

Method and Effect of Adjustment for Heterogeneous Variance

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ABSTRACT

Lactation records were standardized for differing genetic and error variances across herds and over time based on phenotypic variance for each herd-year-parity group. Each herd-year-parity phenotypic variance estimate was combined with those of adjacent years and regressed toward a region-year-parity variance. Heritability was assumed to be .25 at mean variance within year and to range from .2 for herds with smallest phenotypic SD to .3 for herds with largest phenotypic SD. Lactation deviations from management group mean were adjusted by ratio of base genetic SD to genetic SD estimated from heritability and phenotypic SD. The base was defined as 1987 calvings for first parity and 1988 calvings for later parities. Records were weighted according to heritability by multiplying lactation length weight by herd error weight defined as ratio of base error variance to error variance in the adjusted record. Estimated genetic trend for milk increased by nearly 5 kg/yr for Holsteins with this adjustment, which caused predicted breeding values of oldest animals to be lower by about 100 kg. Most correlations of parent and progeny information were slightly higher with adjusted data. Cows in high variance herds were most likely to have large reductions in their evaluations. Adjustment for heterogeneous variance was implemented in July 1991 for national evaluations for yield traits. (Key words: animal model, genetic evaluation, heterogeneous variance)

Abbreviation key: DYD = daughter yield deviation, MF\$ = economic index of PTA for milk and fat yields, PA = parent average.

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INTRODUCTION

Accuracy of genetic evaluations depends on how well the assumptions of the model match the data. For the USDA-DHIA animal model (24, 25), genetic variance has been assumed to be constant and error variance to be affected by length of lactation. Numerous studies (1, 2, 3, 4, 19) have found that genetic variance is not constant but increases with herd yield and herd phenotypic variance. Henderson's mixed model equations (10) can provide solutions with BLUP properties if appropriate variance components are used. Gianola (9) suggested a multitrait approach that considers performance in each variance category as a separate trait. Foulley et al. (7) described a method to model variances so that heterogeneity of variance could be represented by few parameters. Unfortunately, these methods require more information than usually is available, particularly if estimation of individual herd-year variances is required.

Several types of correction for heterogeneity of variance have been investigated and implemented. In the Northeast, a log transformation has been applied (5). Studies (17, 20) have shown that, with this transformation, herds with lowest yields tend to have the largest number of elite cows. A simple Bayesian approach is used to stabilize phenotypic variance in Australia (13). Individual herd variances are regressed toward a population variance, and data for each herd are divided by this estimated phenotypic SD (Goddard, 1990, personal communication). This approach has the benefit of relying on a statistic that is simple to compute and has a higher correlation with the variances of interest than does herd mean. Meinert et al. (16) found that herd mean was only moderately correlated ($\leq .5$) with variance. Brotherstone and Hill (2) developed procedures based on either phenotypic SD or CV that were similar to Australian procedures.

A disadvantage of these approaches is that constant heritability is assumed across all

phenotypic variances. Most studies have found increasing heritability with increasing phenotypic variance (4, 12, 15, 18). Accuracy of evaluations may not improve if phenotypic variance is adjusted without accounting for differing heritability, because records from low heritability herds will have more influence (8, 19).

Rankings of animals have been improved only modestly (1, 16) or not at all (21, 26) by adjusting for heterogeneous variance. Several studies (3, 15) divided data into groups based on variance or mean. Famula (6) described the potential problem from magnified differences with this type of selection. Visscher (23) showed the effect to be relatively small in a simulation.

The small size of many herds could give highly variable estimates of variances within herd or herd-year (23, 26) unless estimates are regressed toward population values. Separate population values by year are necessary to account for rising yields and variances of yields across time. Region also should be considered, because sizable regional differences for yield exist in the US. Separate estimates for first and later parities are desirable, because age adjustment factors and selection bias may cause different variances. The heritability estimate can be a function of phenotypic SD to accommodate higher heritability in higher variance herds. Although a multitrait analysis might yield greater accuracy, genetic correlations of 1 usually are assumed for yields in different herds, regions, or parities to reduce parameters and numbers of equations required.

One goal of this study was to develop genetic evaluation procedures to account for 1) differing phenotypic variances across time, region, herd, and parity and 2) changing heritability with changing phenotypic variance. A second goal was to implement these procedures and assess their impact on national rankings of cows and bulls.

MATERIALS AND METHODS

Changes in phenotypic variances by region, calving year, and parity (first or later) were investigated with data from 1,897,600 herd-years, which were used in calculating July 1990 USDA-DHIA evaluations of Holsteins and Red and Whites. Only variances for milk

yield were analyzed; variances for fat and protein were assumed to be proportional to those for milk to simplify computation of the three single-trait analyses. Factors to adjust for heterogeneous variance were computed from these variance estimates and applied to milk and fat evaluations to investigate potential benefits.

Phenotypic variances were computed for each year-state-parity group pooled over individual herd. These variances were analyzed with a model that included effects of calving year, state, and parity group. State solutions were the basis for defining three regions with some consideration given to geographical location. Region-year-parity variances were computed. Base variances according to parity were defined: weighted mean of variances for 1987 calvings across region for first parity and weighted mean of variances for 1988 calvings across region for later parities. This definition corresponds to the evaluation base of 1985 birth year. For estimation of heritability in routine evaluations, variances also were pooled across region within year and parity.

Regressed variance within each herd-year-parity then was computed as a weighted mean of variation in that herd-year-parity, variation in adjacent years for the same herd-parity, and the region-year-parity variance. Region-year-parity variance received a relative weight of 20; adjacent years within herd-parity, relative weights of one-half their degrees of freedom for estimating that variance; and actual herd-year-parity, a relative weight of its degrees of freedom. For example, in a herd with 21 sire-identified, first lactation cows entering the herd each year, region-year-parity variance would receive a weight of $20/(20 + 10 + 10 + 20)$ or one-third of total weight. Similar reliance on population variance was proposed by Goddard (1990, personal communication) and by Brotherstone and Hill (2).

Variation in the other parity group for each herd-year also could have aided in estimating variance for that herd-year-parity group but was not used because of estimation complexity and possible parity differences in average variance. The multiplicative age adjustment factors remove most but perhaps not all differences in variation across parities.

Relationship between heritability and phenotypic variance reported by Powell et al.

(19) was adapted to provide estimates of genetic variance compatible with heritability assumed for the base group (.25). Heritability was estimated from phenotypic SD according to

$$\hat{h}^2 = .05 + .2 \text{SD}_{\text{regressed}}/\text{SD}_{\text{base}}$$

where \hat{h}^2 is estimated heritability, $\text{SD}_{\text{regressed}}$ is square root of regressed variance, and SD_{base} is square root of base variance. To avoid excessive extrapolation from data, a floor of .15 and a ceiling of .3 were placed on \hat{h}^2 . Because division by SD_{base} gave mean \hat{h}^2 as low as .19 for early years, the denominator was changed to SD_{yr} , the square root of year-parity variance, to provide a standard heritability of .25 for each year, and the floor for \hat{h}^2 was changed to .2. The formula for \hat{h}^2 can be applied to other traits and breeds and also to dairy goats because the ratio of SD is unitless.

Genetic variance for each herd-year-parity was estimated as \hat{h}^2 times regressed phenotypic variance. Lactation records were deviated from management group mean, and that deviation was multiplied by the ratio of base genetic SD to herd-year-parity genetic SD. The adjusted record was management group mean plus adjusted deviation.

The corresponding change in error variance was accounted for by multiplying lactation length weights by a herd error weight. This herd error weight was the ratio of base error variance to estimated error variance in adjusted records: $.45/[(.25/\hat{h}^2) - .55]$, where .45 is base error variance as a fraction of base phenotypic variance, and .55 is base repeatability of records. Herd error weights were less than 1 in low variance herds, which reflected the increased error variance introduced when a large factor was applied to raise genetic variance to the base. Correspondingly, weights were more than 1 in high variance herds, which had reduced deviations but highest heritability.

In addition to adjustment for heterogeneity of variance due to herd-year differences, an adjustment to standardize genetic variance of records with less than 305 d was employed as proposed by VanRaden et al. (22). Expansion factors for projected records were all greater than 1 and were determined by parity and lactation length. New lactation length weights

were less than 1 and lower than those of Wiggans et al. (24). Expansion factors increased variance of records in progress, terminated records, and records of cows dried off before 305 d.

An animal model evaluation including both heterogeneous variance adjustments and expansion of projected yields was computed. The model included a fixed management (m) and random animal breeding value (a), permanent environmental (p), herd-sire interaction (c), and residual (e) effects:

$$y_{ijkl} = m_{ij} + a_{kl} + p_{kl} + c_{ik} + e_{ijkl}$$

where y_{ijkl} = milk or fat yield (with genetic variance standardized) of cow kl (daughter l of sire k) in herd i in year-season, parity, and registry group j. For cows that change herd, i' is the first herd. Additive genetic covariances among a_{kl} were included, and effects for unknown-parent groups also contributed to a_{kl} . Variance components scaled to a phenotypic variance of 1 were genetic = .25, permanent environmental = .16, herd-sire interaction = .14, and residual = .45, which resulted in heritability of .25 and repeatability of .55 for herd-years with phenotypic variances equal to that of the base group. Differing variances of e_{ijkl} were accommodated in the mixed model equations by weighting y_{ijkl} by lactation length weights multiplied by herd error weights.

Evaluations for bulls and cows were compared with corresponding July 1990 evaluations computed without adjustments that were distributed to the dairy industry. For bulls, correlations were computed between parent average (PA) and daughter yield deviation (DYD) within birth year for the 23,230 bulls born in 1975 or later with reliability of .5 or greater. The reliability minimum was imposed to ensure adequate accuracy of DYD. Correlations between evaluations with and without adjustment for these bulls also were computed after removing effects of birth year.

Correlations between PA and yield deviation were computed for cows born in 1980, 1985, and 1987. Characteristics of elite cows were investigated by selecting the top 1% of evaluations with and without adjustment based

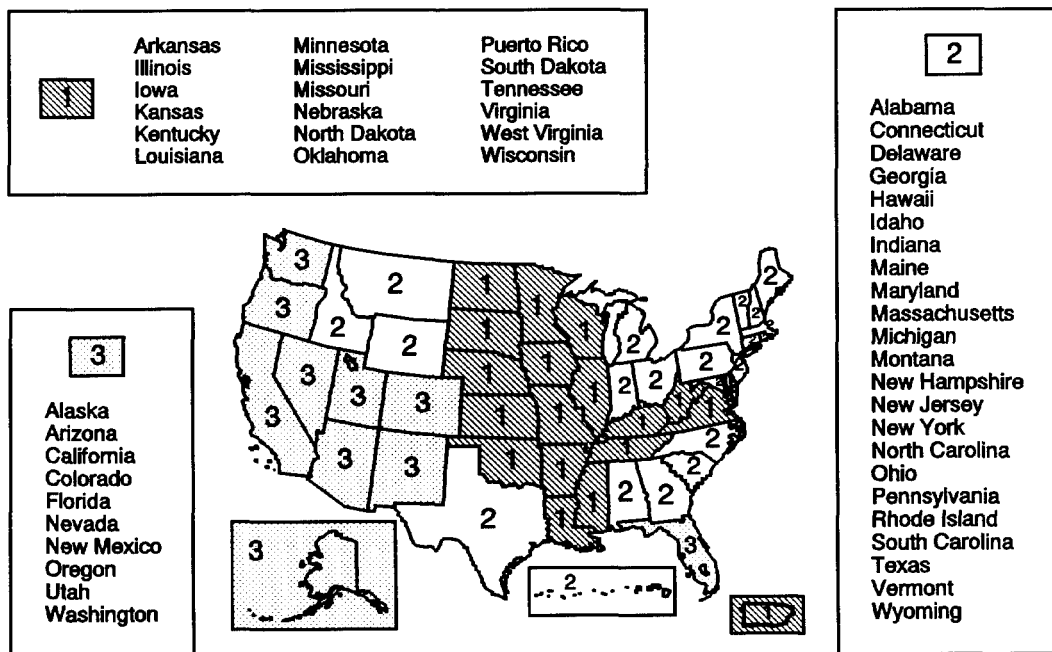


Figure 1. Definition of geographic regions for heterogeneous variance adjustment.

on an economic index for milk and fat yields (MF\$) calculated as

$$MF\$ = (\$.1614/kg)PTA_{milk} + (\$.326/kg)PTA_{fat}$$

which is equivalent to an index distributed to the industry of $(\$.0732/lb)PTA_{milk} + (\$.148/lb)PTA_{fat}$. Distributions of elite cows by relative error variance (ratio of lactation error variance to base error variance) were determined.

RESULTS

Assignments of states to three geographic regions based on phenotypic variance is shown in Figure 1. Regional calving year differences are illustrated by parity for numbers of cows in Figure 2 and for phenotypic SD milk in Figure 3. Weighted mean SD across regions was 1249 kg of milk for the 1987 first parity base and 1343 kg of milk for the 1988 later parity base. Region 1 (central states) had the lowest variance; region 2 (eastern states), intermediate

variance; and region 3 (western states), highest variance. Later parities had slightly higher variance than did first parity despite effects of culling and multiplicative age factors. Variance increased steadily over time, and differences between regions and parities were consistent. Figure 4 shows CV milk by parity and region.

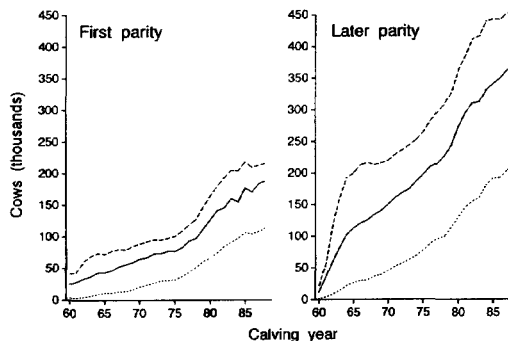


Figure 2. Distribution of Holstein cows according to parity, calving year, and geographic region 1 (—), 2 (---), or 3 (- - -) for heterogeneous variance adjustment.

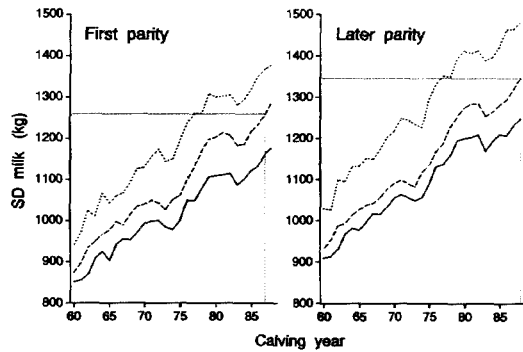


Figure 3. Phenotypic SD of Holstein milk yield according to parity, calving year, and geographic region 1 (—), 2 (---), or 3 (· · ·) for heterogeneous variance adjustment. Base for first parity is cows calving in 1987, which have a weighted mean SD across regions of 1249 kg of milk; base for later parity is cows calving in 1988, which have a weighted mean SD across regions of 1343 kg of milk.

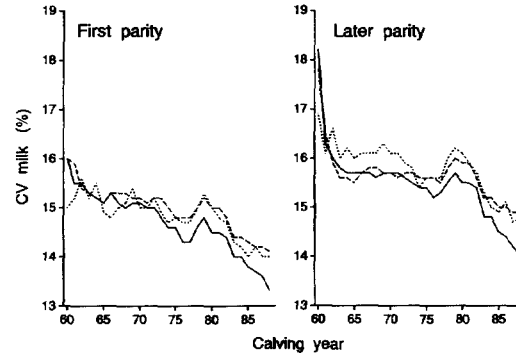


Figure 4. Coefficient of variation for Holstein milk yield according to parity, calving year, and geographic region 1 (—), 2 (---), or 3 (· · ·) for heterogeneous variance adjustment.

Distributions of herd-years according to adjustment factors and herd error weights are shown in Figure 5. Because variances have increased and a recent year was selected as the base, most herd-years were adjusted by a factor greater than 1. Most herd error weights were slightly less than 1 even though mean heritability was held constant across years by using SD_{yr} to calculate \hat{h}^2 . The floor of .2 and the ceiling of .3 for \hat{h}^2 resulted in a minimum herd error weight of .6 and a maximum of 1.6. Correspondence of herd error weight with heritability and repeatability is shown in Figure 6.

The effect of adjustment on genetic trend is illustrated in Figure 7. Estimates of genetic trend were increased by about 5 kg/yr over the last 15 yr with this adjustment. Predicted breeding values were lower by about 100 kg for animals born in 1960 through 1966.

For recent bulls, correlation between evaluations with and without adjustment was .998 for milk and .997 for fat. Correlation between parent and progeny information increased slightly with adjustment from .738 to .740 for milk and from .715 to .719 for fat. On a population basis, changes were not expected to be large; however, evaluations of individual bulls might change substantially. Of the 9751 AI bulls born since 1975 with 10 or more daughters and from an AI organization that samples 10 or more bulls per year, 12 had MF\$ that were \$25 to \$37 lower with adjust-

ment, and 9 had MF\$ that were \$25 to \$39 higher. Four of the top 20 bulls were replaced because of this adjustment.

Adjusting for heterogeneous variance was expected to reduce the apparent disadvantage of progeny-tested bulls in low variance herds even though no adjustment can overcome the reduced amount of information from these herds because of lower heritability. Effect of the adjustment is shown in Table 1 according to AI organization. Organizations A, D, and H have national sampling programs and, therefore, were expected to be affected little by the adjustment. Organizations B, C, E, F, G, and I all have regional sampling programs, but or-

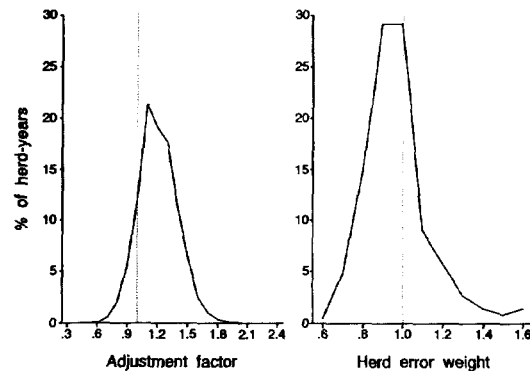


Figure 5. Distribution of herd-years according to adjustment factors and herd error weights for Holstein lactation records with heritability standardized to .25 for each year and limited to values from .2 to .3.

TABLE 1. Effect of heterogeneous variance and expansion adjustments on animal model evaluations of AI-sampled Holstein bulls born in 1980 through 1985 by semen processing organization.

Organization	Number of bulls	Mean daughter milk yield (kg)	Mean difference in MF\$ with adjustment ¹	MF\$ - MF\$ _{PA} ²				Reliability	
				Without adjustment		With adjustment		Without adjustment	With adjustment
				\bar{X}	SD	\bar{X}	SD		
				(\$)					
A	808	8857	1.37	-4.19	45	-2.72	46	.80	.79
B	849	8486	3.34	-1.06	47	-.77	48	.79	.79
C	474	8688	1.53	-6.76	48	-5.86	48	.80	.80
D	583	9039	.51	-1.55	46	-.54	46	.76	.76
E	308	8646	1.22	-8.22	54	-6.39	56	.77	.76
F	52	8243	5.31	-3.28	37	-.76	41	.76	.75
G	618	8448	3.62	-11.97	44	-10.64	48	.79	.78
H	1157	9007	.82	-3.09	44	-1.86	44	.76	.76
I	139	9475	.00	3.42	39	5.34	37	.64	.65
All	4988	8781	1.77	-4.33	46	-3.20	47	.77	.77

¹Difference = MF\$_A - MF\$_S where MF\$ is an economic index of PTA for milk and fat yields computed with the standard system without adjustment (S) and with heterogeneous variance and expansion adjustment (A).

²MF\$_{PA} = Economic index of parent averages for milk and fat yields.

organizations E, F, and G sample primarily in states with low phenotypic and genetic variances and should be affected most by the adjustment. Mean difference between MF\$ with and without adjustment was smallest for organizations D, H, and I and largest for organizations B, F, and G. In addition, variance of MF\$ - MF\$_{PA} (where MF\$_{PA} is an economic index of PA for milk and fat yields) increased most for organizations E, F, and G.

Slight reductions in reliability also were found for bulls from these organizations.

Mean milk yield was highest for daughters of bulls from organization I. Mean reliability of these bulls increased, which reflects herd error weights greater than 1. The SD of MF\$ - MF\$_{PA} for these bulls was reduced, which reflects lactation adjustment factors averaging less than 1. Overall, MF\$ - MF\$_{PA} was reduced; for organization G, MF\$ - MF\$_{PA} remained inexplicably large.

For cows, correlations between PTA with and without adjustment were .996 for milk and .995 for fat. Correlations between PA and yield deviations are in Table 2. Correlations decreased with increasing birth year, which reflects the lower accuracy of yield deviation estimates that include fewer lactations. Correlations were similar regardless of whether evaluations had been adjusted. Correlations were slightly higher with adjustment for cows born in the most recent years. As predicted by Hill (11), the adjustment affected elite cows (Figure 8) such that there was a shift away from high variance herds and a corresponding concentration in average variance herds. Lofgren et al. (14) also found that such adjustments "decreased differences among cow indexes in high variance herds and increased differences in low variance herds."

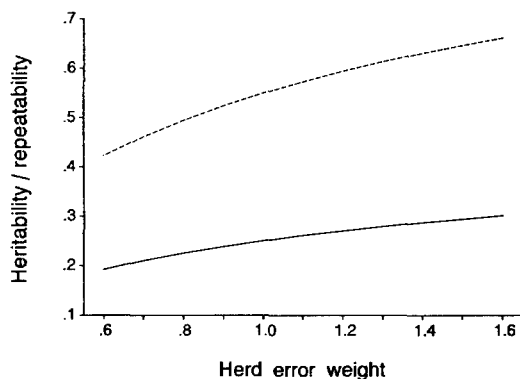


Figure 6. Relationship between heritability (—), repeatability (---), and herd error weight (w) where heritability = .25/[.55 + (.45/w)] and repeatability = .55/[.55 + (.45/w)].

TABLE 2. Correlations between parent average and yield deviation from evaluations with and without heterogeneous variance and expansion adjustment for Holstein cows born in 1980, 1985, and 1987.

Birth year	Number of cows	Without adjustment		With adjustment	
		Milk	Fat	Milk	Fat
1980	542,554	.593	.595	.586	.589
1985	620,141	.574	.564	.579	.571
1987	566,130	.465	.465	.471	.471

DISCUSSION

Evaluations of US dairy cattle for yield traits now include adjustment for heterogeneous variance. The adjustment is based on phenotypic variance with regression toward region-year-parity variance. The greater heritability in higher variance herds is accommodated by assuming that genetic variance increases relatively more than phenotypic variance. The adjustment adds little to overall computing requirements. The primary changes are to calculate herd-year-parity variances and individual herd-year variances and to adjust lactation records and length weights. Means of lactations reported with evaluations are from unadjusted records so that the current definition of lactation average is retained. Unadjusted length weights also are retained so that average amount of adjustment to a cow's data could be represented as the ratio of adjusted to unadjusted weights.

Adjustments for heterogeneous variance and expansion of projected records are related ad-

justments designed to standardize genetic variance in all classes of records. The expansion factors are based on lactation length, type of test, and parity, whereas the heterogeneous variance adjustment uses phenotypic variance within herd-year-parity to indicate genetic variance. Further research may reveal better methods for standardizing variance. This method makes relatively modest changes in the evaluations, and the changes generally improve evaluations, as evidenced by increased correlations between parent and progeny information. Increased SD for bulls sampled in low variance regions and a shift in the herds that contribute elite cows toward those with average variance should make evaluations more accurate and fair for all breeders.

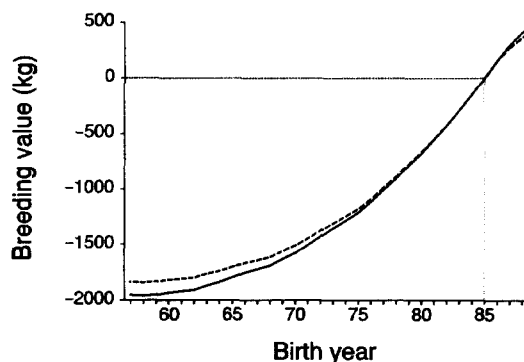


Figure 7. Genetic trend for Holstein milk yield from evaluations computed with the standard system without adjustment (---) and with heterogeneous variance and expansion adjustment (—).

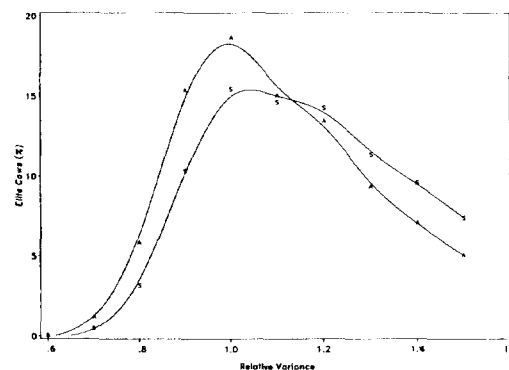


Figure 8. Distribution according to relative error variance (ratio of lactation error variance to base error variance) of the top Holstein cows for an economic index of PTA for milk and fat yields from evaluations computed with the standard system without adjustment (S) and with heterogeneous variance and expansion adjustment (A). Base error variances are defined as $.45 \times 1249$ kg of milk for first parity (cows born in 1985, calving in 1987) and $.45 \times 1343$ kg of milk for later parity (cows born in 1985, calving in 1988).

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