Maternal effects on traits measured during postweaning performance test of swine from four breeds

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ABSTRACT: The objective of this study was to investigate the importance of maternal genetic effects on postweaning performance traits of Yorkshire, Landrace, Duroc, and Hampshire breeds of swine. Data consisted of performance test records collected in a commercial swine operation from 1992 to 1999. Boars from 60% of the litters were culled at weaning based on a combination of maternal and performance indexes that differed by breed. Remaining boars and all females were grown to 100 d of age. At this time all pigs were weighed (WT100) and selected for testing using recalculated breed-specific indexes (n = 15,594, 55,497, 12,267, and 9,782 for Landrace, Yorkshire, Duroc, and Hampshire, respectively). All pigs were weighed at the end of the 77-d test, and backfat (BF) and loin eye area (LEA) were measured over the 12th rib by ultrasound. Average daily feed intake was calculated for boars, and ADG was calculated for all animals. Genetic parameters were estimated for each breed and trait using multiple-trait DFREML procedures. Fixed effects were contemporary groups and either initial or final test age as a covariate. Four models were examined. Model 1 included only the additive genetic effect of the animal. Model 2 added the common litter environmental effect; Model 3 added the maternal genetic value assumed to be uncorrelated with additive genetic effects. Model 4 was the same as Model 3 with additive and maternal genetic effects assumed to be correlated. All models were two-trait models with WT100 as the second trait. Ratios of likelihoods were used to compare models. Maternal effects were important (P < 0.05) for WT100, ADG, ADFI, LEA, and BF in Landrace; for WT100, ADG, LEA, and BF in Yorkshire; for WT100 and ADG in Duroc, and for WT100 in Hampshire. Estimates of heritabilities for direct additive effects using the appropriate model for ADG, ADFI, LEA, and BF were 0.28, 0.34, 0.48, and 0.63 for Landrace; 0.26, 0.31, 0.39, and 0.65 for Yorkshire; 0.14, 0.20, 0.26, and 0.35 for Duroc; and 0.17, 0.23, 0.25, and 0.31 for Hampshire, respectively. Heritability estimates for maternal genetic effects for ADG, ADFI, LEA, and BF were 0.02, 0.05, 0.06, and 0.07 for Landrace and 0.02, 0.05, 0.06, and 0.07 for Yorkshire; 0.02, 0.05, 0.06, and 0.07 for Landrace and 0.02, 0.04, and 0.06 for Yorkshire, respectively. They were zero for all traits except ADG (0.03) in Duroc and for all traits in Hampshire. Maternal effects may need to be considered in genetic evaluation of performance traits in some breeds of swine.

Key Words: Genetic Parameters, Maternal Effects, Performance Traits, Pigs


Introduction

Genetic progress depends on accurate estimates of variances and heritabilities for traits of selection. Accurate estimates of these variances and heritabilities depend on application of the appropriate model for those traits. Estimates may be biased by failure to account for appropriate genetic or environmental sources of variation, such as maternal effects. Robison (1972) reported that there is substantial evidence that maternal effects account for a significant portion of the variance for most traits in swine, including those that are manifested relatively late in life. Bryner et al. (1992) reported significant maternal effects for ADG and backfat for centrally tested Yorkshire boars. If maternal genetic effects are important for performance traits, a model containing these effects along with direct genetic effects should provide more precise predictive ability of future progeny performance than a model that contains only direct genetic effects (Roehe and Kennedy, 1993a; Lykens et al., 2000). Improvement of maternal response in addition to direct response can lead to greater overall response (Roehe and Kennedy, 1993a). It was the objective of this study to investigate the importance of materi-
nal genetic effects on performance traits of Landrace, Yorkshire, Duroc, and Hampshire breeds of swine.

Materials and Methods

Data for this study consisted of performance test records of Landrace, Yorkshire, Duroc, and Hampshire pigs collected in a commercial swine operation (The Pork Group, A Division of Tyson Foods, Inc., Rogers, AR) from 1992 to 1999. These herds were established in 1992. Most founding animals came from Canada with some infusion of European breeding. Two indexes (breeding values) for each animal were calculated at birth. One was a maternal index based on number born alive, farrowing interval, and litter weaning weight. The other was based on growth rate, leanness, and feed efficiency (Grow-Fin). The maternal index was computed using a three-trait model that included terms for the additive genetic effect, litter effects, and maternal genetic effects along with appropriate fixed effects. The Grow-Fin index was computed using a model that included only additive genetic effects and appropriate fixed effects. These two indexes were combined into an overall ranking depending on the breed. For Landrace equal emphasis was given to both indexes; for Yorkshire more emphasis was given to the maternal index; for Duroc more emphasis was given to the Grow-Fin index; and for Hampshire all emphasis was on the Grow-Fin index. Boars from approximately 60% of the litters were culled at weaning based on the breed-specific index. Culled boars (barrows) were grown out and slaughtered. For economic reasons, these animals were not performance-tested. Remaining boars and all females were grown to 100 d of age. At this time, all pigs were weighed and a second culling event occurred with recalculated indexes using any new information collected on animals in the breed. Litter records for the individual were included in the maternal index, and the individual’s own record for 100-d weight was available. Feed efficiency and leanness records for the individual were not available at this time; therefore, changes in the Grow-Fin index resulted from 100-d weight and additional performance records on relatives obtained since pigs were weaned. Fifty to sixty percent of the females and 20 to 25% of the remaining Yorkshire, Landrace, and Duroc boars were put on performance test for approximately 77 d. A higher percentage (37%) of Landrace boars were performance-tested. Females culled at this time were moved down the production pyramid and mated to produce crossbred offspring that then served as parents of commercial offspring. Females that were not culled at this time were retained and mated to purebred boars to produce progeny for the purebred nucleus herd.

Boars were individually penned in 2.79-m² pens with slotted gating on slatted concrete floors. Barns were curtain-sided buildings that were tunnel-ventilated in the winter. Boars were fed for ad libitum consumption a pelleted corn-soybean meal diet that was 1.14% lysine, 19% protein, and 3,344 kcal/kg ME. Exact composition of the diet varied due to ingredient cost. Gilts were fed this same diet in groups of 8 to 10 pigs in a pen with each pig having an area of 1.2 m². Pens of different sizes were available in different facilities; pens in some barns held 8 pigs and in other barns 10 pigs. All pigs had ad libitum access to water. All pigs were weighed at the end of the 77-d performance test, and backfat (BF) and loin eye area (LEA) were measured at approximately the 12th rib using B-mode ultrasound equipment. Average daily feed intake (ADFI) was calculated for boars, and ADG was calculated for all animals.

Contemporary group was defined as all pigs of the same sex reared in the same house and started on test within a 3-mo period (quarter of a year). Data were edited to remove records of animals with missing sire or dam. Records were omitted if any trait measurement was greater than 4 SD away from the overall mean (Bryner et al., 1992). The data sets are described in Tables 1 and 2. The number of records for various traits, along with means and standard deviations, is given in Table 3. There were 15,594, 55,497, 12,267, and 9,782 observations at 100 d of age for Landrace, Yorkshire, Duroc, and Hampshire, respectively. Of these, 7,951 Landrace, 26,656 Yorkshire, 5,240 Duroc, and 3,615 Hampshire had ADG records, with approximately the same number of observations for LEA and backfat. Since ADFI was only recorded for boars, a much lower number of observations was available for this trait (Table 3).

Genetic parameters were estimated for each breed and trait using multiple-trait DFREML procedures (Boldman and Van Vleck, 1991; MTDFREML; Boldman et al., 1993). Fixed effects were contemporary group and initial test age as a covariate for 100-d weight, ADG, and ADFI. Final test age was the covariate for BF and LEA. Four models were examined for each trait. There were 16,028, 56,943, 12,581, and 9,915 animals in A−2 in the analysis of Landrace, Yorkshire, Duroc, and Hampshire, respectively. Model 1 included the additive genetic effect of the animal and appropriate fixed effects. Model 2 included the additive genetic effect plus

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### Table 1. Number of contemporary groups, sires, litters, and dams in the data sets for four breeds of swine

<table>
<thead>
<tr>
<th>Item</th>
<th>Landrace</th>
<th>Yorkshire</th>
<th>Duroc</th>
<th>Hampshire</th>
</tr>
</thead>
<tbody>
<tr>
<td>100-d Weight</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No. of contemporary groups</td>
<td>104</td>
<td>160</td>
<td>98</td>
<td>86</td>
</tr>
<tr>
<td>No. of sires</td>
<td>204</td>
<td>550</td>
<td>168</td>
<td>87</td>
</tr>
<tr>
<td>No. of litters</td>
<td>2,707</td>
<td>11,143</td>
<td>2,120</td>
<td>1,666</td>
</tr>
<tr>
<td>No. of dams</td>
<td>1,016</td>
<td>3,771</td>
<td>755</td>
<td>481</td>
</tr>
<tr>
<td>ADG</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No. of contemporary groups</td>
<td>104</td>
<td>160</td>
<td>96</td>
<td>84</td>
</tr>
<tr>
<td>No. of sires</td>
<td>196</td>
<td>513</td>
<td>157</td>
<td>82</td>
</tr>
<tr>
<td>No. of litters</td>
<td>2,035</td>
<td>9,105</td>
<td>1,791</td>
<td>1,296</td>
</tr>
<tr>
<td>No. of dams</td>
<td>940</td>
<td>3,364</td>
<td>692</td>
<td>421</td>
</tr>
</tbody>
</table>

---
Table 2. Description of the data sets for four breeds of swine

<table>
<thead>
<tr>
<th>Item</th>
<th>Landrace</th>
<th>Yorkshire</th>
<th>Duroc</th>
<th>Hampshire</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>Range</td>
<td>Mean</td>
<td>Range</td>
</tr>
<tr>
<td>100-d Weight</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
| No. of observations/
  contemporary group                | 150      | 14–327   | 347      | 14–931    | 125      | 26–248   | 114      | 23–194    |
| No. of observations/
  sire                                    | 76       | 1–612    | 101      | 1–15      | 5.79     | 1–14     | 5.88     | 1–13      |
| No. of observations/
  litter                                   | 5.76     | 1–15     | 4.98     | 1–15      | 5.79     | 1–14     | 5.88     | 1–13      |
| No. of litters/
  contemporary group             | 22       | 5–93     | 96       | 6–224     | 38       | 6–72     | 36       | 9–64      |
| No. of observations/
  dam                                    | 15.35    | 1–69     | 14.72    | 1–98      | 16.25    | 1–88     | 20.35    | 1–93      |
| No. of litters/dam                  | 2.66     | 1–9      | 2.95     | 1–13      | 2.81     | 1–11     | 3.46     | 1–13      |
| ADG                                 |          |          |          |           |          |          |
| No. of observations/
  contemporary group             | 76       | 6–188    | 173      | 4–499     | 55       | 7–164    | 43       | 10–111    |
| No. of observations/
  sire                                    | 41       | 1–306    | 54       | 1–425     | 33       | 1–244    | 44       | 1–196     |
| No. of observations/
  litter                                   | 3.45     | 1–12     | 3.04     | 1–11      | 2.93     | 1–10     | 2.79     | 1–12      |
| No. of litters/
  contemporary group             | 34       | 4–73     | 71       | 4–201     | 26       | 4–61     | 23       | 4–50      |
| No. of observations/
  dam                                    | 8.46     | 1–42     | 8.22     | 1–59      | 7.57     | 1–44     | 8.59     | 1–37      |
| No. of litters/dam                  | 2.45     | 1–9      | 2.71     | 1–13      | 2.59     | 1–10     | 3.08     | 1–10      |

Table 3. Mean, standard deviation, minimum, and maximum values for performance traits of four breeds of swine

<table>
<thead>
<tr>
<th>Trait*</th>
<th>n</th>
<th>Mean</th>
<th>SD</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Landrace</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age at 100 d</td>
<td>15,594</td>
<td>98.67</td>
<td>2.93</td>
<td>71.00</td>
<td>109.00</td>
</tr>
<tr>
<td>Weight at 100 d, kg</td>
<td>15,594</td>
<td>45.92</td>
<td>7.64</td>
<td>16.33</td>
<td>76.20</td>
</tr>
<tr>
<td>ADG, kg</td>
<td>7,951</td>
<td>0.85</td>
<td>0.15</td>
<td>0.27</td>
<td>1.41</td>
</tr>
<tr>
<td>ADFI, kg</td>
<td>2,523</td>
<td>2.65</td>
<td>0.36</td>
<td>1.46</td>
<td>3.95</td>
</tr>
<tr>
<td>LEA, cm²</td>
<td>7,942</td>
<td>39.56</td>
<td>5.72</td>
<td>18.65</td>
<td>62.26</td>
</tr>
<tr>
<td>Backfat, cm</td>
<td>7,946</td>
<td>1.71</td>
<td>0.47</td>
<td>0.55</td>
<td>3.56</td>
</tr>
<tr>
<td>Age at 177 d</td>
<td>7,951</td>
<td>175.66</td>
<td>4.13</td>
<td>146.00</td>
<td>188.00</td>
</tr>
<tr>
<td>Weight at 177 d, kg</td>
<td>7,951</td>
<td>114.51</td>
<td>14.27</td>
<td>67.59</td>
<td>170.10</td>
</tr>
<tr>
<td>Yorkshire</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age at 100 d</td>
<td>55,497</td>
<td>99.34</td>
<td>2.90</td>
<td>71.00</td>
<td>117.00</td>
</tr>
<tr>
<td>Weight at 100 d, kg</td>
<td>55,497</td>
<td>44.33</td>
<td>7.68</td>
<td>14.06</td>
<td>74.84</td>
</tr>
<tr>
<td>ADG, kg</td>
<td>27,656</td>
<td>0.87</td>
<td>0.14</td>
<td>0.31</td>
<td>1.42</td>
</tr>
<tr>
<td>ADFI, kg</td>
<td>2,523</td>
<td>2.58</td>
<td>0.39</td>
<td>1.36</td>
<td>3.95</td>
</tr>
<tr>
<td>LEA, cm²</td>
<td>27,638</td>
<td>40.89</td>
<td>6.03</td>
<td>17.48</td>
<td>70.71</td>
</tr>
<tr>
<td>Backfat, cm</td>
<td>27,647</td>
<td>1.66</td>
<td>0.48</td>
<td>0.46</td>
<td>3.61</td>
</tr>
<tr>
<td>Age at 177 d</td>
<td>27,656</td>
<td>176.37</td>
<td>3.83</td>
<td>146.00</td>
<td>207.00</td>
</tr>
<tr>
<td>Weight at 177 d, kg</td>
<td>27,656</td>
<td>114.13</td>
<td>13.05</td>
<td>61.69</td>
<td>166.02</td>
</tr>
<tr>
<td>Duroc</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age at 100 d</td>
<td>12,267</td>
<td>98.98</td>
<td>2.83</td>
<td>62.00</td>
<td>118.00</td>
</tr>
<tr>
<td>Weight at 100 d, kg</td>
<td>12,267</td>
<td>42.05</td>
<td>7.78</td>
<td>11.79</td>
<td>70.31</td>
</tr>
<tr>
<td>ADG, kg</td>
<td>5,240</td>
<td>0.88</td>
<td>0.13</td>
<td>0.38</td>
<td>1.37</td>
</tr>
<tr>
<td>ADFI, kg</td>
<td>998</td>
<td>2.67</td>
<td>0.37</td>
<td>1.42</td>
<td>3.78</td>
</tr>
<tr>
<td>LEA, cm²</td>
<td>5,230</td>
<td>39.64</td>
<td>4.97</td>
<td>23.61</td>
<td>59.05</td>
</tr>
<tr>
<td>Backfat, cm</td>
<td>5,235</td>
<td>1.82</td>
<td>0.44</td>
<td>0.71</td>
<td>3.61</td>
</tr>
<tr>
<td>Age at 177 d</td>
<td>5,240</td>
<td>175.98</td>
<td>3.87</td>
<td>160.00</td>
<td>199.00</td>
</tr>
<tr>
<td>Weight at 177 d, kg</td>
<td>5,240</td>
<td>113.76</td>
<td>12.31</td>
<td>66.23</td>
<td>160.12</td>
</tr>
<tr>
<td>Hampshire</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age at 100 d</td>
<td>9,782</td>
<td>100.09</td>
<td>2.94</td>
<td>70.00</td>
<td>132.00</td>
</tr>
<tr>
<td>Weight at 100 d, kg</td>
<td>9,782</td>
<td>39.10</td>
<td>7.34</td>
<td>11.79</td>
<td>68.04</td>
</tr>
<tr>
<td>ADG, kg</td>
<td>3,615</td>
<td>0.83</td>
<td>0.13</td>
<td>0.32</td>
<td>1.30</td>
</tr>
<tr>
<td>ADFI, kg</td>
<td>1,094</td>
<td>2.45</td>
<td>0.34</td>
<td>1.38</td>
<td>3.46</td>
</tr>
<tr>
<td>LEA, cm²</td>
<td>3,613</td>
<td>41.94</td>
<td>5.61</td>
<td>24.45</td>
<td>61.74</td>
</tr>
<tr>
<td>Backfat, cm</td>
<td>3,615</td>
<td>1.50</td>
<td>0.36</td>
<td>0.46</td>
<td>2.90</td>
</tr>
<tr>
<td>Age at 177 d</td>
<td>3,615</td>
<td>177.17</td>
<td>4.03</td>
<td>145.00</td>
<td>209.00</td>
</tr>
<tr>
<td>Weight at 177 d, kg</td>
<td>3,615</td>
<td>107.32</td>
<td>13.29</td>
<td>59.88</td>
<td>160.57</td>
</tr>
</tbody>
</table>

*ADG = average daily gain, ADFI = average daily feed intake, LEA = loin eye area.
a common litter environmental effect along with appropriate fixed effects. Model 3 was the same as Model 2, with the addition of the maternal genetic value assumed to be uncorrelated with additive genetic effects; Model 4 was the same as Model 3 with additive and maternal genetic effects assumed to be correlated. The appropriate model for 100-day weight was determined, then 100-d weight using this model was included in the analysis of each other trait in an attempt to remove bias due to selection at 100 d of age; not all pigs weighed at 100 d of age were performance-tested. Thus, a series of two-trait models, each with 100-day weight as the second trait, were used in estimation of genetic parameters for ADG, ADFI, BF, and LEA. In the REML analyses, the convergence criterion (i.e., variance of the simplex values) for all runs was $10^{-9}$. The program was restarted with estimates at previous apparent convergence used as initial values until an apparent global minimum was found and estimates of genetic parameters did not change between runs. Ratios of likelihoods as described by Ferraz and Johnson (1993) and Irgang et al. (1994) were used to compare models. Log likelihoods were obtained after convergence was reached. Minus twice the difference between two log likelihoods is asymptotically distributed as chi-square with degrees of freedom equal to the difference in the number of parameters in the two models. Genetic parameters for the appropriate models were obtained and are reported.

### Results and Discussion

Likelihood-ratio tests (Table 4) indicated that litter environmental effects (Model 1–Model 2) and maternal effects (Model 2–Model 3) were important ($P < 0.01$) for 100-day weight in all breeds. The correlation between direct and maternal effects (Model 3–Model 4) was important for Yorkshire ($P < 0.05$) and Hampshire ($P < 0.01$). For ADG, litter environmental effects were important ($P < 0.01$) for all breeds. Maternal effects were important ($P < 0.05$) in Duroc, and the correlation between direct and maternal effects was important in Landrace ($P < 0.01$) and Yorkshire ($P < 0.05$). Litter environmental effects were important ($P < 0.01$) in all breeds for ADFI. Maternal effects were not important for ADFI for any breed, although the correlation between direct and maternal effects was important ($P < 0.01$) for Landrace. Litter environmental effects were important ($P < 0.01$) in all breeds for both LEA and BF. Maternal effects ($P < 0.05$) and the correlation ($P < 0.01$) between direct and maternal effects were important for LEA in Landrace and Yorkshire. For BF the correlation between direct and maternal effects was important ($P < 0.01$) for Landrace, and both maternal effects and the correlation between direct and maternal effects were important ($P < 0.01$) for Yorkshire. Ferraz and Johnson (1993), using data from two herds each of Landrace and Large White pigs, reported that common litter environmental effects were important ($P < 0.01$) for BF and ADG. Bryner et al. (1992) found significant maternal effects on both ADG and BF using centrally tested Yorkshire boars. Ferraz and Johnson (1993), using data from two herds each of Landrace and Large White pigs, reported maternal effects ($P < 0.05$) for BF but not ADG.

Estimated genetic parameters for 100-d weight using single-trait analyses and appropriate models are presented in Table 5. Effects found to be unimportant (Table 4) were not estimated and are reported as 0. Estimates of heritability of direct additive effects were 0.18 for Landrace, 0.14 for Yorkshire, 0.05 for Duroc, and 0.20 for Hampshire (Table 5). Estimates of heritability of maternal genetic effects were 0.05, 0.06, 0.05, and 0.11, for Landrace, Yorkshire, Duroc, and Hampshire, respectively. The correlation between direct additive effects and maternal genetic effects ($r_{am}$) was negative for the two breeds for which this effect was important ($-0.25$ for Yorkshire and $-0.68$ for Hampshire). Com-

### Table 4. Values of minus two times the differences between the likelihood functions of two different animal models for weight at 100 d average daily gain (ADG), average daily feed intake (ADFI), loin eye area (LEA), and backfat thickness (BF) for four breeds of swine

<table>
<thead>
<tr>
<th>Breed and trait</th>
<th>Model 1 – Model 2</th>
<th>Model 2 – Model 3</th>
<th>Model 3 – Model 4</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Landrace</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>WT100</td>
<td>1,181.76**</td>
<td>17.57**</td>
<td>1.89</td>
</tr>
<tr>
<td>ADG</td>
<td>209.15**</td>
<td>0.01</td>
<td>8.40**</td>
</tr>
<tr>
<td>ADFI</td>
<td>102.28**</td>
<td>0.01</td>
<td>9.42**</td>
</tr>
<tr>
<td>LEA</td>
<td>159.80**</td>
<td>5.70*</td>
<td>26.71**</td>
</tr>
<tr>
<td>Backfat</td>
<td>123.62**</td>
<td>2.71</td>
<td>20.87**</td>
</tr>
<tr>
<td><strong>Yorkshire</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>WT100</td>
<td>3,772.44**</td>
<td>122.24**</td>
<td>5.37**</td>
</tr>
<tr>
<td>ADG</td>
<td>941.97**</td>
<td>3.25</td>
<td>5.39**</td>
</tr>
<tr>
<td>ADFI</td>
<td>127.57**</td>
<td>1.04</td>
<td>3.71</td>
</tr>
<tr>
<td>LEA</td>
<td>859.31**</td>
<td>4.33**</td>
<td>58.24**</td>
</tr>
<tr>
<td>Backfat</td>
<td>572.89**</td>
<td>14.58**</td>
<td>73.46**</td>
</tr>
<tr>
<td><strong>Duroc</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>WT100</td>
<td>882.81**</td>
<td>24.00**</td>
<td>3.59</td>
</tr>
<tr>
<td>ADG</td>
<td>150.73**</td>
<td>5.50*</td>
<td>0.01</td>
</tr>
<tr>
<td>ADFI</td>
<td>33.56**</td>
<td>0.70</td>
<td>1.24</td>
</tr>
<tr>
<td>LEA</td>
<td>117.80**</td>
<td>0.10</td>
<td>1.47</td>
</tr>
<tr>
<td>Backfat</td>
<td>112.47**</td>
<td>0</td>
<td>0.27</td>
</tr>
<tr>
<td><strong>Hampshire</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>WT100</td>
<td>1,079.35**</td>
<td>10.44**</td>
<td>11.73**</td>
</tr>
<tr>
<td>ADG</td>
<td>133.32**</td>
<td>0</td>
<td>1.29</td>
</tr>
<tr>
<td>ADFI</td>
<td>41.69**</td>
<td>0</td>
<td>0.44</td>
</tr>
<tr>
<td>LEA</td>
<td>220.27**</td>
<td>0</td>
<td>0.01</td>
</tr>
<tr>
<td>Backfat</td>
<td>62.05**</td>
<td>0</td>
<td>0.01</td>
</tr>
</tbody>
</table>

*Asymptotically distributed as chi-square with 1 degree of freedom.

*Model 1 includes direct additive genetic effects only; Model 2 includes additive direct genetic and common litter environmental effects; Model 3 includes direct genetic effects, litter environmental effects, and maternal genetic effects; Model 4 is Model 3 with the correlation between additive direct and maternal genetic effects added. A single-trait model was used for WT100. Analyses of all other traits were two-trait models including WT100. Landrace and Duroc used Model 3 for WT100 and Yorkshire and Hampshire used Model 4 for WT100.

$^*P < 0.05$.

$^{**}P < 0.01$. 

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Maternal effects in swine 1473
Table 5. Estimated genetic parameters for weight at 100 d of age (WT100) using the appropriate single-trait model and two-trait models with average daily gain (ADG), average daily feed intake (ADFI), loin eye area (LEA), and backfat for Landrace, Yorkshire, Duroc and Hampshire pigs

<table>
<thead>
<tr>
<th>Item</th>
<th>Landrace</th>
<th>Yorkshire</th>
<th>Duroc</th>
<th>Hampshire</th>
</tr>
</thead>
<tbody>
<tr>
<td>Single-trait analysis</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$h^2_a$</td>
<td>0.18</td>
<td>0.14</td>
<td>0.05</td>
<td>0.20</td>
</tr>
<tr>
<td>$h^2_m$</td>
<td>0.05</td>
<td>0.06</td>
<td>0.05</td>
<td>0.11</td>
</tr>
<tr>
<td>$r_{am}$</td>
<td>0</td>
<td>-0.25</td>
<td>0</td>
<td>-0.68</td>
</tr>
<tr>
<td>$c^2$</td>
<td>0.20</td>
<td>0.21</td>
<td>0.21</td>
<td>0.25</td>
</tr>
<tr>
<td>With ADG</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$h^2_a$</td>
<td>0.19 (0.19)</td>
<td>0.14 (0.14)</td>
<td>0.05</td>
<td>0.17</td>
</tr>
<tr>
<td>$h^2_m$</td>
<td>0.04 (0.04)</td>
<td>0.05 (0.05)</td>
<td>0.05</td>
<td>0.10</td>
</tr>
<tr>
<td>$r_{am}$</td>
<td>0</td>
<td>-0.20 (-0.19)</td>
<td>0</td>
<td>-0.60</td>
</tr>
<tr>
<td>$c^2$</td>
<td>0.21 (0.21)</td>
<td>0.21 (0.21)</td>
<td>0.21</td>
<td>0.25</td>
</tr>
<tr>
<td>$r_{ga}$</td>
<td>0.46 (0.50)</td>
<td>0.44 (0.46)</td>
<td>0.17</td>
<td>0.43</td>
</tr>
<tr>
<td>$r_c$</td>
<td>0.12 (0.12)</td>
<td>0.09 (0.09)</td>
<td>0.24</td>
<td>0.22</td>
</tr>
<tr>
<td>With ADFI</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$h^2_a$</td>
<td>0.20 (0.19)</td>
<td>0.14</td>
<td>0.05</td>
<td>0.18</td>
</tr>
<tr>
<td>$h^2_m$</td>
<td>0.03 (0.03)</td>
<td>0.05</td>
<td>0.05</td>
<td>0.10</td>
</tr>
<tr>
<td>$r_{am}$</td>
<td>0</td>
<td>-0.23</td>
<td>0</td>
<td>-0.61</td>
</tr>
<tr>
<td>$c^2$</td>
<td>0.21 (0.21)</td>
<td>0.21</td>
<td>0.21</td>
<td>0.25</td>
</tr>
<tr>
<td>$r_{ga}$</td>
<td>0.47 (0.57)</td>
<td>0.50</td>
<td>0.14</td>
<td>0.60</td>
</tr>
<tr>
<td>$r_c$</td>
<td>0.35 (0.35)</td>
<td>0.32</td>
<td>0.42</td>
<td>0.31</td>
</tr>
<tr>
<td>With LEA</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$h^2_a$</td>
<td>0.19</td>
<td>0.14</td>
<td>0.06</td>
<td>0.18</td>
</tr>
<tr>
<td>$h^2_m$</td>
<td>0.03</td>
<td>0.05</td>
<td>0.05</td>
<td>0.08</td>
</tr>
<tr>
<td>$r_{am}$</td>
<td>0</td>
<td>-0.17</td>
<td>0</td>
<td>-0.57</td>
</tr>
<tr>
<td>$c^2$</td>
<td>0.21</td>
<td>0.21</td>
<td>0.21</td>
<td>0.26</td>
</tr>
<tr>
<td>$r_{ga}$</td>
<td>0.26</td>
<td>0.17</td>
<td>0.26</td>
<td>0.31</td>
</tr>
<tr>
<td>$r_c$</td>
<td>0.43</td>
<td>0.43</td>
<td>0.44</td>
<td>0.64</td>
</tr>
<tr>
<td>With backfat</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$h^2_a$</td>
<td>0.19 (0.19)</td>
<td>0.16</td>
<td>0.05</td>
<td>0.19</td>
</tr>
<tr>
<td>$h^2_m$</td>
<td>0.04 (0.04)</td>
<td>0.06</td>
<td>0.05</td>
<td>0.08</td>
</tr>
<tr>
<td>$r_{am}$</td>
<td>0</td>
<td>-0.30</td>
<td>0</td>
<td>-0.58</td>
</tr>
<tr>
<td>$c^2$</td>
<td>0.21 (0.21)</td>
<td>0.21</td>
<td>0.21</td>
<td>0.26</td>
</tr>
<tr>
<td>$r_{ga}$</td>
<td>0.31 (0.37)</td>
<td>0.31</td>
<td>0.57</td>
<td>0.45</td>
</tr>
<tr>
<td>$r_c$</td>
<td>0.28 (0.28)</td>
<td>0.32</td>
<td>0.29</td>
<td>0.39</td>
</tr>
</tbody>
</table>

*The model for Landrace and Duroc included additive direct effects, litter environmental effects, and maternal genetic effects. The correlation between additive direct and maternal genetic effects is reported as 0 because this effect was found to be unimportant for WT100 (see Table 4). The model for Yorkshire and Hampshire included the correlation between additive direct and maternal genetic effects.

**Notation:** heritability for additive direct effects ($h^2_a$); heritability for maternal genetic effects ($h^2_m$); correlation between direct and maternal effects ($r_{am}$); proportion of common litter environmental effects ($c^2$); genetic correlation of WT100 with each other trait ($r_{ga}$); and covariance between litter environmental effects for WT100 and each other trait ($r_c$).

*Estimates in parentheses were obtained from Model 2 analyses for situations in which maternal effects were not significant but the correlation between maternal and additive effects was (see Table 4).

Common environmental litter effects ($c^2$) explained from 20 to 25% of the phenotypic variance.

Estimates of genetic parameters for 100-d weight in the two-trait analyses with other traits (Table 5) were similar to those obtained in the single-trait analyses. Genetic correlations of 100-d weight with ADG were consistent for Landrace, Yorkshire, and Hampshire (0.43 to 0.46) but lower for Duroc (0.17). Genetic correlations for 100-d weight with ADFI followed the same pattern, ranging from 0.47 to 0.60 for Landrace, Yorkshire, and Hampshire and lower for Duroc (0.14). Lower genetic correlations, ranging from 0.17 to 0.31, were found between 100-d weight and LEA. Correlations of 0.31 between 100-d weight and BF were obtained for Landrace and Yorkshire breeds, and higher correlations were observed for Duroc (0.57) and Hampshire (0.45). Common environmental litter effects were consistent in all analyses, explaining from 21 to 26% of the phenotypic variance. No comparable estimates of genetic parameters for 100-d weight were found in the literature; however, Kuhlers and Jungst (1992) reported a realized heritability of 70-d weight in Landrace of 0.13 ± 0.06. This estimate is very close to the 0.14 to 0.16 estimated in this study for Landrace.

The covariance between litter environmental effects ($c^2$) for 100-d weight and ADG was 0.12 and 0.09 for Landrace and Yorkshire, respectively, and higher for Duroc and Hampshire (0.24 and 0.22, respectively). The covariance between litter environmental effects for 100-d weight and ADFI ranged from 0.31 to 0.42. For LEA, $r_c$ was similar for Landrace, Yorkshire, and Duroc (0.43 or 0.44) but higher for Hampshire (0.64). For backfat, this covariance ranged from 0.28 for Landrace to 0.39 for Hampshire. Li and Kennedy (1994) reported sizable negative litter correlations that ranged from −0.10 to −0.26 between backfat and days to 100 kg.

Estimates of heritability of direct additive effects for ADG were 0.28 for Landrace, 0.26 for Yorkshire, 0.14 for Duroc, and 0.17 for Hampshire (Table 6). Ferraz and Johnson (1993) reported a lower estimate of 0.16 in one herd of Landrace and a larger estimate of 0.37 in another herd of pigs tested on-farm. Other estimates in the literature ranged from 0.098 ± 0.070 for Duroc and Yorkshire gilts tested in littermate groups (Bereskin, 1986) to a realized heritability of 0.38 ± 0.43 and 0.65 ± 0.19 for postweaning ADG in Canadian Yorkshire and Hampshire pigs, respectively (McKay, 1990). Other estimates reported were 0.52 ± 0.20 for Hampshire and Duroc boars using regression procedures (Bates and Buchanan, 1988), 0.427 ± 0.055 for Yorkshire, Duroc, and Landrace littermate boars (Mrode and Kennedy, 1993), 0.36 ± 0.07 for Duroc and Landrace pigs (Lo et al., 1992), 0.24 for centrally tested Yorkshire boars (Bryner et al., 1992), 0.16 and 0.20 for Yorkshire and Landrace pigs tested on-farm, respectively (Hofer et al., 1992), 0.23 and 0.32 for two commercial populations of Large White and Landrace in Nebraska (ten Napel and Johnson, 1997), and 0.30 ± 0.06 for centrally tested mixed strains of boars (Van Steenbergen et al., 1990).

Estimates of maternal heritability for ADG were low, being unimportant (reported as 0) for Hampshire, 0.02 for Landrace and Yorkshire, and 0.03 for Duroc. With performance-tested Yorkshire boars, Bryner et al. (1992) found a higher maternal heritability of 0.23; however, litter environmental effects were not included in their model. Ferraz and Johnson (1993) also reported
very small estimates of heritability of maternal effects on ADG (between 0.5% and 1.5%). Correlations between direct additive and maternal effects were reported as 0 for Duroc and Hampshire and were −0.62 and −0.33 for Landrace and Yorkshire, respectively. Litter environmental effects explained approximately 15% (14 to 18%) of the phenotypic variation. This is higher than the 7% reported by Ferraz and Johnson (1993) and ten Napel and Johnson (1997) with Large White and Landrace herds but lower than the approximately 45% reported by Hofer et al. (1992) with on-farm-tested Yorkshire (42%) and Landrace (49%).

Additive direct heritability for ADFI ranged from 0.20 for Duroc to 0.34 for Landrace. Literature estimates varied from 0.105 ± 0.214 for Duroc and Yorkshire gilts tested in littermate groups (Bereskin, 1988), to 0.24 ± 0.06 for mixed strains (Van Steenbergen, 1990), to 0.452 ± 0.050 for Yorkshire, Duroc, and Landrace littermate boars (Mrode and Kennedy, 1993). Maternal heritability of ADFI was important (P < 0.05) for Landrace pigs and was estimated as 0.05 for this breed with a negative correlation of −0.73 between direct additive and maternal genetic effects. Hall et al. (1999) with Large White pigs on test from 45 to 95 kg estimated additive direct heritability of ADFI to be 0.21 ± 0.02 (ranging from 0.18 to 0.26 over four test periods). The proportion of common litter environmental effects ranged from 0.20 for Yorkshire to 0.24 for Duroc and Hampshire. With Large White pigs, Hall et al. (1999) estimated c² to be lower (0.12), ranging from 0.09 to 0.13 over four test periods.

Estimates of additive direct heritability of LEA varied for breeds, ranging from 0.25 for Hampshire to 0.48 for Landrace (Table 6). Lo et al. (1992) using data from a 2 × 2 diallel mating system involving Landrace and Duroc pigs and an animal model estimated heritability of LEA measured ultrasonically at the last rib at 103.6 kg BW to be 0.46 ± 0.08. Swiger and Harvey (1979), using swine tested at the Ohio Swine Evaluation Station, estimated heritability of LEA from carcass data to be 0.56 ± 0.06. Estimates of maternal heritability are reported as 0 for Duroc and Hampshire and are low for Landrace and Yorkshire (0.06 and 0.04, respectively) with correlations between direct and maternal effects found to be unimportant for Duroc and Hampshire and −0.67 for both Landrace and Yorkshire breeds. No comparable estimates of these effects were found in the literature. The proportion of common litter environmental effects ranged from 0.09 for Landrace to 0.18 for Hampshire.

For backfat depth, estimates of direct heritability were 0.63, 0.65, 0.35, and 0.31 for Landrace, Yorkshire, Duroc, and Hampshire, respectively (Table 6). Li and Kennedy (1994) using a model that included animal and litter effects reported lower estimates for Landrace and Yorkshire (0.53 and 0.55) and higher estimates for Duroc and Hampshire (0.51 and 0.50). Bryner et al. (1992) reported a direct heritability estimate of backfat of 0.24 for centrally-tested Yorkshire boars. Kennedy et al. (1985), using data for Yorkshire, Landrace, Duroc, and Hampshire performance-tested pigs, reported heritabilities of BF ranging from 0.40 for Hampshire to 0.61 for Landrace. Bereskin (1986), using performance records of purebred Duroc and Yorkshire gilts tested in littermate groups, estimated heritability of average BF thickness as 0.423. Kuhlers and Jungst (1983) reported heritability of backfat thickness for Duroc and Hampshire pigs estimated by two methods (regression of offspring on midparent and ratio of the selection response to the selection differential from one generation of divergent selection) to be 0.79 ± 0.07 and 0.78 ± 0.09, respectively, for BF at 105 kg and 0.58 ± 0.06 and 0.65 ± 0.10, respectively, for BF at 135 kg. Lo et al. (1992) using data from a 2 × 2 diallel mating system involving Landrace and Duroc pigs and an animal model estimated heritability of BF thickness measured ultrasonically at the last rib at 103.6 kg BW to be 0.54 ± 0.09. Mrode and Kennedy (1993), using data on Yorkshire, Landrace, and Duroc littermate pairs of boars, estimated heritability of BF to be 0.587 ± 0.048. In a study using data for purebred Large White and Lan-

### Table 6. Estimated genetic parameters for average daily gain (ADG), average daily feed intake (ADFI), loin eye area (LEA), and backfat using appropriate two-trait models, including weight at 100 d of age (WT100) as the second trait for each breed

<table>
<thead>
<tr>
<th>Trait</th>
<th>Landrace</th>
<th>Yorkshire</th>
<th>Duroc</th>
<th>Hampshire</th>
</tr>
</thead>
<tbody>
<tr>
<td>ADG</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>h²ₐ</td>
<td>0.28 (0.23)</td>
<td>0.26 (0.25)</td>
<td>0.14</td>
<td>0.17</td>
</tr>
<tr>
<td>h²ₘ</td>
<td>0.02 (0)</td>
<td>0.02 (0)</td>
<td>0.03</td>
<td>0</td>
</tr>
<tr>
<td>rₘₐ</td>
<td>-0.62 (0)</td>
<td>-0.33 (0)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>c²</td>
<td>0.14 (0.14)</td>
<td>0.17 (0.17)</td>
<td>0.15</td>
<td>0.18</td>
</tr>
<tr>
<td>ADFI</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>h²ₐ</td>
<td>0.34 (0.25)</td>
<td>0.31</td>
<td>0.20</td>
<td>0.23</td>
</tr>
<tr>
<td>h²ₘ</td>
<td>0.05 (0)</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>rₘₐ</td>
<td>-0.73 (0)</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>c²</td>
<td>0.22 (0.22)</td>
<td>0.20</td>
<td>0.24</td>
<td>0.24</td>
</tr>
<tr>
<td>LEA</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>h²ₐ</td>
<td>0.48</td>
<td>0.39</td>
<td>0.26</td>
<td>0.25</td>
</tr>
<tr>
<td>h²ₘ</td>
<td>0.06</td>
<td>0.04</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>rₘₐ</td>
<td>-0.67</td>
<td>-0.67</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>c²</td>
<td>0.09</td>
<td>0.14</td>
<td>0.12</td>
<td>0.18</td>
</tr>
<tr>
<td>Backfat</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>h²ₐ</td>
<td>0.63 (0.44)</td>
<td>0.65</td>
<td>0.35</td>
<td>0.31</td>
</tr>
<tr>
<td>h²ₘ</td>
<td>0.07 (0)</td>
<td>0.06</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>rₘₐ</td>
<td>-0.66 (0)</td>
<td>-0.69</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>c²</td>
<td>0.08 (0.09)</td>
<td>0.10</td>
<td>0.12</td>
<td>0.10</td>
</tr>
</tbody>
</table>

*The models for WT100 are the same as those reported in Table 5. Models for other traits included effects that were found to be important (Table 4). When maternal genetic effects or the correlation between additive direct and maternal effects were found to be unimportant these effects are reported as 0.

*Notation: heritability for additive direct effects (h²ₐ); heritability for maternal genetic effects (h²ₘ); correlation between direct and maternal effects (rₘₐ); and proportion of common litter environmental effects (c²).

*Estimates in parentheses were obtained from Model 2 analyses for situations in which maternal effects were not significant but the correlation between maternal and additive genetic effects was (see Table 4).
drace pigs from two commercial breeding herds, ten Napel and Johnson (1997) estimated heritability of BF adjusted for body weight to be 0.49 and 0.43 for the two farms, respectively, using a model that included additive genetic effects and common environmental litter effects. Ferraz and Johnson (1993), using a model that included direct additive effects and common litter environmental effects and data on Landrace pigs, reported estimates of 0.54 and 0.33 for two farms. In a further analysis including both Large White and Landrace and maternal effects, they estimated direct additive heritability to be 0.42. McKay (1990) reported realized heritabilities of probed backfat of 0.41 ± 0.04 for Yorkshire and 0.34 ± 0.18 for Hampshire. Van Steenberggen et al. (1990) reported a similar estimate (0.37 ± 0.07) for mixed strains. Merks (1988) estimated heritabilities of 0.28 and 0.23 for on-farm tested Dutch Landrace and Dutch Yorkshire, respectively.

Estimates of maternal heritabilities of BF were 0.07 for Landrace and 0.06 for Yorkshire and were unimportant for Duroc and Hampshire (Table 6). Correlations between direct and maternal effects were negative and similar for Landrace and Yorkshire (−0.66 and −0.69, respectively). Bryner et al. (1992) reported a similar maternal heritability of 0.11 for BF. Ferraz and Johnson (1993) also reported a low estimate of maternal heritability (3%) and a smaller but still negative \( r_{ma} \) (−0.26).

Common environmental litter effects explained from 8 to 12% of the phenotypic variance for BF (Table 6). Comparable estimates were reported by Kennedy et al. (1985) and Li and Kennedy (1994) for Yorkshire, Landrace, Duroc, and Hampshire breeds. Estimates by ten Napel and Johnson (1997) for Large White and Landrace were slightly lower (5 and 6% for two different farms). An earlier study by Ferraz and Johnson (1993) reported \( c^2 \) values of 0.04 and 0.06 for Landrace from two different farms and 0.05 for Landrace and Large White combined. Merks (1988) reported higher \( c^2 \) effects for on-farm-tested Dutch Landrace and Dutch Yorkshire (0.20 and 0.21, respectively).

The likelihood-ratio test (Table 4) indicated that the correlation between additive direct and maternal genetic effects was significant \( (P < 0.05) \) but that maternal genetic effects were unimportant in four instances: ADG, ADFI, and BF in Landrace and ADG in Yorkshire. Perez-Enciso and Gianola (1992) suggest that it is unreasonable to expect a high covariance when there is negligible variance for maternal effects. Irgang et al. (1994) also obtained some very high correlations between additive direct and maternal genetic effects with very low maternal genetic effects, but with very high standard errors. Roehe and Kennedy (1995) also reported negative correlations between maternal and direct effects based on nonsignificant maternal genetic effects for total number of pigs born and number of pigs born alive. They also reported (Roche and Kennedy, 1993b) that even small maternal genetic effects have a great influence on the response in litter size. Estimates were obtained from Model 2 for those four instances cited above to see whether they differed when maternal effects (and the correlation between direct and maternal effects) were omitted. Estimates of \( h^2_a, h^2_m, r_{am}, \) and \( r_c \) were almost identical for 100-d weight (Table 5). Differences in estimates of genetic correlation with the other trait ranged from 0.02 to 0.10. Numerically, estimates of \( h^2_a \) were lower for ADG, ADFI, and backfat depth for Landrace and nearly the same for ADG in Yorkshire (Table 6). The \( c^2 \) effects were nearly identical for the two models. We are unable to say whether these differences are statistically important or are little more than random deviations. They do suggest, however, that even though the likelihood-ratio test indicated that maternal genetic effects were unimportant, when the correlation between direct and maternal effects is shown to be significant, it is possible that these effects should be included in estimation of genetic parameters. The direction of the bias on the heritability estimate depends partly on the size of the additive maternal variance and the size and sign of the maternal genetic covariance. A negative genetic correlation between the direct and maternal effect can lead to conflict in the improvement of a trait (Southwood and Kennedy, 1990). A large negative covariance between direct and maternal genetic effects indicates that improvements in one effect will lead to reductions in the second.

In summary, the importance of maternal effects differed by breed and trait. They were important \( (P < 0.01) \) for 100-d weight in all breeds, although the correlation between direct and maternal effects was unimportant for Landrace and Duroc. Maternal effects were important \( (P < 0.05) \) for ADG in Duroc, and the correlation between direct and maternal effects were important \( (P < 0.01) \) for ADG in Landrace and Yorkshire. The correlation between direct and maternal effects was important \( (P < 0.05) \) for ADFI in Landrace. Maternal effects were important \( (P < 0.05) \) for LEA in Landrace and for both LEA \( (P < 0.05) \) and backfat depth \( (P < 0.01) \) in Yorkshire. The correlation between direct and maternal effects was important \( (P < 0.01) \) for both LEA and BF in Landrace and Yorkshire. Perhaps these results are related to the selection program for each breed. No emphasis was given to maternal traits for Hampshire, less emphasis on maternal traits for Duroc, equal emphasis with grow-finishing traits for Landrace, and more emphasis is given to maternal traits for Yorkshire.

Implications

Maternal effects may be important for some traits in some breeds and should be examined in large commercial herds. If important, they need to be included in genetic evaluation systems to get unbiased estimates of direct breeding values. Improvement of maternal response in addition to direct response can lead to greater overall response in a trait.
Literature Cited


