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# Animal Model Estimation of Genetic Parameters and Response to Selection for Litter Size and Weight, Growth, and Backfat in Closed Seedstock Populations of Large White and Landrace Swine<sup>1,2</sup>

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**ABSTRACT:** Records from 2,495 litters and 14,605 Landrace and Large White pigs from two farms, but established from the same base population and run as replicated selection lines, were analyzed. Selection within herd was on estimated breeding values weighted by economic values. Animal models and REML procedures were used to estimate genetic, phenotypic, and environmental parameters for the number of pigs born alive (NBA), litter weight at 21 d (LW), average daily gain from approximately 30 to 104 kg (ADG), and backfat thickness adjusted to 104 kg (BF). Random animal genetic effects (**o**), permanent (NBA and LW) or litter (ADG and BF) environmental effects, maternal genetic effects (m), and the covariance between o and m were sequentially added to the model. Estimates of total heritability calculated from all data ( $h_t^2 = \sigma_o^2 + 1/2\sigma_m^2 + 3/2\sigma_{om}$ ) ranged from .01 to .14 for NBA, from .18 to .22 for LW, from .23 to .34 for ADG, and from .40 to .50 for BF. Maternal genetic variance was from 2.4 to 3.8% of phenotypic variance in NBA, from 1.2 to 3.6% in LW, from .5 to 1.5% in ADG, and from 1.9 to 3.4% in BF. The correlation between **o** and **m** was -.07 for NBA, -.25 for LW, -.34 for ADG, and -.26 for BF. Permanent environmental effects explained from 16 to 17% of total phenotypic variation for NBA and from 1.6 to 5.3% for LW. Approximately 7% of the variation in ADG and 5% in BF was due to litter environmental effects. Genetic trends were .012 pigs/yr for NBA, .25 kg/yr for LW, 5.91 g/yr for ADG, and -.063 mm/yr for BF.

Key Words: Pigs, Mixed Models Methods, Genetic Parameters, Genetic Trend

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#### Introduction

Mixed-model methodologies under animal models have become the method of choice to estimate breeding values, not only because they provide best linear unbiased predictors (BLUP) of breeding values, but because they also simultaneously estimate genetic and environmental effects, taking into account the relationship among animals (Sorensen and Kennedy, 1986; Henderson, 1988; Kennedy et al., 1988; Meyer, 1989). Animal models also account for the effects of selection and nonrandom mating when the complete

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covariance matrix is used (Kennedy et al., 1988), and they allow evaluations across herds.

Whole-herd, on-farm testing of pigs in seedstock herds is becoming more common. Data from these herds are a valuable resource for analysis by mixedmodel methods to provide estimates of genetic parameters and to evaluate the effectiveness of applied breeding programs (Hofer et al., 1992a,b).

The objectives of this study were to estimate genetic and phenotypic parameters and genetic trends for litter size, litter weight, growth rate, and backfat in two herds, each with the Landrace and Large White breeds. The herds were established from the same base population and then managed as replicated selection lines.

## **Materials and Methods**

*Herds.* The data came from two herds that produced purebred Landrace and Large White pigs. One herd was located in central Nebraska (Herd N), the other in north central Kansas (Herd K).

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	Large White			Landrace		
Trait <sup>a</sup>	x	SD	n	x	SD	n
			Her	d N		
NBA	10.1	2.7	893	9.8	2.7	517
LW, kg	55.5	9.1	872	59.5	8.7	510
ADG, g	761.9	93.7	4,568	752.8	95.0	2,916
BF, mm	16.6	3.2	5,377	16.4	3.3	3,415
			Her	d K		
NBA	10.1	2.7	698	10.0	2.5	387
LW, kg	57.8	6.4	653	61.5	6.0	373
ADG, g	766.4	84.5	3,431	741.5	82.9	2,382
BF, mm	14.4	2.5	3,431	14.1	2.3	2,382

Table 1. Means, standard deviations, and number of records by trait, breed, and herd

<sup>a</sup>NBA = number of pigs born alive per litter, adjusted to third-parity; LW = litter weight adjusted to weaning age of 21 d, 10 pigs given to the sow to nurse, and third-parity; ADG = average daily gain on test; BF = average probe backfat thickness of boars and gilts, adjusted to 104 kg.

Herd N was established in 1986 from 10 Large White and 8 Landrace boars, none of which had a common sire, purchased from a breeding company based in Canada, and 100 Large White and 50 Landrace gilts purchased from an Illinois breeder. These base animals were randomly mated within breed. Subsequently, all replacements were selected from within the herd.

Whole-herd performance testing was implemented with the first litters born in Herd N. In the 1st yr, selection was based on the pig's days to 104 kg, as only final weights were recorded, backfat at 104 kg (BF), and on the dam's litter size at birth (NBA) and litter weight at 21 d (LW). All records were expressed as deviations from contemporary group means. In late 1988, on-test-weight was recorded so average daily gain (ADG) could be calculated. At the same time, a computer program was developed that calculated breeding values and provided an index to rank animals for selection. Breeding values for ADG and BF were estimated using deviations from contemporary group averages of the individual, its contemporary full-sibs, and all half-sibs. Breeding values for NBA and LW were estimated using records for all litters of the dam.

The relative economic values used for the traits were \$12/pig for NBA, \$1.54/kg for LW.  $35.80 \cdot \text{kg}^{-1} \cdot \text{d}^{-1}$  for ADG, and  $- \frac{78}{\text{mm}}$  for BF. The values for NBA and LW are those recommended by the National Swine Improvement Federation (NSIF, 1988), but values for ADG and BF are larger than values found in the NSIF publication. The magnitude of the coefficients reflect the breeder's goal of improving efficiency of lean growth, relative to maternal traits, more rapidly than recommended by NSIF. The economic values were multiplied by 3 to increase variation among pigs. The selection index was I = 100+ 36  $EBV_{NBA}$  + 4.62  $EBV_{LW}$  + 107.4  $EBV_{ADG}$  - 2.34 EBV<sub>BF</sub>.

Herd K was established in 1989. Nine boars and 85 gilts of the Landrace breed and 10 boars and 136 gilts of the Large White breed were selected on the index from Herd N, moved to Herd K, and randomly mated within breed. Herd K was then closed and subsequently all replacement pigs were selected from within Herd K. Procedures for recording data and estimating breeding values were as described for Herd N.

The data included 1,410 litters from Herd N and 1,085 from Herd K. There were 8,792 pigs with growth and backfat records in Herd N and 5,813 in Herd K. The traits analyzed were NBA, LW, ADG, and BF, measured by ultrasound probing.

Management. At each farm, contemporary groups were all litters born within three weeks. The average was 32 litters per group in Herd N and 29 in Herd K. Number of pigs per group on which growth rate and backfat were measured averaged 208 in Herd N and 168 in Herd K.

The number of live pigs at birth was recorded for each litter, some cross-fostering of pigs among sows was done, and the number of pigs given each sow to nurse was recorded. Litters were weaned and weighed at approximately 20 d of age ( $\bar{x} = 19.8$  d, SD = .9, in Herd N; and  $\overline{x} = 20.4$  d, SD = 1.4, in Herd K). Pigs were in nursery rooms until approximately 5 to 6 wk of age, then in a grower building until approximately 85 d of age, when they were moved to another building and weighed. Growth rate was measured from this age  $(\bar{x} = 86 \text{ d}, \text{SD} = 11.3 \text{ in Herd N}; \bar{x} = 83 \text{ d}, \text{SD} = 8.6 \text{ in}$ Herd K) to average weights of 101.2 kg (SD = 13.1) in Herd N and 91.0 kg (SD = 10.2) in Herd K. At these weights, backfat of pigs in Herd N was measured approximately 4 cm off the midline approximately at the 4th and last ribs and at the last lumbar vertebra. Backfat of pigs in Herd K was measured only at the last rib. Table 1 contains the number of animals, means, and SD for each trait. The number of individuals in the pedigree file was 1,695 for NBA and LW and 15,867 for ADG and BF.

During the period in which growth rate was measured, there were 20 to 25 pigs of one sex per pen. They had ad libitum access to a diet of corn, soybean meal, and a mineral-vitamin premix formulated to contain 16% CP.

Before calculating estimated breeding values, litter size was adjusted for parity; litter weight was adjusted for age at weaning, number of pigs the sow was given to nurse, and parity; and backfat and age were adjusted to a weight of 104 kg. Adjustment factors used were those published by NSIF (1988). Genetic parameters published in NSIF (1988) were used to calculate breeding values.

Data Analyses. Although NSIF (1988) adjustment factors had been used to adjust the records before estimated breeding values were calculated, several of these adjustment factors did not fit the data for these breeds in these herds. Therefore, before genetic analyses were done, the original records were analyzed with PROC GLM<sup>®</sup> (SAS, 1985) to obtain specific adjustment factors for these data.

To obtain factors for effects considered to be discrete (effects of parity on NBA and LW, and effects of number nursed on LW), the model was as follows:  $Y_{ijklm} = H_i + G_{j(i)} + B_k + S_l + F_m + BS_{kl} + BF_{km} + SF_{lm}$ + BSF<sub>klm</sub> + e<sub>ijklm</sub>. Adjustment factors for continuous effects (effects of age at weaning on LW, and effects of weight on BF) were obtained from analyses with the model as follows:  $Y_{ijkl}$  =  $H_i$  +  $G_{j(\,i)}$  +  $B_k$  +  $S_l$  +  $BS_{kl}$  +  $b_1F$  +  $b_2F^2$  +  $b_3F^3$  + I +  $e_{ijkl}$ , where Y = the dependent variable, H = herd, G = contemporary group within herd, B = breed, S = sex, and F = effect for which adjustment factors were estimated (parity, age at weaning, number of pigs nursed by sow, or weight off test, as appropriate). The regression coefficients for the linear  $(b_1)$ , quadratic  $(b_2)$ , and cubic  $(b_3)$  effects of F and their interactions (I) with breed and sex were fitted when F was considered to be continuous. The random error term, e, was assumed to be normally and independently distributed  $(0, \sigma_e^2)$ .

Significance of effects was tested at the level of P < .05. The least squares means for each level of significant effects or interactions were deviated from a given standard (e.g., third-parity sows, 10 pigs nursed, and weaning age of 21 d) to calculate adjustment factors. Interaction effects and highest-order regression coefficients that were not significant were deleted from the model and data were analyzed with a final model that included herd and contemporary group and other effects that were significant for each trait. Both multiplicative and additive adjustment factors were calculated, following the same methods proposed by NSIF (1988). Original data were preadjusted with these factors before genetic analyses were done.

Variance components, genetic parameters, and breeding values were estimated by four different animal models, using DFREML (Meyer, 1988a,b,

1989), adapted to use SPARSPAK (George et al., 1980), a sparse matrix solver package, and output of breeding values as modified by Boldman and Van Vleck (1991). The basic linear model was as follows: Y =  $X\beta$  + Zu + e, where X = incidence matrix for fixed effects:  $\beta$  = vector of fixed effects of herd, contemporary group within herd, breed, and sex (for ADG and BF); Z = incidence matrix for random effects; u = vector of random effects (animal genetic, permanent environmental effect of the sow for NBA and LW, litter as a common environmental effect for ADG and BF, and maternal genetic, depending on the model); and, e =vector of environmental effects normally and independently distributed  $(0, \sigma_{e}^{2})$ . Model 1 included only the additive genetic effect of the animal (o), Model 2 included (o) and permanent environmental effect of sow (for NBA and LW) or common litter environmental effect (for ADG and BF), Model 3 included (**o**), the maternal genetic value (m), assumed to be uncorrelated with o, and permanent or common environmental effect, and Model 4 was the same as Model 3, but with o and m assumed to be correlated. Genetic parameters estimated were direct heritability  $(h_{\mathbf{0}}^2)$ , maternal heritability  $(h_{\mathbf{m}}^2)$ , correlation between o and m (r) and total heritability (Dickerson, 1947, 1970;  $h_t^2 = [h_o^2 + .5h_m^2 + 1.5 \sigma_{(o,m)}]/\sigma_p^2$ , where  $\sigma_{(o,m)}$  is the estimate of covariance between direct and maternal genetic effects and  $\sigma_{\rm p}^2$  is the estimate of phenotypic variance). The environmental parameter estimated was the ratio of variance of permanent environmental effects for NBA and LW (associated with the dam) or of common environmental effects (associated with the litter, c<sup>2</sup>) for ADG and BF to  $\sigma_{\rm p}^2$ .

The method described by Rao (1973) and Mood et al. (1974) to calculate ratios of likelihoods was used to compare models. The ratio  $-2[\log \Lambda_i - \log \Lambda_j]$  is asymptotically distributed as chi-square with degrees of freedom equal to the difference in the number of parameters in the Models i and j, where  $\Lambda$  is the value of the likelihood function for the model, after the convergence criterion was reached.

The software used to set up and solve the mixedmodel equations, DFREML (Meyer, 1988a,b), considers all the pedigree information available back to the foundation of the herd to calculate the inverse of the numerator relationship matrix  $(A^{-1})$ . The direct (**o**) and maternal (**m**) breeding values for the traits were estimated for all animals, including those without records and base animals. The average breeding values per year of birth of the pig were regressed on year of birth of the pigs and plotted to illustrate trends. Aggregate breeding values (H), the sum of the direct and maternal breeding values (Azzam and Nielsen, 1987), were also estimated for each trait and the trend was calculated.

Data for each herd-breed subclass also were fitted independently to Model 2 that included the additive

Herd-Breed	h <sub>o</sub> <sup>2</sup>	$\hat{\sigma}_{ m p}^2$	$\hat{\sigma}^2_{ extsf{PE}}/\hat{\sigma}^{ extsf{2b}}_{ extsf{p}}$	$e^{2^c}$		
	]	No. born alive per litter (NBA)				
Herd N-Landrace	.11	7.06	0	_		
Herd N-Large White	0	7.30	.28			
Herd K-Landrace	0	6.13	.11	_		
Herd K-Large White	.10	7.15	.11			
	<b></b>	Litter wt (LW), kg				
Herd N-Landrace	.20	75.0	0	_		
Herd N-Large White	.19	82.0	0			
Herd K-Landrace	.18	36.1	.03	_		
Herd K-Large White	.06	41.3	.06	—		
	Average daily gain (ADG), g					
Herd N-Landrace	.16	9,029		.10		
Herd N-Large White	.21	8,782		.07		
Herd K-Landrace	.37	6,870		.07		
Herd K-Large White	.26	7,136		.06		
	Backfat (BF), mm					
Herd N-Landrace	.54	10.7		.04		
Herd N-Large White	.41	10.3		.06		
Herd K-Landrace	.33	5.4	—	.06		
Herd K-Large White	.36	6.2		.07		

Table 2. Estimates of genetic, environmental, and phenotypic parameters, obtained with Model 2<sup>a</sup>, for each breed-herd subclass

<sup>a</sup>Model 2 included animal genetic effects (o) and permanent or common environmental effects. <sup>b</sup>Ratio of variance of permanent environmental effects ( $\hat{\sigma}_{PE}^2$ ) to phenotypic variance ( $\hat{\sigma}_p^2$ ).

<sup>c</sup>Ratio of variance of common litter environmental effects to phenotypic variance.

genetic effect of the animal and either permanent or common environmental effects as appropriate for the trait. Comparisons among models within subclasses were not done because this would have required a large number of computer runs. Maternal genetic effects were not included in the subclass analyses because, as discussed below, the component of variance for maternal effects computed in the combined analysis was small for all traits, even though maternal genetic effects were significant for two traits.

### **Results and Discussion**

Within-Herd-Breed Analyses. Estimates of parameters for each herd-breed subclass are presented in Table 2. There is no consistent pattern in these values that suggests parameters differ between breeds. For NBA, two estimates of heritability of direct effects were approximately .10 (one for each breed), but the other two estimates were zero. Three of four estimates of the heritability of LW were from .18 to .20, the fourth value was .06. Estimates of heritability of ADG ranged from .16 to .37, with the largest values for Herd K; heritabilities of BF were from .33 to .54, with the largest values for Herd N. The only consistent pattern was that the phenotypic variances of both LW and BF were lower in Herd K than in Herd N.

We do not know of an objective procedure to test whether parameters differ for the subclasses. Variation among estimates was expected because subclass sample sizes are not large. Therefore, the remainder of the discussion will focus on results of the combined analyses.

Choice of Model. A property of REML methods is that the larger the value of the likelihood function, the better the model explains the variation in the data. Generally, every time a parameter is added to mixedmodel analyses, the value of the likelihood function increases. So values of the likelihood function were expected to increase when data were analyzed first by Model 1, and then by Models 2, 3, or 4. The likelihood ratio test described by Rao (1973) and Mood et al. (1974) was used to test significance of the changes in the likelihoods, and results of those tests are presented in Table 3.

For NBA, significantly larger likelihood values were obtained when Model 2 was used, compared with Model 1, and when Model 3 was compared with Model 2. Thus, both permanent environmental effects of sows and maternal genetic effects were important. Models 3 and 4 did not have statistically different logs of the likelihood, and the values of  $h_{o}^2$ ,  $h_{m}^2$ , and  $h_t^2$  were similar for the two models. Consequently, including the correlation between direct and maternal genetic effects did not add significant information. This does not agree with the conclusions of Southwood and Kennedy (1990), who found that additive maternal genetic effects did not contribute extra information to selection for litter size.

Trait	Mod 1 – Mod 2	Mod 2 – Mod 3	Mod 3 – Mod 4
NBA	13.7**	7.1**	.1
LW	.2	.3	.4
ADG	1,555.5**	1.9	.6
BF	114.8**	5.5*	6.1*

<sup>a</sup>Number of degrees of freedom = 1.

\*P < .05.

 $*^{*}P < .01.$ 

The results obtained for LW suggest that Model 1 is appropriate. Maternal genetic effects and permanent environmental effects were not important; however, a small reduction in  $h_t^2$  was observed when permanent environmental effects were added to the model.

Common environmental effects of litter on ADG added significant information when Model 2 was compared with Model 1, but adding maternal effects (Models 3 and 4) did not contribute significantly. For BF, common environmental effects of litter and maternal genetic effects, correlated with direct genetic effects, contributed significantly to Model 1 that included only direct effects.

Genetic, Phenotypic, and Environmental Parameters. Estimates of genetic, environmental, and phenotypic parameters obtained with each animal model are presented in Table 4. Results obtained with each model are presented for comparison purposes, but the estimates most appropriate for these breeds and herds are those from Model 3 for NBA, Model 1 for LW, Model 2 for ADG, and Model 4 for BF.

The estimate of  $h_0^2$  for NBA was .002, much smaller than values found in many other studies (Avalos and Smith, 1987; Jorgensen, 1989; Long et al., 1990; Southwood and Kennedy, 1990; Kaplon et al., 1991a; Lamberson et al., 1991) but close to the value of .007 obtained by Haley and Lee (1992) with DFREML. Using Model 1, Southwood and Kennedy (1990) estimated, for Canadian pigs,  $h_0^2$  of .13, very close to the value of .14 found here.

The estimates of  $h_m^2$  for NBA, .012 and .036, are small and close to the values reported by Southwood and Kennedy (1990) but larger than the estimates of Haley and Lee (1992). Although not significant, a small negative correlation between direct and maternal genetic effects was found for NBA (-.07). The correlation was similar to values of -.013 and .112 obtained for Canadian Large White and Landrace (Southwood and Kennedy, 1990) but in disagreement with the estimate of -.98 reported by Haley and Lee (1992). Permanent environmental effects of sows explained 16 to 17% of the total phenotypic variation, values close to the 12.6% reported by Haley and Lee (1992) but larger than the 1% reported by Keele et al. (1991).

The estimates of  $h_0^2$  for LW did not change much with the different models. The value from Model 1 was .22, larger than the value of .06 found by Kaplon et al. (1991a). Estimates of maternal genetic effects, their correlation with direct effects, and permanent environmental effects all were small.

The estimate of  $h_{\mathbf{o}}^2$  for ADG decreased when environmental effects of litters were introduced from Model 1 to Model 2, but the addition of maternal effects in Models 3 and 4 did not cause important changes in the estimate. The estimate of  $h_0^2$ , approximately .24, is larger than that found in other studies of pigs tested on-farm (Merks, 1988, 1989; Hofer et al., 1992a) or in experimental herds (Keele et al., 1991), for which estimates varying from .12 to .16 were found, but is close to values reported by Savoie and Minvielle (1988), Long et al. (1990), and Kaplon et al. (1991a). McKay (1990) found a realized heritability of .38 for Canadian Yorkshire pigs. The estimates of heritability of maternal effects on ADG were very small, between .5 and 1.5%. Litter environmental effects explained approximately 7% of the phenotypic variation. The estimate of  $c^2$  is similar to those reported by Smith (1984) and Haley and Lee (1992) but is smaller than values found by Merks (1988, 1989), Van Diepen and Kennedy (1989), and Hofer et al. (1992a).

The estimates of  $h_0^2$  for BF were high and varied from .39 to .50. Permanent environmental effects, maternal effects, and the correlation of direct and maternal effects were important. However, the estimates of  $h_{f m}^2$  were small (from 1.9 to 3.4%), and the estimate of  $r_{o,m}$  was -.26. Those values, although statistically significant, had little effect on the estimates of  $h_t^2$  for BF, which were approximately .40 for all models that included litter environmental effects. For practical purposes, both maternal effects and the correlation between maternal and direct effects could be ignored. The estimates for  $h_{\boldsymbol{o}}^2$  and  $h_t^2$  for BF agree with those from several studies (Savoie and Minvielle, 1988, for Large White pigs; Van Diepen and Kennedy, 1989, for Canadian pigs tested on-farm; Long et al., 1990; McKay, 1990), but some other studies found smaller values at approximately .27 (Merks, 1988; Van Diepen and Kennedy, 1989, for station-tested pigs; Kaplon et al., 1991a). Other authors have reported larger estimates of  $h_0^2$  for BF, approximately .55 (Savoie and Minvielle, 1988, for Landrace pigs; Keele et al., 1991). The common environmental effect

Trait <sup>a</sup> and parameter <sup>b</sup>	Model 1	Model 2	Model 3	Model 4
NBA, pigs				
$h_o^2$	.14	.03	.00	.00
$h_{\mathbf{m}}^2$		_	.01	.04
$\sigma_{0,\mathbf{m}}/\sigma_{\mathbf{p}}^{2}$				01
$h_t^2$	.14	.03	.01	.01
<sup>r</sup> o,m		—	—	07
c <sup>2</sup> _2		.16	.17	.16
σ <sub>p</sub>	7.64	7.56	7.5	7.57
LW, kg				
hő	.22	.18	.19	.19
$h_m^2$			.01	.04
$\sigma_{\mathbf{o},\mathbf{m}}/\sigma_{\mathrm{p}}^{2}$				02
$h_t^2$	.22	.18	.19	.18
r <b>o,m</b>		— 	— 02	25
$\sigma^2$		00. 80.80	.05	.02
°p	63.57	63.08	63.35	63.38
h <sup>2</sup>	0.4	84	20	0.7
<sup>11</sup> 0 h2	.34	.24	.23	.20
<sup>II</sup> m , 2		—	.01	.02
$\sigma_{\mathbf{o},\mathbf{m}}/\sigma_{\mathbf{p}}^{2}$		—	—	02
$h_t^z$	.34	.24	.24	.23
r <sub>o,m</sub>		07	- 07	34 07
$\sigma_{\rm p}^2$	8 421 34	8 199 96	8 187 93	8 1 7 8 0 8
BF mm	0,121.01	0,100.00	0,101100	0,210100
$h^2_{-}$	50	49	30	49
$h^2$	.00		.00	.12
$\sigma_{\rm m} = 1/\sigma^2$		—	.02	.05
՝ <b>o,m</b> /՝°p ե2			—	04
"t	.50	.42	.41	.40 - 26
$c^2$		.06	.05	.05
$\sigma_{\rm p}^2$	8.88	8.63	8.65	8.56

Table	4.	Estimates of	genetic,	environme	ntal, and	l phenotypi	c parameters,	obtained
		by fou	r animal	models, fo	r NBA,	LW, ADG,	and BF	

<sup>a</sup>NBA = number born alive, LW = litter weight, ADG = average daily gain and BF = backfat. <sup>b</sup>h<sub>o</sub><sup>2</sup> = heritability for direct animal effects;  $h_m^2$  = heritability for maternal effects;  $\sigma_{o,m}/\sigma_p^2$  = covariance between direct and maternal genetic effects as a proportion of phenotypic variance;  $r_{o,m}$  = correlation between direct and maternal genetic effects;  $h_t^2$  = heritability of the total genetic contribution of the animal (total heritability);  $c^2$  = relative contribution of the permanent environmental effects of sow (for reproductive traits) or litter (for growth traits) and  $\sigma_p^2$  = phenotypic variance.

of litters explained only approximately 5% of the phenotypic variance but was significant. The value found agrees with results reported by Smith (1984) but is smaller than the values of 10 to 20% reported by other authors (Merks, 1988; Van Diepen and Kennedy, 1989; Keele et al., 1991; Haley and Lee, 1992; Hofer et al., 1992a).

Generation Interval. The average age of sires and dams when their first litter was born, average number of litters produced per parent, and approximate generation intervals were calculated for each herdbreed subclass, and these statistics are presented in Table 5. Approximate generation interval was calculated for each parent as its mean age when its first and last litters were born, and these values were averaged for each subclass.

In both herds, boars were young when first used as breeders; their average age when their first litters

	He	rd N	Herd K	
Item	Large White	Landrace	Large White	Landrace
		Sir	es	
Age at birth of first litter, d	336.8	345.3	302.4	296.7
Age at birth of last litter, d	457.2	450.0	470.6	461.0
No. of litters	8.8	7.7	16.6	12.1
Length of time used as breeder, d	120.4	104.7	168.2	164.3
Approximate generation interval <sup>a</sup> , d	397.0	397.6	386.5	378.8
		Dai	ms	
Age at birth of first litter, d	361.2	354.2	339.6	340.0
No. of litters	2.2	2.2	2.2	2.0
Approximate generation interval, d	424.4	422.4	412.4	389.5

Table 5. Mean utilization as breeders of sires and dams

<sup>a</sup>Average of age of parents at birth of first and last litters.

were born ranged from 297 to 345 d. Boars were first mated at a younger age but remained in the breeding herd longer and produced more litters in Herd K than in Herd N. Therefore, the approximate generation interval of sires was approximately 15 d longer in Herd N. Averaged across subclasses, the approximate generation interval of sires was 390 d.

The average age of gilts when their first litters were born was approximately 17 d less in Herd K than in Herd N, and the average female had 2.2 litters in Herd N and 2.1 litters in Herd K. Because Landrace gilts in Herd K were younger when their first litter was born and had fewer litters than gilts in other subclasses, the approximate generation interval for these females was only 390 d, compared with 412 to 424 d for females in the other subclasses. Overall, the generation interval for females averaged 412 d, and the average for males and females was 401 d, 1.1 yr per generation.

Selection Applied. The average realized and standardized selection differentials for boars and gilts selected from within the herd are presented in Table 6. On average, approximately 1.2 standard deviations of selection for the index were realized, although the breeder placed more emphasis on ADG and BF and less on NBA and LW in selection of boars than in selection of gilts. The realized selection differentials for boars for the index are lower than could have been achieved because the breeder seldom selected littermate boars, emphasizing selection of boars from several paternal half-sib families, and some emphasis was put on foot and leg structure. Family structure was not considered in selection of gilts.

Selection of replacements was based on the index; therefore, selection differentials for other traits were secondary selection differentials. Because these are the average selection differentials of animals that were selected, they are selection differentials per generation. To place them in the same units as the genetic changes per year discussed in the next section, the average values for boars and gilts were divided by 1.1, the generation interval, to obtain the average selection differential per year.

Genetic Trends. The average breeding values for base animals were adjusted to zero to illustrate genetic change in further generations. Graphs of genetic trends of aggregate breeding values are given in Figures 1 to 4.

The estimate of genetic trend for NBA was consistently positive, although small, for all models except Model 4, for which a small negative change in direct effects was found. The trend for aggregate breeding value is shown in Figure 1. The genetic change in litter size obtained with Model 3 was approximately .12% of the mean, .012 pigs/yr, similar to values reported by Kaplon et al. (1991b) and Southwood and Kennedy (1991). When selection was applied only to litter size or to traits related to litter size, such as ovulation rate and embryonic survival, larger changes in litter size have been reported (Neal et al., 1989; Lamberson et al., 1991).

The genetic trend for LW obtained with all models was positive (Figure 2). The estimated trend for

Table 6. Number of selected animals and selection differentials, as deviation from contemporary groups, by sex

Trait <sup>a</sup>	Males <sup>b</sup>	Females <sup>b</sup>	Average per year <sup>c</sup>
n	133	687	
NBA, pigs	1.84 (.65)	2.32 (.84)	1.89 (.68)
LW, kg	3.70 (.48)	2.82 (.36)	2.96 (.38)
ADG, g	109.25 (1.23)	49.98 (.64)	72.38 (.85)
BF, mm	10 (41)	09 (24)	09 (30)
INDEX	9.60 (1.25)	8.91 (1.16)	8.4 (1.10)

<sup>a</sup>NBA = number of pigs born alive; LW = weight of litter at weaning; ADG = average daily gain on test; BF = average backfat, measured by ultrasound; INDEX = selection index.

<sup>b</sup>Values in parentheses are standardized selection differentials. <sup>c</sup>Mean values for males and females divided by the average generation interval of 1.1 yr.



Figure 1. Genetic trend of aggregate breeding value for number of pigs born alive (see text for description of models). Equation for Model 3, that best fitted data, is as follows: Y = -.0002 + .0118X.

Model 1 was .245 kg/yr, .44% of the mean, larger than the average of .045 kg/yr reported by Kaplon et al. (1991b).

The trend for ADG was positive and similar for all models (Figure 3). Genetic progress was estimated to be 6.91 g/yr or .80% of the mean by Model 2, very close to the value reported by Hofer et al. (1992b) of 6.5 g/ yr for Large White pigs tested on-farm in Switzerland, but smaller than the 10.3 g/yr observed by those authors for Landrace pigs and the 9 g/yr reported by McKay (1990) for Canadian Large White pigs. Genetic trends for ADG found in this study are larger than the values of 1.5 to 4 g/generation reported by Kaplon et al. (1991b) and the changes of -.027 to .016% of the mean reported by Smith (1984).

Average breeding values obtained for BF for 1988 were large compared with those obtained in other



Figure 2. Genetic trend of aggregate breeding value for litter weight at 21 d (see text for description of data). Equation for Model 1, that best fitted data, is as follows: Y = .0211 + .2447X.



Figure 3. Genetic trend of aggregate breeding value for average daily gain (see text for description of models). Equation for Model 2, that best fitted data, is as follows: Y = -4.3636 + 6.9059X.

years (Figure 4). The reason is not apparent, but these large values, followed by little additional change, caused average changes to be low. Genetic reduction in direct effects on BF were approximately .06 mm/yr (.40% of the mean). Values from -.02 to -.04 mm/yr were reported by Kaplon et al. (1991b). Higher trends of -.12 mm/yr (for Large White) and -.18 mm/yr (for Landrace) were reported by Hudson and Kennedy (1985a,b). David et al. (1985) found average values of .4 to .5 mm/yr in Nebraska SPF herds, and McKay (1990) found genetic change was -.7 mm/generation in Canadian pigs.



Figure 4. Genetic trend of aggregate breeding value for backfat thickness (see text for description of models). Equation for Model 4, that best fitted data, is as follows: Y = .1194 - .0627X.

Implications

Mixed-model procedures are useful for obtaining estimates of genetic parameters specific to populations and for monitoring, and then improving, industry selection programs. This can be done by analyzing data with different models that consider both direct and maternal genetic effects and the correlation between them and permanent or common environmental effects, identifying the most appropriate model, and then using it for subsequent calculations of breeding values. Selection in industry herds can be effective, but most progress can be made when breeding values are estimated with parameters specific to the population so optimum emphasis can be given to each trait for specific breeding objectives.

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