A simple approach to finding optimum fractions when selecting from both environments was suggested. If p_1 and p_2 represented the fraction selected from each environment, weighted average responses for environments one and two could be calculated for $p_1 + p_2 = p$ combinations. Thus, optimum weights could be determined.

This study (65) gave examples focusing on the importance of heritability as well as within-herd variance in developing strategies to optimize genetic gain in different environments. In fact, differences in heritability were considered potentially more important than differing residual variances.

Heterogeneous Within-Herd Variance for Type

Research indicating heterogeneous within-herd variances for milk production is well documented. The genetic and environmental nature of differences among herds, and the relationship between within-herd variance and herd level for milk has been established. Research investigating this relationship and differences among herds in within-herd variance is less extensive (1,32,53,54) for conformation traits.

Potential differences in within-herd variance for type could originate from environmental or genetic sources. In the mid sixties, factors that directly influenced variation in type appraisal were studied. Using 29,000 records on Canadian Holsteins, Carter et al. (8) determined that less than 1% of the variation in final score was due to classification round while inter-herd differences and sire-within-herd differences accounted for 8% and 7% of the variation respectively. Their results indicated round of classification, classifier, and month of classification had no significant effect on variability in final score. They concluded that little would be gained by using contemporary comparisons in genetic evaluation for type.

Using type records on U.S. Holsteins, VanVleck (60) found environmental differences among herds accounted for less than 10% of the variation in classification score. He maintained the need to include herd effects in sire evaluation for type was minimal unless large numbers of sires had daughters distributed over a small number of herds.

Hansen et al. (21) used records from 41 Wisconsin herds to determine the effects of age, stage of lactation, and age by stage of lactation interaction on classification score. Similar to VanVleck (60), he found less than 10% of the variation in classification score was due to inter-herd differences. However, effects due to age and stage of lactation were highly significant. This study strongly suggested age and stage of lactation effects could have significant effects and certainly warranted consideration as factors impacting variation in classification scores.

Vinson et al. (67) analyzed records on 78,151 U.S. Holsteins to estimate the effects of herd, classifier, and their interaction on differences in final score. Herd and classifier accounted for 13.8% and 2.6% of total variance in final score respectively. Herd by classifier interaction was more important than classifier effects alone. Work at Guelph (47) revealed that some environmental factors had a significant effect on final score. Their study included 51,044 Canadian records, and partitioned variation for appraisals on 11 traits. Effects of herd round, age at classification, stage of lactation, and season of classification were significant sources of variation for most traits. However, coefficients of determination for the entire model were extremely low, and heritability estimates using adjusted and unadjusted data were quite similar for all traits except final score.

In the early-to-mid seventies, genetic evaluation for type was undergoing

changes in both the United States and Canada. The Holstein-Friesian Association of Canada had introduced a new score card and introduced revised sire evaluation methods using statistical techniques similar to those used for milk production. Schaeffer et al. (51) were charged with developing a linear model for the purpose of sire evaluation. This model reflected the environmental effect of age on classification score as indicated by previous research (47). It also included an effect due to dam's classification score to adjust for possible assortative mating for type traits in the Canadian Holstein population. Approximately one year later, Burnside and Stewart (7) published results indicating assortative mating for type was practiced. Schaeffer's model (51) did not include effects of herd-round or stage of lactation. Stage of lactation effects were not included because most type data did not include calving dates. Additionally, the authors cited earlier papers (47,60) which suggested small influence of herd differences on classification score. However, the primary reason for not including herd round was attributed to limited computing capabilities. In 1984, Sorensen and Kennedy (54) noted failure of the Schaeffer model to include herd round and stage of lactation effects and they indicated that the Canadian sire evaluation did eventually add these effects to the model. They assessed the impact of including herd round by estimating heritabilities of various type traits on more recent data with and without herd round in the model. Evidence suggested failure to account for herd-round effects overestimates heritability since sires were not randomly used across all herds. This result provided support to VanVleck's (60) warning about non-random daughter distributions across herds.

In the United States, the Holstein-Friesian Association of America (HFAA) introduced Predicted Difference type (PDT) in 1971. This estimate of transmitting

ability for final classification score accounted for the environmental effect of age and adjusted for the proof of a sire's mate. However, as in the Canadian evaluation, herd effects were presumed minimal and not taken into consideration. Daughters of sires were compared to some age-adjusted breed average for final score. Although this evaluation procedure did account for some effects which could bias proofs, Jamieson et al. (26) suggested environmental differences among herds might be important. They reported 20% of the total variance in classification scores was due to herds. Still a much smaller percentage than for milk production, they postulated these herd differences might consistently bias proofs when the possibility of certain bulls being used predominately in higher or lower scoring herds was considered. This study evaluated the system used by HFAA in relation to various herdmate comparison methods. Correlations between PDT and adjusted herdmate averages indicated that, under the system being used, PDT was highly affected by the overall quality of the herd in which the bull was used. These results lead to use of a herdmate comparison procedure in 1976 which made genetic evaluations for type more similar to those for milk production.

In the next few years, further refinements regarding genetic/environmental herd differences were considered. Bell et al. (2) stated that, under genetic theory, progeny of different bulls should be compared with herdmates of the same genetic merit. They proceeded to evaluate the impact of ignoring this requirement in sire evaluations for type. Additionally, refinements in 1976 evaluation methods were investigated. Classification records of 755,744 progeny were stratified into three groups by herdmate average for final score. The low group contained records with a herdmate average below 79.75 while middle and high groups had herdmate averages of (79.75 to 81.75) and (> 81.75), respectively. Transmitting abilities for the same

670 sires were estimated within each herdmate average group. Average transmitting abilities were .12, -.28, and -.45 from low to high groups which suggested that estimates of sire transmitting ability were affected by the quality of herdmates of their progeny. Eighty-three percent of sire transmitting abilities estimated in low herds exceeded those estimated in high herds while seventy-seven percent of transmitting abilities estimated in low herds exceeded those in middle herds. Correlation coefficients between herdmate average and average PDT of herdmates sires/average cow index of herdmates were .48 and .45, respectively.

In an attempt to reduce bias created by non-random sire usage, Bell et al. (2) estimated new transmitting abilities on the same sires within the same herdmate-average groups. They used two iterative procedures and a mixed model comparison to calculate the new estimates. Each method was evaluated as an alternative to herdmate comparison. Results demonstrated that all methods were effective in reducing effects of differences in herdmate groups. Mixed model methods were most effective, but estimates calculated in low herdmate average groups were still at an advantage.

A possible explanation for the remaining bias was differential culling levels for females in different herdmate average groups. In this study, 14% of the variation among high herds was genetic in nature. Forty-six percent of the inter-herd variation was genetic in the other groups. It appeared that selection decreased within-herd variation and increased likeness among cows in high herds. Group average final scores were 78.96, 80.77, and 82.79 from low to high groups. Corresponding within-herd standard deviations were 4.54, 3.81, and 3.58. Later work by Smothers et al. (53) reported similar results. They divided herds into ten groups based on herd-average final score. Within-herd standard deviation for final score declined

dramatically as herd-average final score increased. These results demonstrated an inverse relationship between mean and variance compared to those reported for milk production (4,11,12,28,30,37,41,58,71).

Additional evidence for decreasing within-herd variance with increasing herd mean was reported by Mansour et al. (32). Means and variances for final score were estimated on six populations of Holsteins. Each population was categorized by number of times scored. Mean and variance first score at approximately 27.5 months of age was as follows:

Population	1	2	3	4	5	6
Mean	76.65	77.83	78.40	78.79	79.03	79.65
Variance	20.11	13.58	12.56	11.68	11.47	11.15

These values reflect selection across populations and a negative association between mean and variance for final score. Bell (1) characterized the association between herd mean, variance, and selection intensity for type. He noted intensive selection procedures reduced within-herd variation for final score. In addition to raising the mean and reducing variance, selection also decreased the range of herdmate deviations. Smaller deviations in progeny performance would be reflected in estimates of sire transmitting ability for type. Vinson (68) suggested potential bias in genetic evaluation of cows was much more serious because from cows usually expressing all their records in one herd. Cow evaluations would favor high performers in high-variance herds.

In a Canadian study, Sorensen and Kennedy (54) examined associations between herd level for final score and genetic and environmental variances for eleven type traits. Data included 354,308 records taken between 1976 and 1981. Herd means for final score were computed and twenty groups were formed in

descending order based on herd-mean final score. Each group contained approximately 18,000 records representing approximately 2,000 sires. Within each group, sire and residual variances were approximated for ten type traits using Henderson's new method (22) with a model including effects of herd-round, stage of lactation, age at classification, sire, and a dam covariate to account for nonrandom mating.

Regression of environmental variances, genetic variances, and heritabilities on group number was used to evaluate any trends with herd level for final score. Linear and quadratic terms were fitted in the regression model. Significant genetic trends were noted for rump and feet and legs. Increased genetic variances were linearly associated with higher type appraisals. Environmental variances were higher in lower scoring groups for final score, final class, dairy character, and capacity. This trend was opposite for size. Quadratic trends in environmental variances were significant for rump, feet and legs, fore udder, and rear udder. Although genetic and environmental variances were heterogeneous for many traits, results gave minimal evidence that heritabilities were affected by herd level for final score.

Most recently, genetic evaluations for conformation in the U.S. have undergone additional refinements (17). Daughter score nearest 30 days has replaced last score. The model now accounts for merit of mates and additive genetic covariances due sires of sire and maternal grandsires. These refinements have strengthened the reliability of the evaluations. However, with regard to heterogeneity of within-herd variance, further improvements must be considered.

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Relationships Among Phenotypic Standard Deviation and Herd Level for Type and Their Effect on Selection Response in U. S. Holsteins

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Abstract

Type records, representing 151,443 classification scores, were analyzed to estimate phenotypic relationships among various herd parameters and examine their impact on selection response. Data, adjusted for age and stage of lactation, were from first-parity cows classified from 1983 through 1986 by the Holstein-Friesian Association of America. Herd mean and within-herd standard deviation for final score demonstrated a strong negative association ($r = -.59$). Correlations among herd-mean final score and within-herd standard deviations for linear traits ranged from -.33 to -.05.

Herds were stratified into deciles according to herd mean for final score. Within-herd standard deviation for final score declined curvilinearly (concave up) as mean final score increased. Negative trends of less magnitude were noted for within-herd variability of linear traits. Herds were also stratified by mean PD type of herd-sires to obtain genetic classes for final score. Again, within-herd standard deviation for final score demonstrated a negative decline of less range than when stratification was by herd-mean final score. Trends with linear traits were small and inconsistent in direction.

Regression of daughter contemporary deviation type on her sire's PD Type within 25 mean/standard deviation subclasses indicated selection response differed across herd levels for those parameters. Response to selection on PD Type was greatest in high-mean/variance herds and least in low-mean/variance herds.

Introduction

Correlations between within-herd variability and herd mean for production has been reported (3,4,5,7) as positive and moderate. Coefficients have ranged from

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.21 (4) to .49 (7). This relationship negates assumptions that herd mean and within-herd variance are independent for production traits. Vinson (13) discussed the selection problems associated with heterogeneous variances.

Some research (1,5,12) suggests phenotypic variation may be reduced in herds at high levels for type. Mansour et al. (5) categorized Holsteins within age groups according to number of times scored. For first score, mean final score increased while variance decreased across categories. Bell (1) reported a similar trend with Holsteins stratified into three groups according to herdmate average for final score. Means and standard deviations for each group were 78.96, 80.77, 82.79, and 4.54, 3.81, 3.58, respectively. He ascribed this trend to heavier use of high PD type (PDT) bulls and more intensive culling in higher classifying herds. Using Canadian type records, Sorensen and Kennedy (12) also reported decreasing variances for final score with increasing herd-mean final score.

Heterogeneous within-herd variances could affect genetic evaluations and selection of bull mothers (3,11,13). Additionally, herds at different levels of variability and mean for traits could differ in response to selection. Research with production traits (2,7,9,10) has demonstrated that regressions of daughter yield on sire PD can vary drastically among herd-level categories. If within-herd variability for type differs substantially across the Holstein population, response to sire selection for PDT could be affected. Objectives of this study were: (1) to examine relationships between estimates of phenotypic within-herd variation for final score and linear descriptive traits and herd mean for final type score, (2) to estimate response to selection using PDT in herds differing in mean and variance for final score.

Materials and Methods

Data provided by the Holstein-Friesian Association of America (HFAA) included type classifications from 1983 through 1986. Records for final score and fifteen linearly-scored descriptive traits were obtained for herds with codes ending in 2, 5, and 8, 1/3 of all cows scored during the time period.

Data were edited to include only first-parity classification scores. Also, records without calving dates, classification dates, or on cows over 45 months of age were deleted. Only herd rounds with at least 10 records were used to estimate within-herd standard deviations. Records were adjusted for age and stage of lactation with factors used by HFAA (D. A. Funk, personal communication, 1988). After edits, the data set contained 151,443 records representing 7,466 herd rounds of classification.

Herd-round means were estimated for final score, PDT of sires, herd size, and age of individuals at classification. Estimates of within-herd-round standard deviation were calculated for final score and linear type traits. Linearly-scored traits included: stature, strength, body depth, angularity, rump angle, rump length, rump width, rear legs (side view), foot angle, fore udder attachment, rear udder height, rear udder width, udder support, udder depth, and teat placement. Definitions of linear descriptive traits are given in Appendix 1. Phenotypic correlations between age and herd-size, and within-herd standard deviations were estimated to determine associations among various herd parameters.

Trends with herd level for final type score

Relationships between within-herd phenotypic standard deviation for various type traits and herd level for final score were determined using regression

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techniques. Initially, herd rounds were stratified into deciles of approximately equal size by herd-mean final score. Group 1 consisted of herd-rounds with the lowest mean final score, while group 10 comprised those herds at the highest mean. Mean final score, herd rounds, and cow numbers are presented in Table 1 by group. Each group contained approximately 750 herd rounds of classification while cow numbers ranged from 13,267 to 16,177. Subsequently, herd rounds were restratified into deciles according to mean PDT of herd sires. Again, herd-round numbers were similar for each group. However, this stratification more closely reflected the genetic level of a herd. Mean PDT ranged from -.06 in group 1 to 1.83 in group 10.

Mean within-herd standard deviations for final score and fifteen linear type traits for each group were regressed on group means for final score and PDT of sires. The model fitted linear and quadratic terms. Models including non-significant quadratic regressions were reanalyzed using only linear terms. Changes in herd size and average age of individuals within a herd, accompanying changes in herd mean and within-herd variance, were also examined. Phenotypic correlations were utilized to investigate associations among these other herd parameters.

Response to selection for final type score

Response to selection for final score was estimated in herds having different means and within-herd variances. The original data set was stratified into quintiles, with similar numbers of herd-rounds, according to herd-mean final score. Similarly, herd-rounds were again stratified into quintiles by within-herd standard deviation for final score. Simple linear regression was utilized to determine response to sire selection for type within groups. Daughter contemporary deviation type (CDT) was

regressed on her sire's PDT. Regressions were computed within mean group, within standard-deviation group, and within 25 subclasses representing all mean group/standard-deviation group combinations.

Results and Discussion

Relationships between herd level and within-herd standard deviation

Overall means and standard deviations for all type traits are in Appendix 2. Means ranged from 23.0 (udder depth) to 30.5 (body depth) for linear traits. Final score mean was 80.4. Stature had the largest standard deviation (8.2) while udder depth (4.6) and final score (4.6) had the smallest.

Regression of group mean final score on group mean standard deviation for final score is shown in Figure 1. This graph illustrates a curvilinear decrease in within-herd standard deviation final score as herd mean final score increases. This decline is rather dramatic and constitutes an approximate two-fold decrease from the highest mean group to the lowest. This supports other work (1,5) that suggests phenotypic variance of final score was reduced by selection for type. A similar trend was noted by Sorensen and Kennedy (12) for Canadian data. The downward trend in within-herd variation most likely reflects intensified selection and culling practices for herds at higher levels for final score type. Additionally, upper limits on classification score certainly play a role.

Significant linear and quadratic coefficients were noted for regressions of group-average within-herd standard deviations for linear traits on group-mean final score (Appendices 3-17). Generally, linear terms were negative and large relative to quadratic terms that were positive and small. Although quadratic terms were not significant (P > .05) for rump angle and rear udder, linear regressions were highly

significant (P < .01) and negative. Thus, herds with higher mean final score displayed decreased phenotypic variability in all linear traits. However, as expected, trends were of smaller magnitude than for final score.

Regressions, fitting linear and quadratic terms, of group-average within-herd standard deviation for final score and linear traits on group-mean PDT of herd sires also suggested some trends. A negative linear relationship between within-herd, standard-deviation final score and average PD type of herd sires is illustrated in Figure 2. The trend was similar to that when stratification was by phenotypic herd level; however, the magnitude of decline was less. Phenotypic variance appears more heavily influenced by environmental factors. This question will be investigated in more detail in a companion study.

Group-mean standard deviations for most linear traits demonstrated less change and were varied in direction as group-mean PDT changed. Quadratic terms were not significant (P > .05) for any linear traits. Significant (P < .05) positive coefficients were noted for: stature, body depth, rump width and fore udder attachment. Significant (P < .05) negative coefficients were noted for: angularity, rump angle, rear legs, foot angle, udder support, and teat placement. For most linear traits, the range of within-herd standard deviations was much less than that for final score.

Phenotypic correlation among herd parameters

Table 2 contains estimates of phenotypic correlations for various herd parameters and within-herd standard deviation for final score and fifteen linearly scored conformation traits. Herd-mean final score and within-herd standard deviation final score demonstrated the strongest negative association (r = -.59). The

correlation coefficient was somewhat larger and opposite in sign to those estimated (3,4,8) for production traits. The negative correlation between herd mean and within-herd standard deviation for final score was supportive of other research (1,5) on conformation traits. Correlations between within-herd standard deviations for linear traits and herd mean final score were all negative and moderately-low to low. Coefficients ranged from -.33 for rear legs (side view) to -.05 for rump width and fore udder attachment.

Results were more variable with regard to associations among other herd parameters and within-herd standard deviations for type traits. Average transmitting ability of herd sires for final score demonstrated a small negative correlation ($r = -.26$) with within-herd standard deviation for the trait. Coefficients for mean PDT and within-herd standard deviations for linear traits were variable in sign and small.

Correlations among average age/size of herds and within-herd standard deviations for final score and linear traits gave no indication of any strong linear connection among those herd parameters. Most coefficients estimated between herd size and within-herd standard deviations for type traits were positive, but most were near zero. Using production data, Meinert (8) estimated phenotypic correlations between herd size and within-herd-year standard deviations at .22 and .20 for mature equivalent milk and fat yields, respectively. For average age of herd, coefficients were variable in sign and were between .11 and -.11.

Overall, herd mean and within-herd standard deviation for final score demonstrated the greatest antagonistic association. Table 3 illustrates the reduction in estimates of within-herd standard deviation with increasing herd-mean final score. Mean sire transmitting abilities of herd sires within each group show a steady

increase with increasing mean and decreasing herd variability for final score. Thus, decreasing within-herd standard deviations seem related to a herd's genetic level as well as its phenotypic level for final score. As indicated by near zero correlations, average age and herd size remained relatively constant as group-mean final score increased.

Response to selection for final type score

Results of regressing daughter CDT on her sire's PDT within quintiles based on herd-round-mean final score are in Table 4. Regression coefficients ranged from 1.13 in the lowest mean group to 1.01 in the highest. Decreases from lowest to highest mean groups reflect a trend opposite than that found for production (2,7,8,10). As seen in Table 5, increased selection response accompanied increased within-herd standard deviation for final score. The 75% increase in selection response was in general agreement with that reported by Meinert et al. (9) for production under the same grouping strategy. Directional divergence in selection response when herd rounds were categorized differently was expected. It was anticipated given the strong negative relationship between herd mean and within-herd standard deviation for final score.

Regression coefficients and distribution of cows in 25 subclasses representing all mean group/standard-deviation group combinations are in Table 6. The average coefficient across all subclasses was approximately 1.05. Herd numbers were greatest in the (1,5) and (5,1) cells and least in the (1,1) and (5,5) cells. This distribution reflects the antagonistic relationship between the two herd parameters and was nearly opposite to that reported for milk (9).

Averaged across standard-deviation groups, regression coefficients ranged

from .92 (lowest mean group) to 1.17 (highest mean group). Generally, coefficients for each mean class demonstrated larger increases across mean classes as standard deviation class increased. The increases in coefficients within standard-deviation groups with increasing herd mean class was somewhat surprising. If increased culling in high-mean herds is a major contributor to the inverse relationship between mean and within-herd variance, differences among sire groups should lessen. This should reduce the regression.

The greater increase in coefficients was as standard-deviation class increased within mean class. Averaged across mean classes, coefficients ranged from .71 (lowest standard-deviation class) to 1.4 (highest standard-deviation class). The large increase in regression coefficients with increased within-herd, standard-deviation classes was in agreement to similar work (9) with production traits. In general, these data suggest rather large differences in selection response for final score.

Conclusions

An analysis of conformation scores on U. S. Holsteins indicated that differences in phenotypic estimates of within-herd variance exist in the population. The correlation between within-herd standard deviation and herd mean for final score was strong and negative. Estimates of within-herd standard-deviation final score decreased curvilinearly as herd-mean final score increased. Negative relationships of lesser degree were noted between within-herd variability of fifteen linear traits and herd-mean final score. Thus, heterogeneous within-herd variances should be a matter of concern in genetic evaluations for type. Average age of herd and herd size were relatively constant across groups with increasing herd-mean final score.

Regressing group estimates of within-herd standard deviation on group estimates of herd genetic level for final score indicated a moderately-low negative trend. Thus, genetic as well as environmental factors contribute to differences in within-herd variance for final score. Trends for group estimates of within-herd variability of linear traits were not strong and were inconsistent in direction.

Differences in response to selection for type were apparent in herds characterized by differing herd levels for mean and within-herd standard deviation for final score. Response to selection increased slightly within standard-deviation groups as herd-mean final score increased. Within mean groups, substantial increases in response were noted as within-herd standard deviation for final score increased. These differences could affect accuracy of sire evaluations if daughters were not randomly distributed across herds. The extent of influence would depend on differences among herds in estimates of heritability. Changes in genetic and environmental variance and heritability with changes in herd-mean final score will be examined in a companion study.

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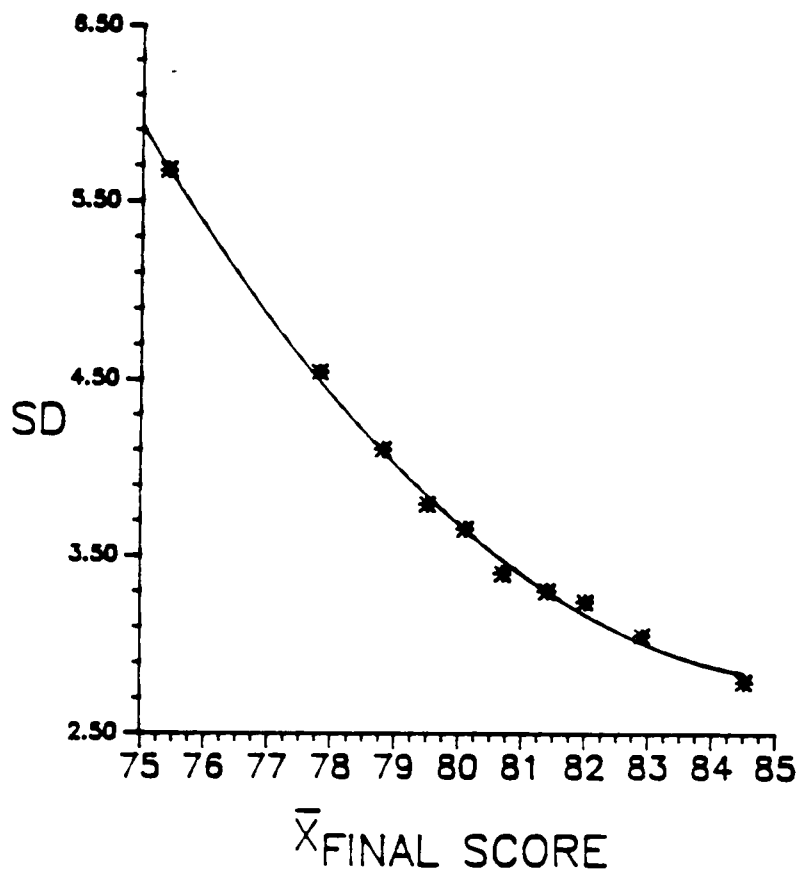
Figure 1. Regression of group average for within-herd
standard deviation (final score) on group
average for herd-mean final score.
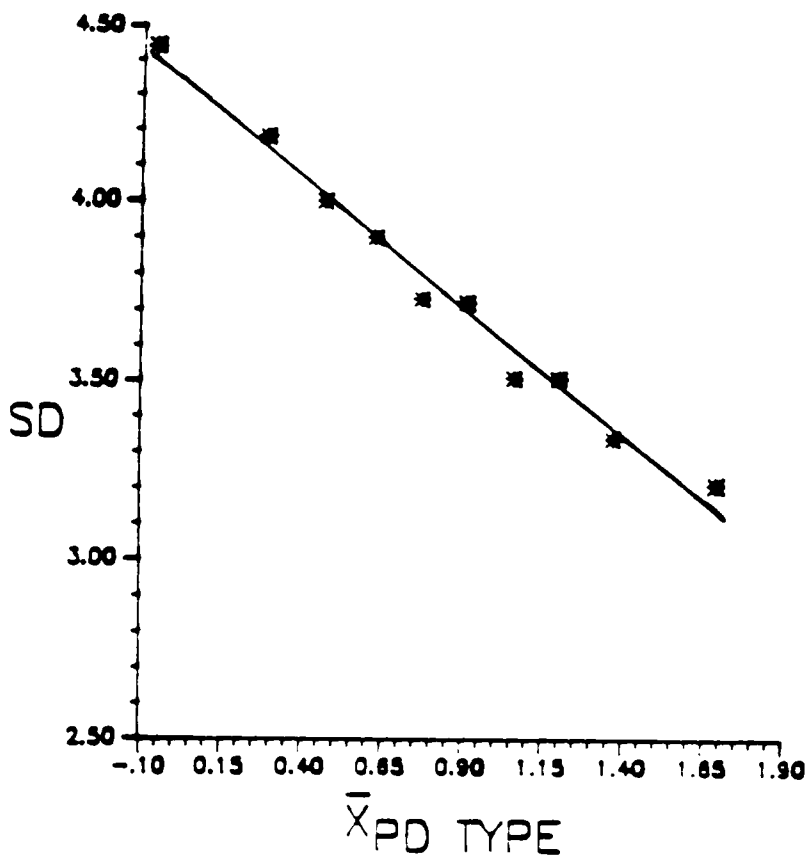
Figure 2. Regression of group average for within-herd standard-deviation (final score) on group average for herd-mean PD type.

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Table 1. Mean within-herd-round final score, numbers of herd rounds, and numbers by group.

Group[1]	$\overline{X}$ Final Score	Herd-Rounds	Cows
#	pts	#	#
1	75.4	749	13,267
2	77.8	750	15,369
3	78.8	750	14,517
4	79.5	750	14,858
5	80.1	750	15,867
6	80.7	750	15,926
7	81.4	750	16,177
8	82.0	750	15,641
9	82.9	750	15,854
10	84.5	717	13,967

[1]Group stratification according to herd-round mean for final score.

Table 2. Phenotypic correlations among various herd characteristics and within-herd standard deviations for conformation traits.

Trait	Means			
Standard Deviation for:	Final Score	PD Type[1]	Age[2]	Herd Size[3]
Final Score	-.59**	-.26**	.05**	.05**
Stature	-.10**	.03**	-.08**	.02
Strength	-.08**	.00	-.07**	.04**
Body Depth	-.06**	.05**	-.11**	.03**
Angularity	-.14**	-.04**	.03*	.03**
Rump Angle	-.31**	-.15**	.07**	.04**
Rump Length	.07**	.02	-.04**	.06**
Rump Width	-.05**	.04**	-.07**	.01
Rear Legs (side view)	-.33**	-.10**	.05**	-.04
Foot Angle	-.24**	-.12**	.07**	.01
Fore Udder Attachment	.05**	.12**	-.03*	.04**
Rear Udder Height	-.12**	.00	-.01	.04**
Rear Udder Width	-.13**	-.02	-.04**	.03**
Udder Support	-.14**	-.03**	.06**	.04**
Udder Depth	-.24**	-.12**	.11**	.06**
Teat Placement	-.15**	-.05**	.04**	.03**

[1]Based on daughters' score nearest 30 months.
[2]Mean age at first classification.
[3]Number of cows with first scores in the herd rounds.
*(P<.05)   **(P<.01)

Table 3. Mean within-herd-round standard deviations for final score,
         predicted differences for type, age at classification, and
         number scored for herd rounds stratified by mean final score
         (group).

Group[1]	Mean			
	Standard Deviation	PD Type[2]	Age[3]	Herd Size[4]
1	5.67	.37	36.2	17.7
2	4.54	.47	35.8	20.5
3	4.10	.59	35.9	19.4
4	3.78	.70	35.5	19.8
5	3.65	.79	35.4	21.2
6	3.40	.85	35.2	21.2
7	3.29	.96	35.2	21.6
8	3.24	1.07	35.0	20.9
9	3.05	1.16	34.8	21.1
10	2.79	1.33	35.0	19.5

[1]Group stratification in ascending order according to herd-round mean
 for final score.
[2]Based on daughters' score nearest 30 months.
[3]Age at first classification.
[4]Number of cows with first classification scores.

Table 4. Within-mean group regressions of
         daughter contemporary deviation type on
         sire PD type.[1]

Group[2]	Mean Final Score	B**
1	76.7	1.13
2	79.1	1.07
3	80.4	1.07
4	81.4	1.05
5	83.6	1.01

[1]Based on daughters' score nearest 30 months.
[2]Group stratification according to herd-round
 mean for final score.
**(P<.01)

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Table 5. Within-standard-deviation group regressions of daughter contemporary deviation type on sire PD type.[1]

Group[2]	Mean Standard Deviation (Final Score)	B[**]
1	2.33	.76
2	2.95	.94
3	3.44	1.08
4	4.14	1.18
5	5.86	1.33

[1]Based on daughters' score nearest 30 months.
[2]Group stratification according to within-herd standard deviation for final score.
**(P<.01)

Table 6. Regression of daughter contemporary deviation type on sire PD type[1] within 25 herd standard deviation/mean subclasses.[2]

Within-herd[3] Standard Deviation Group	Herd Mean Groups[4]					Unweighted Mean Coefficient
	1	2	3	4	5	
1	.67	.69	.69	.77	.75	.71
	858	3124	4210	6228	10,117	
2	.82	.84	.87	.93	.98	.89
	1356	4151	6639	8081	8812	
3	.82	.98	1.11	1.11	1.16	1.04
	2928	5789	7815	7968	7134	
4	.98	1.12	1.23	1.21	1.40	1.19
	6470	8928	8446	6369	2857	
5	1.29	1.33	1.38	1.48	1.54	1.40
	16438	7090	3731	2265	678	
Mean Coefficient	.92	.99	1.06	1.10	1.17	1.05

[1]Based on daughters' score nearest 30 months.
[2]Number of cows per subclass.
[3]Group stratification in ascending order according to within-herd standard deviation for final score.
[4]Group stratification in ascending order according to herd mean for final score.

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Herd Level for Final Score and its Relationship

to Genetic and Environmental Parameters of

Conformation Traits in U. S. Holsteins

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Abstract

First-parity conformation scores, representing 7410 herd-rounds of classification were analyzed to determined relationships between genetic and environmental parameters and herd mean for type. Herd-rounds were stratified into quintiles according to herd mean for final score. Within each group, REML estimates of sire and error variance were approximated, using the tilde-hat method. Average heritability estimates were: final score .21; stature .36; strength .28; body depth .33; angularity .27; rump angle .37; rump length .19; rump width .26; rear legs (side view) .19; foot angle .13; fore udder attachment .24; rear udder height .23; udder support .17; udder depth .31; teat placement .27. Heritabilities and genetic and environmental variances for final score and linear descriptive traits were regressed on group mean for herd-average final score. For final score, environmental variance decreased curvilinearly as group-mean final score increased while genetic variance exhibited a linear decline. For most descriptive traits, environmental variance decreased linearly with increasing herd-mean final score. Significant linear decreases in genetic variance were seen for foot angle, udder depth, and rump angle. Heritability estimates for final score demonstrated no significant trends with increasing herd mean. Significant positive trends were noted for body depth, angularity, rear udder height, udder support, and teat placement as herd-mean final score increase.

Introduction

Differences in within-herd variance for yield traits are well documented (3,4,5,11,13,15,16,22,24). Meinert et al. (13) reported a positive correlation between herd mean and within-herd variance for milk production. Some studies (2,4,11,14)

have reported increases in both genetic and environmental variances at increased production levels. Boldman and Freeman (2) reported increases in genetic, permanent environmental, and residual variance with increasing herd levels for production. Genetic variances demonstrated the largest increase. Their estimates doubled from lowest to highest production levels.

With regard to conformation traits, research has been somewhat limited. Some work (1,10,17) has suggested that phenotypic variance for final score is reduced in herds at higher means for final score. Sorensen and Kennedy (18), using Canadian records, examined relationships among genetic and environmental variances in Holsteins. As herd final score decreased, they reported higher environmental variances for final score, final class, dairy character, and capacity. Significant quadratic trends were reported for genetic variance in mammary system, feet and legs, and size. Mammary system and fore udder exhibited curvilinear trends for heritability estimates. Higher genetic variances were found in average herds for type, while lower estimates were at the extremes of herd-mean final score. The trend was opposite for feet and legs.

Information regarding relationships between herd level for final score and genetic/environmental parameters for the U. S. population does not exist. These relationships are needed in order to document the extent of heterogeneity of genetic variances, environmental variances, and heritability. Heterogeneity of variances affects accuracy of genetic evaluations and the proportion of animals selected from different environments. If not accounted for, genetic progress is reduced to an extent depending on the relationship between within-herd variance and within-herd heritability (7,15,25). If heritability decreases with increasing variance, loss in genetic progress may be substantial. The objective of this study was to investigate

relationships between herd mean for final score and genetic/environmental parameters for final score and fifteen linearly-scored descriptive traits in the U. S. Holstein population.

Materials and Methods

Data were conformation records provided by the Holstein-Friesian Association of America (HFAA). Records included cows scored under HFAA's Linear Classification Program from 1983 through 1986. Original data included herd identifications ending in 2, 5 or 8. Included were appraisals for final score and fifteen linearly-scored descriptive traits. Records were edited to include only first-parity individuals. Cows without calving dates, classification dates, or those over 45 months of age at first appraisal were deleted. Additionally, sires were required to have at least ten progeny in at least five herds. (After edits, data represented approximately 7400 herd-rounds of classification having first scores on at least ten cows and represented 112,077 records.) Records were adjusted for age and stage of lactation with multiplicative factors provided by HFAA, (D. A. Funk, personal communication, 1988).

Means for final score type were calculated for each herd-round, and herd-rounds were stratified into quintiles based on herd-mean final score. Average herd-mean final score, number of herd-rounds, cow numbers, and sire numbers are in Table 1. Average mean final scores ranged from 76.6 in quintile one to 83.7 in quintile five. Each group contained approximately 1480 herd-rounds, while cow numbers ranged from 19,035 to 24,844. A total of 590 sires were included over all quintiles. Sires were represented in more than one group and ranged from 244 in quintile five to 459 in quintile one. Obviously, lower sire numbers in the highest

mean final-score group reflects increased selection intensity for type.

Relationships between herd level for final score and genetic/environmental parameters were investigated for final score and the following linear descriptive traits: stature, strength, body depth, angularity, rump angle, rump length, rump width, leg set (rear view), foot angle, fore udder attachment, rear udder height, rear udder width, udder support, udder depth, and teat placement (rear view). Descriptive traits were scored on a linear scale from 1 to 50, while final score values had a potential range from 50 to 100.

Genetic and Environmental Parameters

Within each group, Restricted Maximum Likelihood estimates of sire and error variances were approximated using the tilde-hat approach of VanRaden and Jung (21). For linear traits, genetic and residual components of variance and covariance were estimated using five multiple-trait analyses within 5 groups based on average final score. Since final score is not a composite of linear traits, variance components for final score were estimated separately using single-trait analyses. The linear model used for final score and each linear trait was:

$$\underset{\sim}{y} = \underset{\sim\sim}{Xh} + \underset{\sim\sim\sim}{ZQg} + \underset{\sim\sim}{Zs} + \underset{\sim}{e}$$

where: y : vector of final score or linear scores for a particular type trait

h : vector of fixed herd-round effects

g : vector of fixed genetic group effects

s : vector of random sire effects

X,Z : incidence matrices relating y to h and s

Q : incidence matrix relating s to g

e : vector of random residuals

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Dispersion assumptions were:

$$s \sim (0, A\sigma_s^2)$$

$$e \sim (0, I\sigma_e^2)$$

Relationship matrix A was due to sires and maternal grandsires. Genetic $(4\sigma_s^2)$ and environmental $(\sigma_e^2 - 3\sigma_s^2)$ variances and heritabilities $[4\sigma_s^2 | (\sigma_s^2 + \sigma_e^2)]$ were calculated within each quintile. Genetic groups effects were added to account for genetic trend in type traits, and were according to year of birth of sires. Sire birth years ranged from 1959 through 1981. Regression on merit of mates was not included because cow index was not always available and its effect on parameter estimates is small (VanRaden, personal communication, 1988).

Relationships with mean final score

Linear and quadratic trends associated with changing herd mean for final score were examined for genetic/environmental variances and heritabilities for final score and linearly-scored descriptive traits. Within-group estimates of these parameters were regressed on linear and quadratic terms for group-average herd mean for final score. If the quadratic regression was not significant, a model was run using only the linear term. Linear and quadratic regression lines were plotted for data where coefficients were significant.

Results and Discussion

Within-group estimates of genetic variances, environmental variances, and heritability are reported in Appendices 18-20. Table 2 contains minimum, maximum, and average values within each herd-mean group obtained for estimates of genetic variance, environmental variance, and heritability for each trait. Averaged

over groups, heritability estimates were highest for stature (.36) and rump angle (.37) and lowest for foot angle (.13) was lowest. Some estimates were slightly higher than those reported by Klei et al. (9) from data from Eastern AI Cooperative. Estimates for most traits were intermediate those reported by Thompson et al. (19) in 1981 using data from an AI cooperative, and estimates later reported by Thompson et al. (20) on data provided by the HFAA. Foster et al. (6) reported estimates on data from an AI cooperative that were in general agreement to estimates obtained in this study. Estimates were similar to those officially reported by HFAA (VanRaden, 1988, Personal Communication) based on records from 799,391 classifications. Note that heritability estimates in this study were obtained as unweighted averages of estimates computed within subsets of the data which is generally not equivalent to analyzing the complete data set.

Significant negative relationships between herd-mean final score and genetic/environmental variance for final score are shown in Figure 1. Environmental variance demonstrated a curvilinear decline with increasing group-mean final score. The largest decrease occurred between the two groups with the lowest mean final score, in agreement with Sorensen and Kennedy (18). Other studies (1,10,17) have reported decreases in phenotypic variance with increasing level for final score. Contrary to results of the Canadian study (18), genetic variance for final score declined in a linear fashion. Heritability estimates for final score varied little and demonstrated no significant trend with herd-mean final score. They ranged from .19 to .25 (Table 2) with group three yielding the highest estimate. Heritability estimates for final score were slightly lower than expected. Potential causes are the approximation procedure and/or estimating within groups. Sorensen and Kennedy (18) reported that heritability for final score ranged from .07 to .17

across herd-mean groups.

These results were in contrast to relationships between herd mean, within-herd variance, and heritability for production. For yield traits, (3,4,12,13,14,16,22,23) within-herd variance increased with increases in herd mean. Estimates of heritability for production traits have also been shown to increase (8,11,14,23) with increasing herd mean.

Relationships between within-group estimates of genetic variance, environmental variance, and heritability for many linear traits are in Appendicies 21-30. Stature, as did most other linear traits, showed a linear decrease in environmental variance with increasing herd-mean final score (Figure 2). The range was from 38.0 (group 1, $\overline{X} = 76.6$) to 29.2 (group 5, $\overline{X} = 83.7$). Other traits in which environmental variance behaved similarly were: strength, body depth, angularity, rump angle, rump length, rump width, rear legs (side view), rear udder height, rear udder width, udder support, udder depth, and teat placement. Greatest linear decreases in environmental variance with increasing herd-mean final score were noted for rear legs (47.4 to 23.0) and angularity (41.0 to 27.3). Rump length had the minimum linear decrease (24.2 to 20.7). In traits demonstrating linear decreases in environmental variance, declines were usually more uniform between groups than for final score. Foot angle decreased curvilinearly (38.5 to 25.0) and was the only descriptive trait behaving similarly to final score. Estimates of environmental variance for fore udder attachment changed very little across mean groups and no significant trends were detected.

Estimates of genetic variance for final score declined linearly (6.0 to 2.0) with increasing herd-mean final score (Figure 1). Udder depth (6.3 to 4.3) and foot angle (5.2 to 4.0) rump angle were the only traits exhibiting significant linear declines in

genetic variance. Although for estimates of genetic variances for other descriptive characters differed across groups, no significant trends with herd-mean final score were noted.

Heritability estimates demonstrated some significant trends with the increase in herd-mean final score. Estimates for angularity (.21 to .35) and body depth (.28 to .41) increased linearly and are illustrated in **Figures 3 and 4**. Other descriptive traits with significant linear increases in heritability included: rear udder height (.20 to .25), udder support (.15 to .20), and teat placement (.23 to .32). Although no significant trends in heritability estimates were detected in most descriptive traits, estimates for stature, strength, rump angle, rear legs (side view), and rump width were generally highest in higher scoring groups. In the Canadian study (18), some differences in heritabilities were found. However, only mammary system showed a significant curvilinear trend. Overall, they concluded heritabilities were not greatly affected by mean herd score. In U. S. data, the only trait for which heritability remained fairly stable across groups was fore udder attachment. As seen in Figure 5, changes in genetic variance, environmental variance, and heritability were extremely small.

Genetic and phenotypic correlations among linear traits are reported in Appendicies 31-35. Correlations were generally similar among groups based on herd-mean final score. Some coefficients near 0 varied in sign among groups.

Differences in within-herd variance and heritabilities across populations present certain problems with regard to selection and genetic evaluations. As pointed out by Hill (7), more individuals would be selected from more variable populations. The problem magnifies as selection intensity increases. Following Hill (7), Vinson (25) noted that high-variance herds would have the advantage in bull

dam selection. The extent of this depends on how heritability changes with variance. Also, differences in heritability could affect the accuracy of genetic evaluations. For production, Van Vleck (24) observed that higher heritabilities, in more variable herds, would increase accuracy of bull evaluations based on daughter performance. Alternatively, equal accuracy could be obtained with fewer daughters. In addition, response to selection of bull dams would be greater in environments where heritability was greater. For milk production, higher heritabilities found in more variable environments justify selecting a greater proportion of individuals from this group. For some type traits in this study, heritability decreased when variance increased. Using angularity as an example, environmental variance declined sharply as herd-mean final score increased. Genetic variance was fairly stable across groups, but was largest in the highest mean group. Heritability increased from low to high mean groups. Since phenotypic variability for angularity was highest in the low group, a larger proportion of individuals would be selected from this group which had the lowest heritability. Consequently, genetic gain in the overall population would be reduced if the genetic evaluation procedure does not account for heterogeneity of variance components and heritability.

Conclusions

Heterogeneous variances for type traits do exist in the U.S. Holstein population. Thus, the assumption of equal variances in genetic evaluations for type does not hold. Selection and limits in the range of score values are potential causes of heterogeneity. Linear traits, in addition to final score, also showed heterogeneous variances with increasing herd-mean final score. Because increasing or constant heritability, in some linear traits, also accompanied increasing within-herd variance,

accuracy of sire and cow evaluations would be decreased. Also, a larger proportion of bull dams would come from highly variable herds if within-herd variances are assumed constant.

In future research, extent of heterogeneity of variances and heritability estimates should be examined by grouping herd-rounds according to phenotypic standard deviations of the linear traits. If heterogeneity exists, transformation of records must be considered. If score distributions were approximately normal, linear transformations could be considered. Otherwise, nonlinear methods are an alternative. Since linear traits are correlated and require multiple-trait analysis, finding a suitable transformation could be difficult.

Acknowledgements

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Table 1. Group average herd-mean final score, herd-round numbers, cow numbers and sire numbers.

Group[1]	Average Final Score	Herd-Rounds	Cows	Sires
no.	pts.	no.	no.	no.
1	76.6	1479	19035	459
2	79.1	1473	20403	390
3	80.4	1488	24084	353
4	81.7	1487	24844	297
5	83.7	1483	23711	244

[1]Group stratification according to herd-round mean for final score.

Table 2. Minimum (min.), maximum (max.), and mean ($\bar{X}$)[1] for genetic and environmental variances and heritability of final score and linear descriptive traits estimated within each of 5 herd-mean final score groups.

Trait	Genetic Variance			Environmental Variance			Heritabilities[2]		
	Min.	Max.	$\bar{X}$	Min.	Max.	$\bar{X}$	Min.	Max.	$\bar{X}$
Final Score	2.0	6.0	3.4	7.4	23.9	13.1	.19	.25	.21
Stature	16.3	20.3	18.6	29.2	38.0	33.6	.32	.41	.36
Strength	10.5	13.5	11.6	27.3	34.4	30.7	.24	.33	.28
Body Depth	12.4	16.7	13.9	24.5	32.3	28.5	.28	.41	.33
Angularity	11.2	14.8	12.2	27.4	41.0	33.3	.21	.35	.27
Rump Angle	7.6	9.9	9.0	12.4	21.5	16.0	.32	.40	.37
Rump Length	4.4	5.6	5.0	20.7	24.2	22.0	.17	.21	.19
Rump Width	8.3	12.2	9.6	24.2	30.0	27.5	.22	.33	.26
Rear Legs (side view)	6.3	8.7	7.8	23.0	47.4	33.5	.15	.25	.19
Foot Angle	4.0	5.2	4.6	25.0	38.5	29.7	.12	.14	.13
Fore Udder Attachment	8.8	10.9	9.5	28.3	31.5	30.0	.23	.26	.24
Rear Udder Height	9.8	10.4	10.0	29.1	39.2	33.1	.20	.25	.23
Rear Udder Width	7.3	9.0	8.3	31.2	39.1	34.1	.18	.22	.20
Udder Support	4.1	5.0	4.6	20.0	28.0	22.7	.15	.20	.17
Udder Depth	4.3	6.3	5.1	9.3	14.1	11.3	.29	.33	.31
Teat Placement	7.4	8.9	8.1	19.1	27.0	22.6	.23	.32	.27

[1]Minimum, maximum, and mean for quintiles according to herd-mean for final score.
[2]Standard errors ranged from .03 to .05.

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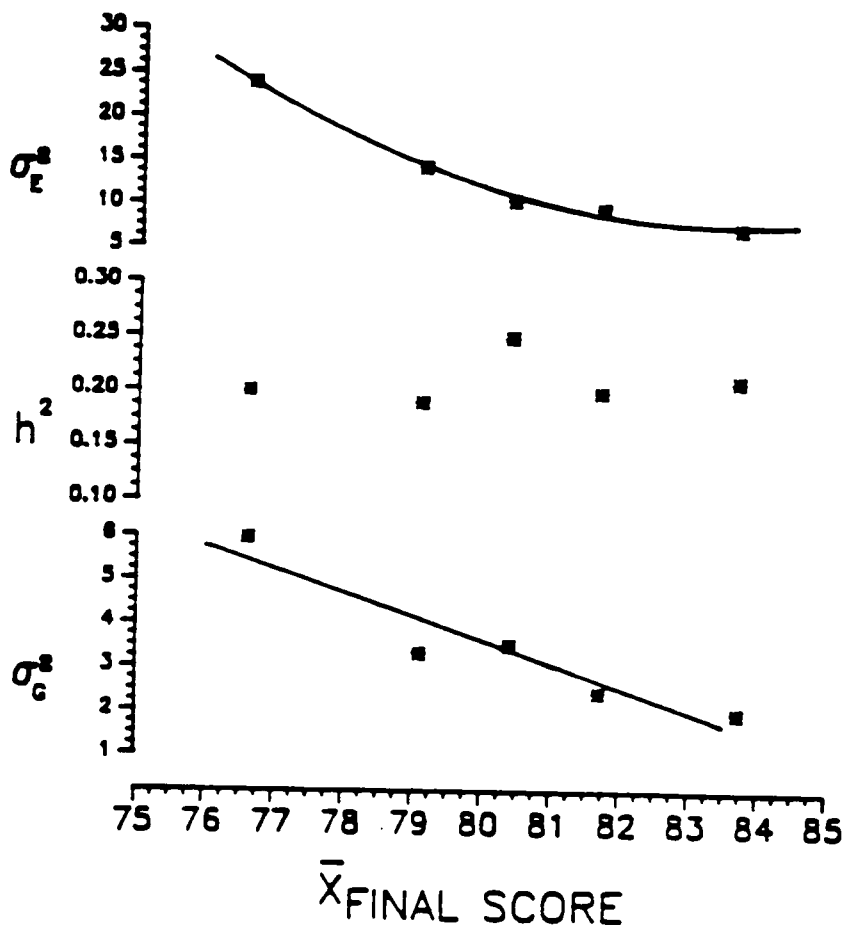
Figure 1. Regression of within-group estimates of
genetic variance, environmental variance,
and heritability for final score on
group-mean final score.
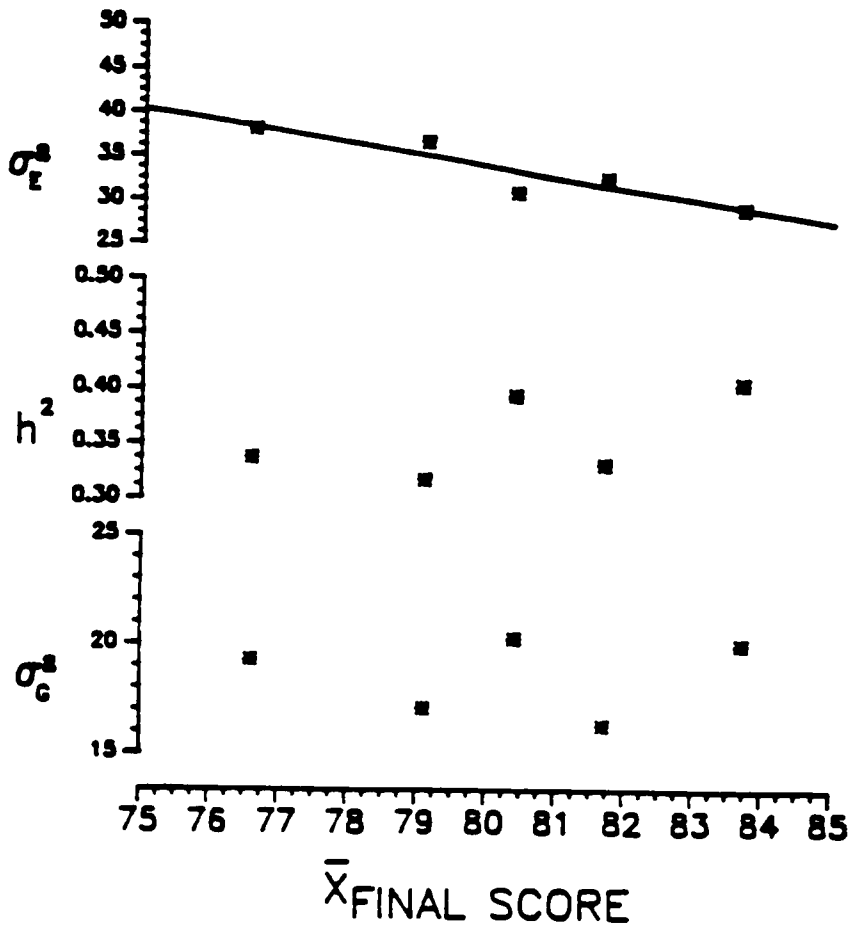
Figure 2. Regression of within-group estimates of genetic variance, environmental variance, and heritability for stature on group-mean final score.
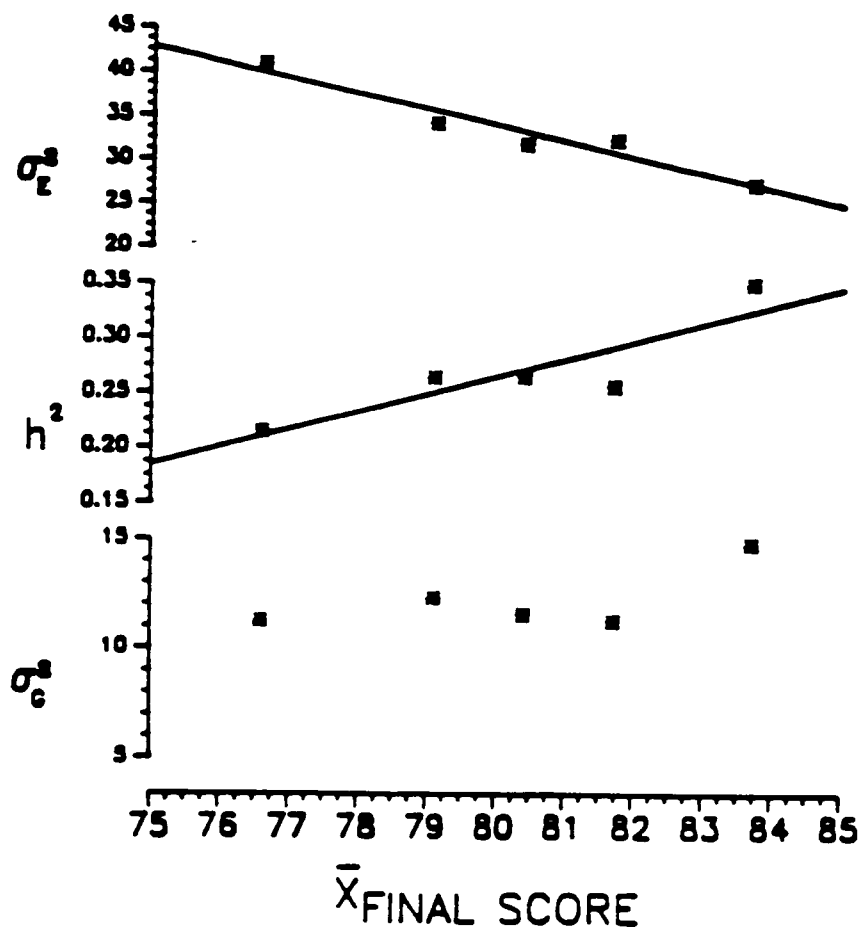
Figure 3. Regression of within-group estimates of
          genetic variance, environmental variance,
          and heritability for angularity on
          group-mean final score.
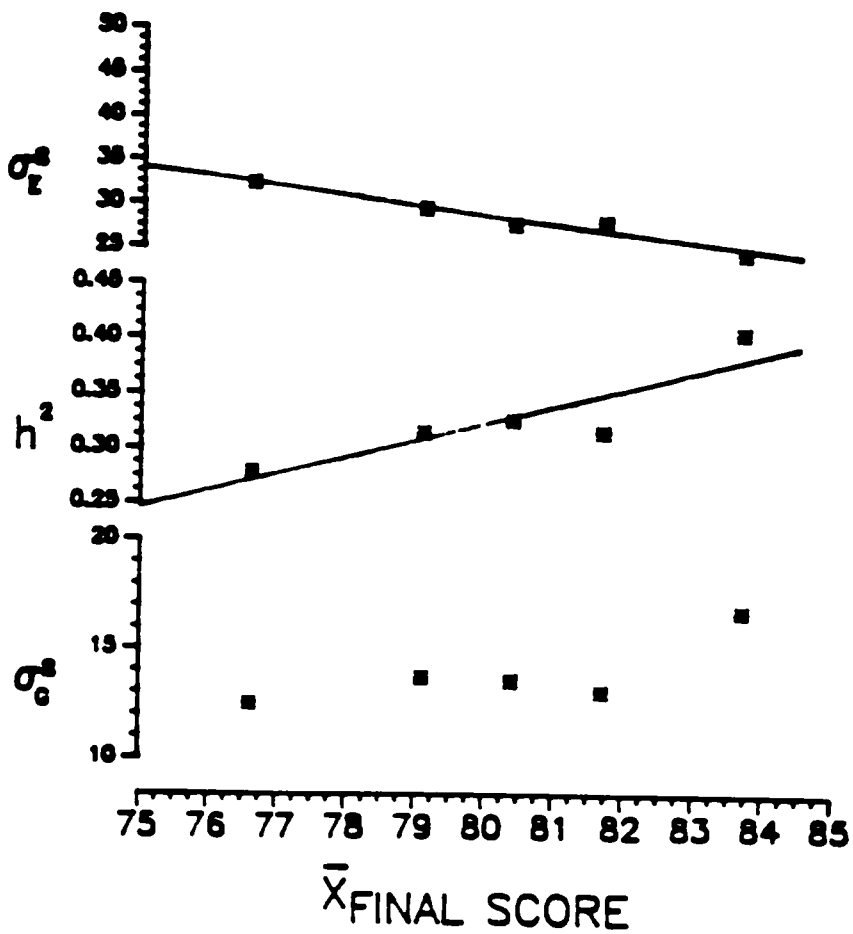
Figure 4. Regression of within-group estimates of
genetic variance, environmental variance,
and heritability for body depth on
group-mean final score.
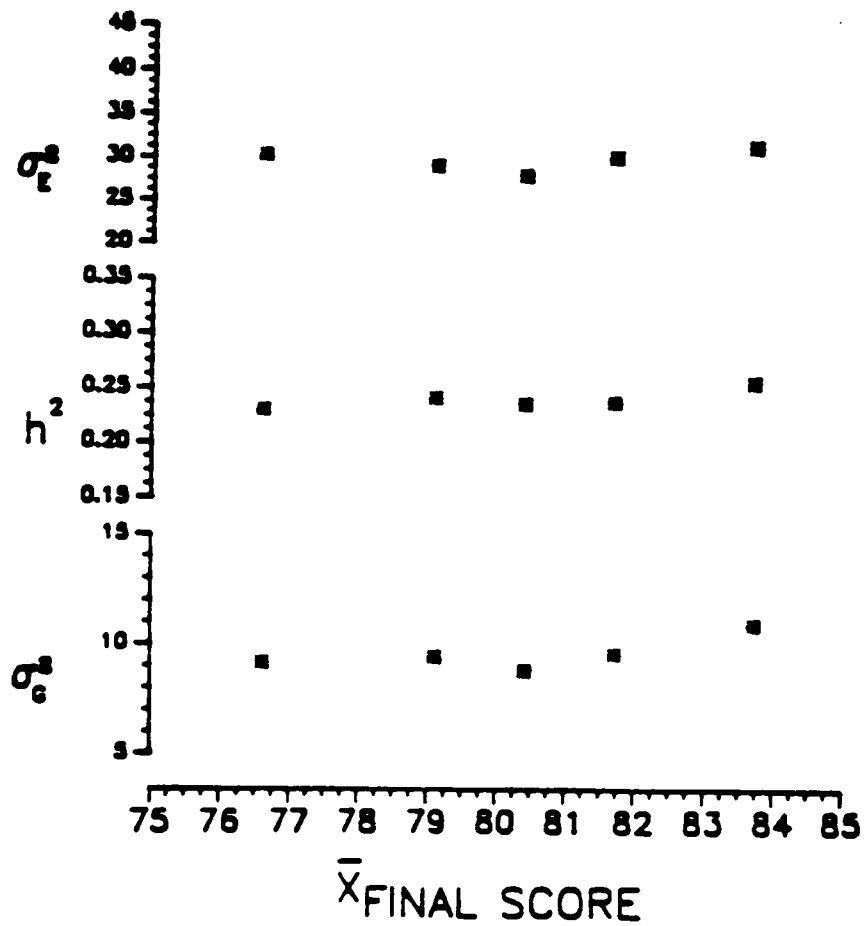
Figure 5. Data points representing within-group
estimates of genetic variance,
environmental variance, and heritability
for fore udder attachment across group
mean for final score.

Effects of Time Trend and Selection Differential on Within-Herd Variation for Final Score

C. D. Smothers

R. E. Pearson

and

T. Lawler

Abstract

First-parity classification records on 391,414 U.S. Holsteins in 20101 herd-rounds were examined to determine the relationship between within-herd variance and herd-mean final score, and the effects of time and selection on the relationship. Data covered herd classifications from 1967 through 1986.

The correlation between herd-mean and within-herd standard deviation for final score was -.55. Average PD type of herd sires, herd size, and average age at classification had little or no association with variability within herds.

Positive curvilinear trends over time were noted for within-herd standard deviation for final score (2.97 to 3.86) and for the negative association between herd-mean and within-herd variability ($r = -.26$ to $r = -.61$). Curves were convex upward and concave upward, respectively. Herd-mean PD type increased linearly (-.54 to .91) as did negative correlation coefficients between average PD type of herd sires and within-herd standard deviation for final score. Repeatability of within-herd standard deviation for herd-rounds over time was quite low (.23).

Mean differences between a cow's first classification score and the average of all first-parity scores in the herd-round increased (-.78 to 1.20) as the number of times a cow was scored increased. Differences in first score deviation within-herds accounted for 24% of the differences seen in within-herd standard deviation for final score. Larger first score deviations were associated with higher variance herds.

Introduction

Previous studies (1,8,9,10) have revealed heterogeneous within-herd variances and a negative relationship between herd mean and within-herd variance for final score. Sorensen and Kennedy (10) used Canadian records and reported

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decreasing variances for final score with increasing herd-mean final score. Smothers et al. (9) found decreasing within-herd standard deviations for final score and many linear traits decreased with increases in herd-mean final score. Bell et al. (1) proposed that declining variability in final score was attributable to more uniform and intensive sire selection and increased culling for type in higher scoring herds.

Variance for milk production has been shown to increase over time (5,6,11). Within-herd, sire, and total variance of both mature equivalent and herdmate deviation milk records increased with time (11). Mirande (6) found increased residual variation for milk from 1960 to 1982. This increase was most noticeable after 1975. Although earlier studies (8,9) examined relationships between phenotypic and genetic/environmental variances and herd-mean final score in U. S. Holsteins, data included only 4 years of classification. A larger data set was needed to confirm earlier results, examine time trends, and determine the influence of selection for type. Objectives of this study were: (1) to examine the phenotypic relationship between herd-mean and within-herd variance for final score over a period of 20 years, (2) to estimate trends for within-herd parameters over time, and (3) to determine the effect of selection for type on within-herd variability for final score.

Materials and Methods

Data provided by the Holstein-Friesian Association of America (HFAA) included type classifications from 1967 through 1986. Records for final score were obtained for herds with codes ending in 2, 5, and 8. Unedited data were approximately 1/3 of all cows scored during the time period and contained 1,744,024 records.

Originally, the data contained multiple records for final score on each individual. These records were used to determine number of times a cow was classified. Data were edited to include only first classification scores. Records without classification dates or sire identification were excluded. Cows over 43 months or under 19 months of age at first score were deleted. Additionally, only herd-rounds with at least 10 usable scores were included. All classification records were adjusted for age with multiplicative correction factors used by the HFAA (D. A. Funk, personal communication, 1989). After edits, the data contained 391,414 first-parity records representing 20,101 herd-rounds of classification.

Association with final type score

Herd-round means were estimated for final score, PD type (PDT) of sires, herd size, and age of individuals at classification. Estimates of within-herd-round standard deviation were calculated for final score. Herd-rounds were stratified into deciles by herd-mean final score. Groups were in ascending mean order from 1 to 10. Details of this stratification were given in an earlier study (9).

Trends over time

For each year from 1967 through 1986, the average within-herd standard deviation for final score, the average herd-mean PDT, correlation coefficients between herd mean and within-herd standard deviation for final score, and correlation coefficients between average herd-mean PDT and within-herd standard deviation for final score were estimated. Estimates of these herd parameters were regressed on linear and quadratic forms for year of classification to examine any trends over time. Repeatabilities of within-herd standard deviation and herd-mean

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final score were estimated from a nested analysis (7) within and among herds.

Influence of selection

A subset of the data was utilized to determine if selection had contributed to population differences in within-herd standard deviation for final score. Only data on cows initially scored prior to 1981 was included. This edit insured that all cows had an opportunity to be scored at least 5 times. Number of times each cow was classified was used to measure selection for type within a herd. The mean of all cows scored for the first time in the herd round and the mean of subsets of the cows that were subsequently rescored 0 to 5 times were calculated. The difference between each subset mean and the herd-mean is an estimate of the selection being practiced. If selection was occurring, the average first score deviation for those cows scored once should be negative and average deviations would increase with number of times scored. Average within-herd first score deviations for cows scored 5 and more than 5 times were regressed on years to examine time trends.

In determining if selection influenced within-herd standard deviation for final score, average differences for cows scored 1 through over 5 times were calculated within herd-rounds. Only herd-rounds ($n = 2599$) with animals scored in all categories 1 to over 5 were included in this part of the study. Regressions of within-herd standard deviation on mean differences for each selection group were examined. The procedure was repeated placing all cows scored more than twice into group 3. Requiring herd-rounds to contain only three selection groups substantially increased numbers ($n = 7717$) for the regression. R-square values were used to determine if selection decisions might have influenced within-herd standard deviation for final score. Correlations between the mean difference for each

selection group (1-over 5) within a herd and within-herd standard deviation for final score were estimated. The coefficients would indicate associations among selection differentials and within-herd variance.

To examine sire selection in herds with different means and variances for final score, 25 subclasses were created. Initially, herd-rounds were stratified into equal sized quintiles according to within-herd-round standard deviation for final scored. Herd-rounds were also stratified in quintiles by mean final score. Herd-rounds were then placed in 25 herd-round standard deviation/mean subclasses. Within each subclass, average herd-mean PD type of sires was calculated.

Results and Discussion

Herd mean and within-herd variability

Table 1 contains mean final score, mean within-herd standard deviation, number of herd-rounds, and cow numbers by groups of ascending herd-mean final score. Each group represented approximately 2010 herd-rounds and between 34,909 and 40,200 cow records. Herd-mean final scores ranged from 76.1 (group 1) to 84.6 (group 10). As groups increased from 1 to 10, estimates of within-herd standard deviation for final score decreased from 5.41 (group 1) to 2.74 (group 10). This decrease was similar to that reported in an earlier study (9) using Holsteins classified from 1983 through 1986. As in (9), the largest decrease was between groups 1 and 2. This result supports other studies (1,10) that reported reduced phenotypic variation in herds at higher means for final score.

Phenotypic correlations among various herd parameters and within-herd-round standard deviation for final score are in Table 2. Herd-mean final score demonstrated a strong negative association ($r = -.55$) with within-herd

variability. This correlation was estimated at -.59 in the previous study (9). Both estimates reflect an opposite relationship to that reported for production (2,4,5). The association between within-herd standard deviation and herd size (r = .07) was positive but weak while the correlation between within-herd variability and mean age at classification (r = .01) was not different from 0. Mean PDT of herd sires was associated only slightly (r = -.08) with within-herd standard deviation. This correlation was somewhat larger (-.26) with more recent data (9).

Trends over time

Figure 1 illustrates significant trends over time for mean within-herd standard deviation for final score, correlations between herd-mean and within-herd standard deviation final score, and herd-mean PDT of sires. Estimates of within-herd standard deviation increased curvilinearly from 1967 (2.97) to 1986 (3.86). Other studies (5,6,11) have reported increased variances over time for production data. The negative correlation between herd mean and within-herd standard deviation has become larger over time. The range was from -.26 in 1967 to -.61 in 1986. In early years, coefficients were more variable and averaged approximately -.41. However after the mid-seventies, correlations were more stable and averaged approximately -.57. During these 20 years, more herds were joining classification programs. Some of the herds were undoubtedly concerned with higher average appraisals and used sire selection, cow culling, and management strategies to obtain them. Over time, divergence of herds seriously concerned with type from those that were not could have strengthened the negative correlation. Herd-mean for PDT of sires increased linearly (-.54 to .91) over time. All PDTs were interpreted relative to a single fixed base for the entire time period. Thus if superior individuals were identified and

selection policies were effective, sire transmitting abilities would generally increase over time.

Figure 2 illustrates the linear decrease over time (0 to -.28) in estimates of correlation between herd-mean PDT and within herd standard deviation for final score. This time trend sheds light on the difference found in coefficients estimated with recent data (-.26) and with data covering 20 years of herd classification (-.08). Although the correlation became increasingly more negative within years, the increasing yearly trends for both herd-mean PDT and within-herd variance for final score weakened the correlation estimated over all years.

Repeatability of herd-mean final score was .62 while repeatability of within-herd standard deviation was estimated at .23. The latter was slightly lower than an estimate obtained for milk production (.33) as part of another study (T. R. Meinert, personal communication, 1989). The low repeatability was unfortunate since with a high repeatability for herds across years, more accurate estimates of variance would have been obtainable. Adjustment techniques could operate on a herd level instead of a herd-round level.

Influence of selection

Table 3 contains mean differences between a cow's first classification score and the average of all first-parity scores in the herd-round, for groups scored different number of times during their lifetime. For cows scored only once, the mean difference was -.78. As number of times scored increased, mean difference also increased. The largest mean difference (1.20) was for cows scored more than five times. A negative mean difference for the lowest selection group and subsequent increases in higher selection groups indicates that some of the selection

being practiced was for final score. Time trends for mean difference of two selection groups are in Figure 3. Time trend for cows scored 5 times was positive and linear. A positive trend for cows scored more than 5 times approach significance.

Table 4 contains phenotypic correlations between within-herd standard deviation for final score and the mean difference for each selection group within a herd-round. Coefficients range from -.42 in selection group 1 to .23 for cows scored more than 5 times. These correlations suggest larger deviations for cows at the extremes in higher variance herds. If cows are selected assuming equal variability within herds, cows in higher variance herds are at a selective advantage because of larger deviations. Vinson (14) suggested that cows at upper extremes would be over-evaluated in high-variance relative to low-variance herds. For cows at lower extremes, the opposite would be true. Other studies (2,3,13) have addressed this situation. Unless heritability is higher in high-variance herds (12), the accuracy of selection and genetic evaluations could be compromised.

Only herd-rounds having cows in all 6 selection groups were used to calculate regression of within-herd standard deviation for final score on herd-round first score deviations for group. The R-square suggests a low to moderate relationship between the differences in within-herd standard deviation for final score and within-herd first score deviations. When the regression was rerun using only three selection groups, the R-square was .18. Generally, it seems that selection plays some role in affecting within-herd standard deviation. This would support the contention of Bell et al. (1) that higher classifying herds select more intensely for final score.

Table 5 gives average herd-mean PD type of sires for each of 25 subclasses based on within-herd-round standard deviation/mean for final score. Average PD

type clearly increases with herd-mean final score. Thus, reflecting more sire selection emphasis for type in higher scoring herds. Additionally, average PD type increases slightly with increases in within-herd-round standard deviation for final score. The reason for this was not clear.

Summary and Conclusions

Within-herd-round variance was shown to vary greatly across herds. This was partially due to a strong negative ($r = -.59$) relationship between mean and variance. However, the repeatability of within-herd standard deviation, across rounds within a herd, was low (.23). Thus, any method of adjusting for within-herd standard deviation must consider individual herd rounds when estimating mean and variance.

Significant time trends over the 20 years were found for within-herd standard deviation (convex upward), PDT (linear upward), correlations between mean and standard deviation within-herd (concave upward), and PDT and within-herd standard deviation (linear downward). The increasing negative relationship between mean final score and herd-mean PDT, and within-herd standard deviation may reflect increasing diversity in the objectives of herds scored over time.

In herds on the classification program for at least 6 rounds of classification, significant emphasis was placed on final score in deciding which cows were to be culled. The magnitude of the deviations had a slight relationship to within-herd variance. However, a cause and affect relationship between the two variables was unclear.

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Table 1. Mean final score ($\bar{X}$), mean within-herd standard deviation (SD) for final score, numbers of herd-rounds, and cow numbers by group.[1]

	Mean			
Group[1]	Herd $\bar{X}$	Herd SD	Herd Rounds	Cows
	pts	pts	#	#
1	76.1	5.41	2009	38044
2	78.3	4.19	2010	39979
3	79.2	3.81	2010	39978
4	79.9	3.64	2010	40072
5	80.5	3.48	2010	40154
6	81.0	3.35	2010	39995
7	81.6	3.26	2010	39645
8	82.2	3.17	2010	40200
9	83.0	3.04	2010	38618
10	84.6	2.74	2012	34909

[1]Group stratification according to ascending herd-round mean for final score.
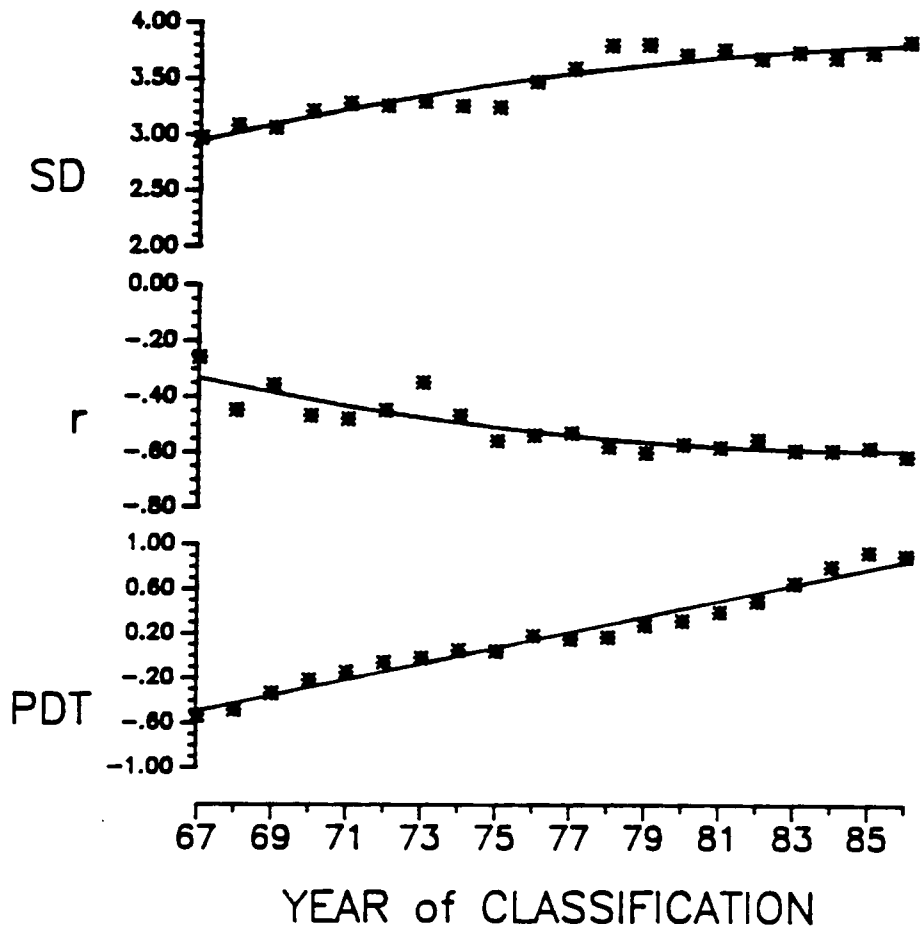
Figure 1. Regressions of mean within-herd standard deviation (SD) for final score, correlation (r) between herd mean and standard deviation final score, and herd-mean PD type (PDT), on year of classification.

Table 2. Phenotypic correlations among various herd parameters and within-herd standard deviation for final score.

Herd-round mean for:	Coefficient
Final Score	-.55**
PD Type of Herd Sires[1]	-.08**
Age[2]	.01
Herd Size	.07**

[1]Based on daughters' score nearest 30 months.
[2]Mean age at first classification.
[3]Number of cows with first scores in the herd-rounds.
**(P<.01)

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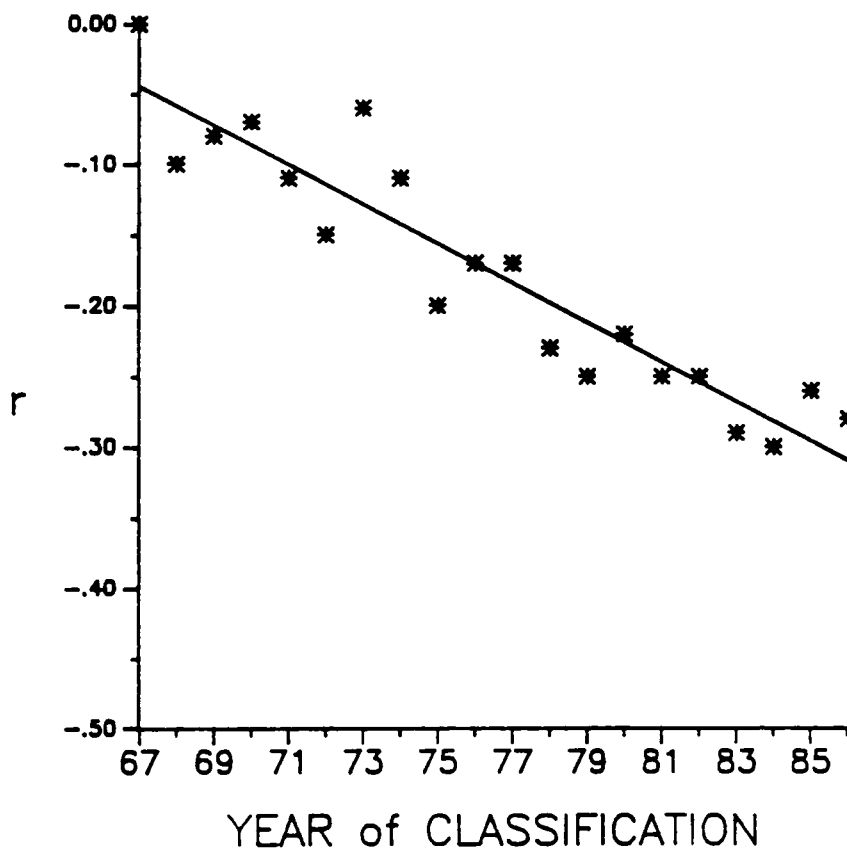
Figure 2. Regression of correlation coefficients (r), estimated within-year, between herd-mean PDT and within-herd standard deviation for final score, on year of classification.

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Table 3. Mean-differences between a cow's first classification score and the average of all first-parity scores in the herd-round, by the number of times scored.[1]

Number of Times Classified	Mean Difference[2]
#	pts.
1	-.78
2	.09
3	.37
4	.60
5	.81
5 or more	1.20

[1]Data collected from 1967-1980.
[2]Difference between a cow's first score and the herd-round mean of first scores.
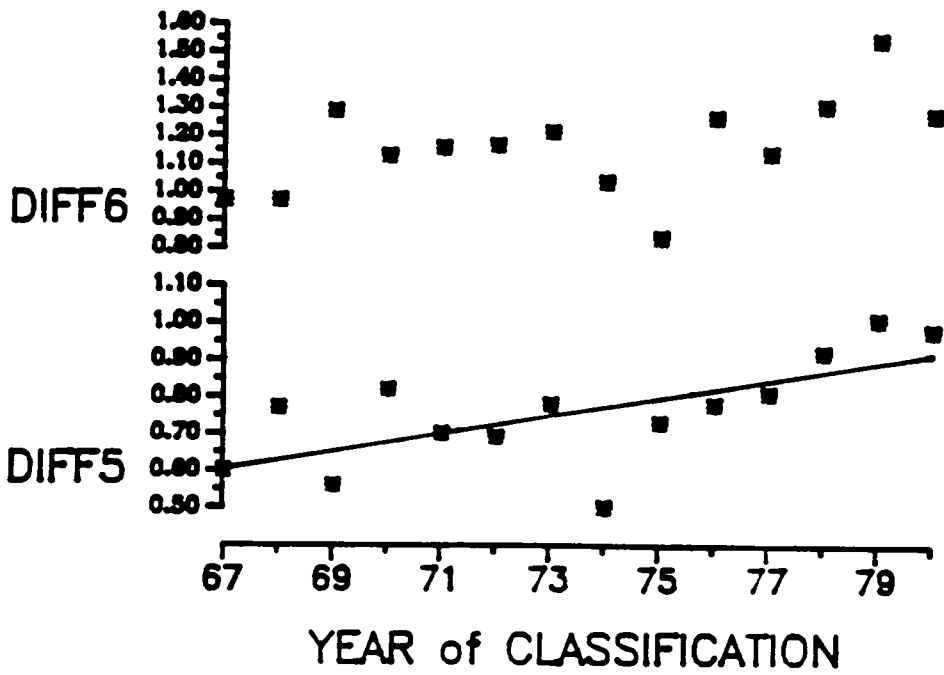
Figure 3. Data points representing change in mean selection
differentials over years for cows scored 5 times
(DIFF5) and those scored over 5 times (DIFF6).

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Table 4. Phenotypic correlations
          between within-herd standard
          deviation for final score
          and the mean difference
          between average first-parity
          scores in the herd-round and
          first-parity scores of cows
          classified from 1 to 6
          times.[1]

Number of Times Classified	Coefficient
#	pts.
1	-.42**
2	.05*
3	.12
4	.16
5	.22
over 5	.23

[1]Data collected from 1967-1980.
*(P<.05)
**(P<.01)

Table 5. Average PD type of herd sires for herd-rounds stratified into 2-5 herd-round standard-deviation/mean subclasses.

Within-herd Standard-Deviation Group[1]	Herd Mean Groups[2]				
	1	2	3	4	5
1	-.45	-.26	-.08	.02	.35
2	-.41	-.18	-.04	.14	.38
3	-.31	-.18	.07	.24	.38
4	-.29	-.02	.13	.28	.47
5	-.19	.07	.24	.36	.54

[1]Group stratification in ascending order according to within-herd-round standard deviation for final score.
[2]Group stratification in ascending order according to herd-round mean for final score.

General Conclusions

These studies demonstrate heterogeneity of within herd variances exist in the U.S. Holstein population. Consequently, assuming constant within-herd variances for genetic evaluations is not valid. The relationship between within-herd-round standard deviation for final score and herd-mean final score was large and negative. The relationship between within-herd-round standard deviation for final score and herd-mean PD type of sires was also negative but not as strong. Both negative relationships suggest within-herd-round variability for final score was influenced by environmental and genetic factors.

Within-herd-round standard deviations for linear traits also declined with increasing herd-mean final score. The declines were less than for final score. Declines in within-herd variability for linear traits may have been more dramatic if stratification were by herd-mean for each linear trait instead of herd-mean final score. In any case, within-herd-round variances for linear traits were heterogeneous and should be accounted for in multiple-trait genetic evaluations.

Differences in herd-mean and phenotypic within-herd standard deviations for final score on response to selection for type was substantial. Herds characterized by high-mean/within-herd variance for final score obtained two times the selection response as that obtained in low-mean/within-herd variance herds. Large differences across herds in selection response would effect sire evaluation if progeny were nonrandomly distributed. They could also lead to responses to sire selection significantly greater or lesser than expected.

When sire and residual variance components were estimated within quintiles based on herd-mean final score, decreases in genetic and environmental variance for final score accompanied increasing herd-mean final score. Many linear traits

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exhibited similar trends. Most importantly, heritability estimates remained constant or increased with decreases in within-herd variability. If higher proportions of individuals were selected from more variable herds with equal or lower heritabilities than low variance herds, genetic progress in the population would suffer. Accounting for within herd variance, is more important for type traits than for production where h^2 increases with variance.

Phenotypic within-herd standard deviations for final score and average herd mean for PD type of herd sires increased over time. These trends partially negated the overall negative correlation between within-herd variability for final score and herd-mean PD type of sires. However, within years the correlation has become increasingly negative since 1967. Improvements in estimation of sire breeding values could have influenced the trend.

Generally, herd means for final score have been constant over years, while average within-herd variance for final score has increased. Thus, the negative relationship between these parameters grew larger over time. Across rounds within herds, repeatability of within-herd standard deviation for final score was low. Consequently, the same estimate of the within herd variability cannot be used across rounds of the same herd. Estimation of standard deviations for each individual herd round creates problems both in the number of parameters estimated and in their accuracy. Both culling and sire selection appear to affect within-herd variance. Most of the influence came through their effect on herd 90 mean final score and its relationship to within-herd variance.

APPENDICES

Appendix 1. Definition of conformation traits in the Holstein Friesian Association of America linear classification program (scoring is based on scale of 1 to 50).

I. Body Characteristics

1) Stature
   1-5, Very short
   25, Intermediate
   45-50, Very tall

2) Strength
   1-5, Extremely narrow and frail
   25, Intermediate
   45-50, Extremely strong and wide

3) Body Depth
   1-5, Extremely shallow body
   25, Intermediate
   45-50, Extremely deep body

4) Angularity
   1-5, Thick & coarse
   25, Sharp & angular
   45-50, Extremely sharp and angular

II. Rump

1) Rump Angle
   1-5, Pins clearly higher than hooks
   25, Slight slope from hooks to pins
   45-50, Extremely sloped from hooks to pins

2) Rump Length
   1-5, Extremely short
   25, Intermediate length
   45-50, Extremely long

3) Rump Width
   1-5, Extremely narrow
   25, Intermediate width
   45-50, Extremely width

III. Udder

1) Fore Udder Attachment
   1-5, Extremely loose
   25, Intermediate strength
   45-50, Extremely snug and strong

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Appendix 1. Definition of conformation traits in the Holstein Friesian Association of America linear classification program (scoring is based on scale of 1 to 50). - con't

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III.   Udder - con't

2) Rear Udder Height
   1-5, Extremely low
   25, Intermediate height
   45-50, Extremely high

3) Rear Udder Width _
   1-5, Narrow rear udder
   25, Intermediate width
   45-50, Extremely wide rear udder

4) Udder Support
   1-5, Negative celft, broken support
   25, Clearly defined halving, cleft and support
   45-50, Extreme cleft and strong support

5) Udder Depth
   1-5, Very deep udder floor well below the hock
   25, Udder floor above hocks
   45-50, Extreme height of udder floor above hock

6) Teat Placement (rear view)
   1-5, Extremely wide, placement on outside of quarter
   25, Centrally placed on quarter
   45-50, Extremely close, base of teat on inside quarter

Appendix 2. Means and standard deviations for final
score and linear descriptive traits on cows
classified from 1983 through 1986.[1]

Trait[2]	Mean	Standard Deviation
Stature	29.9	8.2
Strength	28.3	7.3
Body Depth	30.5	7.4
Angularity	29.7	7.4
Rump Angle	25.2	5.2
Rump Length	29.8	6.0
Rump Width	26.9	6.9
Rear Legs (side view)	27.4	6.8
Foot Angle	23.9	6.3
Fore Udder Attachment	24.2	6.8
Rear Udder Height	25.9	7.3
Rear Udder Width	25.5	7.3
Udder Support	26.3	5.6
Udder Depth	23.0	4.6
Teat Placement	24.0	5.9
Final Score[3]	80.4	4.6

[1]Cows 45 months of age or less at first score.
[2]Linear scores adjusted for age and stage of lactation.
[3]Final scores adjusted for age.

Appendix 3. Regression of group average for within-herd
            standard deviation (stature) on group average
            for herd-mean final score.
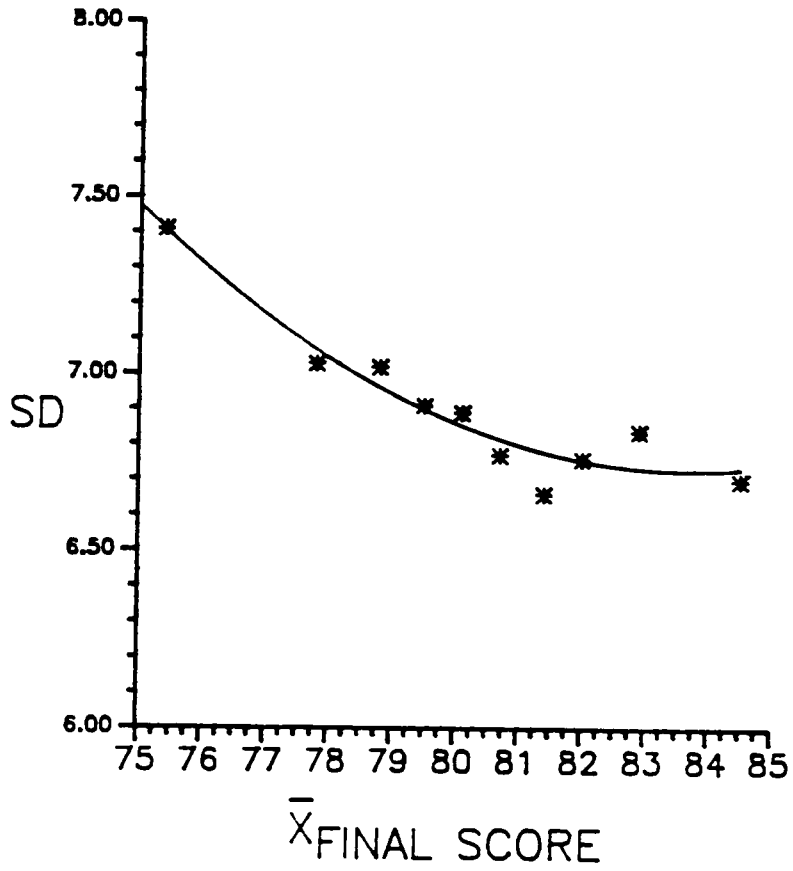
Appendix 4. Regression of group average for within-herd
standard deviation (strength) on group
average for herd-mean final score.
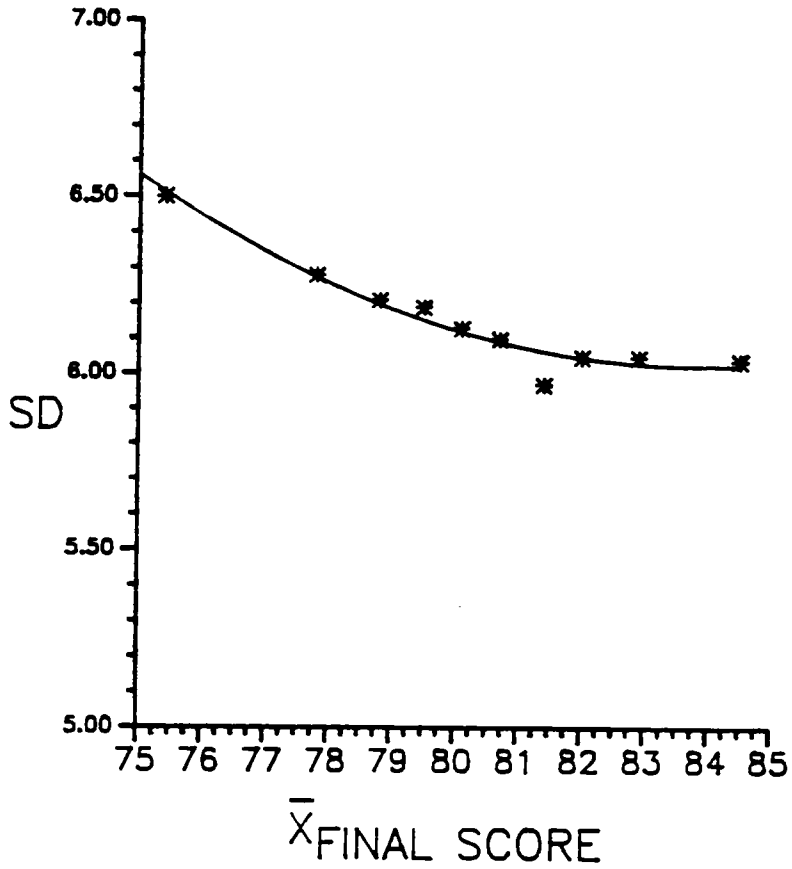
Appendix 5. Regression of group average for within-herd
standard deviation (body depth) on group
average for herd-mean final score.

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Appendix 6. Regression of group average for within-herd standard deviation (angularity) on group average for herd-mean final score.

Appendix 7. Regression of group average for within-herd standard deviation (rump angle) on group average for herd-mean final score.

Appendix 8. Regression of group average for within-herd
            standard deviation (rump length) on group
            average for herd-mean final score.

Appendix 9. Regression of group average for within-herd standard deviation (rump width) on group average for herd-mean final score.
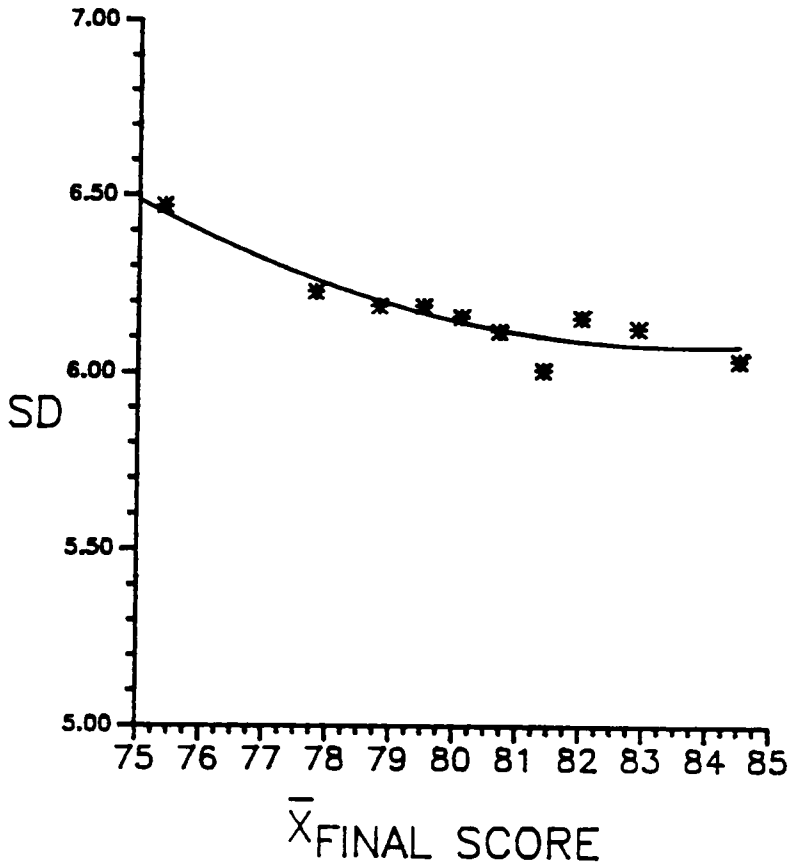
Appendix 10. Regression of group average for within-herd
standard deviation (rear legs) on group
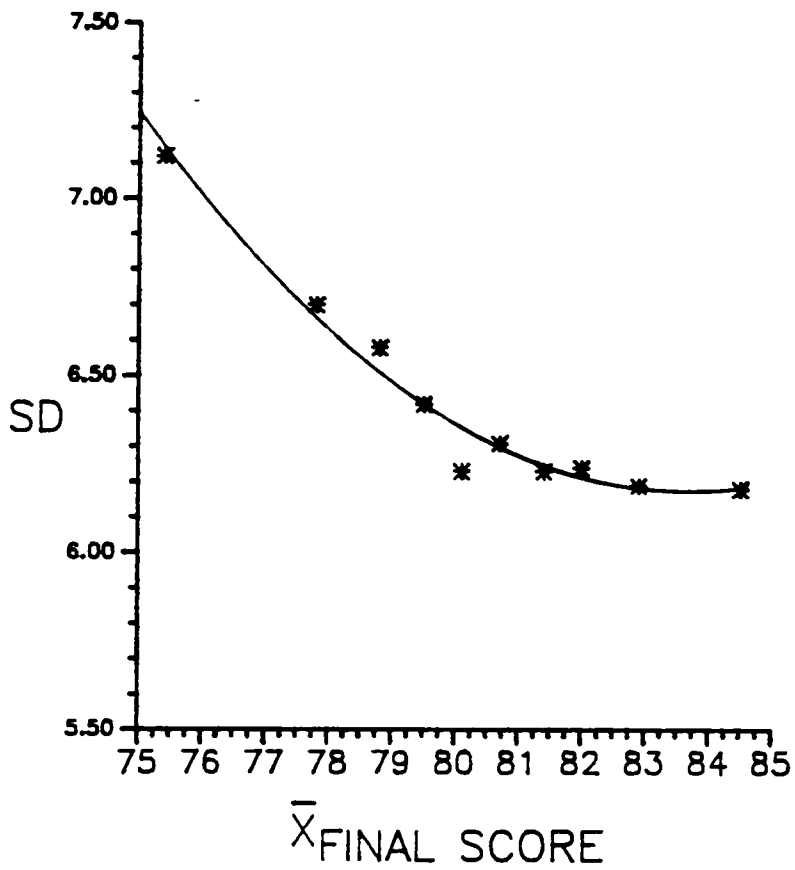average for herd-mean final score.

Appendix 11. Regression of group average for within-herd
standard deviation (foot angle) on group
average for herd-mean final score.

Appendix 12. Regression of group average for within-herd
standard deviation (fore udder attachment) on
group average for herd-mean final score.

Appendix 13. Regression of group average for within-herd
standard deviation (rear udder height) on
group average for herd-mean final score.

Appendix 14. Regression of group average for within-herd
standard deviation (rear udder width) on
group average for herd-mean final score.
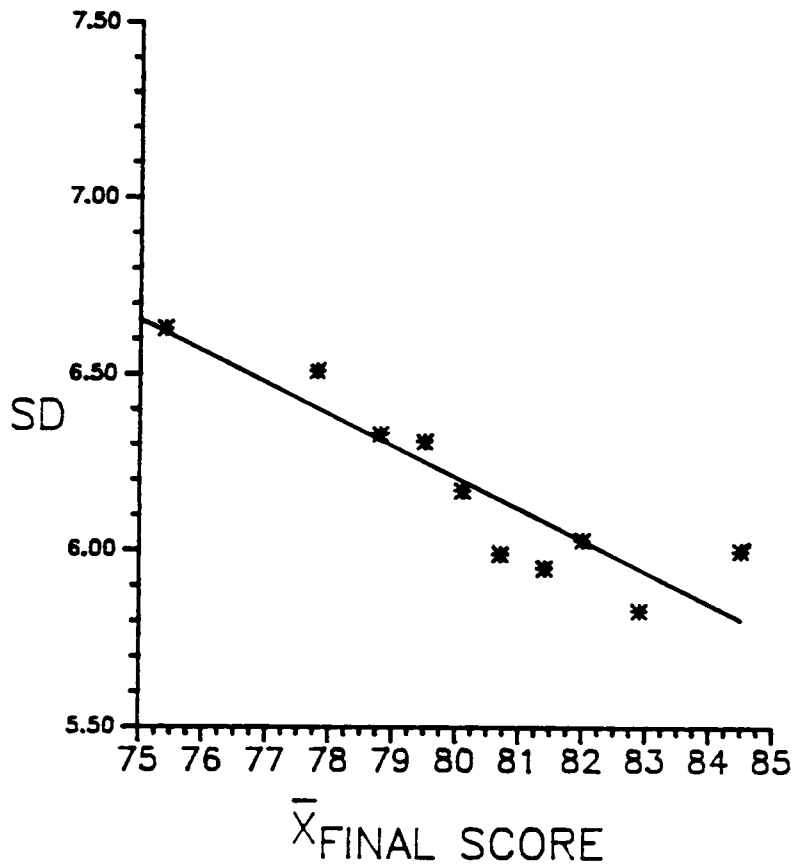
Appendix 15. Regression of group average for within-herd
              standard deviation (udder support) on group
              average for herd-mean final score.
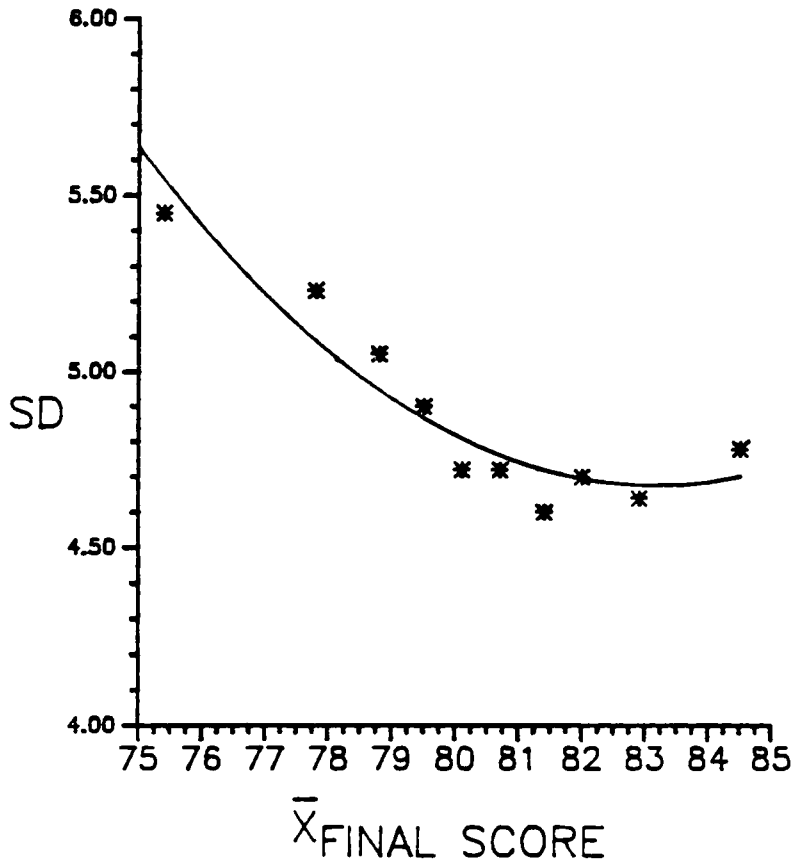
Appendix 16. Regression of group average for within-herd
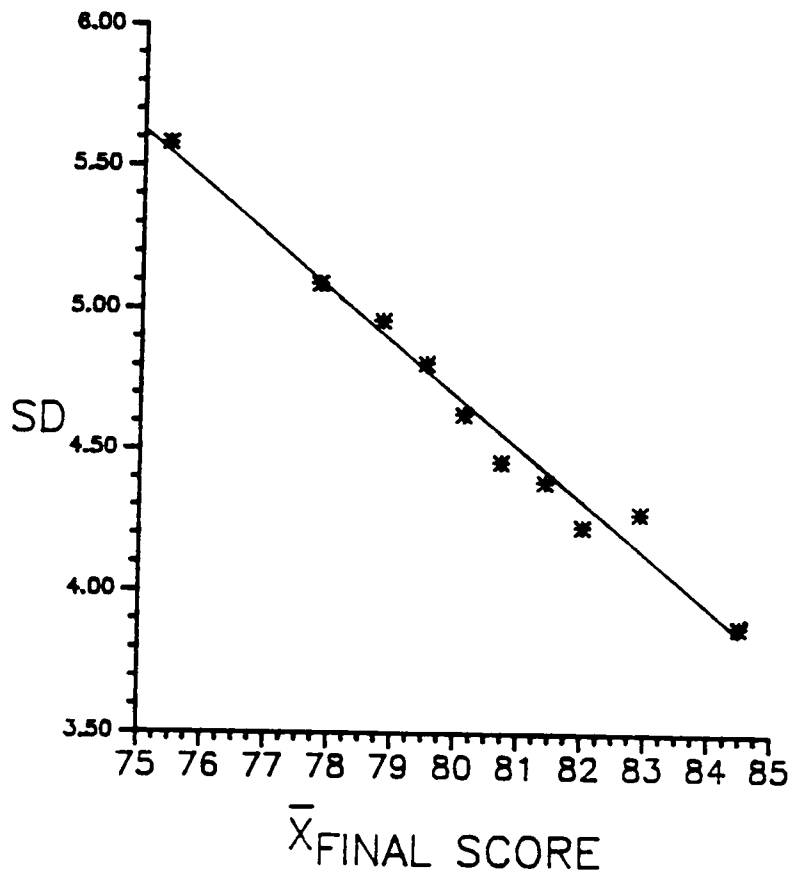standard deviation (udder depth) on group
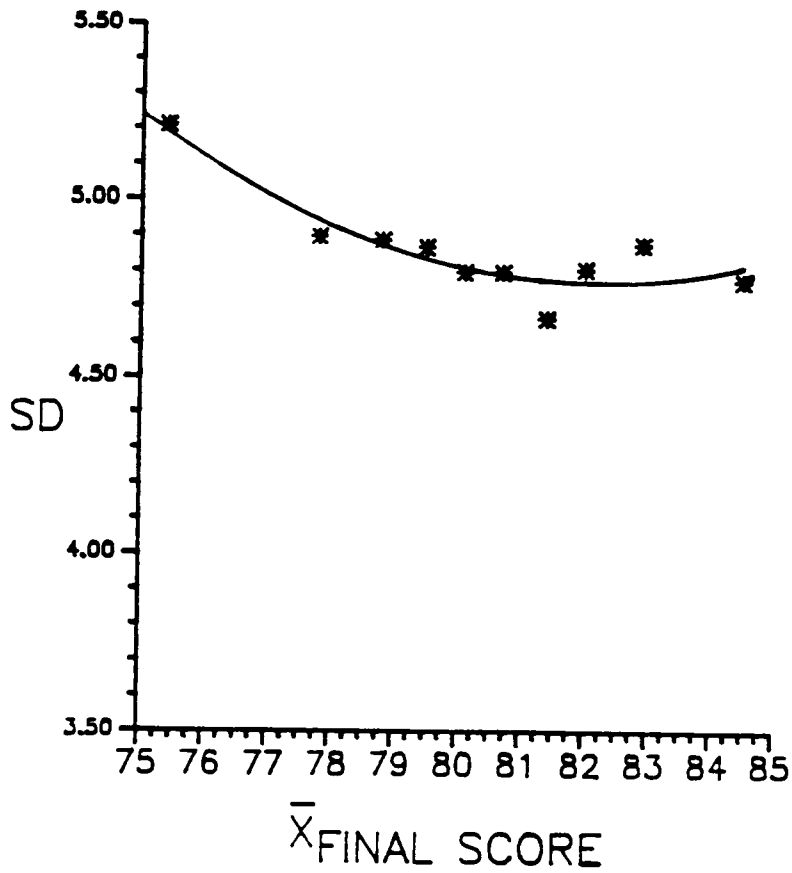average for herd-mean final score.

SD
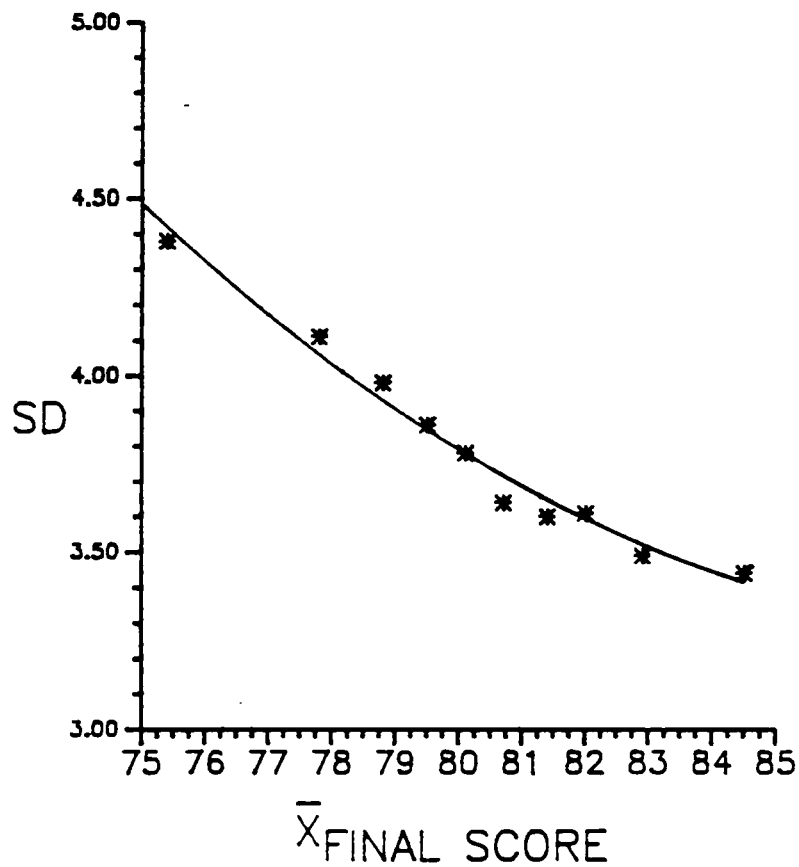
$\bar{X}$FINAL SCORE
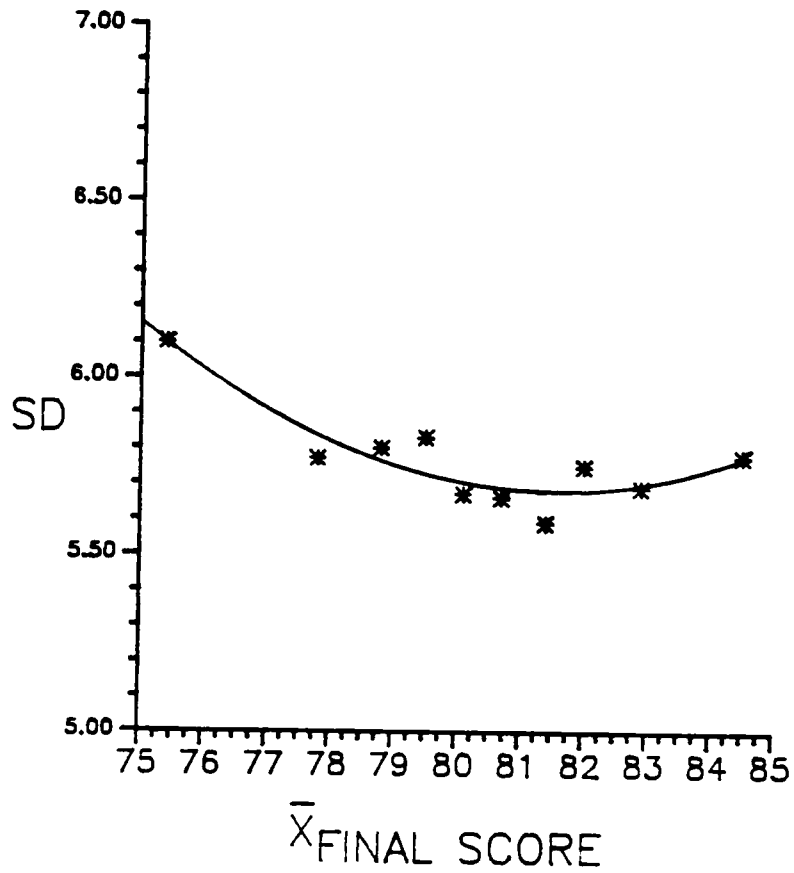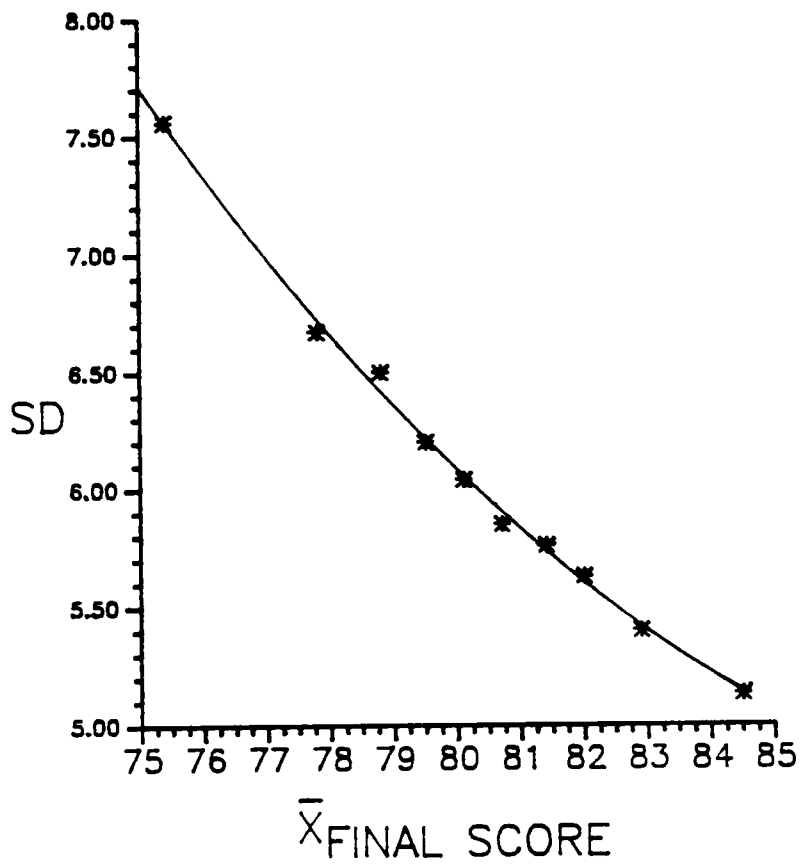
Appendix 17. Regression of group average for within-herd
             standard deviation (teat placement) on group
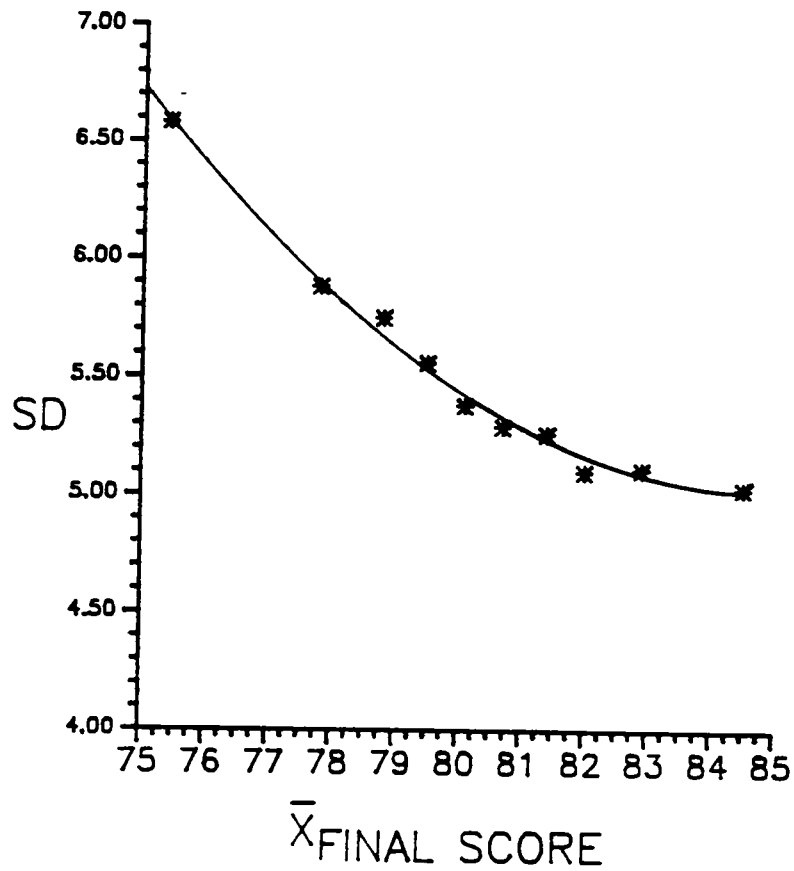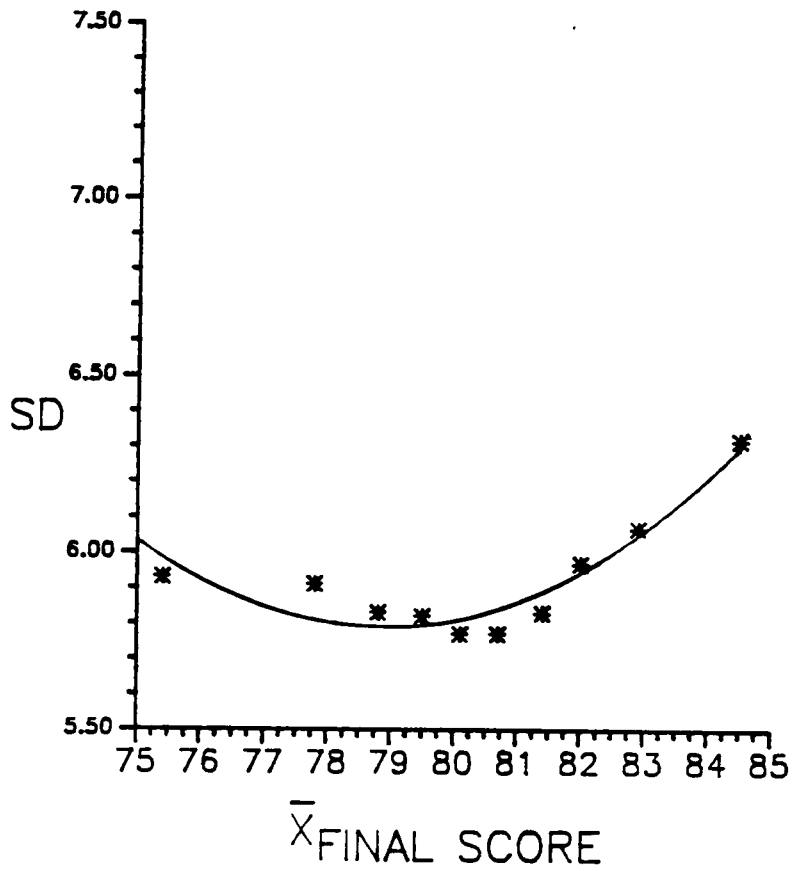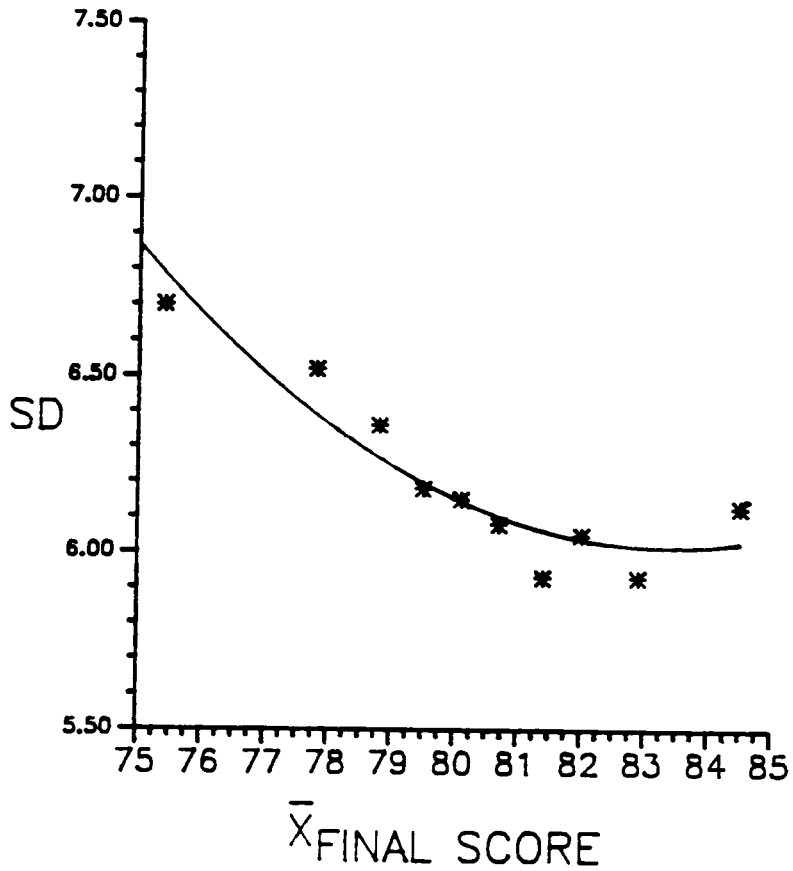   average for herd-mean final score.
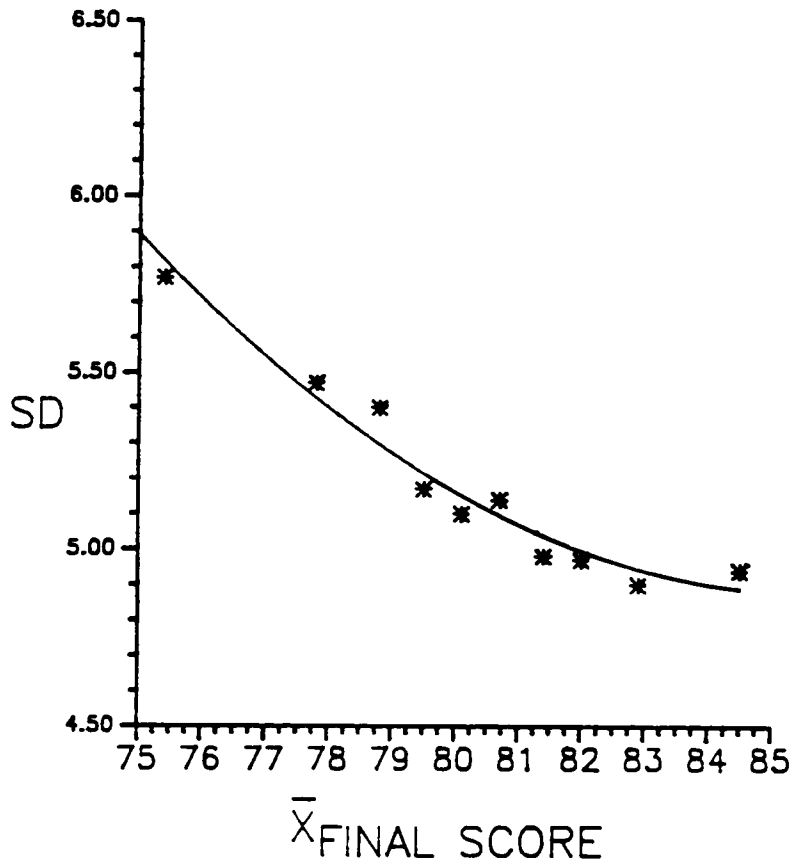
Appendix 18. Estimates of genetic variance for final score and linear descriptive traits by group.

Trait	Group Number[1]				
	1	2	3	4	5
Stature	19.27	17.07	20.7	16.29	20.03
Strength	11.33	10.63	12.16	10.48	13.45
Body Depth	12.43	13.66	13.52	13.01	16.73
Angularity	11.22	12.26	11.50	11.24	14.81
Rump Angle	9.90	9.61	9.72	8.39	7.59
Rump Length	5.09	4.82	5.15	4.36	5.62
Rump Width	9.34	8.26	9.35	8.96	12.20
Rear Legs	8.69	8.05	8.47	6.30	7.64
Foot Angle	5.14	5.22	4.35	4.09	3.98
Fore Udder Attachment	9.13	9.37	8.76	9.54	10.87
Rear Udder Height	9.95	9.79	10.35	9.94	9.98
Rear Udder Width	9.02	7.72	9.07	8.46	7.33
Udder Support	4.96	4.12	4.27	4.58	4.93
Udder Depth	6.31	5.73	4.45	4.43	4.34
Teat Placement	7.96	7.49	7.35	8.72	8.91
Final Score	5.95	3.31	3.50	2.42	1.97

[1]Groups based on average herd-mean for final score, range from group 1 (76.6) to group 5 (83.7).

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Appendix 19. Estimates of environmental variance for final score and linear descriptive traits by group.

Trait	Group Number[1]				
	1	2	3	4	5
Stature	37.98	36.71	31.09	32.75	29.23
Strength	34.35	32.95	29.31	29.78	27.27
Body Depth	32.32	29.68	27.89	28.18	24.46
Angularity	41.01	34.11	31.81	32.38	27.37
Rump Angle	21.48	17.93	14.43	13.68	12.43
Rump Length	24.25	22.74	21.20	21.00	20.74
Rump Width	30.02	29.98	26.40	26.85	24.25
Rear Legs	47.38	37.24	31.13	28.87	23.04
Foot Angle	38.53	31.36	27.79	25.75	24.99
Fore Udder Attachment	30.43	29.31	28.30	30.38	31.49
Rear Udder Height	39.16	34.14	31.16	31.24	29.63
Rear Udder Width	39.05	36.15	32.13	31.99	31.16
Udder Support	28.02	24.12	20.94	20.60	19.95
Udder Depth	14.07	11.81	10.86	10.62	9.32
Teat Placement	27.02	24.31	22.58	20.18	19.10
Final Score	23.89	14.22	10.52	9.70	7.36

[1]Groups based on average herd-mean for final score, range from group 1 (76.6) to group 5 (83.7).

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Appendix 20. Estimates of heritability for final score and linear
descriptive traits by group.

Trait	Group Number[1]				
	1	2	3	4	5
Stature	.34	.32	.39	.33	.41
Strength	.25	.24	.29	.26	.33
Body Depth	.28	.32	.33	.32	.40
Angularity	.21	.26	.27	.26	.36
Rump Angle	.32	.35	.40	.38	.38
Rump Length	.17	.17	.20	.17	.21
Rump Width	.24	.22	.26	.25	.33
Rear Legs	.15	.18	.21	.18	.25
Foot Angle	.12	.14	.13	.14	.13
Fore Udder Attachment	.23	.24	.24	.24	.26
Rear Udder Height	.20	.22	.25	.24	.25
Rear Udder Width	.19	.18	.22	.21	.19
Udder Support	.15	.15	.17	.18	.20
Udder Depth	.31	.33	.29	.29	.32
Teat Placement	.23	.24	.25	.30	.32
Final Score	.20	.19	.25	.20	.21

[1]Groups based on average herd-mean for final score, range from group 1 (76.6)
to group 5 (83.7).

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Appendix 21. Regression of within-group estimates of genetic variance, environmental variance, and heritability for rump angle on group-mean final score.

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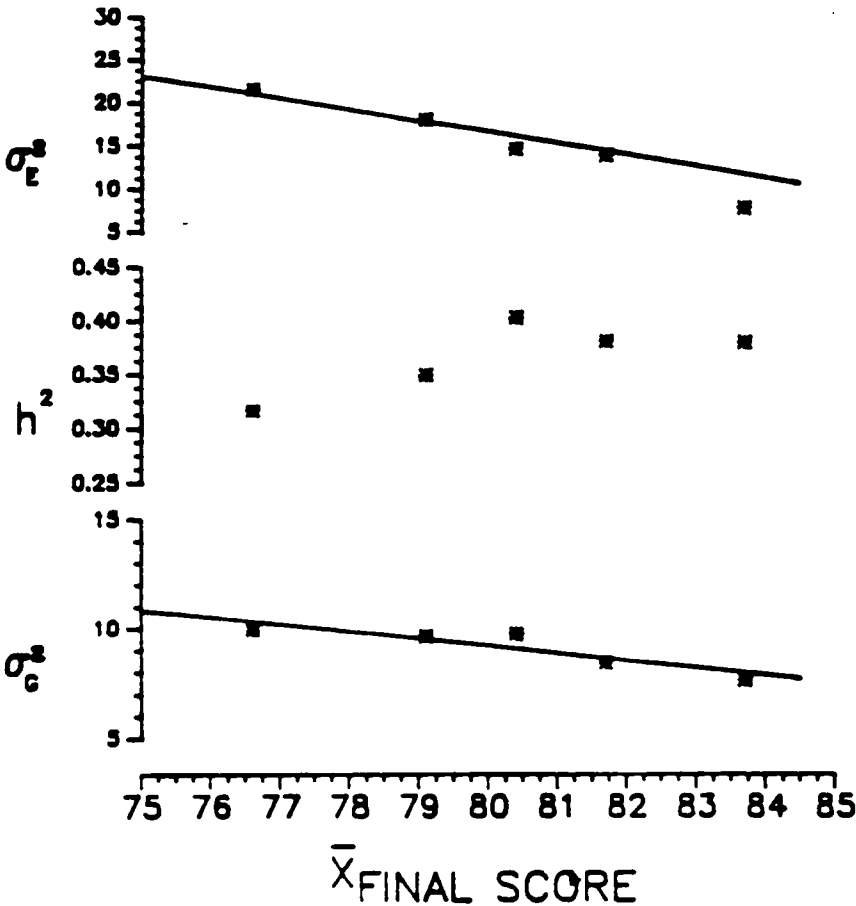
Appendix 22. Regression of group estimates of genetic variance, environmental variance, and heritability for rump length on group-mean final score.
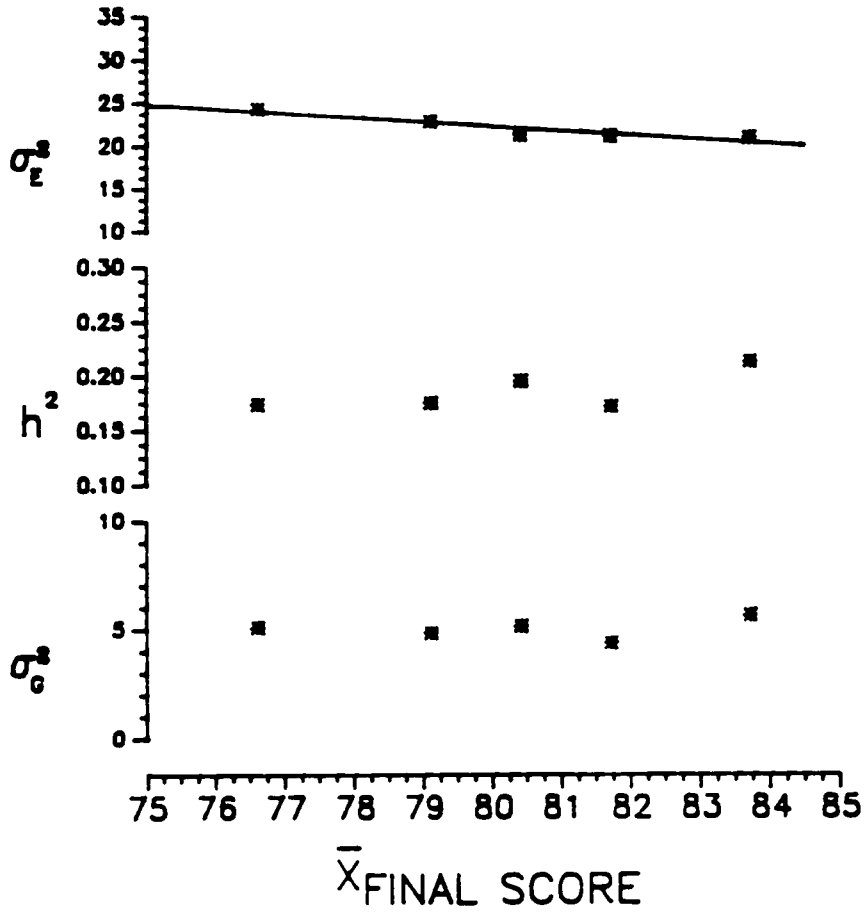
Appendix 23. Regression of within-group estimates of genetic variance, environmental variance, and heritability for rump width on group-mean final score.

Appendix 24. Regression of within-group estimates of genetic variance, environmental variance, and heritability for rear legs on group-mean final score.

-Appendix 25. Regression of within-group estimates of genetic variance, environmental variance, and heritability for foot angle on group-mean final score.

Appendix 26. Regression of within-group estimates
of genetic variance, environmental variance,
and heritability for rear udder height on
group-mean final score.

Appendix 27. Regression of within-group estimates of genetic variance, environmental variance, and heritability for rear udder width on group-mean final score.

Appendix 28. Regression of within-group estimates
of genetic variance, environmental variance,
and heritability for udder support on
group-mean final score.
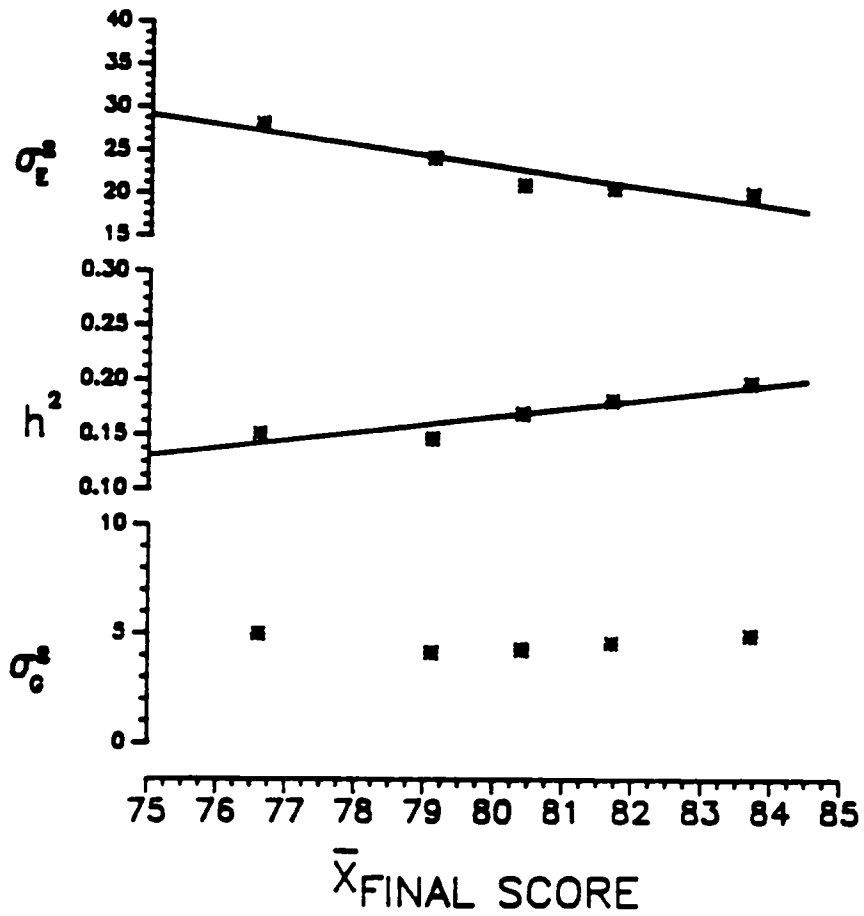
Appendix 29. Regression of within-group estimates of genetic variance, environmental variance, and heritability for udder depth on group-mean final score.
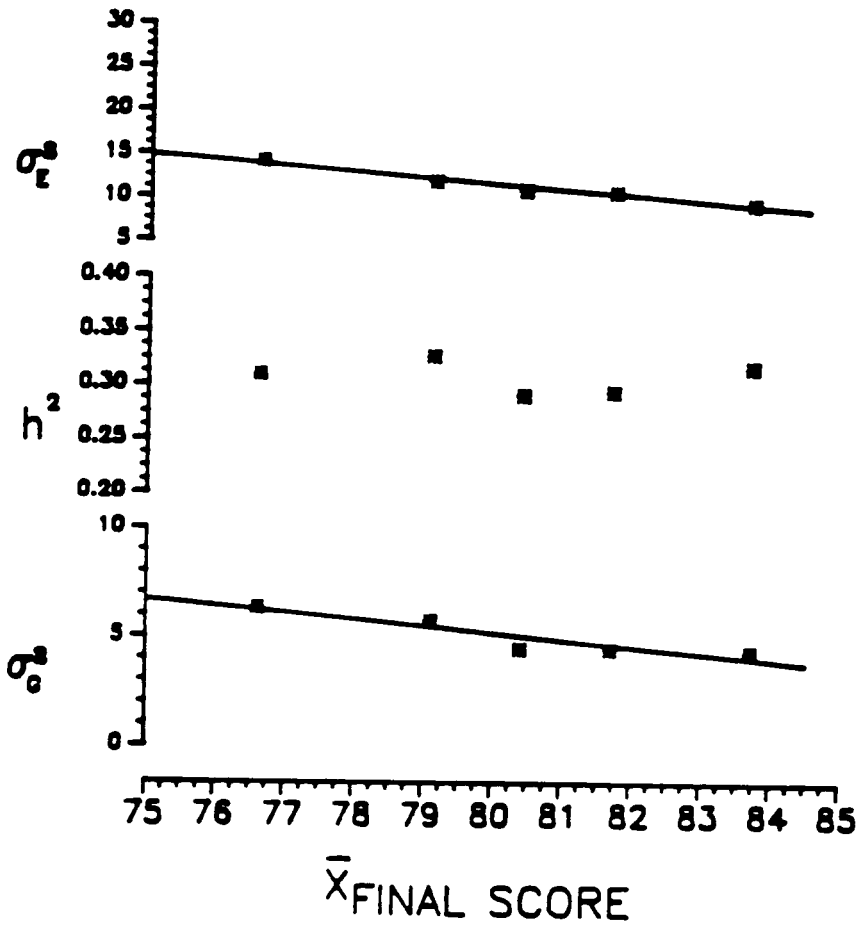
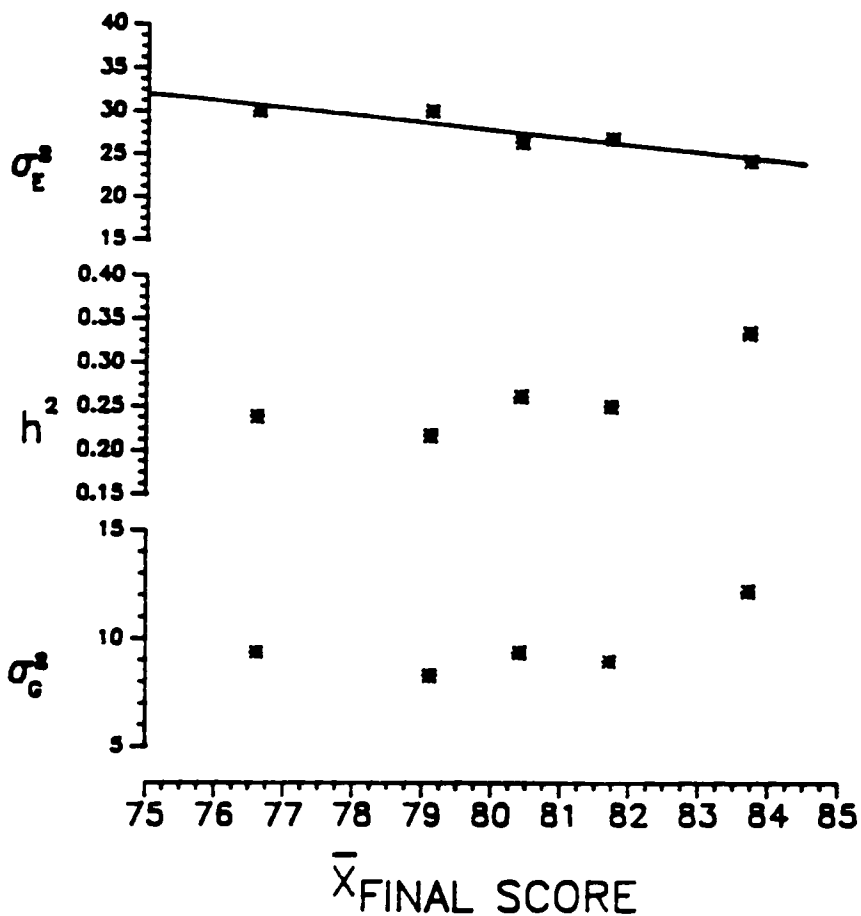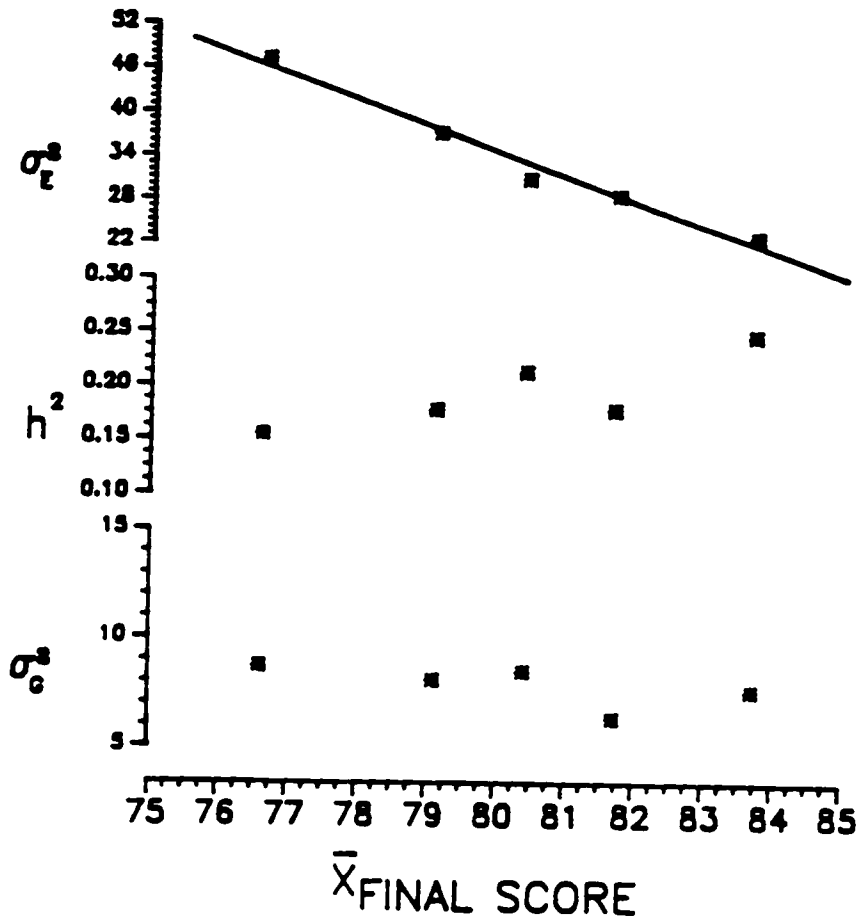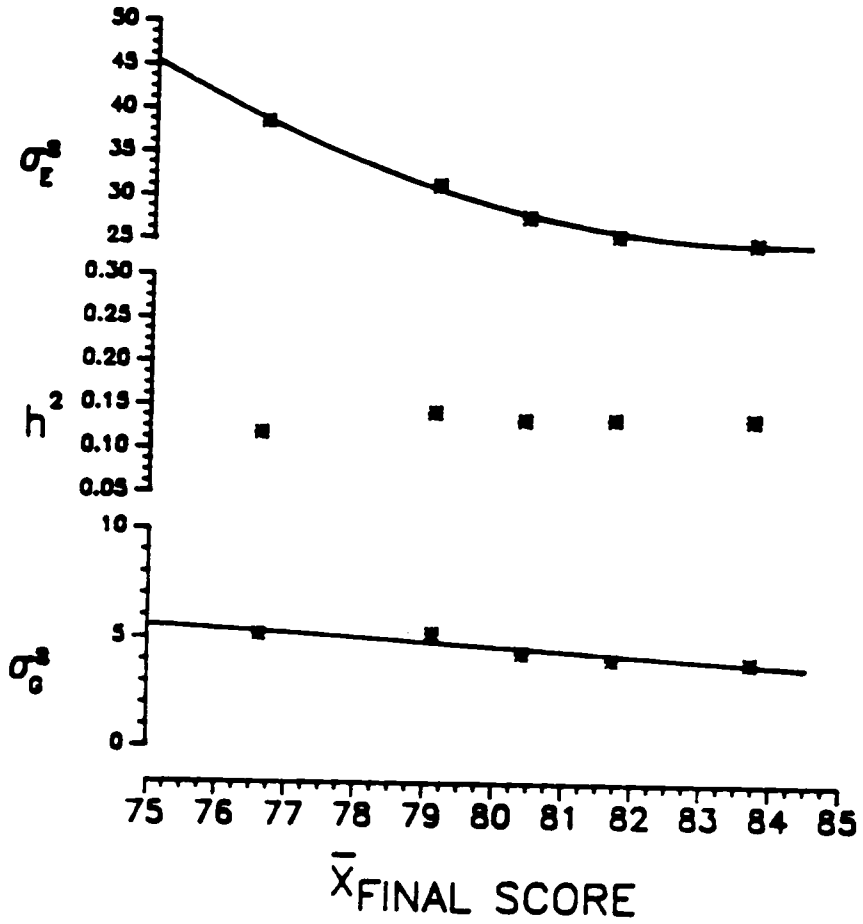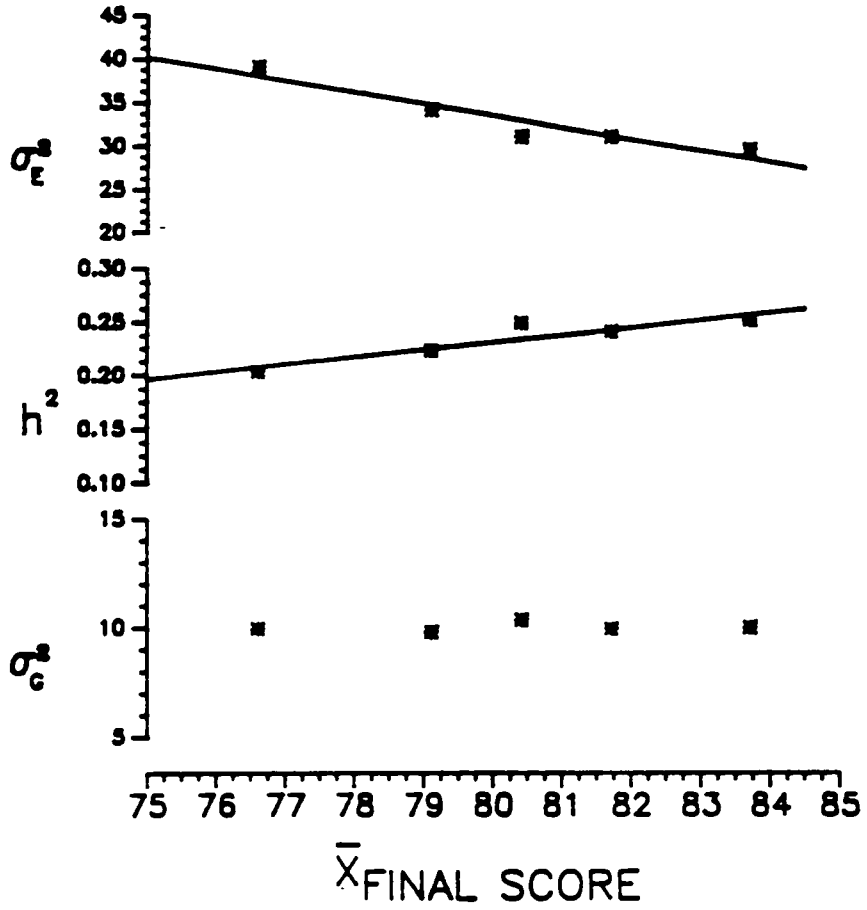Appendix 30. Regression of within-group estimates of genetic variance, environmental variance, and heritability for teat placement on group-mean final score.
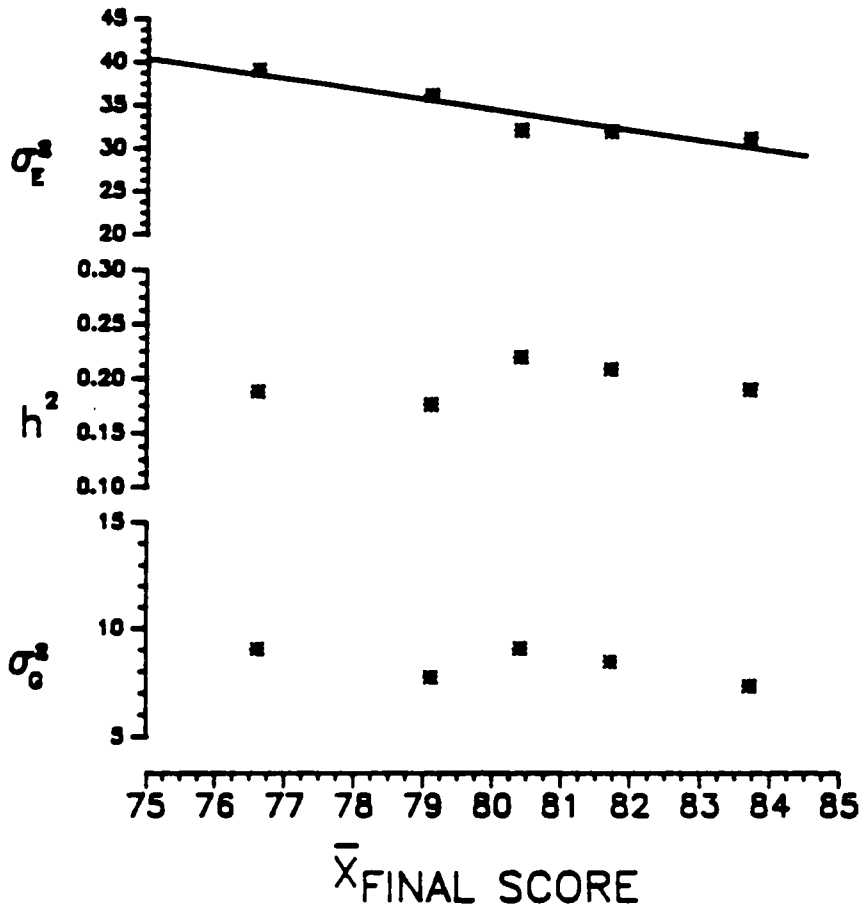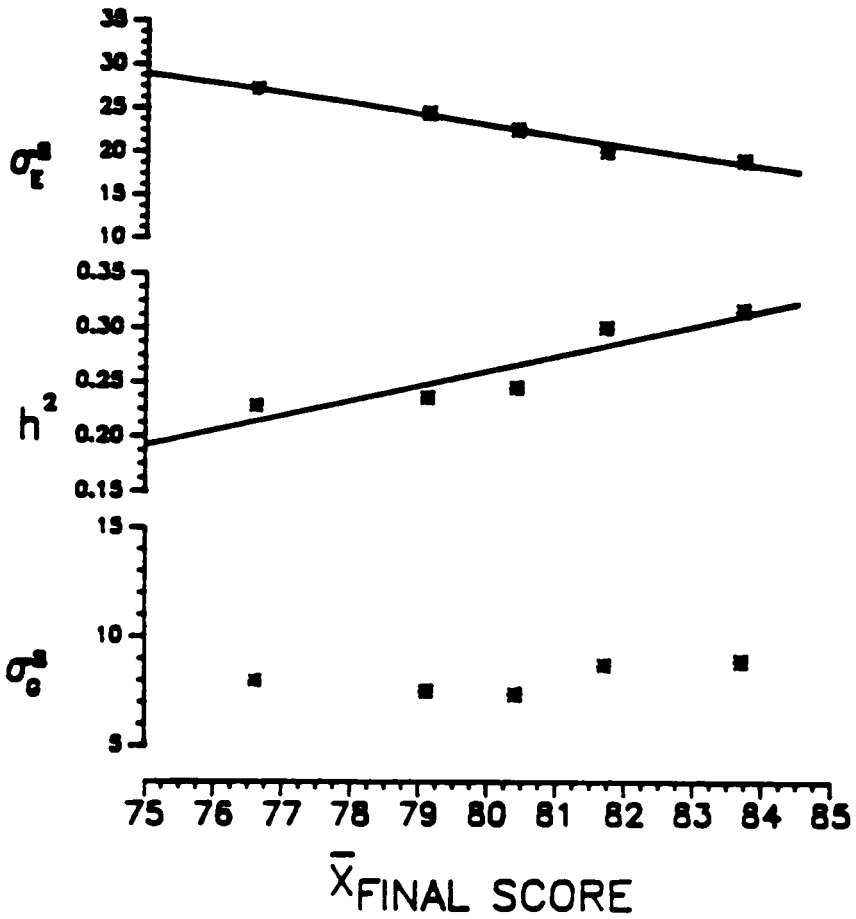
Appendix 31. Genetic (above diagonal) and phenotypic (below diagonal) correlations for linear descriptive traits of cows in group 1 ($\bar{X}$ herd-mean final score of 76.6).[1]

Trait	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Stature		.70	.81	.32	-.07	.87	.49	-.07	.24	.16	.21	.15	.21	.26	.15
Strength	.57		.91	-.20	.08	.77	.66	-.34	.43	.31	.29	.32	.27	.22	.14
Body Depth	.66	.76		.21	-.03	.79	.62	-.15	.26	.19	.22	.26	.27	.05	.13
Angularity	.14	-.16	.09		.10	.11	.01	.37	-.25	-.13	.00	.02	.06	-.20	.09
Rump Angle	.03	-.03	-.01	-.03		.06	-.01	.09	-.07	-.22	-.37	-.37	-.14	-.16	-.12
Rump Length	.59	.47	.53	.09	-.01		.74	-.15	.37	.33	.32	.28	.24	.32	.19
Rump Width	.42	.47	.47	.02	-.07	.52		-.19	.34	.26	.24	.31	.14	.12	.08
Rear Legs	-.07	-.14	-.08	.16	.01	-.02	-.07		-.55	-.06	-.20	-.23	-.25	-.07	-.05
Foot Angle	.13	.19	.16	-.04	-.06	.11	.14	-.21		.22	.28	.26	.38	.26	.29
Fore Udder Attachment	.11	.15	.13	.01	-.13	.12	.13	-.06	.15		.52	.50	.42	.81	.57
Rear Udder Height	.12	.15	.16	.11	-.14	.12	.16	-.07	.15	.43		.92	.43	.44	.30
Rear Udder Width	.15	.22	.23	.11	-.11	.17	.23	-.08	.16	.39	.71		.41	.28	.35
Udder Support	.06	.05	.06	.11	-.07	.05	.06	-.00	.08	.32	.30	.29		.47	.80
Udder Depth	.12	.01	-.03	-.08	-.08	.06	.03	-.04	.08	.45	.20	.11	.33		.51
Teat Placement	.05	.05	.06	.07	-.07	.06	.06	-.01	.09	.41	.25	.26	.49	.33	

[1]First parity scores adjusted for age and stage of lactation.

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Appendix 32. Genetic (above diagonal) and phenotypic (below diagonal) correlations for linear descriptive traits of cows in group 2 ($\bar{X}$ herd-mean final score of 79.1).[1]

Trait	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Stature		.63	.75	.34	.00	.80	.37	-.10	.31	.28	.11	.14	.19	.32	.11
Strength	.56		.91	-.16	-.07	.63	.55	-.19	.40	.31	.11	.36	.18	.11	.11
Body Depth	.65	.76		.18	-.03	.68	.54	-.09	.34	.18	.09	.24	.11	.00	.06
Angularity	.18	-.10	.14		.11	.25	.03	.20	-.08	-.14	-.16	-.02	.00	-.15	.02
Rump Angle	.06	-.01	.00	.00		.04	.00	.07	-.10	-.27	-.18	-.20	-.12	-.24	-.09
Rump Length	.56	.44	.50	.12	.01		.62	.07	.25	.38	.16	.23	.26	.31	.22
Rump Width	.39	.45	.45	.06	-.05	.50		.06	.29	.22	.04	.14	.04	.01	.05
Rear Legs	-.06	-.11	-.05	.14	-.01	.00	-.02		-.62	.00	-.21	-.18	-.17	-.07	.00
Foot Angle	.14	.20	.17	-.02	-.05	.11	.15	-.17		.20	.25	.28	.30	.19	.20
Fore Udder Attachment	.12	.15	.13	.01	-.12	.12	.11	-.03	.14		.55	.56	.58	.86	.64
Rear Udder Height	.11	.17	.16	.11	-.12	.13	.15	-.08	.14	.42		.90	.41	.50	.35
Rear Udder Width	.15	.24	.23	.11	-.07	.18	.23	-.08	.16	.38	.72		.39	.35	.36
Udder Support	.05	.04	.06	.11	-.08	.06	.06	.02	.08	.31	.29	.27		.61	.84
Udder Depth	.15	.00	-.04	-.06	-.08	.07	.02	-.03	.08	.44	.20	.11	.30		.59
Teat Placement	.06	.06	.07	.07	-.07	.07	.06	.03	.08	.41	.26	.26	.46	.32	

[1]First parity scores adjusted for age and stage of lactation.

Appendix 33. Genetic (above diagonal) and phenotypic (below diagonal) correlations for linear descriptive traits of cows in group 3 ($\bar{X}$ herd-mean final score of 80.4).[1]

Trait	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Stature		.75	.81	.30	-.01	.91	.46	-.08	.38	.33	.14	.18	.43	.37	.30
Strength	.58		.93	-.09	-.05	.73	.60	-.30	.48	.28	.21	.31	.43	.15	.16
Body Depth	.65	.77		.20	-.06	.77	.59	-.10	.37	.22	.14	.26	.37	.07	.21
Angularity	.19	-.08	.14		.02	.25	.09	.26	-.12	-.01	.10	.14	.14	-.07	.21
Rump Angle	.06	.00	.00	.00		-.05	-.03	.03	.45	-.24	-.27	-.28	-.15	-.11	-.05
Rump Length	.57	.44	.49	.14	.00		.68	-.08	.45	.34	.14	.19	.32	.36	.21
Rump Width	.40	.43	.44	.10	-.05	.50		.05	.37	.19	.03	.16	.11	.10	.03
Rear Legs	-.04	-.10	-.05	.13	-.02	-.01	-.02		-.59	-.09	-.30	-.29	-.23	-.06	.04
Foot Angle	.15	.21	.18	-.02	-.05	.14	.15	-.19		.33	.36	.40	.44	.28	.27
Fore Udder Attachment	.14	.15	.13	.04	-.12	.13	.13	-.05	.15		.50	.44	.60	.84	.63
Rear Udder Height	.13	.16	.16	.12	-.12	.13	.15	-.09	.16	.43		.96	.49	.41	.29
Rear Udder Width	.17	.23	.23	.13	-.09	.18	.23	-.09	.17	.39	.73		.47	.28	.32
Udder Support	.09	.07	.08	.13	-.09	.09	.08	.01	.09	.31	.31	.29		.53	.69
Udder Depth	.15	.01	-.03	-.04	-.06	.09	.04	-.03	.07	.43	.19	.11	.31		.53
Teat Placement	.10	.07	.08	.11	-.06	-.09	-.06	.02	.07	.40	.25	.26	.45	.32	

[1]First parity scores adjusted for age and stage of lactation.

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Appendix 34. Genetic (above diagonal) and phenotypic (below diagonal) correlations for linear descriptive traits of cows in group 4 ($\bar{X}$ herd-mean final score of 81.7).[1]

Trait	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Stature		.68	.76	.27	.12	.83	.38	-.16	.29	.16	-.05	-.13	.11	.29	.01
Strength	.58		.93	.17	.03	.62	.42	-.31	.41	.17	.07	.14	.17	.03	.10
Body Depth	.65	.77		.17	.11	.63	.41	-.23	.32	.07	-.02	.05	.07	-.08	.03
Angularity	.17	-.11	.11		.26	.20	.03	.19	-.06	-.21	.05	.03	.03	-.21	-.01
Rump Angle	.06	.00	.02	.00		.06	-.05	.14	.06	-.20	-.28	-.34	-.11	-.22	-.11
Rump Length	.57	.46	.50	.11	.00		.65	-.04	.35	.29	.05	.03	.19	.31	.19
Rump Width	.40	.44	.44	.04	-.05	.51		.04	.22	.17	.03	.14	.09	.06	.07
Rear Legs	-.05	-.12	-.07	.13	-.02	-.02	-.03		.55	-.07	-.19	-.11	-.04	.06	.10
Foot Angle	.14	.20	.17	-.02	-.05	.14	.16	-.17		.15	.17	.12	.34	.09	.20
Fore Udder Attachment	.13	.15	.12	.03	-.01	.12	.13	-.06	.14		.59	.52	.47	.75	.60
Rear Udder Height	.13	.15	.15	.14	-.11	.13	.15	-.09	.14	.43		.92	.45	.31	.38
Rear Udder Width	.16	.22	.22	.14	-.09	.18	.24	-.08	.14	.39	.72		.46	.18	.44
Udder Support	.07	.04	.06	.15	.07	.07	.05	.01	.08	.30	.31	.29		.37	.79
Udder Depth	.15	.01	-.04	-.06	-.07	.08	.03	-.03	.07	.43	.18	.10	.26		.37
Teat Placement	.07	.07	.07	.10	.06	.08	.07	.00	.09	.40	.26	.26	.43	.29	

[1]First parity scores adjusted for age and stage of lactation.

Appendix 35. Genetic (above) and phenotypic (below) correlations for linear descriptive traits of cows in group 5 ($\bar{X}$ herd-mean final score of 83.7).[1]

Trait	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Stature		.70	.76	.28	.29	.88	.54	-.01	.23	.16	-.16	-.09	.03	.31	.08
Strength	.57		.93	-.13	.33	.66	.58	-.24	.30	.08	-.18	.05	-.07	-.01	-.07
Body Depth	.63	.76		.13	.35	.67	.60	-.09	.17	-.01	-.19	-.01	-.15	-.09	-.14
Angularity	.20	-.07	.14		.24	.13	.06	.24	-.07	-.10	-.09	-.02	.16	-.05	.04
Rump Angle	.09	.04	.05	.02		.21	.05	-.01	.08	-.10	-.29	-.26	-.09	-.13	.11
Rump Length	.56	.45	.49	.11	-.01		.74	.01	.29	.18	-.21	-.12	.02	.34	.12
Rump Width	.39	.45	.44	.04	-.04	.51		.06	.21	.01	-.20	-.10	-.09	.22	-.08
Rear Legs	-.04	-.12	-.05	.14	-.04	.01	-.01		.52	-.16	-.26	-.29	-.21	-.09	.14
Foot Angle	.16	.20	.17	-.01	-.03	.14	.15	-.14		.16	.14	.14	.28	.13	.24
Fore Udder Attachment	.15	.16	.12	.04	-.09	.13	.12	-.05	.15		.43	.45	.61	.81	.69
Rear Udder Height	.12	.14	.15	.15	-.09	.12	.13	-.08	.13	.42		.90	.42	.21	.38
Rear Udder Width	.16	.22	.21	.14	-.05	-.17	.23	-.08	.14	.38	.70		.49	.13	.41
Udder Support	.05	.04	.05	.16	-.06	.05	.05	.01	.07	.29	.30	.28		.54	.82
Udder Depth	.16	.01	-.04	-.04	-.05	.09	.04	-.03	.07	.43	.17	.11	.27		.59
Teat Placement	.08	.05	.05	.11	-.07	.07	.05	.02	.08	.38	.24	.24	.43	.31	

[1]First parity scores adjusted for age and stage of lactation.