

# JOURNAL OF ANIMAL SCIENCE

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*J Anim Sci* 2003. 81:46-53.

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# Genetic parameters and trends for litter traits in U.S. Yorkshire, Duroc, Hampshire, and Landrace pigs<sup>1</sup>

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**ABSTRACT:** Records on 251,296 Yorkshire, 75,262 Duroc, 83,338 Hampshire, and 53,234 Landrace litters born between 1984 and April of 1999 in herds on the National Swine Registry Swine Testing and Genetic Evaluation System were analyzed. Animal model and restricted maximum likelihood procedures were used to estimate variances of animal genetic (a), maternal genetic (m), permanent environmental, and service sire, and the covariances between a and m for number born alive (NBA), litter weight at 21 d (L21WT), and number weaned (NW). Fixed effects of contemporary groups were included in the analysis. Based on a single-trait model, estimates of heritabilities were 0.10, 0.09, 0.08, and 0.08 for NBA; 0.08, 0.07, 0.08, and 0.09 for L21WT; and 0.05, 0.07, 0.05, and 0.05 for NW in the Yorkshire, Duroc, Hampshire, and Landrace breeds, respectively. Estimates of maternal genetic effects were

low and ranged from 0.00 to 0.02 for all traits and all breeds. Estimates of permanent environmental effects ranged from 0.03 to 0.08. Estimates of service sire effects ranged from 0.02 to 0.05. A bivariate analysis was used to estimate the genetic correlations among traits. Average genetic correlations over the four breeds were 0.13, 0.15, and 0.71 for NBA with L21WT, NBA with NW, and L21WT with NW, respectively. Average genetic trends were 0.018 pigs/yr, 0.114 kg/yr, and 0.004 pigs/yr for NBA, L21WT, and NW, respectively. Although estimates of heritabilities for litter traits were low and similar across breeds, genetic variances for litter traits were sufficiently large to indicate that litter traits could be improved through selection. This study presents the first set of breed-specific estimates of genetic parameters available from large numbers of field records. It provides information for use in national genetic evaluations.

Key Words: Genetic Parameters, Genetic Trend, Litter Traits, Pigs

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J. Anim. Sci. 2003. 81:46–53

## Introduction

Selection for litter traits is attractive to breeders because lean growth traits, which have been selection objectives for many years, may be approaching an optimal point (Webb, 1998). A successful genetic improvement program requires accurate genetic parameter estimates. Several studies (Southwood and Kennedy, 1990; Crump et al., 1997; Kaufmann et al., 2000) have reported estimates of genetic parameters for litter traits based on different commercial populations and limited field data. Parameter estimates in the literature for litter traits vary substantially among studies or breeds (Southwood and Kennedy, 1990; Ferraz and Johnson, 1993; Kaufmann et al., 2000). Genetic parameters cur-

rently recommended by the National Swine Improvement Federation (NSIF, 1997) for genetic evaluation programs are not breed-specific. Therefore, the objective of this study was to estimate breed-specific genetic parameters and genetic trends for number born alive (NBA), number weaned (NW), and litter weight at 21 d (L21WT) for the U.S. Yorkshire, Duroc, Hampshire, and Landrace populations.

## Materials and Methods

### Data Source

Data were obtained from the National Swine Registry Swine Testing and Genetic Evaluation System (STAGES) on Yorkshire, Duroc, Hampshire, and Landrace litters born from 1984 to April 1999. Details of data collection can be found in STAGES (NSR, 2000). Data included pedigree information for each sow, contemporary group, parity of the sow, farrowing and weighing dates, NBA, number after transfer (NAT), NW, and L21WT. The NW included adopted pigs but excluded pigs transferred to other sows. Contemporary

<sup>1</sup>Journal paper No. J-19676 of the Iowa Agric. and Home Econ. Exp. Stn., Ames, Project No. 3456, and supported by Hatch Act and State of Iowa funds.

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Received December 20, 2001.

Accepted August 8, 2002.

**Table 1.** Number of records and means for litter traits by breed

| Item                | Yorkshire | Duroc  | Hampshire | Landrace |
|---------------------|-----------|--------|-----------|----------|
| Records             | 251,296   | 75,262 | 83,332    | 53,234   |
| Animals             | 128,773   | 45,970 | 46,861    | 26,134   |
| Sires               | 12,415    | 4,729  | 4,982     | 2,815    |
| Dams                | 48,875    | 18,413 | 18,795    | 9,241    |
| Service sires       | 12,415    | 5,299  | 5,947     | 3,737    |
| Contemporary groups | 31,487    | 10,404 | 12,086    | 7,191    |
| Number born alive   |           |        |           |          |
| $\bar{x}^a$         | 10.61     | 9.16   | 9.54      | 10.44    |
| SD                  | 2.67      | 2.37   | 2.36      | 2.54     |
| Litter weight, kg   |           |        |           |          |
| $\bar{x}^b$         | 59.48     | 55.64  | 54.57     | 62.41    |
| SD                  | 14.34     | 14.11  | 13.81     | 13.84    |
| Number weaned       |           |        |           |          |
| $\bar{x}^c$         | 11.31     | 10.77  | 10.49     | 11.42    |
| SD                  | 2.45      | 1.85   | 1.71      | 1.81     |

<sup>a</sup>Mean adjusted for parity and age at farrowing.

<sup>b</sup>Mean adjusted for parity, age at farrowing, number after transfer, and age at weighing.

<sup>c</sup>Mean adjusted for parity and number after transfer.

groups were defined by the breeder as a group of sows that were bred, gestated, and farrowed in a group under the same management and environmental conditions. The traits NBA and L21WT were adjusted according to breed-specific procedures developed by Culbertson et al. (1997). Number weaned was adjusted according to breed-specific procedures developed by Culbertson (1997). Both NBA and L21WT were adjusted for parity and age at farrowing. Litter weight at 21 d was also adjusted for NAT and age at weighing. Number weaned was adjusted for parity and NAT. Single-sire contemporary group records were removed, as were records from sires not connected across contemporary groups. Numbers of records, animals, sires, dams, service sires, and contemporary groups by breed are in Table 1, along with means and SD for NBA, L21WT, and NW. After editing, distribution of records across years for each breed is shown in Table 2. In the Yorkshire dataset, only records since 1992 were used to estimate variance

components due to computational limitations on dataset size.

### Statistical Analysis

*Univariate Analysis.* Within-breed univariate analyses were conducted using REMLF90 (Misztal, 2000) to estimate single-trait variance components. The model fitted was:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{Pm} + \mathbf{W}_1\mathbf{ss} + \mathbf{W}_2\mathbf{pe} + \mathbf{e}$$

where  $\mathbf{y}$  represents a vector of observations;  $\mathbf{b}$  is a vector of fixed contemporary group effects;  $\mathbf{a}$  is a vector of random additive genetic effects of animals, which is assumed to be distributed  $N(\mathbf{0}, \mathbf{A}\sigma_a^2)$ ;  $\mathbf{A}$  is the numerator relationship matrix among animals;  $\mathbf{m}$  is a vector of random additive maternal genetic effects, assumed to be distributed  $N(\mathbf{0}, \mathbf{A}\sigma_m^2)$  and correlated with random

**Table 2.** Data distribution by year and breed

| Year              | Yorkshire | Duroc | Hampshire | Landrace |
|-------------------|-----------|-------|-----------|----------|
| 1984              | 8,636     | 15    | 444       | 1,400    |
| 1985              | 14,469    | 34    | 994       | 1,759    |
| 1986              | 16,138    | 1,123 | 2,323     | 2,484    |
| 1987              | 18,137    | 3,019 | 3,844     | 3,423    |
| 1988              | 19,697    | 3,294 | 4,823     | 3,255    |
| 1989              | 20,434    | 3,638 | 5,751     | 3,555    |
| 1990              | 21,870    | 4,150 | 6,799     | 4,128    |
| 1991              | 20,913    | 5,026 | 8,240     | 4,520    |
| 1992              | 20,392    | 5,474 | 9,113     | 5,231    |
| 1993              | 18,349    | 6,860 | 8,725     | 4,479    |
| 1994              | 16,960    | 7,969 | 8,815     | 4,218    |
| 1995              | 14,907    | 7,686 | 7,830     | 3,959    |
| 1996              | 14,939    | 8,909 | 6,914     | 4,027    |
| 1997              | 12,400    | 8,471 | 5,010     | 3,417    |
| 1998              | 7,404     | 5,796 | 2,762     | 2,108    |
| 1999 <sup>a</sup> | 5,651     | 3,798 | 951       | 1,271    |

<sup>a</sup>Partial year—records included the litters born up to April 1999.

animal effects ( $\sigma_{am}$ );  $\mathbf{ss}$  is a vector of service sires, assumed to be distributed  $N(\mathbf{0}, \mathbf{I}\sigma_{ss}^2)$  and uncorrelated with other random effects;  $\mathbf{pe}$  is a vector of permanent environmental effects, assumed to be distributed  $N(\mathbf{0}, \mathbf{I}\sigma_{pe}^2)$  and uncorrelated with other random effects; and  $\mathbf{e}$  is a vector of residual effects, which is assumed to be distributed  $N(\mathbf{0}, \mathbf{I}\sigma_e^2)$ . Incidence matrices  $\mathbf{X}$ ,  $\mathbf{Z}$ ,  $\mathbf{P}$ ,  $\mathbf{W}_1$ , and  $\mathbf{W}_2$  relate records to fixed, additive genetic, maternal genetic, service sire, and permanent environmental effects, respectively. A simplified model in which maternal genetic effects were excluded was also fitted. Standard errors of heritability estimates were calculated using the approximation of Swiger et al. (1964).

*Bivariate Analyses.* Bivariate analyses were conducted to estimate genetic and phenotypic correlations among traits using REMLF90 (Misztal, 2000). The model was the same as for the univariate analyses except maternal genetic effects were excluded. Standard errors of genetic correlations ( $\hat{\sigma}_{r_A}$ ) were calculated using the approximate formula given by Falconer (1989):

$$\hat{\sigma}_{r_A} = \frac{1 - \hat{r}_A^2}{\sqrt{2}} \sqrt{\frac{\hat{\sigma}_{\hat{h}_x^2} \hat{\sigma}_{\hat{h}_y^2}}{\hat{h}_x^2 \hat{h}_y^2}}$$

where  $\hat{h}_x^2$ ,  $\hat{h}_y^2$  are the heritability estimates of traits  $x$  and  $y$ , respectively, and  $\hat{\sigma}_{\hat{h}_x^2}$  and  $\hat{\sigma}_{\hat{h}_y^2}$  are the standard errors of the heritability estimates of traits  $x$  and  $y$ , respectively. In the restricted maximum likelihood analyses, the convergence criterion was set to  $10^{-8}$  for all analyses.

*Maternal Effects.* Breeding values for litter traits were estimated using two single-trait models with and without maternal effects using BLUPF90 (Misztal, 2000). Spearman rank correlations between the two sets of EBV for sows were estimated to examine the consequences of ignoring maternal effects.

*Genetic Trends.* Breeding values for litter traits were estimated using a three-trait model without maternal effects using BLUPF90 (Misztal, 2000). The average breeding values per birth year were regressed on birth year of the sows and plotted to illustrate trends.

## Results and Discussion

### Genetic Variances

Estimates of genetic variances and covariances are in Tables 3 to 5. Differences in estimates of variance components among breeds were found. Genetic variances for NBA, L21WT, and NW were highest in the Yorkshire breed. Landrace had the highest additive maternal genetic variance for NBA, and Yorkshire had the highest for NW and L21WT. Interpreting differences in variance component estimates from the literature is difficult because these estimates depend on the population and the data collected. Estimates of animal genetic variance for NBA in Tables 3 to 5 generally tend to be smaller than those reported in the literature

(Southwood and Kennedy, 1990; Crump et al., 1997; Kaufmann et al., 2000). However, estimates of animal genetic variances for L21WT are in agreement with the values reported by Ferraz and Johnson (1993). Negative genetic covariances between direct and maternal genetic effects were found for all traits in each breed.

### Heritabilities

Estimates of heritabilities from single-trait models are in Tables 3 to 5, and those from bivariate analyses are in Table 6. Estimates of heritability for each trait within breed obtained from single- and bivariate-trait analyses differed by 1% or less; therefore, only those from single-trait analyses are discussed. Very little difference in estimates of heritability with and without maternal genetic effects occurred. This result agrees with the findings of Southwood and Kennedy (1990) in Canadian Yorkshire. However, the results of this study are not consistent with the findings of Southwood and Kennedy (1990) in Canadian Landrace who found estimates of heritability were reduced considerably by not accounting for maternal effects and their covariance with animal direct effects. Crump et al. (1997) also reported that the estimates of heritability for litter traits changed very little with maternal genetic effects in the model.

Estimates of heritability for NBA are 0.10, 0.09, 0.08, and 0.08 for the Yorkshire, Duroc, Hampshire, and Landrace breeds, respectively (Table 3). These are in agreement with literature estimates of approximately 0.10 (Southwood and Kennedy, 1990; Crump et al., 1997). See et al. (1993) reported estimates of 0.12 to 0.13 from field data of Hampshire, Landrace, and Spotted breeds, which were included in the current analysis. However, the estimates in this study are much lower than the estimate of 0.22 reported by Kaufmann et al. (2000). These results are also consistent with the heritability of 0.10 recommended by NSIF (1997).

Estimates of heritability for L21WT are 0.08, 0.07, 0.08, and 0.09 for Yorkshire, Duroc, Hampshire, and Landrace breeds, respectively (Table 4). These estimates are similar to those reported by Kaplon et al. (1991a) in Polish Large White sows; however, the data in that study was not adjusted for litter size, and cross-fostering was stated to be infrequent. However, Ferraz and Johnson (1993) reported an average heritability of 0.19 over four models for L21WT in Landrace and Large White sows. The results in this study are also lower than the heritability of 0.15 recommended by NSIF (1997).

Estimates of heritability for NW are 0.05, 0.07, 0.05, and 0.05 for the Yorkshire, Duroc, Hampshire, and Landrace breeds, respectively (Table 5). These estimates are in the range of previous estimates (Kaplon et al., 1991a; Roehe and Kennedy, 1995), but lower than the estimated heritability of 0.10 reported by Southwood and Kennedy (1990) in Canadian sows and Chen et al. (2001) from a selection experiment with a synthetic

**Table 3.** Estimates of (co)variance components and genetic parameters from univariate analyses for number born alive by breed using models without (Model 1) and with (Model 2) maternal genetic effects

| Component <sup>a</sup> | Yorkshire |         | Duroc   |         | Hampshire |         | Landrace |         |
|------------------------|-----------|---------|---------|---------|-----------|---------|----------|---------|
|                        | Model 1   | Model 2 | Model 1 | Model 2 | Model 1   | Model 2 | Model 1  | Model 2 |
| $\sigma_a^2$           | 0.5931    | 0.5917  | 0.4627  | 0.4113  | 0.4046    | 0.4045  | 0.5050   | 0.4418  |
| $\sigma_m^2$           |           | 0.0592  |         | 0.0514  |           | 0.0450  |          | 0.1262  |
| $\sigma_{am}$          |           | -0.0495 |         | -0.0618 |           | -0.0553 |          | -0.1653 |
| $\sigma_{ss}^2$        | 0.2372    | 0.2368  | 0.1542  | 0.1542  | 0.1011    | 0.1010  | 0.2525   | 0.2525  |
| $\sigma_{pe}^2$        | 0.4152    | 0.4142  | 0.4113  | 0.4113  | 0.3034    | 0.3035  | 0.4417   | 0.4418  |
| $\sigma_e^2$           | 4.6856    | 4.6149  | 4.1129  | 4.1131  | 4.248     | 4.2478  | 5.1132   | 5.0498  |
| $\sigma_p^2$           | 5.9311    | 5.9168  | 5.1411  | 5.1413  | 5.0571    | 5.0568  | 6.3124   | 6.3121  |
| $h^2$                  | 0.10      | 0.10    | 0.09    | 0.08    | 0.08      | 0.08    | 0.08     | 0.07    |
| $m^2$                  |           | 0.01    |         | 0.01    |           | 0.00    |          | 0.02    |
| $ss^2$                 | 0.04      | 0.04    | 0.03    | 0.03    | 0.02      | 0.02    | 0.04     | 0.04    |
| $pe^2$                 | 0.07      | 0.07    | 0.08    | 0.08    | 0.06      | 0.06    | 0.07     | 0.07    |
| $r$                    | 0.17      | 0.17    | 0.17    | 0.16    | 0.14      | 0.14    | 0.15     | 0.15    |
| $r_{am}$               |           | -0.27   |         | -0.43   |           | -0.41   |          | -0.70   |

<sup>a</sup> $\sigma_a^2$  = animal genetic variance;  $\sigma_m^2$  = maternal genetic effect;  $\sigma_{am}$  = covariance between animal genetic and maternal genetic effects;  $\sigma_{ss}^2$  = service sire variance;  $\sigma_{pe}^2$  = permanent environmental variance;  $\sigma_e^2$  = residual variance;  $\sigma_p^2$  = phenotypic variance;  $h^2$  = heritability (standard errors ranged from approximately 0.004 to 0.008);  $m^2$  = fraction of variance due to maternal genetic effects;  $ss^2$  = fraction of variance due to service sire effects;  $pe^2$  = fraction of variance due to permanent environmental effects;  $r_{am}$  = genetic correlation between animal genetic and maternal genetic effects; and  $r$  = repeatability.

line of Yorkshire-Meishan pigs. The estimates from this study are also similar to the value of 0.06 recommended by NSIF (1997).

#### Additive Maternal Genetic Effects

Additive maternal genetic effects were not large sources of variation. The percentage of the variance accounted for by maternal genetic effects ranged from 0.00 to 0.02 for all traits and breeds (Tables 3 to 5). This result is in agreement with the results of Perez-Enciso and Gianola (1992), Roehe and Kennedy (1995),

and Crump et al. (1997). However, these estimates of maternal genetic effects are considerably lower than those reported by Southwood and Kennedy (1990), Ferraz and Johnson (1993), and See et al. (1993). Negative correlations between direct and maternal additive genetic effects were found for all traits across breeds (Tables 3 to 5). The estimated correlations ranged from -0.27 to -0.70 for NBA, -0.11 to -0.21 for L21WT, and -0.53 to -0.71 for NW. These results are in the range of previous estimates reported by Southwood and Kennedy (1990), Haley and Lee (1992), and Crump et al. (1997). These correlations were stronger for NW than

**Table 4.** Estimates of (co)variance components and genetic parameters from univariate analyses for litter weight at 21 d (kg) by breed using models without (Model 1) and with (Model 2) maternal genetic effects

| Component <sup>a</sup> | Yorkshire |          | Duroc    |          | Hampshire |          | Landrace |          |
|------------------------|-----------|----------|----------|----------|-----------|----------|----------|----------|
|                        | Model 1   | Model 2  | Model 1  | Model 2  | Model 1   | Model 2  | Model 1  | Model 2  |
| $\sigma_a^2$           | 14.8214   | 15.2861  | 8.5931   | 8.5071   | 9.0515    | 8.9656   | 13.0831  | 12.9783  |
| $\sigma_m^2$           |           | 3.7140   |          | 1.3125   |           | 0.9921   |          | 1.7971   |
| $\sigma_{am}$          |           | -0.8355  |          | -0.5013  |           | -0.6264  |          | -0.6279  |
| $\sigma_{ss}^2$        | 7.7908    | 7.7374   | 3.7837   | 3.6988   | 4.3866    | 4.5214   | 5.8671   | 5.7834   |
| $\sigma_{pe}^2$        | 7.4107    | 7.5134   | 8.1471   | 8.4952   | 6.8137    | 6.8117   | 7.5534   | 7.5134   |
| $\sigma_e^2$           | 159.9955  | 154.4059 | 102.2471 | 97.3011  | 91.0826   | 88.9876  | 123.9932 | 121.7461 |
| $\sigma_p^2$           | 190.0184  | 188.6568 | 122.7710 | 119.3147 | 111.3344  | 110.2784 | 150.4968 | 149.8183 |
| $h^2$                  | 0.08      | 0.08     | 0.07     | 0.07     | 0.08      | 0.08     | 0.09     | 0.09     |
| $m^2$                  |           | 0.02     |          | 0.01     |           | 0.00     |          | 0.01     |
| $ss^2$                 | 0.04      | 0.04     | 0.03     | 0.03     | 0.04      | 0.04     | 0.04     | 0.04     |
| $pe^2$                 | 0.04      | 0.04     | 0.07     | 0.07     | 0.06      | 0.06     | 0.05     | 0.05     |
| $r$                    | 0.12      | 0.12     | 0.14     | 0.14     | 0.14      | 0.14     | 0.14     | 0.14     |
| $r_{am}$               |           | -0.11    |          | -0.15    |           | -0.21    |          | -0.13    |

<sup>a</sup> $\sigma_a^2$  = animal genetic variance;  $\sigma_m^2$  = maternal genetic effect;  $\sigma_{am}$  = covariance between animal genetic and maternal genetic effects;  $\sigma_{ss}^2$  = service sire variance;  $\sigma_{pe}^2$  = permanent environmental variance;  $\sigma_e^2$  = residual variance;  $\sigma_p^2$  = phenotypic variance;  $h^2$  = heritability (standard errors ranged from approximately 0.004 to 0.008);  $m^2$  = fraction of variance due to maternal genetic effects;  $ss^2$  = fraction of variance due to service sire effects;  $pe^2$  = fraction of variance due to permanent environmental effects;  $r_{am}$  = genetic correlation between animal genetic and maternal genetic effects; and  $r$  = repeatability.

**Table 5.** Estimates of (co)variance components and genetic parameters from univariate analyses for number weaned by breed using models without (Model 1) and with (Model 2) maternal genetic effects

| Component <sup>a</sup> | Yorkshire |         | Duroc   |         | Hampshire |         | Landrace |         |
|------------------------|-----------|---------|---------|---------|-----------|---------|----------|---------|
|                        | Model 1   | Model 2 | Model 1 | Model 2 | Model 1   | Model 2 | Model 1  | Model 2 |
| $\sigma_a^2$           | 0.2554    | 0.2597  | 0.2216  | 0.2118  | 0.1363    | 0.1383  | 0.1577   | 0.1540  |
| $\sigma_m^2$           |           | 0.0583  |         | 0.0279  |           | 0.0257  |          | 0.0126  |
| $\sigma_{am}$          |           | -0.0652 |         | -0.0469 |           | -0.0423 |          | -0.0299 |
| $\sigma_{ss}^2$        | 0.1996    | 0.2118  | 0.1547  | 0.1517  | 0.1055    | 0.1044  | 0.1072   | 0.0944  |
| $\sigma_{pe}^2$        | 0.2557    | 0.2612  | 0.1234  | 0.1214  | 0.1061    | 0.1037  | 0.1041   | 0.0951  |
| $\sigma_e^2$           | 4.6116    | 4.5108  | 2.6220  | 2.6056  | 2.3252    | 2.2893  | 2.7824   | 2.7887  |
| $\sigma_p^2$           | 5.3223    | 5.3018  | 3.1217  | 3.1184  | 2.6731    | 2.6614  | 3.1514   | 3.1448  |
| $h^2$                  | 0.05      | 0.05    | 0.07    | 0.07    | 0.05      | 0.05    | 0.05     | 0.05    |
| $m^2$                  |           | 0.01    |         | 0.01    |           | 0.01    |          | 0.00    |
| $ss^2$                 | 0.04      | 0.04    | 0.05    | 0.05    | 0.04      | 0.04    | 0.03     | 0.03    |
| $pe^2$                 | 0.05      | 0.05    | 0.04    | 0.04    | 0.04      | 0.04    | 0.03     | 0.03    |
| $r$                    | 0.10      | 0.10    | 0.11    | 0.11    | 0.09      | 0.09    | 0.08     | 0.08    |
| $r_{am}$               |           | -0.53   |         | -0.61   |           | -0.71   |          | -0.68   |

<sup>a</sup> $\sigma_a^2$  = animal genetic variance;  $\sigma_m^2$  = maternal genetic effect;  $\sigma_{am}$  = covariance between animal genetic and maternal genetic effects;  $\sigma_{ss}^2$  = service sire variance;  $\sigma_{pe}^2$  = permanent environmental variance;  $\sigma_e^2$  = residual variance;  $\sigma_p^2$  = phenotypic variance;  $h^2$  = heritability (standard errors ranged from approximately 0.003 to 0.007);  $m^2$  = fraction of variance due to maternal genetic effects;  $ss^2$  = fraction of variance due to service sire effects;  $pe^2$  = fraction of variance due to permanent environmental effects;  $r_{am}$  = genetic correlation between animal genetic and maternal genetic effects; and  $r$  = repeatability.

for NBA in the Yorkshire, Duroc, and Hampshire breeds, but they were relatively strong for both NW and NBA in the Landrace.

Spearman rank correlations between the two sets of EBV for direct genetic effects for litter traits under the models with and without maternal genetic effects ranged from 0.93 to 0.98 across breeds. Little change in ranking of sows on estimated breeding values from models with and without maternal genetic effects occurred. This result is consistent with those of other studies (Southwood and Kennedy, 1990; Crump et al.,

1997) indicating models with only direct genetic effects are sufficient.

In this dataset, 50% of litters had cross-fostering. The small maternal genetic effects may be explained by the large amount of cross-fostering practiced, as argued by Crump et al. (1997), which means that sows that are littermates at birth do not share the same postnatal environment. This implies the maternal genetic effect applies postnatally rather than in utero or cytoplasmically. This was supported by Southwood and Kennedy (1990), who found that estimates of maternal genetic

**Table 6.** Estimates of heritability<sup>a</sup> (diagonal), genetic<sup>b</sup> (above diagonal), and phenotypic (below diagonal) correlations from bivariate analysis by breed

| Trait                 | Number born alive | Litter weight at 21 d | Number weaned |
|-----------------------|-------------------|-----------------------|---------------|
| Yorkshire             |                   |                       |               |
| Number born alive     | 0.10              | 0.14                  | 0.19          |
| Litter weight at 21 d | 0.06              | 0.08                  | 0.75          |
| Number weaned         | 0.06              | 0.80                  | 0.04          |
| Duroc                 |                   |                       |               |
| Number born alive     | 0.09              | 0.10                  | 0.07          |
| Litter weight at 21 d | 0.03              | 0.07                  | 0.65          |
| Number weaned         | 0.02              | 0.77                  | 0.06          |
| Hampshire             |                   |                       |               |
| Number born alive     | 0.08              | 0.13                  | 0.20          |
| Litter weight at 21 d | 0.04              | 0.08                  | 0.71          |
| Number weaned         | 0.06              | 0.79                  | 0.03          |
| Landrace              |                   |                       |               |
| Number born alive     | 0.08              | 0.15                  | 0.14          |
| Litter weight at 21 d | 0.07              | 0.09                  | 0.73          |
| Number weaned         | 0.05              | 0.78                  | 0.02          |

<sup>a</sup> $h^2$  is the average of two estimates from bivariate analyses.

<sup>b</sup>Standard errors of  $r_g$  ranged from 0.05 to 0.09 for number born alive with litter weight at 21 d, from 0.06 to 0.10 for number born alive with number weaned, and from 0.02 to 0.04 for litter weight at 21 d with number weaned, respectively.

effects for NW were generally higher than for NBA. However, in this study, estimates of maternal genetic effects for NW are similar to those for NBA. Roehe and Kennedy (1993) showed that with small maternal heritability ( $h^2_m$ ) and a negative correlation between maternal and direct effects, the response to direct selection for litter size can be reduced.

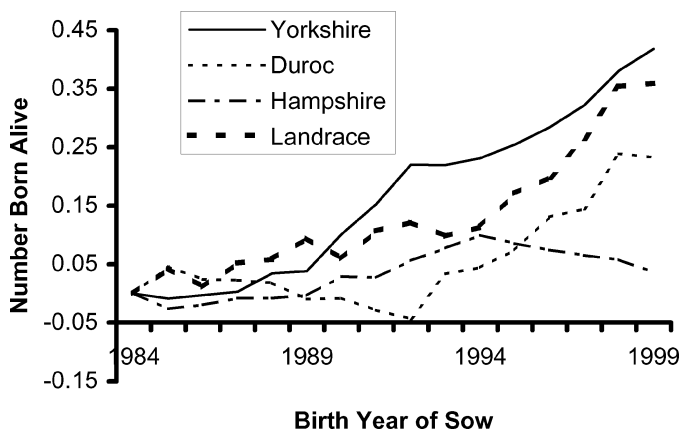
Estimates of maternal genetic effects and their correlations with direct effects have large sampling variances (Meyer, 1992). Also, Gerstenmayr (1992) found that estimates of small magnitude have greater relative and absolute sampling variances than larger estimates. Additionally, Roehe and Kennedy (1993) found substantial confounding between estimates of maternal and direct effects. Therefore, estimates of maternal genetic effects in this study likely have high sampling variances and may be confounded with direct genetic effects.

#### Permanent Environmental Effects

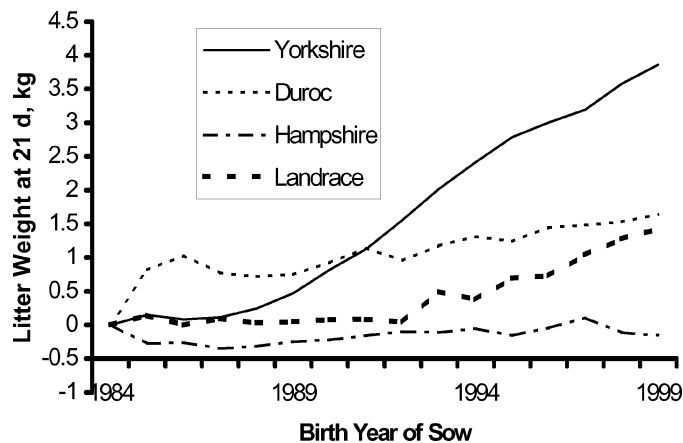
Estimates of the fraction of the total phenotypic variation for litter traits due to permanent environmental effects associated with the sow ranged from 0.03 to 0.08 (Tables 3 to 5). These estimates are consistent with those reported by Crump et al. (1997) and Kaufmann et al. (2000). However, these results for NBA are lower than the estimates of 16 to 17% reported by Ferraz and Johnson (1993) and the estimate of 12.6% reported by Haley and Lee (1992).

#### Service Sire Effects

The proportion of the total variation in litter traits due to the effect of service sire ranged from 0.02 to 0.05 (Tables 3 to 5) across breeds. See et al. (1993) estimated variation due to service sire effects at 0.01 to 0.02 for NBA from field data in the Spotted, Landrace, and Hampshire breeds. Mabry et al. (1988) also reported that service sire effects accounted for 3% of the total



**Figure 1.** Genetic trend for number born alive by breed from 1984 to 1999 National Swine Registry Swine Testing and Genetic Evaluation System data.

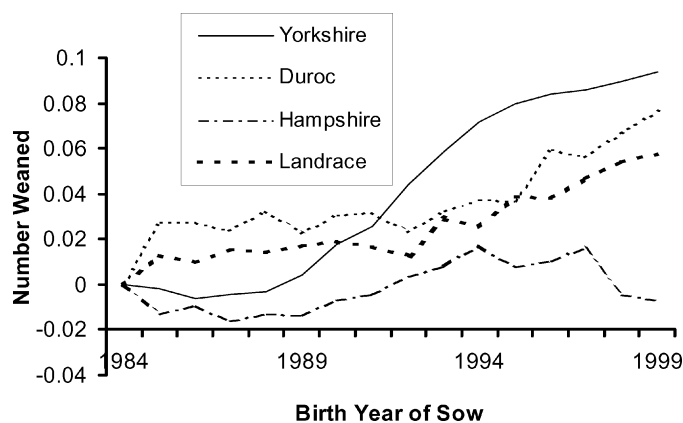


**Figure 2.** Genetic trend for litter weight at 21 d by breed from 1984 to 1999 National Swine Registry Swine Testing and Genetic Evaluation System data.

variation in NBA, and Buytels and Long (1991) found that service sire effects accounted for 1% of the total variation. In general, results from this study indicate stronger service sire effects than these previous studies. The service sire could influence litter size either by semen quality and quantity or by genetic effects that influence embryo development and survival (See et al., 1993).

#### Correlations

Estimates of phenotypic and genetic correlations among traits for each breed are in Table 6. Estimates of phenotypic correlations between NBA and L21WT ranged from 0.03 in the Duroc breed to 0.07 in the Landrace breed. Strong, positive phenotypic correlations between NW and L21WT ranging from 0.77 in the Duroc breed to 0.80 in the Yorkshire breed were found. Small positive correlations between NBA and NW were also found. The weak correlations between



**Figure 3.** Genetic trend for number weaned by breed from 1984 to 1999 National Swine Registry Swine Testing and Genetic Evaluation System data.

**Table 7.** Overall regressions of EBV for number born alive, litter weight at 21 d, and number weaned on birth year by breed

| Item                         | Yorkshire      | Duroc          | Hampshire      | Landrace       |
|------------------------------|----------------|----------------|----------------|----------------|
| Number born alive, pigs/yr   | 0.029 ± 0.002  | 0.013 ± 0.001  | 0.007 ± 0.001  | 0.021 ± 0.002  |
| Litter weight at 21 d, kg/yr | 0.279 ± 0.025  | 0.087 ± 0.020  | 0.007 ± 0.009  | 0.081 ± 0.020  |
| Number weaned, pigs/yr       | 0.008 ± 0.0006 | 0.004 ± 0.0005 | 0.001 ± 0.0005 | 0.004 ± 0.0003 |

NBA and L21WT and between NBA and NW may be due to cross-fostering of pigs. McCarter et al. (1987) reported estimates of phenotypic correlations of 0.08 between NBA and L21WT, 0.48 between NW and L21WT, and 0.59 between NBA and NW.

Estimated genetic correlations between NBA and L21WT were lowest for the Duroc breed (0.10) and highest for the Landrace breed (0.15). A genetic correlation of 0.12 between NBA and L21WT is recommended by NSIF (1997). Estimated genetic correlations between L21WT and NW ranged from 0.65 in the Duroc breed to 0.75 in the Yorkshire breed, while genetic correlations between NBA and NW ranged from 0.07 in the Duroc breed to 0.20 in the Hampshire breed. McCarter et al. (1987) reported estimates of genetic correlations of 0.12 for NBA and L21WT, 0.55 for NW and L21WT, and 0.58 for NBA and NW. Kaplon et al. (1991a) reported estimates of pooled genetic correlations of 0.68 for NBA and L21WT, 0.80 for NW and L21WT, and 0.91 for NBA and NW. These differences, especially between NW and NBA, may be due to the fact that cross-fostering was not practiced in their populations.

### Genetic Trends

All estimated genetic trends for NBA, L21WT, and NW were positive (Figures 1 to 3, Table 7). Estimates of genetic trends were greatest in Yorkshire, averaging 0.029 pigs/yr for NBA, 0.279 kg/yr for L21WT, and 0.008 pigs/yr for NW. Average genetic change in NBA over the four breeds was 0.018 pigs/yr, or 0.18% of the mean, higher than the estimate of 0.01 pigs/yr reported by Kaplon et al. (1991b), Southwood and Kennedy (1991), and Ferraz and Johnson (1993). Average genetic change in L21WT was 0.11 kg/yr or 0.20% of the mean. This is lower than the estimates of 0.245 kg/yr or 0.44% of the mean in Landrace and Large White breeds by Ferraz and Johnson (1993), but larger than the average of 0.045 kg/yr reported by Kaplon et al. (1991b). Genetic trends in NW across breeds were positive and very small (Figure 3, Table 7), which is consistent with the values reported by Southwood and Kennedy (1991) in Canadian breeds and Kaplon et al. (1991b) in Polish sows. Low rates of genetic trends could be because breeders were applying very little selection for them or the selection that was applied was ineffective because of the low heritabilities.

### Implications

This report of breed-specific genetic estimates for litter traits is based on the U.S. national database. Based

on this study, use of a direct model that ignores maternal breeding values would seem sufficient. Genetic variance for litter traits was sufficiently large to indicate that litter traits could be improved through selection. Estimated annual rates of genetic change for litter traits indicate that further improvement in these traits is still possible. Use of appropriate models that include permanent environmental and service sire effects, along with breed-specific genetic parameters, will increase the accuracy of estimated breeding value.

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