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Heterogeneity of (Co)Variance Among Herds for Backfat Measures of Swine^{1,2}

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ABSTRACT: Within-herd variation for the trait of backfat was examined in swine. Backfat depth data ($n = 21,877$) from 11 herds that had each recorded over 1,000 measures were evaluated using univariate animal model procedures in analyses for individual herds and all herds together. Variance components were estimated by a derivative-free REML algorithm, and significance tests for variance components were carried out as likelihood ratio tests. Adjustment for heterogeneous variance by correction for within-herd phenotypic SD was also evaluated. Additive genetic and residual variances were heterogeneous across herds and ranged from 1.39 to 9.78 mm² and from .88 to 7.05 mm², respectively. Eleven parameter estimates from individual herd analyses were significantly

different ($P < .05$) from the analysis for all herds together. However, only small differences were observed between estimates of heritability, which ranged from .37 to .73. Scaling data to a constant within-herd SD resulted in more homogeneous variance. For additive genetic variance, only one herd differed significantly ($P < .01$) from the analysis for all herds together. However, five estimates of residual variance were found to be significantly different ($P < .05$) from the analysis for all herds together. The rank correlation between EPD predicted from the analyses with all herds together, homogeneous variance, and scaled to a constant within-herd SD was .97 ($P < .01$). Effects of heterogeneous variance may need to be accounted for in genetic evaluation procedures for swine.

Key Words: Pigs, Genetic Parameters, Best Linear Unbiased Prediction

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Introduction

Across-herd genetic evaluations using BLUP have improved the response to selection for swine when compared with within-herd BLUP selection (Mabry and See, 1990). However, the validity of genetic evaluations with BLUP depends on how well the assumptions of the model match the data. Current across-herd evaluations for swine in the United States assume that all data come from the same population with constant variation among herds and no genotype \times herd interaction. Potential bias in genetic evaluation from differences in variation within herds has been recognized for some time (Vinson, 1987). If variances are not equal among herds, biases may become more severe as intensity of selection increases (Vinson, 1987). Hill (1984) demonstrated that heterogeneous variance among herds results in selection of a greater proportion of animals from more variable herds,

causing a reduction in response to selection. Vinson (1987) demonstrated that this effect on response to selection depends on the extent to which the greater variability is due to genetic as opposed to environmental factors. If heterogeneity of variance is ignored when computing breeding values of boars and sows, high performers in high-variance herds will be strongly favored over high performers in low-variance herds (Hill, 1984). A potential long-term problem is that biases in the evaluations of sows accumulate over time as daughters and dams tend to express records in the same herd (Vinson, 1987).

The objectives of this study were to determine whether heterogeneity of backfat measures exists among herds and to evaluate appropriate methods of accounting for heterogeneity.

Materials and Methods

Field Data. Backfat measurements on 29,977 pedigreed Duroc hogs collected from 44 herds were supplied by the United Duroc Swine Registry. Herds for which over 1,000 backfat records had been assembled were included in the analyses (Table 1). The data consisted of 21,877 records from 11 such

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Table 1. Numbers of herds, backfat records, sires, and contemporary groups

Herd	Number of records from			Number of	
	Boars	Gilts	Barrows	Sires	Groups
1	763	535	7	38	52
2	1,185	588	54	37	46
3	721	575	12	42	42
4	534	479	35	34	20
5	926	1,103	278	33	38
6	793	756	0	49	112
7	687	856	68	42	20
8	1,525	1,361	24	38	55
9	995	760	36	29	20
10	2,125	2,667	0	110	29
11	721	669	38	51	88
All herds	10,976	10,349	552	397	522

herds. Backfat measures were adjusted to a uniform off-test weight of 104 kg using adjustment factors recommended by the National Swine Improvement Federation (1987). Contemporary groups were defined by breeders as groups of hogs with data that were raised in a common herd, year, and seasonal time frame. A minimum of two generations of ancestral relationships were included for hogs with records. Table 2 describes the numbers of sires and records that provided connectedness among herds.

Statistical Methods. The linear model used to estimate genetic parameters for univariate analyses for individual herds and univariate analyses for all herds together was:

$$y = Xb + Za + e$$

where y is the vector of observations for all traits; b is the vector of common fixed effects that includes effects that are due to contemporary group and sex; a is a vector of random animal effects; e is a vector of residuals; X and Z are incidence matrices that relate observations to the fixed and animal effects, respectively, and $E [y' a' e'] = [b'X' 0' 0']'$. Variances of the random variables were

$$V \begin{bmatrix} a \\ e \end{bmatrix} = \begin{bmatrix} G_0 \otimes A0 \\ 0 \quad R_0 \otimes I \end{bmatrix}$$

where \otimes denotes a direct product operation; G_0 and R_0 are genetic and residual covariance matrices, with order equal to the number of traits in the analysis; and A is the numerator relationship matrix.

(Co)variance components were estimated by a derivative-free REML algorithm (Graser et al., 1987) using the MTDFREML computer programs developed by Boldman et al. (1993). This set of programs minimizes -2 times the restricted log likelihood function (Λ); that is, $-2\Lambda = \text{constant} + \log|R| + \log|G| + \log|C| + y'Py$, where C is a full-rank coefficient matrix for the mixed model equations and

$y'Py$ is the weighted sum of squares for the residuals, with P a projection matrix. Stopping criterion was 10^{-10} for the simplex variance. Convergence was achieved after stopping criterion was obtained and the same or larger -2Λ resulted, after a minimum of two cold restarts with the parameter estimates as new starting values. Expected progeny differences were also calculated at the convergence of these programs. Standard errors for heritability estimates were approximated by the method described by Swiger et al. (1964).

Likelihood ratio tests (Hogg and Craig, 1978) were used to test individual herd variance component estimates for deviation from variance component estimates from the analyses for all herds together. This procedure consists of subtracting the value of -2Λ from the model with more parameters from -2Λ corresponding to the model with fewer parameters (Rodriguez-Almeida et al., 1995). The likelihood for the null hypothesis (H_0) was maximized and compared with the maximum likelihood value from each individual herd analysis (Visscher et al., 1991). This allows the remaining parameter to change when comparing the difference in likelihood. For example, to test an individual herd estimate for deviation in genetic variance from the estimate with all herds together, the likelihood was maximized at a value of the genetic variance of 4.49. The difference between maximum likelihood estimates (Δ_i) was compared with a chi-squared distribution with one degree of freedom. Degrees of freedom are equal to the difference in the number of parameters estimated for the two models. The restricted log likelihood was obtained at convergence of the MTDFREML iterative process.

Correction for within-herd phenotypic standard deviation (Brotherstone and Hill, 1986; Visscher et al., 1991; Wiggans and VanRaden, 1991) was investigated as a method of reducing heterogeneity of variance. Scaling of backfat measures to a constant SD was accomplished by multiplying data by the ratio of the average phenotypic standard deviation to the phenotypic standard deviation for the corresponding

Table 2. Number of common sires between herds (above diagonal) and number of progeny by common sires (below diagonal)

Herd	Common sires between herds and progeny of common sires										
	1	2	3	4	5	6	7	8	9	10	11
1		9	7	11	4	10	5	8	2	4	17
2	300		22	4	4	9	9	5	3	3	9
3	182	1,162		6	3	8	7	4	4	1	8
4	586	88	81		0	4	5	4	3	3	8
5	180	610	140	0		6	9	4	3	5	5
6	429	280	306	65	73		9	5	5	2	10
7	215	203	178	210	1,243	243		4	6	6	8
8	121	107	99	130	58	103	77		20	1	2
9	28	29	77	193	33	89	164	2,689		2	3
10	108	26	2	46	494	12	439	59	37		5
11	947	751	328	242	115	295	194	25	3	190	

herd as follows: $y_{ij}^c = y_{ij}(SD_p/SD_h)$ with SD_p = population SD, SD_h for herd i , and y^c = adjusted record. These SD were calculated ignoring other fixed and random effects.

To determine the degree of reranking of sires, according to EPD obtained from the analyses with all herds together, rank (Spearman) correlation coefficients between sire EPD were calculated. The impact of scaling data by within-herd SD on the selection of sires was also evaluated. Under a 10% selection intensity, the number of sires selected from each herd was determined when selection was based on EPD obtained with and without adjustment for heterogeneity of variance.

When herds were considered to have heterogeneous residual and additive variances, the univariate linear model was applied in a multitrait (herd) analysis to estimate the (co)variance structure (Henderson, 1984; Gianola, 1986). In this analysis, backfat depths in different herds were considered to be different traits. To aid convergence and complete this analysis with available computing resources, the (co)variance structure for the eleven-herd model was estimated by pooling estimates from 24 separate three-herd analyses. For a three-herd model,

$$G_0 = \begin{bmatrix} \sigma_{a_{11}}^2 & \sigma_{a_{12}} & \sigma_{a_{13}} \\ & \sigma_{a_{22}}^2 & \sigma_{a_{23}} \\ \text{symmetric} & & \sigma_{a_{33}}^2 \end{bmatrix}$$

where $\sigma_{a_i}^2$ = additive genetic variance in herd i , σ_{aij} = $\rho_{ij}\sigma_{ai}\sigma_{aj}$ and is the genetic covariance between breeding values of the same animal in different herds, and ρ_{ij} = genetic correlation between expression of the same genes in a pair of herds and is an estimate of genotype \times herd interaction. No animal produced a record in more than one herd; therefore, covariance estimates are based on relationships with primary contributions from the sire (Table 2). In the context of

heterogeneous variance it was assumed that $\rho \neq 1$. Further,

$$R_0 = \begin{bmatrix} \sigma_{e_{11}}^2 & 0 & 0 \\ & \sigma_{e_{22}}^2 & 0 \\ \text{symmetric} & & \sigma_{e_{33}}^2 \end{bmatrix}$$

and $\sigma_{e_i}^2$ = residual variance in herd i . Estimation of the genetic correlations (ρ_{ij}) from the REML (co)variance estimates is straightforward. Standard errors for heritability and genetic correlation were approximated by the methods described by Swiger et al. (1964) and Tallis (1959), respectively.

Results and Discussion

Descriptive Statistics. Estimates of means, SD, and skewness for backfat depth in each herd are given in Table 3. Backfat depth ranged from 16.07 mm (Herd 2) to 21.99 mm (Herd 1). The SD estimate for backfat depth in Herd 10 was generally 50% smaller than that

Table 3. Descriptive statistics for swine backfat data

Herd	Mean \pm SE, mm	SD, mm	Skewness \pm SE
1	21.99 \pm .11	3.87	.35 \pm .07
2	16.07 \pm .10	4.42	1.42 \pm .06
3	17.10 \pm .11	3.94	.84 \pm .07
4	17.68 \pm .15	4.71	.48 \pm .08
5	16.27 \pm .07	3.25	.78 \pm .05
6	20.51 \pm .10	3.82	.58 \pm .06
7	20.33 \pm .11	4.60	.65 \pm .06
8	20.47 \pm .07	3.69	.63 \pm .05
9	20.16 \pm .09	3.72	.86 \pm .06
10	19.13 \pm .03	1.79	.46 \pm .04
11	20.64 \pm .12	4.43	.73 \pm .06
All herds	19.10 \pm .03	4.04	.56 \pm .02

Table 4. Estimates of genetic variance (σ_a^2), residual variance (σ_e^2), and heritability (h^2) for backfat and likelihood ratio tests (Δ_i)^a for individual herd variance component estimates from variance component estimates from the analysis for all herds together

Herd	σ_a^2	Δ_1	σ_e^2	Δ_2	$h^2 \pm SE$
1	7.52	5.47*	4.79	0	.61 ± .14
2	7.02	4.27*	6.50	3.41	.52 ± .12
3	6.23	1.95	7.05	6.00*	.47 ± .12
4	4.25	.06	3.04	13.64**	.58 ± .15
5	2.85	6.92**	3.33	28.39**	.46 ± .11
6	8.74	9.20**	3.27	3.49	.73 ± .14
7	6.03	2.30	4.90	.02	.55 ± .12
8	3.49	1.81	6.62	14.12**	.35 ± .09
9	6.32	3.16	4.64	.06	.58 ± .15
10	1.39	411.57**	.88	1,912.53**	.61 ± .08
11	9.78	17.14**	4.89	.01	.67 ± .13
All herds ^b	4.49		4.80		.48 ± .03

^a $\Delta_i = -2(\Lambda_{\text{herd}} - \Lambda_{H_0})$, the difference between the likelihood function from the individual herd (Λ_{herd}) and the likelihood for the null hypothesis (Λ_{H_0}), asymptotically distributed as chi squared with degrees of freedom = 1. For likelihood ratio tests of genetic and residual variance, i.

^bUsed as null hypothesis (H_0).

* $P < .05$.

** $P < .01$.

for the other herds. This result is similar to those reported by Visscher et al. (1991) for high- and low-variance herds for dairy fat yield with a minimum SD of 25 and a maximum SD of 48.9. The within-herd and combined-herd backfat distributions were all positively skewed.

The correlation between herd mean and skewness was $-.58$ ($P = .08$). The negative correlation with herd mean and the positive skewness of the within-herd and combined backfat distributions are in agreement with the observation by Whittemore (1993) that “as average fatness reduces, so the possibility of normal distribution lessens and that for skewness increases.”

The correlation between herd mean and herd phenotypic SD was $.05$ ($P = .89$). Studies of dairy milk yield have found herd means and variances to be both positively correlated (Legates, 1962; Brotherstone and Hill, 1986; Dong and Mao, 1990) or unrelated (Lofgren et al., 1985; Winkelman and Schaeffer, 1988). One suggested approach to equalizing variances across herds is to transform records to logarithms (Vinson, 1987) as an adjustment for difference in herd variation according to difference in herd mean. The log transformation, however, is only appropriate when the mean and variance are perfectly correlated and was not further evaluated as a procedure to adjust for heterogeneous variance in this data.

Heterogeneity of Variance Among Herds. The results from the analyses of unadjusted data for individual herds and all herds together are presented in Table 4. For the analysis with all herds together when homogeneity of variance among herds was assumed, the heritability estimate for backfat was similar to the

estimate of $.41$ for backfat reported by Stewart and Schinckel (1990) in a review of 175 research papers. Estimates of genetic and residual variance were heterogeneous across herds, and 11 parameters were significantly different ($P < .05$) from the estimate with all herds together. Most estimates of heritability were similar in magnitude. However, the heritability for backfat in Herd 8 was different from that estimated for Herds 1, 6, 10, and 11. The general result suggests that heritabilities are relatively constant and that the phenotypic variance is heterogeneous. Visscher et al. (1991) found similar results in an evaluation of 26 Holstein herds for fat yield where two within-herd heritabilities and eight variance component estimates significantly differed ($P < .05$) from the overall estimates.

Heritability estimates were positively correlated with mean backfat depth ($.58$, $P = .16$) and negatively correlated with skewness ($-.45$, $P = .16$). When a character selected is a component of fitness, asymmetry is expected to occur, and selection toward increased fitness has lower heritability than selection toward decreased fitness (Falconer and Mackay, 1996).

Adjustment of the data with intraherd SD resulted in more homogenous estimates of variance components (Table 5). For additive genetic variance, only Herd 8 differed ($P < .01$) from the combined estimate. However, five estimates of residual variance were found to be different ($P < .05$) from the combined analysis. Differences between maximum likelihood estimates (Δ_i) were generally smaller for a given herd when data were scaled to a constant within-herd SD (Table 5) than with likelihood ratio tests for unad-

Table 5. Estimates of genetic variance (σ_a^2), residual variance (σ_e^2), and heritability (h^2) for backfat data scaled to a constant within-herd SD and likelihood ratio tests (Δ_i)^a for individual herd variance component estimates for deviation from variance component estimates from the analysis for all herds together

Herd	σ_a^2	Δ_1	σ_e^2	Δ_2	$h^2 \pm SE$
1	3.65	.18	3.59	4.32*	.50 \pm .14
2	4.80	.15	4.45	.42	.52 \pm .12
3	4.33	.66	4.91	.02	.47 \pm .12
4	5.39	.03	3.86	2.22	.58 \pm .15
5	4.26	1.15	4.98	.10	.46 \pm .11
6	6.73	1.76	2.51	14.72**	.73 \pm .14
7	5.10	0	4.14	1.58	.55 \pm .12
8	3.20	7.23**	6.05	8.06**	.35 \pm .09
9	5.33	.02	3.92	3.13	.58 \pm .15
10	5.67	.64	3.57	12.8**	.61 \pm .08
11	6.16	1.08	3.08	11.8**	.67 \pm .13
All herds ^b	5.17		4.83		.52 \pm .03

^a $\Delta_i = -2(\Lambda_{\text{herd}} - \Lambda_{H_0})$, the difference between the likelihood function from the individual herd (Λ_{herd}) and the likelihood for the null hypothesis (Λ_{H_0}), asymptotically distributed as chi squared with degrees of freedom = 1. For likelihood ratio tests of genetic and residual variance, i.

^bUsed as null hypothesis (H_0).

* $P < .05$.

** $P < .01$.

justed data (Table 4). Heritability estimates after adjustment for within-herd SD were still similar in magnitude across herds with the exception of heritability in Herd 8, which differed from heritability estimates in Herds 6, 10, and 11. For fat yield of dairy cattle, heterogeneity was reduced (Visscher et al., 1991) by adjustment with within herd-year-season phenotypic SD.

Ranking of Sires. The rank correlation between EPD predicted from the analysis, assuming homogenous variance with EPD from the analysis of data scaled to a constant within-herd SD, was .97 ($P < .01$). Correction for heterogeneity of variance in dairy traits has been reported to result in only a small improvement in rankings (Winkelmann and Schaeffer, 1988; Sullivan and Schaeffer, 1989; Wiggans and Van Raden, 1991). Changes were also observed in the proportions of sires contributed by individual herds to the total of sires selected under 10% selection intensity (Figure 1). For example, Herd 10 contributed 20 more sires when rankings were based on EPD from data scaled to a constant within-herd SD than when rankings were based on uncorrected data.

Hill (1984) showed that standardization to within-group phenotypic SD is justified for the construction of simple selection criteria if the heritability is constant across groups. A disadvantage of this adjustment is that it requires continuous estimation of within-herd SD. For small herds, 75% of these data, these estimates may be subject to large sampling errors. An extension of this method has been implemented (Wiggans and VanRaden, 1991) for national evaluations of dairy yield traits in the United States. Gianola (1986) outlined BLUP procedures that automatically

account for heterogeneous variance, provided that the covariance structure is known. Foulley et al. (1990) has described statistical methods to model variances so that sources of heterogeneity can be assessed. Both of the latter methods require more information than is usually available. Given the results in Tables 4 and 5, it seems practical to scale data to a constant within-herd SD.

Genotype \times Herd Interactions. Heritability and genotype \times herd interactions estimated as genetic correlations between expression of the same genes in

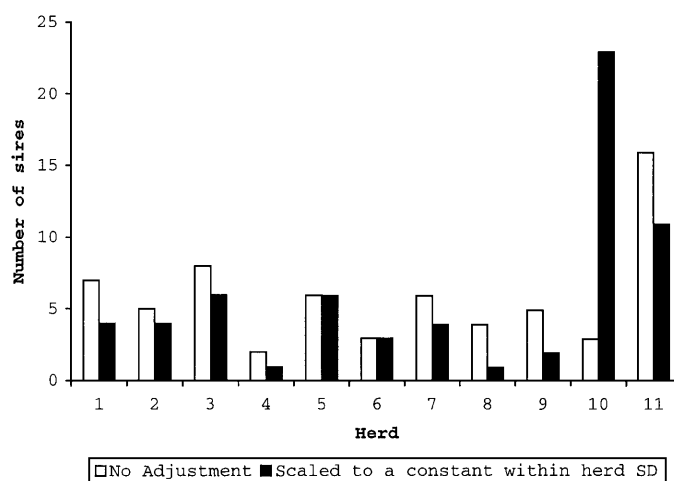


Figure 1. Number of sires selected from herds according to their EPD for backfat when selecting the top 10% with different assumptions and adjustments for heterogeneous variance.

Table 6. Estimates of heritability (diagonal) and genetic correlation^a between expression of the same genes in a pair of herds (above diagonal) for backfat depth

Herd	1	2	3	4	5	6	7	8	9	10	11
1	.61 ± .14	.91 ± .11	.99 ± .12	.90 ± .08	.98 ± .07	.93 ± .06	.99 ± .07	.02 ± .55	.13 ± .03	-.25 ± .57	.81 ± .10
2		.48 ± .12	.95 ± .05	.27 ± .61	-.40 ± .44	.19 ± .39	.44 ± .36	1.00 ± .17	.98 ± .22	1.00 ± .46	.93 ± .07
3			.48 ± .12	.95 ± .14	.01 ± .67	.82 ± .15	.98 ± .08	.67 ± .41	.92 ± .20	.88 ± .32	.82 ± .15
4				.58 ± .15	.91 ± .31	.94 ± .02	.88 ± .14	.01 ± .63	.62 ± .41	.34 ± .73	.48 ± .33
5					.46 ± .11	.58 ± .42	.75 ± .16	-.96 ± .25	.03 ± .95	.75 ± .23	.76 ± .30
6						.69 ± .14	.91 ± .08	.85 ± .30	-.34 ± .53	.53 ± 1.03	.69 ± .21
7							.55 ± .12	-.90 ± .16	.69 ± .28	-.05 ± .44	.52 ± .34
8								.35 ± .09	-.58 ± .16	.75 ± .55	.92 ± .25
9									.58 ± .15	.52 ± .67	.89 ± .14
10										.62 ± .08	.77 ± .22
11											.65 ± .13

^aGenetic correlation is an estimate of genotype × herd interaction.

pairs of herds are presented in Table 6. Heritability estimates for backfat depth ranged from .35 to .69 across herds. Most estimates of heritability were similar in magnitude and were not different from those from the individual herd analyses presented in Table 4. But heritability in Herd 8 differed from heritability estimates in Herds 1, 6, 10, and 11. Estimates of genetic and residual variance components (not presented) were similar in magnitude to those from the single herd analyses shown in Table 4. Genetic and residual variance for backfat ranged from 1.25 to 9.20 and from .98 to 6.83, respectively.

Forty-nine percent of the estimates of genetic correlation were not significantly different from one, 25% were not different from zero, and 3.6% were not different from minus one. However, because of sampling errors and limited connectedness between herds (Table 2), the true correlations may be closer to unity. Of course, the true correlations may also be less than the estimates for the same reason. The estimates of SE for genetic correlation are approximated (Tallis, 1959) and may be underestimated for this data structure.

Genetic correlations (Table 6) may differ from one because of heterogeneity of variance across herds, differences in true breeding value in different herds, or chance. The available data do not allow the cause of genetic correlations different from one to be clearly demonstrated.

Robertson (1959) suggested that if the genetic correlation is less than .80, the genotype × herd interaction is of biological importance. Such a large genotype × herd interaction clearly seems to be associated with Herd 8. All of the negative genetic correlations presented in Table 6 that are significantly different from zero occur with Herd 8. Negative genetic correlations with Herd 8 are shown for Herds 5 (-.90), 7 (-.96), and 9 (-.58). This result could indicate large management differences across herds because Herd 8 and Herd 9 showed the highest level of connectedness between herds (Table 2). Herd 8 also showed the smallest heritability estimate (Tables 4, 5,

and 6) for backfat depth, and this may be influenced by or be a cause of the observed genotype × herd interactions. However, herd management factors are not documented in these data, which makes it difficult to attribute the cause of the observed interactions.

Scaling data to a constant within-herd SD was not evaluated as a correction procedure under the multi-herd model. However, scaling may not account for differences in genetic correlations observed in Table 6. Unlike Herd 10, scaling did not result in smaller differences between maximum likelihood estimates for Herd 8 (Table 5), when compared with the unadjusted results in Table 4. This result may indicate that in these data there are both differences in variance among herds and differences in true breeding value in different herds.

Genotype × herd interactions indicate that a potential influence on sire evaluation would be for sires to be ranked differently in different herds. This result also indicates that a procedure to account for heterogeneity of variance suggested by Winkelman and Schaeffer (1988) should not be applied with these data. Winkelman and Schaeffer (1988) suggested that a practical approach to accounting for heterogeneity of variance without estimating the (co)variance structure among herds would be to assume heritability as constant from herd to herd and that the genetic correlation between genetic values in different herd groups is one. Genotype × environment interactions for backfat depth ranging from .18 ($P > .1$) to .60 ($P < .05$) have been reported between test station and on-farm performance (Bampton et al., 1977; Merks, 1986).

Possible Causes of Heterogeneity and Genotype × Herd Interactions. An interesting question is, what are the causes of the observed heterogeneity and genotype × herd interactions? Differences among herds in variability of performance generally have been thought to result from differences in climatic factors and herd management (Vinson, 1987). Herd management factors are not documented in these data. Variability among herds may include feeding inten-

sity, diet, measurement procedures, ultrasonic equipment, housing, production schedule, and disease control. The factors applied for preadjustment of backfat to a constant weight (NSIF, 1987) may also introduce heterogeneity if they are not appropriate for all herds. The herds that supplied these data may also differ in breeding objectives and how within-herd selection programs are designed and implemented.

Implications

Potential sires from less-variable herds may be undervalued if differences in within-herd variance are not considered in genetic evaluation procedures. Evidence of genotype \times herd interactions also may necessitate further standardization of performance-testing methods.

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